INTRODUCTION

The terms “granivore”, “insectivore” and “herbivore” refer to animals whose diet contains over 50% of seeds, insects (or arthropods in a wider sense), and green plant parts (leaves, stems) respectively, whereas “omnivore” refers to those species in whose diets no particular category prevails (Kerley and Whitford, 1994).

Desert small mammals adopt one of two alternative dietary strategies, either granivory or herbivory/omnivory (Kerley, 1992). In North American deserts granivorous rodents are dominant, according to the information on diets obtained mostly for species of the family Heteromyidae (Reichman, 1975; Mares and Rosenzweig, 1978; Abramsky, 1983). No evidence of strict granivory by small mammals has been found in Australian, South African or South American deserts, where the most frequent dietary strategies are omnivory, insectivory and herbivory (e.g. Glanz, 1977; Morton, 1979; Meserve, 1981a,b; Morton, 1985; Kerley, 1989, 1992; Murray and Dickman, 1994a, b; Murray et al., 1999; Campos et al., 2001).

The diets of these groups of rodents have been examined using the microhistological technique (Baumgartner and Martin, 1939; Dusi, 1949; Butet, 1987) for analyzing fecal and stomach contents. Nonetheless, some food items as hard tissues, for example stems, fruits, seeds, and roots, may be underestimated in the microhistological analysis (Campos, 1997;
Campos et al., 2001). Recently, Dacar and Giannoni (2001) modified this technique in order to increase the likelihood of accurately identifying underestimated plant parts such as stems, seeds, and fruits.

The small mammals that occur in the central-western Monte desert (Argentina) were categorized as omnivores by Campos et al. (2001): *Akodon molinae* (with a strong tendency to insectivory), *Calomys musculinus* (with a strong tendency to granivory), *Eligmodontia typus* and *Graomys griseoflavus* (with a strong tendency to folivory). Campos et al. (2001) characterized the specific composition of diets by using the microhistological technique, this characterization was as accurate as this technique allowed. So, in this study we attempted to improve diet characterization for the same rodent species and the same habitat as those studied by Campos et al. (2001) by using the microhistological technique modified by Dacar and Giannoni (2001), because it allows identification of hard tissues.

**MATERIAL AND METHODS**

**Study site**

The study was conducted in the Biosphere Reserve of Nacuñán, located in the central-western part of the Mendoza plain (34° 02' S, 67° 58' W), 200 km southeast of Mendoza city, Argentina (Ojeda et al., 1998). The Reserve is in the Monte phytogeographical province (Morello, 1958), and comprises approximately 13 000 ha of xerophytic vegetation. The climate is semiarid with a long-term average annual rainfall of 322 ± 103 mm (ISD, range 192-533; N = 17 yrs), concentrated in the summer months (November to March; mean= 235.22 ± 89.5 mm). Mean daily temperatures are lower than 10°C in winter and above 20°C in summer (Ojeda et al., 1998).

The vegetation consists of an open woodland and shrubland steppe (Roig, 1971), and the area has been protected from grazing and human disturbance since 1970. The open mesquite woodland is the most widespread plant community, dominated by *Prosopis flexuosa*, accompanied by *Geoffroea decorticans*, a shrub layer of *Larrea divaricata*, *L. cuneifolia*, *Atriplex lampa*, *Lycium chilense*, and a species-rich herbaceous layer (e.g., *Pappophorum caespitosum*, *Digitaria californica*, *Setaria leucopila*; Roig, 1971).

**Mammal species**

We studied four sigmodontine rodents (less than 100 g) that coexist in the Reserve of Nacuñán: *Graomys griseoflavus*, *Akodon molinae*, *Calomys musculinus*, and *Eligmodontia typus*. In total, 69 samples of feces and intestinal contents were analyzed: 31 *G. griseoflavus*, 21 *A. molinae*, 6 *C. musculinus*, and 11 *E. typus*. The material was taken from animals trapped during the dry season (1996-1997; 2001-2002) when, because of food shortage, animals would be forced to eat a wide variety of items. Fecal samples were obtained from animals captured with Sherman traps, whereas samples of intestinal and stomach contents were taken from animals captured with Victor snap-traps.

Diet composition was determined by a microhistological analysis. We used the technique developed by Dacar and Giannoni (2001) for hard tissues such as stems and seeds. This procedure uses a macerating solution of 17.5% of NaHCO₃ to soften and clarify hard tissues. Fifty microscope fields were systematically examined on each slide under a microscope at 400x. Histological features of epidermis of leaves, seeds, fruits, and stems, and arthropod body parts were used to identify food items on slides prepared from stomach and intestinal contents, and feces. Presence of each food item was recorded, and its percent frequency of occurrence was determined on all microscope fields (Holechek and Gross, 1982).

Food items were grouped into the following categories: leaves, seeds, *Prosopis flexuosa* pods, stems, and arthropods. A multivariate analysis of variance (MANOVA) was used to test for differences among rodent species in the consumption of 5 food categories. The Newman-Keuls test was used to assess differences in the consumption of each food category by all four rodent species (Zar, 1999). The frequency of occurrence of each dietary category was expressed as mean, standard deviation and coefficient of variation (CV). A nonparametric analysis of variance (Kruskall-Wallis) and a Tukey test were used to test for differences among rodent species in the consumption of food categories, per plant species, only considering the most common plant species found in the diets.

**RESULTS**

Significant differences in the consumption of seeds, stems, leaves, *Prosopis flexuosa* pods
and arthropods were observed among mammal species (Fig. 1). *Calomys musculinus* consumed the highest proportion of seeds: nearly 60% of its diet was composed mainly of seeds of *Lycium* spp., *Larrea* spp., and grasses. The highest proportions of arthropods were found in the diets of *Akodon molinae* and *C. musculinus*, although the latter species showed no significant differences compared to *Eligmodontia typus*. The highest proportion of leaves was found in the diet of *Graomys griseoflavus*, the most consumed plant species being *P. flexuosa*. All rodents consumed stems and *P. flexuosa* pods, showing no differences among them (Fig. 1 and Table 1).

In analyzing the proportions of the different food categories present in the diet of each sigmodontine species, *C. musculinus* showed the highest variation in the consumption of the different categories as indicated by the coefficient of variation, which agreed with the high percentages of seed found in its diet, and with the little variation in seed consumption among the individuals studied. On the other hand, *E. typus* exhibited the least variation in the proportions of the categories consumed, since this species showed an even use of all food categories. In the diet of *E. typus*, *P. flexuosa* pods, arthropods and stems were the most highly variable food categories (Table 1). In the case of *G. griseoflavus*, leaves represented more than 50% of its diet, and was the least variable category; arthropods, instead, were the least consumed but most highly variable category. In the diet of *A. molinae*, arthropods and seeds were the most abundant and less variable categories (Table 1).

The most consumed plant species (with a frequency higher than 5% in the diet) were *Capparis atamisquea*, *Larrea* spp., *Lycium* spp., and *P. flexuosa*. All rodent species consumed stems of *C. atamisquea*, *Larrea* seeds, leaves and seeds of *Lycium* spp., and leaves and pods of *P. flexuosa* (Table 2).

![Wilks Lambda= 0.317; F(12, 164.33)= 7.438; p< 0.0001](image)

**Fig. 1.** Categories consumed by sigmodontine rodents of the Monte desert in the dry season. Letters and numbers indicate differences between means (MANOVA and Newman-Keuls test, *P* < 0.001).
Table 1
Means, standard deviations, and coefficient of variation (CV) of percentage of food categories consumed by sigmodontine species of the Monte desert.

<table>
<thead>
<tr>
<th></th>
<th><em>G. griseoflavus</em></th>
<th><em>E. typus</em></th>
<th><em>A. molinae</em></th>
<th><em>C. musculinus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>N = 31</em></td>
<td><em>N = 11</em></td>
<td><em>N = 21</em></td>
<td><em>N = 6</em></td>
</tr>
<tr>
<td><strong>Leaves</strong></td>
<td>55.7 ± 23.6</td>
<td>34.2 ± 21.6</td>
<td>20.5 ± 15.5</td>
<td>14.0 ± 12.9</td>
</tr>
<tr>
<td></td>
<td>(42)</td>
<td>(63)</td>
<td>(75)</td>
<td>(91)</td>
</tr>
<tr>
<td><strong>Pods</strong></td>
<td>10.7 ± 12.9</td>
<td>14.2 ± 15.2</td>
<td>3.5 ± 7.0</td>
<td>2.7 ± 5.6</td>
</tr>
<tr>
<td></td>
<td>(120)</td>
<td>(107)</td>
<td>(206)</td>
<td>(215)</td>
</tr>
<tr>
<td><strong>Seeds</strong></td>
<td>24.5 ± 24.5</td>
<td>29.6 ± 21.3</td>
<td>32.9 ± 18.5</td>
<td>58.3 ± 30.9</td>
</tr>
<tr>
<td></td>
<td>(100)</td>
<td>(72)</td>
<td>(56)</td>
<td>(53)</td>
</tr>
<tr>
<td><strong>Stems</strong></td>
<td>6.8 ± 6.4</td>
<td>4.2 ± 4.6</td>
<td>1.3 ± 3.5</td>
<td>2.0 ± 4.0</td>
</tr>
<tr>
<td></td>
<td>(94)</td>
<td>(110)</td>
<td>(243)</td>
<td>(200)</td>
</tr>
<tr>
<td><strong>Arthropods</strong></td>
<td>2.3 ± 5.8</td>
<td>17.8 ± 20.9</td>
<td>41.7 ± 19.9</td>
<td>23.0 ± 27.2</td>
</tr>
<tr>
<td></td>
<td>(242)</td>
<td>(118)</td>
<td>(48)</td>
<td>(118)</td>
</tr>
</tbody>
</table>

Mean CV: (120) (94) (126) (136)

Table 2
Means and standard error of percentage of food categories, per plant species, consumed by sigmodontine rodents of the Monte desert. Only plant species with over 5% consumed were considered. Letters indicate differences between means (Kruskall-Wallis and Tukey tests).

<table>
<thead>
<tr>
<th>Species</th>
<th><em>G. griseoflavus</em> Mean ± SE</th>
<th><em>E. typus</em> Mean ± SE</th>
<th><em>A. molinae</em> Mean ± SE</th>
<th><em>C. musculinus</em> Mean ± SE</th>
<th><em>P</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Capparis atamisquea</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaves</td>
<td>0.06 ± 0.06</td>
<td>——</td>
<td>0.67 ± 0.48</td>
<td>——</td>
<td></td>
</tr>
<tr>
<td>Seeds</td>
<td>0.71 ± 0.34</td>
<td>0.33 ± 0.33</td>
<td>0.10 ± 0.10</td>
<td>——</td>
<td></td>
</tr>
<tr>
<td>Stems</td>
<td>5.55 ± 1.04 *</td>
<td>3.83 ± 1.31 *</td>
<td>1.33 ± 0.76 *</td>
<td>2.00 ± 1.63 * *b</td>
<td>0.014</td>
</tr>
<tr>
<td>Total</td>
<td>6.32 ± 1.13 *</td>
<td>4.17 ± 1.57 *</td>
<td>2.10 ± 0.89 *</td>
<td>2.00 ± 1.63 * *b</td>
<td>0.029</td>
</tr>
<tr>
<td><strong>Larrea spp.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaves</td>
<td>——</td>
<td>——</td>
<td>0.95 ± 0.43</td>
<td>——</td>
<td></td>
</tr>
<tr>
<td>Seeds</td>
<td>5.03 ± 1.66</td>
<td>1.17 ± 0.63</td>
<td>0.10 ± 0.10</td>
<td>7.00 ± 5.88</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>5.03 ± 1.66</td>
<td>1.17 ± 0.63</td>
<td>1.05 ± 0.43</td>
<td>7.00 ± 5.88</td>
<td></td>
</tr>
<tr>
<td><strong>Lycium spp.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaves</td>
<td>14.00 ± 2.04 *</td>
<td>22.17 ± 4.58 *</td>
<td>5.71 ± 1.22 *</td>
<td>8.00 ± 5.29 * *c</td>
<td>0.006</td>
</tr>
<tr>
<td>Seeds</td>
<td>9.42 ± 2.55 *</td>
<td>10.33 ± 3.42 *</td>
<td>20.48 ± 3.13 *</td>
<td>20.67 ± 9.28 * *b *c</td>
<td>0.011</td>
</tr>
<tr>
<td>Total</td>
<td>23.42 ± 3.63 *</td>
<td>32.50 ± 6.32 *</td>
<td>26.19 ± 3.22</td>
<td>28.67 ± 8.92</td>
<td></td>
</tr>
<tr>
<td><strong>Prosopis flexuosa</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaves</td>
<td>36.77 ± 3.69 *</td>
<td>4.17 ± 3.10 *</td>
<td>8.86 ± 2.11 *</td>
<td>0.67 ± 0.67 * b</td>
<td>0.0001</td>
</tr>
<tr>
<td>Seeds</td>
<td>0.06 ± 0.06</td>
<td>0.17 ± 0.17</td>
<td>1.14 ± 0.83</td>
<td>——</td>
<td></td>
</tr>
<tr>
<td>Pods</td>
<td>10.71 ± 2.32 *</td>
<td>13.00 ± 4.36 *</td>
<td>3.52 ± 1.61 *</td>
<td>2.67 ± 2.29 * *b</td>
<td>0.009</td>
</tr>
<tr>
<td>Stems</td>
<td>1.23 ± 0.36</td>
<td>——</td>
<td>——</td>
<td>——</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>48.77 ± 4.02 *</td>
<td>17.33 ± 4.57 *</td>
<td>13.52 ± 3.08 *</td>
<td>3.33 ± 2.23 * b</td>
<td>0.001</td>
</tr>
</tbody>
</table>
DISCUSSION

Granivory, rather than omnivory, has been frequently considered the most advantageous dietary strategy for desert-dwelling rodents (Price and Brown, 1983; Mares 1993). However, several recent studies on diets and food preferences in African, Australian, and South American deserts have shown that rodents are more usually omnivorous than granivorous (Morton, 1979; Meserve, 1981a, b; Morton, 1985; Kerley, 1989, 1992; Murray and Dickman, 1994b; Campos et al., 2001).

Some anecdotal and casual observations have suggested that *G. griseoflavus* is a folivorous species (Mares, 1973; Rosi, 1983). In Chilean shrublands *E. typus* has been reported to include a large proportion of insects in its diet (Mann, 1945; Hershkovitz, 1972). In the cropfields of central Argentina, the diet of *C. musculinus* is composed primarily of seeds (Maldonado Curti, 1989; Dellafiore and Polop, 1994; Ellis et al., 1998). The trophic status of the four most abundant sigmodontine rodents of the Monte desert is poorly known as yet. Campos (1997) and Campos et al. (2001) made a detailed dietary study using a microhistological analysis that may have underestimated some food items such as stems, fruits, seeds, and roots. According to these authors, small rodents of the Monte desert are omnivorous, with a tendency towards granivory (*C. musculinus*), insectivory (*A. molinae*), and folivory (*G. griseoflavus*).

Results of the present study, using a new technique developed for increasing accuracy in the identification of plant parts, support preliminary indications on the dietary status as stated by Campos et al. (2001), however some interesting differences were found. Campos et al. (2001) found a higher use of leaves by all four rodent species compared to the present study. Although some hard items, such as stems, were found for the first time, others, such as pods and seeds, increased the percentage of occurrence in diets of Monte desert rodents.

Higher proportions of seed found in the diets reveal a higher use of this resource. This is consistent with results of ongoing studies on food hoarding (Giannoni et al., 2001), seed handling ability, and ability of sigmodontine rodents to find buried seeds (P. Taraborelli, 2003, in litt.). *Prosopis* pods are a major source of nutrients for *Dipodomys merriami*, (Reynolds and Glendening, 1949) and also for small mammals such as *G. griseoflavus* and *E. typus*. These results support field experiments that indicate that *P. flexuosa* pods are intensively removed by small rodents of the Monte (C. Campos and C. Borghi, pers. obs.). Moreover, considering that *P. flexuosa* produces fruit during the wet season, consumption of pods and seeds during the dry season strongly suggests that rodents feed on stored pods, especially because *P. flexuosa* seeds were not found in the soil seed-bank during the dry season (Marone et al., 1998). Stems were also consumed by all sigmodontines, particularly by *G. griseoflavus*, the most herbivorous species. For other herbivores of the Monte desert (*Microcavia australis*), bark consumption was recorded during the dry season due to low availability of green vegetation (Borruel et al., 1998; Tognelli et al., 1999), and this could also be related to the high water and carbohydrate contents of bark (Frank, 1988).

In this study, results reflect rodent diets in periods of harsh conditions, such as drought, that coincide with periods of maximum relative abundance of rodents (autumn). So the trophic status of rodents indicates what they are capable of eating for surviving the season of most critical food shortage, rather than their potentially preferred food items in seasons of food abundance. According to definitions of the terms “granivore”, “insectivore”, “herbivore” and “omnivore” (Kerley and Whitford, 1994), the present study supports the suggestion that *C. musculinus* is a granivore, *G. griseoflavus* an herbivore, and that *E. typus* and *A. molinae* are omnivores, although the latter exhibits a strong tendency towards insectivory.

Like in other deserts, species display considerable dietary flexibility, as indicated by the high standard deviations found in all five food categories. This flexibility may be particularly advantageous in arid environments where re-
source availability is unpredictable and heterogeneous (Reichman, 1975; Meserve, 1981b; Glanz, 1982; Meserve et al., 1988; Stafford Smith and Morton, 1990). These results show a new and more complex scenario in the relationship of South American rodents with desert plants, increasing the importance of plant parts other than leaves, i.e. fruits, stems and seeds, in these interactions.

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LITERATURE CITED


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