

RESEARCH PAPERS

Ability of Murid Rodents to Find Buried Seeds in the Monte Desert

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Abstract

Rodents have developed a great capacity to for finding and storing seeds, and the ability of each species to find seeds in sufficient numbers could determine rodent abundance. To investigate this ability, we compared the differential ability of four murid rodents (*Akodon molinae*, *Graomys griseoflavus*, *Calomys musculinus* and *Eligmodontia typus*) to detect buried seeds. We also measured the variables (seed type, number of seeds in caches, soil depth and soil moisture) that would be affecting such ability. Results showed a differential ability to find seeds among rodents, *E. typus* was the most successful species, and *C. musculinus* and *G. griseoflavus* were the least successful. Conditions of wet sand and grouped seeds were the most favourable for murids to find higher number of seeds. These rodents showed preference for the sunflower seed, which is large, with good hygroscopic capacity and high in lipids, whereas millet is the opposite. The use of food storage strategies would give murid species a differential adaptive advantage, providing them with a greater ability to locate and exploit food sources more efficiently in periods of lower food abundance and after rainfall events.

Introduction

Desert areas are extreme environments characterized by limited moisture, temporal and spatial unpredictability of food resources, and a strong temperature contrast (Costa 1995). Rodents are the most diverse and abundant mammal group in deserts, and most of them are omnivorous (Costa 1995). Omnivory is considered to be a strategy and an adaptation in response to food shortage and unpredictability (Kerley & Whitford 1994), and is likely to be favoured as a dietary strategy if it allows individuals to use an array of different food resources when preferred ones become scarce. Such flexibility may be particularly advantageous in arid environments where resource availability is unpredictable (Reichman 1975; Campos et al. 2001). Seeds are a highly energetic source of nourishment, as well as free and met-

abolic water, so they constitute a key resource for the survival of desert rodents (Frank 1988), particularly for heteromyids (Chew & Chew 1970; Brown 1973; Reichman 1975). Heteromyid rodents have developed cache retrieval mechanisms, and the ability of each species to find caches in sufficient numbers could determine rodent abundance (Beatley 1969; Brown 1973). The different abilities to find seeds, such as the olfactory and tactile abilities, would increase the competitive advantage of rodents as they would find buried seeds more efficiently during periods of food shortage (Johnson & Jorgensen 1981).

Environmental agents such as wind and water disperse and bury the seeds at different depths, constituting reserves of nourishing food for periods of low seed production (Reichman 1975). Efficiency in detecting seeds could be the result of the highly

developed sense of smell of heteromyid and murid rodents such as *Dipodomys microps*, *Dipodomys ordii*, *Peromyscus maniculatus* and *Perognathus parvus* (Shaw 1934; Howard & Cole 1967; Howard et al. 1968; Lockard & Lockard 1971; Reichman 1981). The probability of rodents finding seeds decreased as the depth of seed burial increased. *Reithrodontomys megalotis* detected 100% of seeds buried near the soil surface and 0% at 0.6 and 1.3 cm depth. *Perognathus parvus* found 100% of seeds buried near the surface, 42.5% buried at 0.6 cm and 17.5% at 1.3 cm. *Dipodomys ordii* detected 100% of seeds buried just below the surface and 5% at 0.6 and 1.3 cm depth (Johnson & Jorgensen 1981). Soil moisture is also an important variable in the smelling ability of desert rodents to detect buried seeds (Johnson & Jorgensen 1981). Like Johnson & Jorgensen (1981), Vander Wall (1995, 2003) and Vander Wall et al. (2003) found that substrate moisture improved the detection of buried seeds by increasing cache discovery by rodents. Water absorption is associated with the escape of organic solutes and odorous volatile molecules that would increasingly stimulate the sense of smell (Vander Wall 1995, 1998, 2003), permitting the detection of seed caches. Therefore, granivorous rodents use olfaction to find seeds scattered in the soil or on the soil surface, and to locate buried seed caches (Vander Wall 1998; Vander Wall et al. 2003). Reichman & Oberstein (1977) asserted that the size of seeds is important in their detection, and they found a significant negative relationship between the ratio of seed burial depth to seed size and the probability that kangaroo rats dig for seeds.

The Monte has a diverse mosaic of habitats and plant associations, for example, xerophytic hillsides with bromeliads and cacti, forests and woodlands of 'algarrobos' mixed with grasses, shrublands, saltbush, salt basins ('salares') surrounded by rings of halophytic vegetation, sand dunes, bare muddy depressions 'barreales' and bad-lands (Morello 1958). The central portion of the Monte, at the Man and Biosphere Reserve of Nacuñán, Mendoza Province, is characterized by xerophytic vegetation that consists of an open woodland and shrubland steppe. The climate is semiarid and exhibits a marked seasonality of humid summers and dry winters (Ojeda et al. 1998). Sigmodontine rodents considered as nocturnal and burrow-dwelling species coexist in the Reserve (Readford & Eisenberg 1992; Ojeda & Tabeni 2007). *Akodon molinae*, *Eligmodontia typus*, *Graomys griseoflavus* and *Calomys musculus* are regarded as small mammals because they weigh <100 g (Readford & Eisenberg 1992; Campos et al. 2001). *Akodon*

molinae (Ratón Pajizo) utilizes habitats with high cover of shrubs, herbs and litter or undisturbed patches; for example, *Larrea* shrubland and *Prosopis* woodland (Corbalán 2004, 2006; Ojeda & Tabeni 2007). *Eligmodontia typus* (Laucha Colilarga Baya) is a small mouse that is abundant in sand dunes where plant cover by *Larrea* sp. is scarce and in open shrublands (Readford & Eisenberg 1992; Giannoni et al. 2001; Corbalán 2004, 2006; Ojeda & Tabeni 2007). It can exist for long periods with no free water (Readford & Eisenberg 1992) and is a skilful climber (A. Orofino, pers. comm.). *Graomys griseoflavus* (Pericote Común) is a large mouse that occupies highly diverse habitats, among them *Larrea* shrubland and *Prosopis* woodland, but is more abundant in the *Prosopis* woodland with high shrub cover (Gonnet & Ojeda 1998; Corbalán 2004, 2006; Ojeda & Tabeni 2007). It is a good climber and has been seen foraging up to 15 m high on trees (Readford & Eisenberg 1992). *Calomys musculus* (Laucha Bimaculada) is a small mouse that occupies highly diverse habitats; but is more abundant in the *Larrea* shrubland with high forb cover. It is a climber that has been seen up to 0.5 m high on shrubs and grasses (Corbalán 2004; Ojeda & Tabeni 2007).

With regard to foraging behaviour, the rodents studied are omnivorous (Campos et al. 2001). In the field, *E. typus* and *G. griseoflavus* in particular store food in scatterhoards near and far from the seed sources (Giannoni et al. 2001; Taraborelli et al. 2003). In the laboratory, *E. typus*, *G. griseoflavus*, *A. molinae* and *C. musculus* use larderhoarding inside their burrows and scatterhoarding in the foraging area (H. Carroni and C. Fernández, pers. comm.). In analysing ecology partition within the sigmodontine group, Giannoni et al. (2005) found trophic diversity, particularly during the seasons with scarce feeding resources (autumn and winter). Results from the microhistological analyses made to verify diet composition from field-collected faeces revealed high proportions of seed in the diets, and that use of this resource is high in the dry season (Apr.–Oct.) and increases in the wet season (Nov.–Mar.). *Larrea* sp. and *Lycium* sp. seeds and *Prosopis flexuosa* pods were also consumed by all sigmodontines. *Calomys musculus* is considered granivorous because seeds represented 58.3% of all the food it consumed. *Graomys griseoflavus* is herbivorous because it consumed 55.7% of leaves and 24.5% of seeds. *Eligmodontia typus* and *A. molinae* are omnivorous, although the first species presents a tendency to folivory because it consumed 34.2% of leaves, 29% of seeds and 17% of arthropods; and the

second species exhibits a strong tendency to insectivory because it consumed 41.7% of arthropods, 35% of pods and 32.9% of seeds (Campos et al. 2001; Giannoni et al. 2005).

There is no information on the ability to recover seeds by *A. molinae*, *G. griseoflavus*, *C. musculus* and *E. typus* in desert areas of South America. This skill could be important as a strategy and an adaptation to food shortage and unpredictability. Then, to investigate this capacity, we compared the differential ability of four murid rodents to find buried seeds. Also we measured the variables (seed type, number of seeds in caches, soil depth and soil moisture) that would be affecting the ability of these species to detect buried seeds. We expect that soil moisture and number of seeds in caches will positively influence the finding of buried seeds in all rodents. Sunflower seeds will be the most easily found because of their greater size, which is an important feature for their detection. We predict that, being granivorous, *C. musculus* will detect the buried seeds more easily than the other rodents, and that soil depth will have no negative effects on seed finding. Based on diet studies, *G. griseoflavus* should be the murid rodent showing lower cache recovery.

Materials and Methods

Description of Habitat

The Monte is a temperate desert, latitudinally the most extensive arid region in Argentina (Lowe et al. 1973; Mares et al. 1985). The climate is semiarid, with large annual and daily temperature ranges, and a long-term average annual rainfall of 322 mm (SD \pm 103 mm, range 192–533 mm; $n = 17$ yr), concentrated in the summer months from Nov. to Mar. when \bar{x} is 235.22 ± 89.5 mm. Mean daily temperatures are below 10°C in winter and above 20°C in summer (Ojeda et al. 1998; Campos et al. 2001). Field experiments were carried out in the Man and Biosphere Reserve of Nacuñán, located in the central area of the temperate Monte desert, Mendoza Province (34°0.2'S and 67°58'O; Cabrera & Willink 1980). The sand dune community is characterized by islands of vegetation with an herbaceous stratum composed of *Panicum urvilleanum*, *Solanum eucanthum* and *Hyalis argentea*, and a shrub stratum including mainly *Larrea divaricata*, *Larrea cuneifolia* and *Condalia microphylla*, separated by open areas, and its sandy soil is of aeolian and hydric origin (Roig 1971). Some of the murid rodents occurring in this community are: *C. musculus*, *G. griseoflavus*, *E. typus* and

A. molinae (Giannoni et al. 2001). The two most abundant rodent species are *E. typus* (25 individuals) and *G. griseoflavus* (five individuals), also *A. molinae* and *C. musculus* (one individual of each species) occur with less abundance in the sand dune community (Giannoni et al. 2001; Corbalán 2006).

Laboratory Trial

Seeds used were sunflower (*Helianthus annuus*), millet (*Panicum miliaceum*) and creosotebush (*Larrea divaricata*). Commercial seeds (sunflower and millet) were chosen because they represent a nourishing food item unknown to all rodent species, and fall in the range of seed sizes consumed in the Monte (Sassi 2001). *Larrea divaricata* (wild source) was found in the diet of these murids (in *Eligmodontia* it reaches 20% of the total ingested seeds; M. Dacar, pers. comm.). Seed selection was also based on their difference in size, chemical composition (J. Tort, pers. comm.) and scent (*H. annuus* has the most odorous seeds, followed by *L. divaricata*; determined by personal perception). Creosotebush seeds were collected at the sand dune community.

The experiment was carried out in a wooden box of 70 × 70 × 45 cm, with a knitted wire mesh (2 mm) fastened to the bottom that permitted us to sift the sand, and a lid made of the same material. One half of the experimental box was filled with sand (with no vegetation) up to 2.5 cm height and the other half up to 5 cm. Five centimetres was selected as maximum depth because 80% of the seed bank is in the top 2 cm (Marone et al. 1998). The control treatment was carried out in dry sand and the other treatment in wet sand. Dry sand with $0.2 \pm 0.01\%$ of water and wet sand with $1.96 \pm 0.03\%$ of water were the percentages obtained from five samples of moist sand from the sand dune habitat after a rainfall event. In the same treatment, one seed or caches of six seeds of each seed type were buried approx. 20 cm apart, at both depths, in sifted sand from sand dune soil. Therefore, in one treatment, the animal could find six seeds (one millet, one sunflower and one creosotebush at both 2.5 and 5.0 cm depths) and in another trial 36 seeds (six millet, six sunflower and six creosotebush at both depths). From another experiment, we knew the number of seeds with which the rodents became satiated (more than 36 seeds), and we never exceeded this number to encourage the search for seed.

All four rodent species used were adults collected at the sand dune community (eight *A. molinae*, eight *C. musculus*, six *E. typus* and nine *G. griseoflavus*).

Becoming habituated to laboratory conditions took them 1 mo, during which they were provided food *ad lib*; they were fed on sunflower, millet, creosote-bush seeds, carrots and apples. Individuals were subjected to fasting for 24 h in order to stimulate them to search for food, and kept under a 12 h/12 h light–darkness cycle. All experiments were made under the same light cycle. Each treatment was conducted for 24 h. The order of the individuals was random for each species, and the sequence of treatments (dry and wet sand) for each individual was random as well.

We also determined the proportion of moisture absorbed by each whole seed (with its husk) from the wet sand in 24 h, finding 0.328 g H₂O/g seed for sunflower, 0.252 g H₂O/g seed for *L. divaricata* and 0 g H₂O/g seed for millet.

Statistical Analysis

A one-way ANOVA was used to compare the number of seeds consumed (dependent variable) among all four murid species (factor). We tested for differences between treatments in the ability of rodents to find seeds using a three-way ANOVA, with rodent species, soil moisture and depth of buried seeds as factors and number of seeds consumed as the dependent variable. Also a three-way ANOVA was applied separately for each species to compare the means of seeds consumed among seed types and between seed caches in both treatments (dry and wet sand). A *post hoc* test, the Newman–Keuls test, was used to test for differences among the variables considered; in the figures different letters indicate differences between means. Data transformations [$\log(x + 1)$] were carried out to conform to ANOVA assumptions. The results are displayed as mean \pm standard error (SE).

Results

From footprints and holes dug by the rodents in the sand, we were able to determine that animals dug in the same place where seeds had been buried, and made no excavations at random, because no other places were disturbed near seed caches.

One-way ANOVA found significant differences among rodent species in the ability to locate seeds ($F_{3,426} = 80.68$, $df = 3$, $p = 0.001$). *Eligmodontia typus* was the species with greater ability, followed by *A. molinae*, whereas *G. griseoflavus* and *C. musculus* were similarly less efficient (Fig. 1).

Interaction among rodent species, soil moisture and depths of buried seeds was also significant

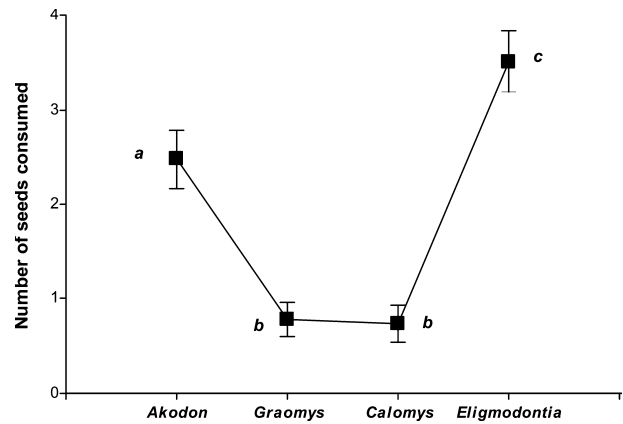


Fig. 1: Number of seeds consumed (all seed types) by murid rodents of the Monte desert: *Akodon molinae*, *Graomys griseoflavus*, *Calomys musculus* and *Eligmodontia typus*. Letters (a, b, c) indicate differences between means (Newman–Keuls test, $p < 0.05$) (mean \pm SE).

($F_{3,426} = 2.78$, $df = 3$, $p = 0.04$). *Eligmodontia typus* and *A. molinae* found more caches and were not significantly affected by either soil moisture or depth. *Calomys musculus* was the most affected by this interaction because the proportion of seeds found was significantly higher when seeds were offered in wet sand and buried at 2.5 cm depth ($F_{1,96} = 5.08$, $df = 1$, $p = 0.027$, Newman–Keuls test, $p = 0.05$). As the depth variable was not significant in ANOVA, this variable is not included in the figures.

To have a clearer view of the effect of studied variables on the ability of Monte desert rodents to find seed, three-way ANOVA was made separately for each species. Seed detection by *A. molinae* was significantly influenced by seed species and the way they were supplied (caches of one seed or caches of six seeds); millet was the least frequently found seed, and this rodent was more able to find seeds when they were offered in caches of six vs. single seeds (seed species: $F_{2,102} = 4.86$, $df = 2$, $p = 0.009$; caches: $F_{1,102} = 57.23$, $df = 1$, $p = 0.0001$). For *A. molinae*, we found a significant interaction among factors: soil moisture and seed species, for caches with grouped seeds only ($F_{2,102} = 3.2995$, $df = 2$, $p = 0.041$; Fig. 2). In dry sand, all three seed species were found in similar proportions, but in wet sand detection of sunflower and creosotebush seeds improved significantly.

Regarding *G. griseoflavus*, its ability to find seeds was significantly affected by soil moisture ($F_{1,102} = 10.29$, $df = 1$, $p = 0.0017$), seed species ($F_{2,102} = 14.98$, $df = 2$, $p = 0.0001$) and number of seeds in caches (singly or grouped; $F_{1,102} = 14.16$, $df = 1$, $p = 0.0002$). This species found significantly more seeds when offered in wet vs. dry sand

Fig. 2: Number of millet, sunflower and creosotebush seeds consumed by *Akodon molinae*, seeds buried singly or grouped in both treatments (control = dry sand and wet sand). Letters (a, b, c) indicate differences between means (Newman–Keuls test, $p < 0.05$) (mean \pm SE).

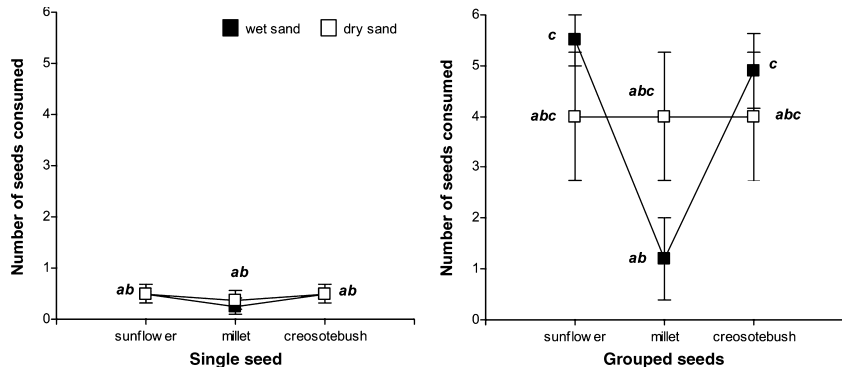
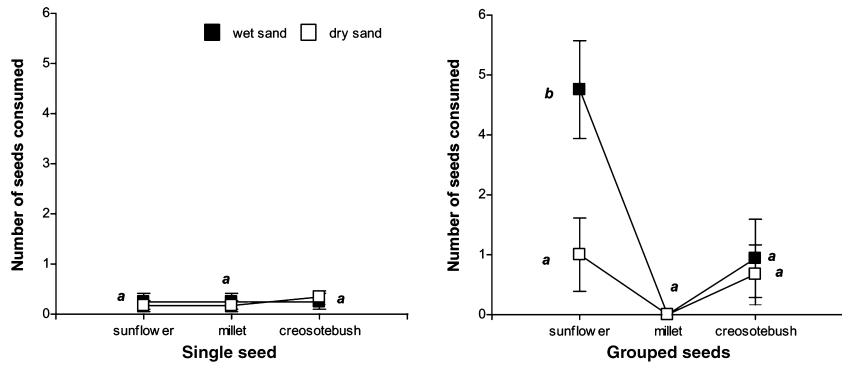


Fig. 3: Number of millet, sunflower and creosotebush seeds consumed by *Graomys griseoflavus*, seeds buried singly or grouped in both treatments (control = dry sand and wet sand). Letters (a, b) indicate differences between means (Newman–Keuls test, $p < 0.05$) (mean \pm SE).



(Newman–Keuls test, $p = 0.05$). Millet was the least frequently found seed, followed by creosotebush, and the most highly found were sunflower seeds (Newman–Keuls test, $p = 0.05$). In dry sand, all three seed species were found in similar proportions. The only significant interaction was that of soil moisture, seed species and number of seeds in caches ($F_{2,12} = 5.98$, $df = 2$, $p = 0.0033$; Fig. 3). Sunflower was the only seed that this species found extensively when offered in groups of six seeds and in a wet substrate.

As for *C. musculus*, the variables significantly affecting this species were soil moisture ($F_{1,96} = 20.72$, $df = 1$, $p = 0.00002$), seed species ($F_{2,96} = 9.89$, $df = 2$, $p = 0.0001$) and number of seeds in caches ($F_{1,96} = 14.17$, $df = 1$, $p = 0.0003$). In dry sand, all three seed species were found in similar proportions. This species was significantly more successful in detecting millet than sunflower and creosotebush, and when these seeds were in wet sand and grouped (Newman–Keuls test, $p = 0.05$). Finally, *C. musculus* found significantly more sunflower seeds, followed by creosotebush, when in wet sand and grouped ($F_{2,96} = 5.15$, $df = 2$, $p = 0.0075$; Fig. 4).

For *E. typus*, seed finding was significantly affected by only two variables: seed species and number of

seeds in caches ($F_{2,108} = 3.196$, $df = 2$, $p = .0448$ and $F_{1,108} = 317.11$, $df = 1$, $p = 0.001$ respectively). This rodent species found significantly more sunflower seeds, with millet being the least frequently found seed (Newman–Keuls test, $p = 0.05$; Fig. 5). On the other hand, grouped seeds were more easily detected than single ones. No significant interactions among variables were observed for *E. typus*.

Discussion

Seeds are a highly energetic source of nourishment, as well as of free and metabolic water, so they constitute a key resource for the survival of desert rodents (Frank 1988). Heteromyid rodents have developed a great capacity for finding seeds, and the ability of each species to find sufficient numbers of seeds could determine its abundance (Beatley 1969; Brown 1973). According to our results, all four murid species could have different abilities to find seeds, for example *E. typus* found more caches than *A. molinae*, and many more than did *G. griseoflavus* and *C. musculus*. *Eligmodontia typus* would have greater ability to exploit seed resources than *G. griseoflavus* and *C. musculus*. *Eligmodontia typus* is the most opportunistic species. It consumes stems, seeds, fruits, leaves and arthropods whereas *G. griseoflavus*

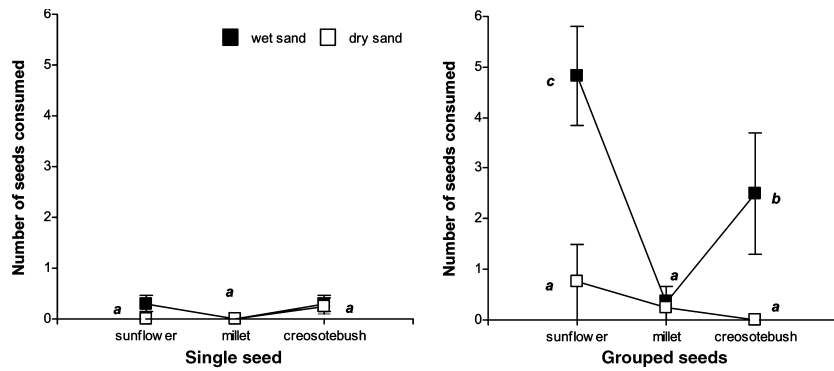


Fig. 4: Number of millet, sunflower and creosotebush seeds consumed by *Calomys musculus*, seeds buried singly or grouped in both treatments (control = dry sand and wet sand). Letters (a, b, c) indicate differences between means (Newman-Keuls test, $p < 0.05$) (mean \pm SE).

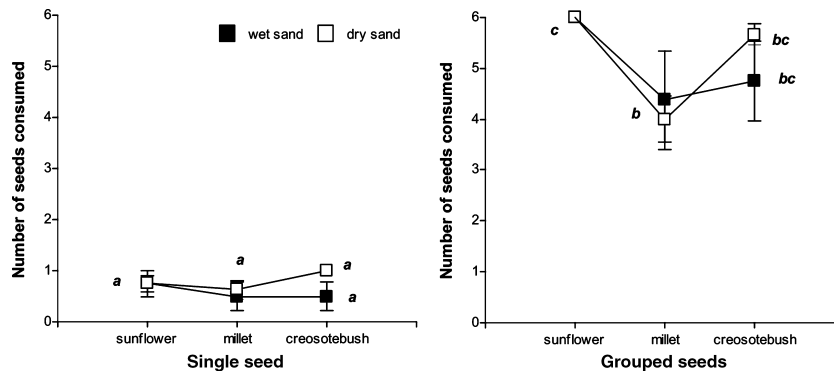


Fig. 5: Number of millet, sunflower and creosotebush seeds consumed by *Eligmodontia typus*, seeds buried singly or grouped in both treatments (control = dry sand and wet sand). Letters (a, b, c) indicate differences between means (Newman-Keuls test, $p < 0.05$) (mean \pm SE).

feeds on leaves and seeds (Giannoni et al. 2005). Also, the Laucha Colilarga Baya is the species most adapted to foraging in open areas with scarce plant cover, i.e. in sand dunes (Giannoni et al. 2001; Corbalán 2004, 2006; Ojeda & Tabeni 2007) or in the experimental box where there was no vegetation. It is the murid that devotes more time to searching for food in these open areas. On the other hand, *C. musculus* is regarded as the most granivorous species (Campos et al. 2001; Giannoni et al. 2005). However, this species showed little ability to find either commercial or natural seeds. This discrepancy could be explained if we differentiated granivory from graminivory, as Kerley et al. (1997) did for the kangaroo rat (*Dipodomys ordii*). *Calomys musculus* is more graminivorous than granivorous, because recent studies on its diet have reported a higher percentage of bracts of gramineous plant species than of seeds of dicotyledonous plant species (M. Dacar, pers. comm.). On the other hand, the Laucha Bimaculada is more abundant on sites with high grass cover (Campos et al. 2001; Corbalán 2004; Ojeda & Tabeni 2007). This species would be foraging seeds in the litter, but this activity would decrease in areas without plant cover. Therefore, this ability could give any of the murid and heteromyid species a competitive advantage by increasing their capacity to find

and exploit seeds more efficiently in periods when nourishing food items are less abundant (Johnson & Jorgensen 1981; Vander Wall 1995).

The number of seeds found by murids was different for all three seed species selected. The murid rodents preferred to consume sunflower, in contrast millet seeds were the least preferred. As these rodents have no pouches, they must transport seeds one at a time, grabbing them with their incisors, so large seeds would provide them with a higher energy intake per travel unit (sunflower = 2343.88 J/100 g vs. millet = 1368.66 J/100 g; Taraborelli et al. 2003). A similar preference for larger seeds was reported by Lima & Valone (1986) for grey squirrels and by Vander Wall (1995) for the yellow pine chipmunk. The sunflower seed is large, high in lipids, and low in carbohydrates and preformed water, whereas millet is the opposite (Price 1983; Tort et al. 1998). Seed handling time, seed size and energy content could be important attributes for Monte Desert rodents in the field in trading off the costs and benefits under predation pressure (Taraborelli et al. 2003). Like Johnson & Jorgensen (1981), Vander Wall (1995, 1998, 2003) and Vander Wall et al. (2003), we could say that substrate moisture affected the encounter of buried seeds by increasing cache discovery by some rodents. For example, *C. musculus* showed a differential

ability to find seeds in the moisture treatment, being more efficient in a moist substrate. This species is distributed in humid areas, and the Monte is the limit of its distribution (Readford & Eisenberg 1992), so this rodent is highly water-dependent. On the other hand, the frequency of detection of sunflower seeds increased when caches were in wet sand, and it was the seed preferred by the rodents. This could be related to the hygroscopic capacity of this seed (0.328 g H₂O/g seed); water absorption, when the soil is moistened, has been linked to the leakage of organic solutes and odorous volatile molecules emanating from seeds (Vander Wall 1995, 1998, 2003). These organic materials apparently contribute to the odour signal emitted by seeds, and an elevated water level of the substrate may help to convey odorant molecules through soil, which would increasingly stimulate the sense of smell, allowing greater detection of seed caches in moist substrate than in dry soils (Vander Wall 1995, 1998, 2003; Vander Wall et al. 2003). Consequently, nocturnal rodents, that forage when relative humidity is higher, are expected to have greater foraging success with buried seeds under dry conditions (Vander Wall et al. 2003).

Grouped seeds would be more easily found by rodents than seeds buried singly. Probably this is also related to the scent of seeds that would be stronger when they are grouped, but this assumption should be made in future chemistry studies. Reichman (1981) detected that large caches probably emit a stronger olfactory signal at ground surface than do smaller caches. The efficiency of rodents in detecting seeds would be the result of smell, and species with a more acute sense of smell would have an adaptive advantage in periods of low seed production (Johnson & Jorgensen 1981). We were able to determine that animals dug in the same place where seeds had been buried, and made no excavations at random, because no other places were disturbed near seed caches. This would indicate that murid rodents of the Monte utilize the scent of seeds to find them, and not the sense of touch as do other rodent species. For example, kangaroo rats detected cache sites from a short distance, went directly to them, and dug to accurately reach the seeds, whereas pocket mice seemed less focused and dug less accurately (Reichman & Oberstein 1977).

The depth at which seeds were buried did not influence the encounter of nourishing items by the most successful rodent species, such as *E. typus* and *A. molinae*. In contrast, *C. musculus*, that is less successful, seemed to be more influenced by substrate

moisture than by the depth of the seed cache. Lockard & Lockard (1971) reported that *Dipodomys deserti* found 100% of the seeds buried up to 6 cm depth, and then seed encounter diminished progressively as depth increased.

Eligmodontia typus and *G. griseoflavus* scatterhoard food near and far from the source of nourishment in the field and in the laboratory, and use larderhoarding inside their burrows in the laboratory (Giannoni et al. 2001; Taraborelli et al. 2003; H. Carroni, pers. comm.). *Akodon molinae* and *C. musculus* also larderhoard and scatterhoard food under laboratory conditions (C. Fernández, pers. comm.), but there is no evidence of how they hoard food in the field. Therefore, the ability to find buried seeds could give advantages to murid rodents when they harvest; and olfaction plays an important role in the foraging behaviour of rodents (Vander Wall et al. 2003). A well-developed sense of smell would allow them to find their own or foreign caches, as observed in *Dipodomys merriami* and *Tamias amoenus* that spread their seed caches widely (scatterhoarding) to prevent seed loss due to theft by other rodents (Jenkins et al. 1995; Vander Wall et al. 2005). *Calomys musculus*, which is less skilful, may be vulnerable to pilferage by other species and may be less able to pilfer caches of other rodents. This type of asymmetrical interaction among species potentially alters competitive relationships and has important consequences to the structure and functioning of rodent communities (Johnson & Jorgensen 1981; Vander Wall 1998; Vander Wall et al. 2003). Therefore the use of food storage strategies would give murid species a differential adaptive advantage, providing them with a greater ability to locate and exploit food sources more efficiently in periods of lower food abundance and after rainfall events.

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