

## Testing detection and discrimination of vegetation chemical cues in the subterranean rodent *Ctenomys talarum*

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Previous studies on the subterranean rodent *Ctenomys talarum* (tuco-tuco) have shown that this species has the ability to use olfaction to orient their digging while foraging. As a continuation of these works, we assess whether direct contact with vegetation chemical signals is required for food odor recognition, and whether this subterranean rodent is also able to discriminate plants of different nutritional quality by the chemical signals released by them into the soil. First, we test animal responses to plant extracts and controls (water) covered with a wire mesh or without it. Also, we assess individual digging response in an artificial Y-maze whose arms were filled with soil in which plants of different nutritional quality have been grown. The results of this study suggest that (i) volatile chemical cues allow food odor recognition and direct contact with the odor source does not enhance such recognition in *C. talarum*, and (ii) olfaction could play a key role in the finding of food patches, allowing individuals to direct their excavation towards plant species of high nutritional quality. 10  
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KEY WORDS: subterranean rodent, *Ctenomys talarum*, olfaction, food odors, foraging.

### INTRODUCTION

Among rodents, the senses used while foraging differ according to the rodent's lifestyle. While above-ground rodents mainly rely on multiple sensorial modalities to locate food sources and to assess their quality, herbivorous subterranean rodents must accomplish these tasks without using their vision or hearing (NEVO 1999; HETH & TODRANK 2007). Finding food underground was first considered a chance event, because animals frequently missed patches of suitable vegetation located only 1 m from their burrows (REICHMANN & JARVIS 1989; JARVIS et al. 1998). Contrary to a random digging pattern, evidence was provided in support of the use of some strategies during 25  
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foraging, since animals dig in straight lines and concentrate digging activity when they 35  
 encounter a food patch (BRETT 1991; BENEDIX 1993). Foraging in subterranean rodents  
 is a highly energetic process as access to food sources depends on digging tunnels  
 (VLECK 1979; LUNA et al. 2002; LUNA & ANTINUCHI 2006). Hence, to assess whether  
 subterranean rodents optimize their use of time and energy while searching for food,  
 several recent studies have focused their attention on the sensorial modalities used by 40  
 these rodents while foraging, especially on the role of olfaction in the searching and  
 selection of food (HETH et al. 2000, 2002; LANGE et al. 2005). These works have shown  
 that four subterranean rodent species (*Nannospalax ehrenbergi*, *Fukomys anselli*, for-  
 merly known as *Cryptomys*, *Spalacopus cyanus* and *Heterocephalus glaber*) use odorous  
 chemicals released from plants to locate soil in which plants have been growing. 45  
 Furthermore, one of these species (*Nannospalax ehrenbergi*) can discriminate between  
 the odors of soils in which edible or poisonous plants had grown (HETH et al. 2000).

Concomitant with these results, we have recently demonstrated that the subter-  
 ranean rodent *Ctenomys talarum* (tuco-tuco) also has the ability to use olfaction to orient  
 its digging while foraging, even though members of this species consume mainly 50  
 above-ground plant parts, a characteristic that differentiates this subterranean rodent  
 from the other studied species (SCHLEICH & ZENUTO 2007). In the latter study, individuals  
 of both sexes were tested in an artificial Y-maze, whose arms were filled with sandy  
 soil in which different plant species present in the natural habitat of *C. talarum* either  
 had or had not been growing (control) for 1 week. Tuco-tucos spent more time 55  
 excavating in the soil in which vegetation had been growing in comparison with the  
 control. Also, the number of individuals that dug to the end of the tube containing soil  
 in which plants had been growing was higher than in the control tube.

However, two main questions related to the use of chemical signals released by  
 the vegetation to orient digging in *C. talarum* remained unanswered. First, is the recog- 60  
 nition of plant cues only possible when individuals have direct contact with the odor  
 source? Second, is *C. talarum* also able to discriminate between plants of different  
 nutritional quality by the odorous substances released from them into the soil? *C.*  
*talarum* provide an excellent model to assess the use of signals from vegetation to opti-  
 mize energy spent digging when they search for suitable patches of vegetation. This 65  
 species occupies coastal grasslands along Buenos Aires Province, Argentina. Individu-  
 als are solitary (BUSCH et al. 1989) and build burrow systems, parallel to the surface,  
 comprising a main axial tunnel, a nest chamber and a variable number of foraging tun-  
 nels (ANTINUCHI & BUSCH 1992). During the construction of these foraging tunnels,  
 tuco-tucos may detect plant chemical signals either through olfaction when sniffing 70  
 the walls of their burrows or through taste when they use their teeth to cut and remove  
 obstacles while excavating their burrows.

Tuco-tucos venture away from burrow openings to collect the aerial parts of  
 vegetation growing in the close vicinities of those entrances (less than 1 m), and later  
 transport to and consume leaves and stems in the burrow (BUSCH et al. 2000; DEL VALLE 75  
 et al. 2001). Hence, searching for food is a costly process since access to food resources  
 depends on digging tunnels. *C. talarum* is a generalist and opportunistic forager on  
 plants in the grassland, changing their diet according to the availability of food plants  
 in the habitat (DEL VALLE et al. 2001). The analysis of their diet revealed that perennial  
 monocots constitute the main fraction of their diet, ingesting those items according to 80  
 the probability of encountering them in the grassland. Nonetheless, tuco-tucos also  
 practice selective foraging, since animals select some monocot species, with prefer-  
 ences changing seasonally (DEL VALLE et al. 2001). Furthermore, cafeteria tests demon-  
 strated that individuals preferred some food items but consume all plants offered.

Also, preference for stems of grasses with a high fiber/protein ratio was detected (BUSCH et al. 2000; DEL VALLE et al. 2001). In response to diet variation, *C. talarum* are able to adjust rapidly the rate of food ingestion, egestion and feces ingestion (ANTINUCHI et al. 2007; MARTINO et al. 2007).

The primary objective of this study was thus to determine whether direct contact with a vegetation odor source is necessary for effective discrimination and secondly whether *C. talarum* is capable of discriminating between plants of different nutritional quality when provided with chemical extracts of the soil. Lastly, we attempted to determine whether odors from high-quality plants influence the directionality of excavations through soil.

## MATERIALS AND METHODS

Adult *C. talarum* individuals of both sexes ( $n = 93$ ) were captured at Mar de Cobo locality (37°45'S, 57°26'W, Buenos Aires Province, Argentina) using plastic live traps set at fresh surface mounds. Animals were carried to our laboratory (30 km distance) and housed individually in plastic cages (42 × 34 × 26 cm) with wood shavings as bedding. A fresh provision of vegetables (carrots, sweet potatoes, lettuce and mixed grasses) was provided daily. Since tuco-tucos do not drink free-standing water, it was not provided. The animal room was maintained at thermoneutral temperature (23 ± 1 °C; BUSCH et al. 1989) and natural photoperiod, which was regularly adjusted according to the day-length pattern in the wild. Relative ambient humidity ranged from 50 to 70%. Individuals were allowed to adapt to captive conditions for 10 days prior to participation in experiments. Animals were food-deprived for 24 hr prior to experimentation to promote investigative behavior during experimental tasks.

### *Plant species*

To characterize plant nutritional value, individual body mass response to each exclusive plant diet during a week was considered. Tuco-tucos fed with *Panicum racemosum* as the only food source maintained their initial body mass (MARTINO et al. 2007). When *Cortaderia* sp. was provided as exclusive diet, females lost 15% of body mass during 1 week of treatment while males showed a decrease of 17% in their body mass, concomitant with a clear decline in activity on the 4th day of treatment (MARTINO et al. 2007). Similarly, animals on a *Raphanus sativus* diet suffered a decrease of 15% of body mass (unpubl. data from five animals). Hence, we considered *P. racemosum* as an item of high nutritional quality whereas *Cortaderia* sp. and *R. sativus* were considered low nutritional quality items. Perennial grasses dominate the grassland biomass, followed by annual monocotyledons and forbs; *P. racemosum*, *Poa bonariensis*, *Bromus unioloides*, *Lagurus ovatus* and *Adesmia incana* are the main plant species (DEL VALLE et al. 2001; FANJUL et al. 2006). While *P. racemosum* is one of the most abundant plant species present in the *C. talarum* diet, *R. sativus* and *Cortadeira* sp. were not reported previously as part of tuco-tucos' diet (DEL VALLE et al. 2001). This may be due to plant species in the grassland are characterized by spatial variation in their densities, and the last two species were not present in the habitat where the diet study was carried out (DEL VALLE et al. 2001). Although this latter work does not describe *R. sativus* and *Cortadeira* sp. as part of *C. talarum*'s diet, tuco-tucos' burrows are frequently found in patches dominated by these two plants species (personal observations).

### *Odor cue presentation*

Discrimination trials were used to test whether *C. talarum*'s ability to detect plant chemical signals relies on the possibility of making direct contact with the odor source. Odor samples were

presented to the animals in glass Petri dishes (50 mm in diameter) covered with a wire mesh located 1 cm above the odor source (closed samples), to prevent them from making direct contact with the sample, or without the wire mesh (open samples), so that animals could touch or lick the sample. Plant extracts were obtained by cutting 300 g of roots from *P. racemosum* into small pieces and immersing them in 500 ml of distilled water for 2 hr. Then, the mixture of roots and water was filtered (0.2  $\mu\text{m}$  pore size) to discard the pieces of vegetation that could provide visual cues, and the remnant extract was collected to be used as a food odor sample in the experiments. Using this procedure, plant chemical signals were not affected by microbial activity occurring in natural soils that creates secondary kairomones, as possibly occurs when natural soil is used. Similarly, LANGE et al. (2005) used kairomones obtained from water that contained carrots for 3 days (showing that those molecules are water soluble) to test food location in mole rats.

The discrimination trials consisted of the simultaneous presentation of two Petri dishes, containing (i) cotton pieces soaked with 5 ml of distilled water (control) or with the same volume of plant water extract (test dish), both covered with wire mesh ( $n = 10$ ), (ii) the control and test dishes without wire mesh ( $n = 10$ ), and (iii) two test dishes, one with wire mesh and one without it ( $n = 10$ ).

The experimental apparatus consisted of two acrylic cages (45  $\times$  30  $\times$  30 cm) that were connected to each other by an acrylic tube (10 cm wide, 20 cm long). During discrimination trials, animals were confined for 15 min in one of the cages (acclimation chamber), which contained soiled shavings from the test animal's own cage. At the start of the trial, the test animal was allowed to enter the second cage that contained the Petri dishes containing the odor samples, located 25 cm apart. The position of the different samples (right or left) was balanced, but the order was randomly determined to control for possible side preferences by the test animals. Cotton soaked with plant extracts (test) and water (control) were replaced for each trial.

For all the trials, the amount of time (in seconds) that individual subjects spent investigating each Petri dish during the tests (open odor vs open control; closed odor vs closed control; open odor vs closed odor) was recorded for 5 min (total trial length). The criterion for investigation of the scents was that the subject's nose had to be within 1 cm of the surface of the Petri dish as it sniffed the scent. Animals were tested only once and returned to the field when the experiment concluded.

After each test, the experimental cages and the dishes were thoroughly washed with tap water and odorless glassware cleaner, wiped with alcohol and allowed to air dry to ensure that no odors remained from previous trials.

Paired t-tests or Wilcoxon matched-pairs signed-ranks (if normality and homoscedasticity assumptions were not met) tests were used to test for significant differences between the time spent investigating each stimulus pair.

#### *Plant odor discrimination*

To test whether *C. talarum* can identify and discriminate between plants of different nutritional quality by the chemical signals released from them into the soil, we offered the following plant species: *P. racemosum* (plants of 300 g in 10 litre pots), *Cortadeira* sp. (plants of 1000 g in 10 litre pots) and *R. sativus* (plants of 80–150 g in 5 litre pots). The size of the pots was calculated according to the characteristics of these plants in the natural habitat. We used pots with volumes that equal the soil volumes that surround the whole root area of each plant in the field. To standardize these soil volumes, we only used plants of similar size and weight. The plants were obtained in the habitat where *C. talarum* individuals were captured and transported to our lab in plastic bags. There, they were held in pots filled with sandy soil for a week and maintained under identical lighting and watering conditions. Sandy soil was obtained from a sand-dune without vegetation located near the *C. talarum* habitat.

Test individuals ( $n = 63$ ) were introduced into a 10-cm-diameter transparent acrylic tube Y-maze composed of an entrance tube (25 cm long) connected to two opposed arms (25 cm long, 10 cm diameter) filled with sandy soil but placed 10 cm from the divergence point of the Y-maze.

Each arm was filled with sandy soil in which one of the plant species had grown for a week. Three different combinations were tested: *P. racemosum* (high quality) vs *Cortadeira* sp. (low quality) ( $n = 23$ ); *P. racemosum* (high quality) vs *R. sativus* (low quality) ( $n = 20$ ); and *Cortadeira* sp. (low quality) vs *R. sativus* (low quality) ( $n = 20$ ). 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 compaction 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 was subsequently allowed access to the tubes filled with soil and the digging choice (i.e. the arm in which the tuco-tuco burrowed to the end of the tube) was recorded. Only the individuals that sniffed both arms before starting to excavate were considered for the analysis. A similar number 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.

Chi-squared tests were used to evaluate whether *C. talarum* randomly chose their direction in the Y-maze or whether they preferred to dig in one of arms. Both the response of individuals to each pair of plants species presented in the discrimination trials and the overall response when data of high quality (*P. racemosum*) vs low quality (*Cortadeira* sp. + *R. sativus*) plants were combined were analyzed with this statistical test.

## RESULTS

### *Odor cues presentation*

Animals spent significantly more time investigating both the dishes with or without the wire mesh containing the food odor samples than their respective controls (Fig. 1, Wilcoxon signed rank test, open samples,  $n = 10$ ;  $P = 0.05$ ; paired t-test, closed samples,  $n = 10$ ,  $P = 0.01$ ). However, no statistical differences were observed in the time spent investigating the dishes provided with or without the wire mesh containing food odors (Wilcoxon signed rank test, open odor samples vs. closed odor samples,  $n = 10$ ,  $P = 0.65$ ).

### *Plant odor discrimination*

Both the number of individuals that completed the excavation in the tube containing soil conditioned with the high-quality plant (*P. racemosum*) against the tubes conditioned with the low-quality plants (both *Cortadeira* sp. and *R. sativus*) and the number of individuals that completed the excavation in the tubes containing soil with *Cortadeira* sp. against *R. sativus* were not statistically significant (Table 1). However,

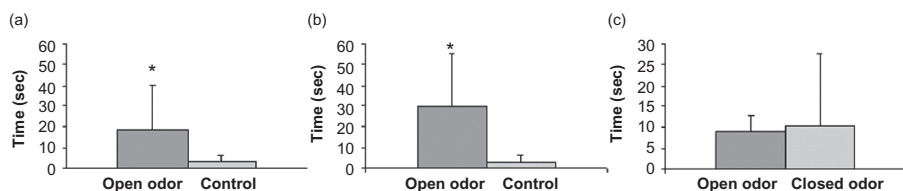


Fig. 1. — Time (mean  $\pm$  SD) spent by *Ctenomys talarum* individuals investigating open or closed Petri dishes containing plant extracts or distilled water presented simultaneously during the tests: (A) open sample vs open control; (B) closed sample vs closed control; (C) open sample vs closed sample. \* indicates at statistically significant differences  $P < 0.05$ , Wilcoxon signed rank test, open samples,  $n = 10$ ; paired t-test, closed samples,  $n = 10$ .

Table 1.

Digging choices of *Ctenomys talarum* for the soils that contained the three analyzed plant species: *Panicum racemosum*, *Cortadeira* sp. and *Raphanus sativus*.

	<i>n</i>	Digging choices		<i>P</i> <sup>a</sup>
<i>P. racemosum</i> vs <i>Cortadeira</i> (high quality vs low quality)	23	<i>P. racemosum</i>	<i>Cortadeira</i> sp.	0.094
	15		8	
<i>P. racemosum</i> vs <i>R. sativus</i> (high quality vs low quality)	20	<i>P. racemosum</i>	<i>R. sativus</i>	0.17
	13		7	
<i>Cortadeira</i> sp. vs <i>R. sativus</i> (low quality vs low quality)	20	<i>Cortadeira</i> sp.	<i>R. sativus</i>	0.65
	11		9	
<i>P. racemosum</i> vs <i>Cortadeira</i> + <i>R. sativus</i> (high quality vs low quality)	43	<i>P. racemosum</i>	<i>Cortadeira</i> sp <i>R. sativus</i>	0.047 *
	28		15	

<sup>a</sup> Chi-squared test.

and although not statistically significant, the proportion of individuals that completed the excavation in the tube containing soil conditioned with the high-quality plant (*P. racemosum*) was higher than in the tubes containing soil conditioned with low-quality plants, contrary to the situation observed with the comparison between low-quality plants, where the proportion of individuals that completed the excavation in the tubes containing soil with *Cortadeira* sp. against *R. sativus* was similar (Table 1). Moreover, when data from both tests involving high- vs low-quality plants were pooled (*P. racemosum* vs *Cortadeira* sp. + *R. sativus*), it is clear that tuco-tucos directed their excavation towards the soil conditioned with the high-quality plant (Table 1).

## DISCUSSION

In a previous study we have demonstrated that *C. talarum* was able to detect substances released by the plants in the soil and orient its digging toward the arms filled with soils containing these compounds (SCHLEICH & ZENUTO 2007). However, neither the importance of the mode of presentation of chemical cues from food to detect them nor the ability to use olfaction to discriminate between plants of different quality by the odorous substances released from them into the soil had been analyzed until the present.

The results of this study show that *C. talarum* do not require to come into direct contact with the odor source to identify food chemical odors. Animals spent more time investigating plant odor samples than controls, reinforcing LANGE et al.'s (2005) findings about the water solubility of plant chemical signals used by subterranean rodents to find food. Also, tuco-tucos devoted the same interest when allowed to come into direct contact (touch and lick) with the odor source or not, and when presented with the same plant extract with or without a wire mesh. As direct contact with the odor sample does not contribute to the discrimination of plant chemical cues in *C. talarum*, and no head bobbing was observed during the investigation of odor samples (a recognized mechanism that facilitates the entry of chemical stimuli into the VNO; WYSOCKI et al.

(1980), also observed in this subterranean rodent), the participation of another olfactory structure, like the VNO, in the discrimination of food odor cues seems unlikely. ZURI et al. (1998) showed that the VNO of *N. ehrenbergi* is well developed and suggested that this organ may also be responsible for the acute olfactory sense observed in the blind mole-rat in intraspecific and food plant recognition, although such possible functionality was not tested. However, physiological studies, recording electrophysiological responses to food odors from the vomeronasal epithelium, are needed to fully rule out the participation of this organ in the foraging behavior of subterranean rodents.

Besides the ability to use olfaction to discriminate between soils conditioned or not conditioned by odorous substances released by plants, it was interesting to know whether this capability could be extended to the discrimination of food palatability or quality from the food odors. HETH et al. (2000) demonstrated that *N. ehrenbergi* discriminate between edible and poisonous bulbs based only on their odors. In an extension of these studies, HETH et al. (2002) also showed that this subterranean rodent can discriminate between the odors from soil in which edible as opposed to poisonous plants had been growing.

As expected, no difference in the proportion of tuco-tucos choosing to dig in soils conditioned with the two low-quality plants used in this study (*Cortadeira* sp. or *R. sativus*) was observed. On the other hand, the number of individuals that completed excavation in the tube containing soil in which the high-quality plant had been growing was higher than in the tubes containing soil in which one of the two low-quality plants had been growing (66 vs 34% and 65 vs 35% for *P. racemosum* vs *Cortadeira* sp. and *P. racemosum* vs *R. sativus* respectively), although not significantly different. Nonetheless, when data were pooled for high- vs low-nutritional-quality plants (*P. racemosum* vs *Cortadeira* sp. + *R. sativus*) it is clear that tuco-tucos discriminated the quality of food items and directed their excavation towards the tube containing high-quality plants. Hence, olfaction is involved not only in the recognition of food patches present in the natural habitat of this subterranean rodent (SCHLEICH & ZENUTO 2007), but also in the capacity to assess plant chemical cues contained in the soil, allowing animals to direct their excavation towards high-quality food items. As is known, although *C. talarum* searches for food underground, most of the food collection occurs above ground, when animals emerge short distances from burrow openings to cut vegetation growing in the soil and run backwards into the burrows where they later consume the leaves and stems (BUSCH et al. 2000). These short excursions above ground may allow tuco-tucos to also use other sensory modalities, such as vision, in food localization and selection, although this possibility needs to be assessed.

In conclusion, the results of this study suggest that direct contact with a food odor source is not required for the recognition of food odors present in the soil. Volatile signals play a key role not only in the finding of food patches but also in the discrimination of the different food plant species.

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