ORIGINAL ARTICLE

# Use of vegetation chemical signals for digging orientation in the subterranean rodent *Ctenomys talarum* (Rodentia: Ctenomyidae)

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## Abstract

Sensory modalities involved in the localization and selection of food represent critical information for understanding the foraging behavior of subterranean rodents. The objective of this study was to determine if a subterranean rodent that forages on aboveground plant parts, *Ctenomys talarum*, is able to detect the presence of odorous chemicals released by the plants into the soil to guide its excavation, as has been shown for subterranean species that forage on roots and bulbs. Individuals were introduced into an artificial Y-maze, whose arms were filled with sandy soil in which plants either had or had not been growing (control). Digging activity exhibited in each soil type was recorded. The following plant species, present in the natural habitat of *C. talarum*, were used: *Panicum racemosum* (three different concentrations), *Cortadeira* sp., *Margiricarpus pignatus*, *Ambrosia* sp. and *Raphanus sativus*. The individuals allocated more time to excavation in the soil in which vegetation had been growing in comparison with the control for the five analysed plant species, except in the case of *P. racemosum* at its lowest concentration. The number of individuals that completed excavation in the tube-containing soil in which plants had been growing was significantly higher than in the tube-containing soil in which no plants had been growing, with the exception of *P. racemosum* at its lowest concentration and *R. sativus*. The results of the present study suggest that *C. talarum* have the ability to use olfaction to orient their digging while foraging even though members of this species consume mainly aboveground plant parts.

## Introduction

Among mammals, subterranean rodents constitute a special group because of the singular characteristics of their habitat. The dark subterranean environment has influenced the evolution of the sensory biology of subterranean rodents. This habitat has led to reductions in sight and hypertrophies of other sensory systems, including olfactory, auditory, taste and tactile modalities (Nevo 1991), although the level of regression or hypertrophy depends on the degree of specialization for life underground. Consequently, the problems faced by subterranean rodents in localizing and selecting their food are different from the ones encountered by surface rodents. While the latter use multiple sensory channels (with emphasis on visual and olfactory ones) to localize food sources, the former must search for their food without using all the senses and signals employed by surface rodents, because vision, audition and vibration are of little value in searching for food while burrowing through the soil (Heth et al. 2000).

Several studies have been conducted to explain the foraging strategies of herbivorous subterranean

rodents. The foraging strategy of these species appears to be a mixture of random and area-restricted searching. It seems that subterranean rodents excavate in straight lines until finding a food-rich area and then dig several feeding tunnels to collect as much food as possible from these areas (Jarvis & Sale 1971; Heth 1989; Brett 1991; Jarvis et al. 1998; Heth et al. 2002). This dual foraging strategy (random and area-restricted searching) presumably maximizes the use of time and energy while searching for food in underground habitats. This pattern of foraging has been widely documented in subterranean rodents, including geomyid pocket gophers (Jarvis & Sale 1971; Benedix 1993), bathyergid and spalacine mole-rats (Heth et al. 1989; Brett 1991), and also ctenomyids (Antinuchi & Busch 1992), for which it was suggested that subterranean herbivores assess their habitat systematically while constructing foraging tunnels (Busch et al. 2000). However, as pointed out by Heth et al. (2002), the sensory mechanisms that underlie the change from linear to reticulate burrowing are not fully understood.

Recent studies have shown that some species of subterranean rodents use odorous substances released from plants to localize soil in which plants have been growing and to identify the palatability of particular types of plants (Heth et al. 2000, 2002; Lange et al. 2005). Using food odours to locate food patches more accurately could allow subterranean rodents to optimize their foraging by reducing the high energetic costs associated with digging during food searching (Heth et al. 2002). These authors obtained similar results when testing four subterranean rodent species (belonging to three families) from three continents representing a variety of social systems [solitary – *Nannospalax ehrenbergi*, colonial – *Fukomys anselli* (formerly known as *Cryptomys*, Kock et al. 2006) and *Spalacopus cyanus*; and eusocial – *Heterocephalus glaber*] and suggested that the ability of these rodents to detect kairomones in the soil and orient their digging toward areas containing food sources could be a convergent characteristic. Geophytes are the main food source for the subject species in Heth et al. (2002), so that these animals are able to respond directly to chemical signals released by their food sources (roots and bulbs). However, some species of subterranean rodents that live in underground burrows and spend the vast majority of their life below the soil surface (*sensu* Lacey et al. 2000) consume the aerial fraction of vegetation. Foraging, however, occurs entirely belowground, and involves the pulling down of vegetation into burrows, as is the case for *Bathyergus* sp., *Georychus* sp.

(Brett 1991), *Thomomys talpoides* (Stuebe & Andersen 1985) and *Geomys bursarius* (Williams & Cameron 1986). In other groups, such as members of genus *Heliophobius* and *Ctenomys*, animals emerge short distances from tunnels to collect plants that they later consume inside their burrows (Delany 1986; Madoery 1993; Comparatore et al. 1995).

The tuco-tucos (*Ctenomys*, Ctenomyidae) provide an excellent model for testing whether the use of odours from vegetation to orient digging toward areas rich in food sources represents a common tactic for subterranean rodents and not one that is restricted to species that forage on underground plant parts. The genus *Ctenomys* comprises around 60 species of subterranean herbivorous rodents that are distributed in the southern parts of South America (Reig et al. 1990); within this genus, one of the most well-studied species is *Ctenomys talarum* (Busch et al. 2000), which inhabits sand dune belts in Provincia de Buenos Aires, Argentina. Individuals of this species are solitary and maintain exclusive territories (Busch et al. 1989). Although *C. talarum* consume, inside their tunnels, the food they have collected, most gathering occurs aboveground; animals emerge short distances (less than one meter) from burrow openings to cut grasses and perennial forbs growing in the soil and run backwards into the burrows where they later consume the leaves and stems (Busch et al. 2000; del Valle et al. 2001). As a result of this foraging modality, burrow entrances are often encircled by an area of cropped vegetation (Comparatore et al. 1995). This foraging modality does not means that animals wander aboveground while searching for food. Instead, tuco-tucos' access to food sources depends on digging tunnels, and they restrict food gathering to the immediate vicinity of burrow openings. Thus, the high energetic costs associated with digging while searching food also apply for *C. talarum*. The burrow system of *C. talarum* exhibits a branching structure, comprising a main axial tunnel, a variable number of foraging tunnels and a nest chamber (Antinuchi & Busch 1992), similar to the general burrow configuration that characterizes most subterranean taxa (Busch et al. 2000). These organisms behave as generalists and opportunists because they consume most of the plant species present in their habitat but also change their diet in relation to the availability of them in their microhabitat (del Valle et al. 2001). Although mainly considered generalists, cafeteria experiments carried out to evaluate the dietary preferences of *C. talarum* have revealed that this rodent has a preference for grasses with higher percentages

of water and higher fiber/proteins ratios (del Valle et al. 2001).

Previous studies on olfaction in this species of subterranean rodent mainly focused on chemical communication, demonstrating the use of chemical signals for individual, sexual and reproductive-state recognition (Zenuto & Fanjul 2002; Fanjul et al. 2003; Zenuto et al. 2004). Until the present study, however, no studies have been conducted exploring the importance of olfaction in the search for, and selection of, food. If *C. talarum* was able to detect the chemical compounds liberated by the plants and altered its excavation based on these signals, this would allow them to improve their foraging efficiency because it would diminish the high energy costs associated with digging during food searching (Vleck 1979; Luna et al. 2002).

Sensory modalities involved in the localization and selection of food represent key information for understanding the foraging behavior of subterranean rodents. Therefore, the objective of this study was to determine if *C. talarum* is able to detect the presence of odorous chemicals released by the plants into the soil to guide its excavation.

## Methods

### Subjects

Adults of both sexes of *C. talarum* (n = 126) were captured in Mar de Cobo (37°45′S, 57°56′W, Buenos Aires Province, Argentina) using plastic live traps set at fresh surface mounds and transported to the laboratory in individual plastic cages. The animals were maintained on a natural photoperiod (10L:14D). Ambient temperature was kept at 24 ± 2°C, whereas relative ambient humidity ranged from 50% to 70%. Animals were fed with mixed grasses, sweet potatoes, lettuce and carrots. Because *C. talarum* do not drink free-standing water, it was not provided to the animals. Before starting the experiments, the animals were food-deprived for 24 h.

### Plant Species and Preparation of Soils

To determine if *C. talarum* is able to use chemical signals released from growing plants to guide its digging, we offered the following plant species that are present in the natural habitat of this subterranean rodent: *Panicum racemosum*, (offered at three different concentrations: 300, 150 and 75 g of plants per 10 l pot, designated as 100%, 50% and 25%, respectively), *Cortadeira* sp. (1000 g of plants per 10 l pot),

*Ambrosia* sp. (100 g of plants per 5 l pot), *Margiricarpus pignatus* (150 g of plants per 5 l pot) and *Raphanus sativus* (80–150 g of plants per 5 l pot). The plants were held in pots with sandy soil and maintained under identical watering and light conditions.

Sandy soil used to fill the pots and reserved for controls was obtained from a sand-dune located near *C. talarum* habitat, in which no vegetation was found growing. The different concentrations of plants used in the experiments were chosen according to their densities at the capture site. The first three species were reported as part of the diet of *C. talarum* while the other two, although not reported in the natural diet of this rodent (del Valle et al. 2001), were present at low availability in the habitat, and consumed when offered as food in captivity. However, the consumption of these items for longer than a week as the only food source has been observed to cause an approximately 15% decrease in body weight in tuco-tucos (unpubl. data). *Panicum racemosum* is the most abundant plant species both in the habitat and diet of *C. talarum* (del Valle et al. 2001) covering the sand dune as the only plant species present, and dominating the coastal grasslands along with other grasses and forbs.

### Test Procedure

Test individuals were introduced into a 10-cm diameter transparent acrylic tube Y-maze comprised of an entrance tube (25-cm long) connected to two opposed arms that were 25-cm long and filled with sandy soil. One of the arms was filled with sandy soil in which no vegetation had been growing (control). The other arm was filled with sandy soil in which the plants had been growing for a week and removed prior to the beginning of the experiments. By transplanting wild plants only 1 wk before trials, we minimized the spread of root hairs that might provide tactile cues to tuco-tucos while digging. The position of each type of soil (right or left arm) was balanced, but the order was randomly determined. Both soil humidity (5–10%) and hardness were held constant throughout the study. Prior to the start of each trial, the experimental subject was confined in an acclimation chamber for 15 min. It subsequently was allowed access to the tubes filled with soil and the following measures were recorded from videotapes: frequency of sniffing at the entrance of each arm filled with soil, time spent digging in each arm and digging choice (i.e. the arm in which the tuco-tuco burrowed to the end of the tube). To be considered sniffing, the subject's nose had to be within 1 cm of the surface of the soil as it sniffed the

**Table 1:** Time spent by *Ctenomys talarum* digging in soil conditioned by each of five plant species or not conditioned at all, and digging choices for the two types of soil. *Panicum racemosum* was tested at three different concentrations (designated as 100%, 50%, and 25%, respectively)

| | (a) Time-digging soil | | | | (b) Digging choices | | | |
|---|---|---|---|---|---|---|---|---|
| | n | Without plants (s) | With plants (s) | p | n | Without plants | With plants | p |
| *P. racemosum* 100% | 17 | 32.10 ± 61.61 | 105.53 ± 59.88 | 0.033 | 17 | 3 | 14 | 0.007 |
| *P. racemosum* 50% | 14 | 23.92 ± 52.11 | 124.07 ± 75.57 | 0.015 | 14 | 3 | 11 | 0.032 |
| *P. racemosum* 25% | 18 | 61.17 ± 82.32 | 69.89 ± 58.79 | 0.78 | 18 | 8 | 10 | 0.64 |
| *Cortadeira* sp. | 20 | 29.55 ± 53.47 | 88.35 ± 58.45 | 0.042 | 20 | 5 | 15 | 0.025 |
| *Margiricarpus pignatus* | 15 | 24.06 ± 42.19 | 98.00 ± 52.78 | 0.006 | 15 | 3 | 12 | 0.020 |
| *Ambrosia* sp. | 11 | 13.91 ± 31.24 | 127.73 ± 94.08 | 0.013 | 11 | 2 | 9 | 0.035 |
| *Raphanus sativus* | 12 | 46.83 ± 71.88 | 138.83 ± 90.45 | 0.059 | 12 | 3 | 9 | 0.08 |

substrate. Similar numbers of animals from each sex were randomly assigned to each experimental condition. Animals were tested only once and returned to the field when the experiment concluded.

To determine if *C. talarum* is able to detect differences in the concentration of plant exudates present in the soil, we studied the digging choices of this rodent after offering them soil that contained two different concentrations (100% and 50%) of *P. racemosum*. Then, the same measurements as before were recorded.

### Data Analysis

A Wilcoxon's signed-rank test for matched pairs was used to compare the frequency of sniffing and the time spent excavating soil in the arm filled with soil conditioned by plants vs. the arm filled with soil-lacking plant chemical cues. A chi-squared test was performed to evaluate if *C. talarum* chose randomly their direction in the Y-maze or if they preferentially chose to dig in one of the arms. Chi-squared tests were also used to evaluate if *C. talarum* can discriminate between soils that contained two different concentrations of *P. racemosum*.

### Results

Before beginning to excavate, the individuals usually sniffed both soil arms without touching or taking the soil into their mouth. Only the individuals that sniffed both arms during the trials were included in the analyses (107 of 114 cases). During the course of this study, animals sniffed both types of soil with similar frequency (2.29 ± 1.43 and 2.12 ± 1.63 times per trial for soil conditioned with plants vs. soil without vegetation, respectively; Wilcoxon's test, p = 0.18).

Individuals of *C. talarum* spent more time excavating the soil conditioned with plants than they did in the control for all five plant species (Wilcoxon's

test, p < 0.05), except for *P. racemosum* (p = 0.78) at its lowest concentration (25%) (Table 1). The proportion of individuals that completed the excavation in the tube containing soil conditioned by plants was significantly higher than in the other tube in most cases (chi-squared test, p < 0.05), although not quite significant for *R. sativus* and not significant for the lowest concentration of *P. racemosum* (Table 1).

Finally, the proportion of individuals that completed the excavation in the tubes containing soil with *P. racemosum* at two different concentrations (100% vs. 50%) was not significantly different (n = 12, chi-squared test, p = 1).

### Discussion

The results of the present study demonstrated that *C. talarum* was able to detect substances liberated by the plants in the soil and orient its digging toward the arms filled with soils containing these compounds. The frequency of sniffing did not differ between sand containing chemical cues from plants and control sand, but clearly allowed animals to discriminate between the different soil types, because they spent more time excavating in sand conditioned with plants, and were more likely to burrow to the end of the tube containing plant-conditioned sand. This discrimination ability could be the key factor mediating the switch from linear to reticulate digging. Le Comber et al. (2005) demonstrated that rodents in burrows of high fractal dimension (burrows that explore the area intensively) are more successful at locating food items than rodents in burrows of low fractal dimension. Therefore, the ability to recognize the presence of growing plants through the odours released by them into the soil, and the use of this information to improve harvest success, could be an adaptive feature that leads to foraging efficiency optimization, even for subterranean rodents that feed mainly on aerial plant parts,

as is the case for *C. talarum*. Previous studies on this foraging strategy have involved species that consume roots and bulbs (Heth et al. 2002), the same structures that release the kairomones used by the animals to orient digging (Lange et al. 2005). Our study extends these findings to subterranean rodents that consume aboveground plant parts, reinforcing the idea that the reliance on olfaction during foraging is a common characteristic of subterranean rodents.

The fact that *C. talarum* recognized plant species occurring in its natural habitat, despite their varying representation in its diet, suggests that the tuco-tucos simply direct their excavation toward areas containing food patches without taking into account the different plant species present in the area. It is possible that the animals just prefer areas where the probability of finding food during aboveground gathering is higher, irrespective of the nutritional value of available plants. However, it is necessary to carry out preference tests comparing soils that contain different plants to determine if *C. talarum* is able to discriminate between different plant quality species by the odorous substances released by them into the soil. The ability to discriminate between the odours of soils in which edible vs. poisonous plants had been growing has been shown in *N. ehrenbergi*, which oriented their digging toward soils in which edible plants grew in preference to those conditioned with poisonous plants (Heth et al. 2000, 2002). Even though *C. talarum* should dig to extend their burrows and locate food resources, the possibility of emerging short distances aboveground may allow animals to fine-tune food localization and selection. In this process, other sensory modalities such as vision may be used, but this possibility remains unstudied.

*Ctenomys talarum* preferred to dig in the tubes that contained soil with high and medium concentrations of *P. racemosum* (designated as 100% and 50%, respectively), although no differences between the number of individuals choosing to dig in soils with low concentrations of *P. racemosum* (25%) or soils without plants were observed. This could be due to the fact that the tuco-tucos are only able to detect the presence of plants at a certain density (in this particular case, densities higher than 75 g of *P. racemosum* per 10 l pot) or that they are also able to detect low densities of plants but choose to dig toward a certain area only when the olfactory signals present in the soil indicate that there is a high density of plants. Related to this possibility, it has been shown that subterranean rodents increase foraging activity in areas of high resource density (Andersen 1988; Benedix 1993).

Previous studies demonstrated that *N. ehrenbergi* is able to distinguish among soils that differ in their proportion of odorous substances, although only at low concentrations of them (Heth et al. 2002). The lack of difference in the proportion of individuals of *C. talarum* choosing to dig in soils with high and medium densities of plants suggests that *C. talarum* is unable to distinguish between different concentrations of plant compounds, at least within the range presented in this study.

Foraging strategies of subterranean rodents appear to be a mixture of random and area-restricted searching. The ability of different taxa to detect plant chemical cues and orient their digging toward food sources, whether subterranean or aerial plant parts, underscores the importance of olfaction to foraging. Nonetheless, to what extends this sense operates in the wild remains poorly understood. The distance over which subterranean rodents can detect chemical cues from plants is not known for any member of this group. Moreover, factors influencing the emission of chemical cues (plant density, spatial distribution, root metabolism, and phenology), as well as the environment in which kairomones are dispersed (soil moisture, granulometry, and hardness), must also be considered. Only then will we be able to evaluate the relative importance of random searching and active soil assessment through the use of kairomones under different ambient conditions. If, as the evidence seems to suggest, subterranean rodents do not forage at random, the aridity-food-distribution hypothesis as a universal explanation for the evolution of sociality in fossorial mammals (Bennett & Faulkes 2000) may have to be reconsidered.

In conclusion, the results of this study demonstrate that *C. talarum* is able to use olfaction to discriminate between soils conditioned or not conditioned by odorous substances released by plants, and to orient its digging toward those soils that retain chemical cues of the presence of plants. Additional studies are needed to determine the possible effect of the different soil characteristics (granulometry, hardness, and humidity) on this discrimination capability and to determine if *C. talarum* is also able to discriminate between plants of different quality by the odorous substances released from them into the soil.

## Acknowledgements

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| Insert comma | (As above) | , |
| Insert single quotation marks | (As above) | Ỷ or ẙ and/or Ỷ or ẙ |
| Insert double quotation marks | (As above) | Ỷ or ẙ and/or Ỷ or ẙ |
| Insert hyphen | (As above) | ⊢⊣ |
| Start new paragraph | ⌐ | ⌐ |
| No new paragraph | ⌐ | ⌐ |
| Transpose | ⊔⊓ | ⊔⊓ |
| Close up | linking ◠ characters | ◡ |
| Insert or substitute space between characters or words | / through character   or ʌ where required | Y |
| Reduce space between characters or words | ǀ between characters or words affected | ↑ |