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DIETARY HABITS OF THE COMMON RODENTS IN AN AGROECOSYSTEM IN ARGENTINA

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Dietary habits of five common rodents in agroecosystems on the central Argentine Pampa were studied for 15 months using microhistological analysis of stomach contents. All five rodent species were omnivorous, but proportions of major dietary items (arthropods, dicot leaves and seeds, monocot leaves and seeds) varied among species and seasons. *Akodon azarae* largely was entomophagous; arthropods formed 41–62% of the diet in all seasons. The other four species (*Calomys musculinus*, *Calomys laucha*, *Bolomys obscurus*, and *Oligoryzomys flavescens*) consumed most diet items throughout the year, but relative proportions varied among seasons. Leaves formed a relatively minor proportion of the diet (12–16% overall for all species) throughout the year. All species except *A. azarae* consumed higher quantities of seeds (50–73% of stomach volume) than arthropods (15–35%) during autumn and winter but switched to higher quantities of arthropods (30–53%) in spring and summer. Diet breadth was narrower and overlap generally highest during winter when all species were forced to subsist on a reduced set of available resources. Of 28 plant species with >2% cover in the environment, 25 were identified in stomachs of one or more of the five rodent species. The most important plant species in the diet were corn and soybeans (mostly grain), seed of Johnson grass (*Sorghum halepense*), chickweed (*Stellaria media*), and *Amaranthus*. High consumption of arthropods, especially by *A. azarae*, contraindicates the broad-scale use of rodenticides until the role of that rodent species in the control of pest insects can be ascertained.

Key words: *Calomys musculinus*, *Calomys laucha*, *Akodon azarae*, *Oligoryzomys flavescens*, *Bolomys obscurus*, dietary selection, food habits

Factors that determine species composition and relative abundance of small mammals in agroecosystems are poorly understood. In many ecosystems, these parameters are influenced by climatic conditions (Hornfeldt, 1994; Mills et al., 1992), social behavior (Brown and Munger, 1985), predation, parasitism and disease (Brown et al., 1988; Desy and Batzli, 1989; Desy et al., 1990; Singleton, 1985) and large-scale landscape composition and structure (Giraudoux et al., 1994; Kaufman and Kauf-

man, 1989). Availability of food resources is one of the more important factors recognized to control small-mammal populations (Hornfeldt, 1994; Moen et al., 1993; Taitt, 1981; Taitt and Krebs, 1981); these studies are of more than purely academic interest in agroecosystems where increasing populations of rodents can result in significant decreases in crop productivity and substantial economic losses. A large number of zoonotic diseases are carried by rodents, and the incidence of these diseases

may reach epidemic proportions when populations of certain species reach high densities. As an example, increased numbers of human cases of Argentine hemorrhagic fever in South America were associated with a temporary increase in abundance of the primary rodent reservoir, *Calomys musculinus* (Mills et al., 1992).

The Argentine Pampa is a temperate sub-humid grassland that has undergone intensive farming for >100 years (Soriano et al., 1991). The rodent assemblage of the central Argentine Pampa consists of six important species, including five sigmodontines *C. musculinus*, *C. laucha*, *Akodon azarae*, *Bolomys obscurus*, and *Oligoryzomys flavescens*, and the naturalized Old-World murine, *Mus musculus* (Mills et al., 1991). Studies of habitat selection show that *C. musculinus*, *B. obscurus*, *A. azarae*, and *O. flavescens* generally are associated with the stable habitats that border crop fields (e.g., roadside, fence line, hedgerow). In contrast, *C. laucha* and *M. musculus* were more frequently captured in cultivated fields (Mills et al., 1992).

Although rodents of the Pampa have been categorized by dietary class (Dalby, 1975; O'Connell, 1982), only two published studies provide data on diets of the rodents in central Argentina (Bilenca et al., 1992; Ellis et al., 1994). In both studies, members of the small-mammal assemblage studied were typified as omnivores. Bilenca et al. (1992) found that *A. azarae* ate higher proportions of insects compared with *C. laucha*, which ate more foliage and seed. In contrast, Ellis et al. (1994) found that these two species consumed fairly equal amounts of insects and seeds. These two studies are difficult to compare, however, given the difference in period of observation. Ellis et al. (1994) studied rodents captured in summer, whereas Bilenca et al. (1992) examined rodents captured in summer and autumn. Barlow (1969) described food habits of the major species captured in grassland habitats of Uruguay by gross examination of stomach contents from a small number of individu-

als of each species. *C. laucha* was predominantly herbivorous (15 stomachs); *A. azarae* and *B. obscurus* ate mostly insects (11 and 7 stomachs, respectively); all 10 stomachs of *O. flavescens* contained plant material and one-half contained some invertebrate remains. None of the cited studies simultaneously measured availability of potential food plants, so that inferences concerning effects of resource availability on diet or on intra- and interspecific interactions were limited.

Our objectives were to: 1) determine the most common food resources exploited by five of the major rodent species from the Argentine Pampa over a 15-month period; 2) relate food use to resource availability by calculating food preference indices; and 3) compare food habits among species and relate this to available information on natural history and habitat associations of rodents of the Pampa.

MATERIALS AND METHODS

Study sites.—Animals were captured from 1 August 1989 to 31 October 1990 from agricultural areas of two provinces (northern Buenos Aires and southern Santa Fe) on the central Argentine Pampa. Anthropogenic disturbance in the study area was universal, except for a few flat low areas where halophytic communities may appear. At least 65% of this area of the Pampa was under cultivation (Hall et al., 1992). Major habitat types included crops (primarily corn, soybeans, wheat), post-harvest crop fields, and the adjacent, more stable border habitats.

Annual rainfall averaged 956 mm based on 80 years of data, with rainfall occurring mainly in autumn and summer (Instituto Nacional de Tecnología Agropecuaria, Pergamino, Argentina). Mean annual temperature was 15.9°C, with a mean minimum and maximum of 9.7° and 40.2°C, respectively.

Kill-trapping was conducted at various sites near (but >2 km from) five sets of permanent mark-recapture grids described by Mills et al. (1992). Those grids and traplines were established on farms near five localities: Maximo Paz (33°29'S, 60°57'W), J.B. Molina (33°30'S, 60°31'W), General Gelly (33°37'S, 60°35'W), Pergamino (33°55'S, 60°35'W), and Oliveros

(32°35'S, 60°51'W). The distance between the two farthest localities was 160 km.

Ten to 20 Victor snap traps (5 by 10 cm) were placed at 5-m intervals along transects in the major habitat types. Each location was visited about every 5 weeks, and a minimum of 225 snap traps were set each night for 3 consecutive nights. Snap traps were baited with peanut butter and checked early each morning.

Stomach content analysis.—Carcasses of captured animals were fixed and stored in 10% neutral-buffered formalin for ≥ 1 month to ensure inactivation of Junin virus, an enveloped RNA virus that causes Argentine hemorrhagic fever. After this time, stomachs were removed and stored in individual containers with 10% formalin until contents were examined. In total, 434 stomachs were analyzed: 141 *C. musculinus*, 139 *C. laucha*, 85 *A. azarae*, 41 *B. obscurus*, and 26 *O. flavescens*. The number of stomachs analyzed from each locality was: Maximo Paz, 164; J.B. Molina, 36; General Gelly, 44; Pergamino, 99; Oliveros, 91.

Histological features of epidermal cells, including occurrence and position of specialized epidermal cell types, were used to identify plant fragments in microscope slides prepared from stomach contents (Holechek et al., 1982). Microhistological techniques for preparation of reference samples and stomach contents followed those used by Holechek (1982) and Sparks and Malechek (1968).

Reference plant material.—Plant reference material was used to confirm and classify plant fragments found in stomachs. Reference plants were collected at peak growing periods, when possible. For grasses, collection was frequently later in the season because they could be identified only at flowering. Plant material was dried (60°C, 48 h) and ground through a 1-mm screen with a micro-Wiley mill. A voucher specimen of each species was retained.

Slide preparation.—For histological examination, stomach contents were rinsed through a 1-mm screen, and a standardized amount was placed on a slide using a metal template 2.5 by 51 cm by 1 mm with openings of 6 mm in diameter spaced at 2.5-cm intervals. Hertwig's solution (Baumgartner and Martin, 1939) was added to the slide, heated to boiling over flame, cooled, and allowed to evaporate. Several drops of Hoyer's solution (Upton, 1993) were placed on the slide and mixed, and a cover slip added.

The solution was again heated to boiling, allowed to cool, and oven-dried (60°C, 1 week). Reference plant material was processed similarly, but dried plant material was mixed with sodium hypochlorite for 20–30 s to clear tissues before rinsing through the 1-mm screen.

Plant species that had $\geq 10\%$ average cover in transects in any given season or locality were collected and chosen for study as reference material. In addition, some species with $< 10\%$ cover but which were known food plants of congeneric rodent species were studied (e.g., *Verbena* is consumed by *Calomys venustus* (= *C. callosus*)—Martinez, 1985). In total, 108 reference vascular plant species, and fungi, moss, and liverworts (not identified to species) were processed prior to making observations of the stomach contents.

Stomach content analysis.—Five slides from each stomach were prepared, and 20 non-overlapping systematically spaced fields were read under a phase contrast microscope at 125 \times (100 microscope fields/sample; a field is the area of a slide visible under a microscope at 125 \times). Twenty observations of five slides per sample provided 80–90% confidence that estimates were within 10% of the mean for plant species that comprise $\geq 20\%$ of the diet (Holechek and Vavra, 1981).

Presence of a food item within a field was recorded, rather than the number or size of fragments, so that the relative frequency for each dietary item was obtained for each stomach. Relative frequency was defined as the number of occurrences of a dietary item divided by the number of occurrences for all items (Holechek and Gross, 1982a). Frequency was defined as the number of fields in which a dietary item occurred among the 100 fields examined. Relative frequency of each dietary item was used as the percentage by weight composition of the diet (Holechek and Gross, 1982a).

The degree of training of the observer greatly influences microhistological results (Holechek and Gross, 1982b). More than 50 known hand-compounded diets were made from reference plant material to train the observer and identify if correction factors were needed (Holechek and Gross, 1982b; Holechek et al., 1984). Hand-compounded test mixtures were made until the observer made estimates within 25% of actual values. Correction factors were not necessary, as neither over- nor underestimation of volumes of

plant species in hand-compounded mixtures occurred (Dearden et al., 1975).

Vegetation analysis.—Plant species composition (percent relative cover) at each capture site was assessed by the line-intercept method (Cox, 1980). A 5-m tape was centered over the trap station and divided into 50-cm intervals. For each plant intercepted by the transect line, the length of the transect intercepted was measured. Aerial coverage by plant species was obtained from these data as: $\text{Cover} = (\sum I/500) \times 100$, where I was the length of the transect intercepted by a given plant species (Cox, 1980).

Due to limitations in time and funding, an assessment of the availability of potential non-plant food items (e.g., arthropods) was not included in the scope of this study.

Data analysis.—Frequency of occurrence and percent volume of major food items in the stomach were examined by rodent species and season for monocots and dicots by seed and leaf, all other plant organs combined (monocot and dicot flowers, dicot stems and fruits, monocot roots), arthropods, other food types (vertebrate muscle, earthworms, feathers, fungi imperfecti, moss, higher fungi), and unidentifiable items. Plant organs then were pooled by plant species to evaluate plant species preferences. Percent volume occupied by endoparasites also was evaluated.

Seasons were defined as: winter, June–August; spring, September–November; summer, December–February; and autumn, March–May. Similar seasons (winter and spring, 1989 and 1990) were combined for statistical analyses.

A two-way analysis of variance was used to test for differences in percent volume of main food categories among rodent species and seasons (Sokal and Rohlf, 1981). All proportions were arcsin-square-root transformed to meet assumptions of normality before testing. If no significant interaction was present, the reduced model was fitted with only main effects. Significant two-way analysis of variance tests were followed by univariate analyses to test for differences among species during each season and among seasons for each species for each of the major food components consumed (Kruskal–Wallis test—Sokal and Rohlf, 1981). Significance level for individual tests was adjusted to $\alpha = 0.002$ for an experiment-wise error rate of $\alpha = 0.05$, according to the Bonferroni approach (Rice, 1989). Sexes were combined in analyses because no statistically significant differences in

consumption of the major food items were observed between sexes for any rodent species within any season (two-way Analysis of Variance on arcsin-square root transformed proportions; data not shown).

Seasonal dietary overlap among rodent species was calculated using Schoener's formula (Abrams, 1980; Schoener, 1970): $100 (1.0 - \frac{1}{2} \sum |p_{xi} - p_{yi}|)$, where p_{xi} and p_{yi} represented proportional use of resource I by species x and y . Seasonal dietary breadth for each rodent species was calculated as: $B = 1 / \sum (p^2)$, where p was the relative frequency of occurrence of each dietary item (Levins, 1968).

Diet and habitat preferences.—Vegetation transect data were used to characterize plant species as border, crop, or both habitat types, based on frequency of occurrence. Plant species were classified as primarily crop or border habitat species if they occurred in that habitat $\geq 75\%$ of the time. To evaluate selective foraging by rodents, proportions of stomach volumes consisting of items from each habitat type were compared among rodent species and season. Again, a two-way analysis of variance was used to test for differences in arcsin-square-root transformed percent volume of plant food items consumed from crop versus border habitats, among rodent species, and seasons. If no significant interaction was present, the reduced model was fitted with only main effects. Significant two-way analysis of variance tests were followed by univariate analyses to test for differences among species during each season and among seasons for each species for each of the plant types consumed (Kruskal–Wallis test—Sokal and Rohlf, 1981). Significance level for individual tests was adjusted to $\alpha = 0.002$ for an experimentwise error rate of $\alpha = 0.05$, according to the Bonferroni approach (Rice, 1989).

A preference index was calculated for each animal as the ratio between the relative volume of each food item consumed and the relative amount of that item available in the animal's environment (Ivlev, 1961). Preference indices were computed only for plant species consumed by: $E = (r - p)/(r + p)$, where r was the proportional consumption of that item by the rodent (percent volume in the stomach) and p was availability of that item in the environment (percent cover in the transect—Jacobs, 1974). Positive values suggested preferred items; negative values indicated that an item was consumed in

TABLE 1.—Probabilities from two-way analysis of variance analyzing differences among five rodent species and four seasons in mean proportion of stomach content consisting of each of five major dietary components. Models were first tested with interaction terms (model 1); if interaction was not significant, significance of only main effects was examined (model 2). All variables were arcsin-square-root transformed prior to analysis (NT = not tested).

Variable	Model	Species	Season	Interaction
Arthropods	1	<0.00001	0.152	0.172
	2	<0.0001	0.002	NT
Dicot leaf	1	0.54	0.05	0.18
	2	0.73	0.35	NT
Monocot leaf	1	0.026	0.487	0.105
	2	0.049	0.015	NT
Total leaf	1	0.314	0.132	0.230
	2	0.688	0.090	NT
Dicot seed	1	0.009	<0.0001	0.009
Monocot seed	1	0.186	<0.0001	0.06
	2	0.040	<0.0001	NT
Total seed	1	<0.0001	<0.0001	0.246
	2	<0.0001	<0.0001	NT

a lower proportion than its availability. Numbers near zero indicated the item was used in roughly the proportion available. Confidence intervals (95%) were computed on mean preference indices. Data were analyzed using SAS version 6.08 (SAS Institute, 1988) and SPSS version 6.0 software (Norusis, 1993).

RESULTS

General diet description.—Although all five rodent species studied were omnivorous, relative proportions of diets consisting of some of the food items differed significantly among seasons and among species (Table 1, Fig. 1). Significant differences in consumption of monocot leaves, monocot seeds, and arthropods were observed among rodent species and seasons.

Consumption of arthropods was generally high in spring and summer and lowest in autumn for all species (Table 2). Arthropods were least commonly consumed in winter for all species except *A. azarae*. Consumption of dicot and monocot leaves was fairly constant throughout the year for all species. Exceptions were the high consumption of dicot leaves by *A. azarae* in spring and *O. flavescens* in summer, and the low consumption of monocot leaves by *C. musculinus* and *A. azarae* in autumn. Con-

sumption of dicot seeds was uniformly low in summer but was high during other seasons. Conversely, consumption of monocot seeds was low in winter and spring, and much higher in summer and autumn.

Among rodent species, relative proportions of major food categories were very similar for *C. musculinus* and *C. laucha* (Fig. 1). *A. azarae* consistently ate higher quantities of arthropods in all seasons than other rodent species (except for *B. obscurus* in summer). In winter when all other species ate large quantities of dicot seeds, *A. azarae*'s specialization on arthropods was most pronounced (Fig. 1, Table 2). *B. obscurus* was the second highest consumer of arthropods and highest consumer of monocot leaves, especially in spring. The two species of *Calomys* and *O. flavescens* ate greater volumes of seeds than either *A. azarae* or *B. obscurus* (Kruskal-Wallis test, $P < 0.0001$, Table 2). Only one *O. flavescens* was examined from spring, and that animal consumed a large quantity of moss.

Rarely eaten food items included earthworms ($n = 4$), feathers ($n = 4$), vertebrate flesh ($n = 5$), filamentous fungi ($n = 36$), moss ($n = 17$), and mushrooms ($n = 2$). Overall, 28% (122 of 434) of rodents had

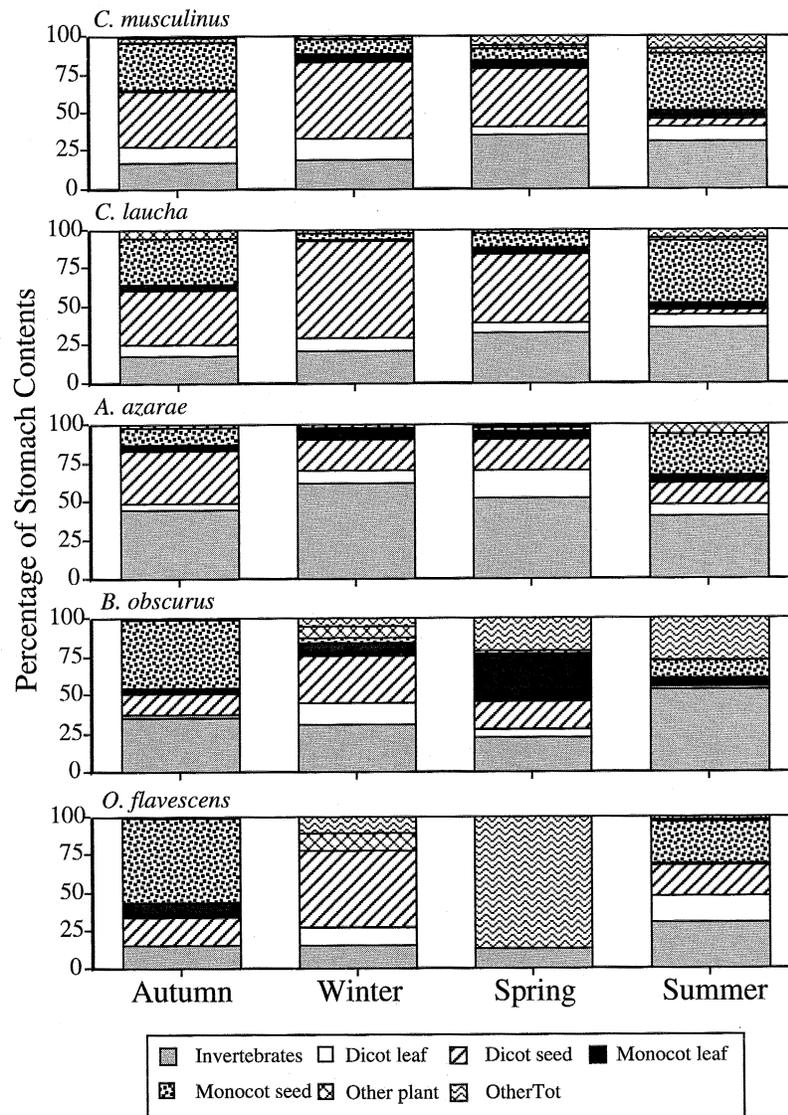


FIG. 1.—Seasonal variation in proportion of stomach content consisting of major food groups for five species of rodents captured from central Argentina, August 1989 through October 1990 (autumn = March–May; winter = June–August; spring = September–November; summer = December–February; other plant = dicot and monocot flowers and stems, dicot fruit, monocot root; othertot = total of other categories, including earthworms, vertebrate flesh, moss, and fungi).

parasites in their stomachs. These numbers were fairly constant among species: 28%, *C. musculus*; 24%, *C. laucha*; 34%, *A. azarae*; 37%, *B. obscurus*; and 19%, *O. flavescens*. Most parasites were nematodes.

Dietary breadth and overlap.—Dietary breadth, based on the seven major cate-

gories of food items, was generally highest in summer and autumn and low in winter and spring, except for *B. obscurus*, which demonstrated the opposite pattern (Table 3). Dietary breadth of *A. azarae* was relatively low in most seasons and when all seasons were combined, probably reflecting its rel-

TABLE 2.—Mean volume of stomach contents (percent of total volume) consisting of major diet items among rodent species by season (CM = *C. musculinus*; CL = *C. laucha*; AA = *A. azarae*; BO = *B. obscurus*; OF = *O. flavescens*). Probability of Kruskal-Wallis test given for each comparison among species for each season and among seasons for each rodent species (NT = not tested because of significant interaction between main effects, Table 1; significance level for individual tests was adjusted to $\alpha = 0.002$ according to an experiment-wise error rate of $\alpha \leq 0.05$, according to the Bonferroni approach; * $P \leq 0.002$; ** $P < 0.0001$; autumn = March–May; winter = June–August; spring = September–November; summer = December–February).

Component/ season	CM	CL	AA	BO	OF	All species	P
Arthropods							
Autumn	16.5	17.4	45.3	35.4	14.8	24.8	**
n	43	43	28	17	8		
Winter	18.5	20.6	62.4	30.6	15.2	36.6	**
n	18	21	37	16	9		
Spring	34.9	32.6	52.6	22.1	13.3	34.2	
n	21	32	7	6	1		
Summer	30.9	35.5	40.5	53.1	30.5	34.1	
n	59	43	13	4	8		
All seasons	25.5	27.0	52.6	33.4	19.7	31.7	**
n	141	139	85	43	26	434	
P	*						
Dicot leaf							
Autumn	11.4	8.2	3.9	2.0	0.7	7.1	
Winter	14.0	9.5	8.3	13.8	11.6	10.7	
Spring	5.3	7.0	17.5	5.5	0.0	7.3	
Summer	9.4	8.8	7.5	2.1	17.2	9.2	
All seasons	10.0	8.3	7.5	6.9	9.5	8.6	
P		*					
Monocot leaf							
Autumn	1.1	4.1	4.4	3.0	9.7	3.4	
Winter	5.6	1.5	5.3	8.2	0.9	4.6	
Spring	5.9	4.6	5.6	31.2	0.0	7.4	
Summer	5.7	4.9	5.8	2.8	0.9	5.0	
All seasons	10.1	11.8	10.3	23.7	14.0	4.8	
P						*	
All leaf							
Autumn	12.4	12.3	8.3	5.0	10.4	10.5	
Winter	19.6	11.0	13.6	21.9	12.5	15.4	
Spring	11.3	11.6	23.1	36.7	0.0	14.8	
Summer	15.0	13.7	13.3	5.0	18.2	14.3	
All seasons	14.2	12.4	12.6	15.7	13.1	13.4	
P							

TABLE 2.—Continued.

Component/ season	CM	CL	AA	BO	OF	All species	P
Arthropods							
Dicot seed							
Autumn	36.0	35.0	34.0	13.9	17.9	31.6	
Winter	50.8	62.4	19.7	31.3	50.0	38.6	*
Spring	38.4	43.9	20.7	17.9	0.0	36.8	
Summer	5.3	3.0	13.7	2.5	19.7	6.2	
All seasons	25.4	31.3	23.6	19.9	28.8	26.6	NT
P	**	**				NT	
Monocot seed							
Autumn	31.3	29.8	10.3	44.5	55.6	29.6	*
Winter	8.9	3.6	1.3	3.5	0.0	3.4	
Spring	6.8	9.9	1.8	2.5	0.0	7.3	
Summer	37.0	40.7	26.6	11.7	27.9	35.8	
All seasons	27.2	24.6	8.2	20.3	25.7	21.9	**
P	**	**	*	*	*	*	
All seed							
Autumn	67.3	64.8	44.3	58.4	73.4	61.2	
Winter	59.6	66.0	21.0	34.8	50.0	42.0	*
Spring	45.2	53.8	22.4	20.4	0.0	44.0	
Summer	42.3	43.6	40.3	14.2	47.6	42.0	
All seasons	52.6	55.9	31.8	40.2	54.5	48.5	**
P	*					**	

actively high intake of a single category (arthropods). Although *O. flavescens* did not demonstrate especially wide dietary breadth in any one season, it had the highest overall breadth (seasons combined). This probably derived from switching dietary items among seasons: primarily monocot seeds in autumn, dicot seeds in winter, and increased consumption of insects and dicot leaves in summer (Fig. 1; Table 2).

TABLE 3.—Dietary breadth (Levin's "B") for rodent species by season calculated with major dietary components; sample sizes given in Table 2 (NC = not calculated, n = 1).

	Au- tumn	Winter	Spring	Sum- mer	All seasons
<i>C. musculinus</i>	3.7	3.0	3.4	3.8	4.3
<i>C. laucha</i>	3.7	2.2	3.1	3.1	3.8
<i>A. azarae</i>	2.9	2.2	2.8	3.6	3.0
<i>B. obscurus</i>	2.9	4.0	3.9	2.7	4.5
<i>O. flavescens</i>	2.7	2.6	NC	4.2	5.2

TABLE 4.—Seasonal dietary overlap (%) for each rodent species pair calculated with major dietary items as listed in Fig. 1 (NC = not calculated, n = 1 *O. flavescens*).

Species pair	Autumn	Winter	Spring	Summer	All seasons
<i>C. musculus</i> - <i>C. laucha</i>	93.6	85.3	89.8	91.5	94.8
<i>C. musculus</i> - <i>A. azarae</i>	67.4	54.7	70.4	81.9	74.4
<i>C. musculus</i> - <i>B. obscurus</i>	65.7	75.1	66.3	58.6	76.1
<i>C. musculus</i> - <i>O. flavescens</i>	66.9	82.0	NC	78.7	79.0
<i>C. laucha</i> - <i>A. azarae</i>	73.1	53.1	68.3	83.0	74.3
<i>C. laucha</i> - <i>B. obscurus</i>	68.4	68.9	61.1	60.0	74.1
<i>C. laucha</i> - <i>O. flavescens</i>	69.6	80.1	NC	76.0	76.2
<i>A. azarae</i> - <i>B. obscurus</i>	65.7	69.1	61.5	65.4	78.2
<i>A. azarae</i> - <i>O. flavescens</i>	48.8	49.9	NC	82.6	64.7
<i>B. obscurus</i> - <i>O. flavescens</i>	51.6	58.4	NC	57.0	56.7

A high degree of dietary overlap was seen with all species pairs; overall overlap ranged from 57% for *B. obscurus*-*O. flavescens* to 95% for *C. musculus*-*C. laucha* (Table 4). Overlap for each of the species pairs differed with seasons, except for *B. obscurus* with *A. azarae*, *C. laucha*, and *O. flavescens*, which showed a relatively constant degree of overlap throughout the year. In most cases, overlap was highest in winter (6 of 10 species pairs) and lowest in summer (7 of 10 pairs). Cases of highest overlap in summer all involved *A. azarae* with *C. musculus*, *C. laucha*, or *O. flavescens*. The three pairs for which overlap was lowest in winter included the two species of *Calomys* and *A. azarae*. Highest overlap for *C. musculus* and *C. laucha*

occurred in autumn (when both species consumed the greatest proportion of crop plants), but the lowest overlap was in winter.

Classification of food plants by habitat.—Significant differences in plant foods consumed from crop and border habitats were observed among rodent species with time (Table 5). Except for *B. obscurus* in summer, *C. laucha* and *B. obscurus* consumed relatively high proportions of crop plants during all seasons (overall 52% and 56% of stomach volume, respectively). *O. flavescens* consumed smaller proportions of crop material throughout the year (27% of stomach volume overall; Table 6). *C. musculus* and *A. azarae* consumed high proportions of crop plants during autumn and winter but switched to plant species growing in crop-field borders (and some ubiquitous species) during spring and summer. The cropland specialist, *C. laucha*, had the lowest consumption of plant species growing in border habitats throughout the year and was the only species that used ubiquitous plant species in all seasons.

Plant species preferences.—In total, 107 plant species were identified from transects where animals were captured, and 70 of those plant species were consumed by the five rodent species studied (Appendix I). Of the plant species consumed, six were not present on transects (*Conium maculatum*, *Cotula australis*, *Physalis viscosa*, *Pisum sativum*, *Salpichroa origanifolia*, *Triodanis*

TABLE 5.—Probabilities from two-way analysis of variance analyzing differences in mean volume of plant items in stomachs classified by habitat type among rodent species and seasons. Models were first tested with interaction terms (model 1); if interaction was not significant, the significance of only main effects was examined (model 2). All variables were arcsin-square-root transformed prior to analysis (NT = not tested).

Variable	Model	Species	Season	Interaction
Crop plants	1	0.01	<0.0001	0.20
	2	0.005	<0.0001	NT
Border plants	1	<0.0001	0.02	0.03
Ubiquitous	1	0.03	0.10	0.51
	2	0.08	<0.0001	NT

TABLE 6.—Mean volume of plant items in stomachs classified by habitat type among rodent species by season (CM = *C. musculus*; CL = *C. laucha*; AA = *A. azarae*; BO = *B. obscurus*; OF = *O. flavescens*). Probability of Kruskal-Wallis test given for each comparison among species across seasons and for each season for a given rodent species (only statistically significant tests are reported after Bonferroni adjustment of probability value, * $P \leq 0.002$; ** $P < 0.0001$). Sample sizes given in Table 2.

Component/ season	CM	CL	AA	BO	OF	All species	P
Crop plants							
Autumn	63.2	59.2	51.3	72.5	32.5	59.1	
Winter	56.3	60.5	48.0	42.4	29.4	49.4	
Spring	26.7	42.7	30.5	65.0	0.0	38.1	
Summer	17.6	49.4	21.0	18.9	21.4	28.7	
All seasons	39.6	52.5	43.5	55.7	26.5	45.3	**
P	**						
Border plants							
Autumn	31.4	25.5	31.9	24.0	67.5	30.8	
Winter	28.3	5.0	38.9	41.8	27.3	29.6	*
Spring	42.8	16.3	61.8	16.9	100.0	30.0	
Summer	67.4	34.9	67.6	34.2	47.0	54.3	**
All seasons	46.0	22.4	42.9	30.6	47.8	36.5	NT
P						NT	
Ubiquitous							
Autumn	5.4	12.6	13.0	3.5	0.0	8.6	
Winter	15.4	29.5	13.0	9.6	21.1	16.9	
Spring	25.4	40.9	7.7	18.1	0.0	30.3	
Summer	10.6	12.8	3.8	13.6	19.1	11.2	
All seasons	12.0	22.7	11.1	8.8	13.7	14.9	**
P		**					

biflora; Appendix I). Plant species unique to the diet of each rodent species include: 1) *C. musculus*—*Conium maculatum*, *Setaria*, and *Briza*; 2) *C. laucha*—*Commelina erecta* and *Pisum sativum*; 3) *A. azarae*—*Calamagrostis*, *Geranium*, *Juncus*, and *Baccharis*; 4) *B. obscurus*—*Galium* and *Plantago*. Plant species consumed in greatest quantities by all five rodent species included *Amaranthus* (leaf and seed), and mostly seed from *Sorghum*, *Stellaria*, corn and soybeans.

Dominant plant species in study areas bordering crop fields included grasses (*Stipa*, *Sorghum*, *Cynodon*, *Lolium*, *Setaria*, and *Bromus*) and the European weed *Carduus* (Appendix I). Aside from the cultivars corn (*Zea mays*), soybeans (*Glycine max*), wheat (*Triticum aestivum*), lentils (*Lens culinaris*), and sunflowers (*Helianthus annuus*), domi-

nant plant species found in crop fields included the invasive European weeds *Cynodon dactylon*, *Digitaria sanguinalis*, *Stellaria media*, and *Sorghum halepense*.

Calculation of preference indices demonstrated that most plant species were not significantly avoided or preferred but consumed in an amount proportional to their abundance (Table 7). A smaller set of plant species was avoided (i.e., consumed in a much smaller amount than that available in the habitat). Significant preference was demonstrated in only a very few cases. *Stellaria media* (chickweed), wheat, and corn were consumed by *C. laucha* in significantly greater proportions than its availability in spring. *Stipa* was consumed by *C. laucha* in greater proportions than its availability in summer. Corn was a preferred food item for both *C. musculus* and *B. obscurus* in Au-

TABLE 7.—Directions of preference indices for plant species consumed and habitats with which plant species occur in greatest frequency where $n \geq 5$ (CM = *C. musculus*; CL = *C. laucha*; AA = *A. azarac*; BO = *B. obscurus*; OF = *O. flavescens*; ubiq = ubiquitous; 0 = no significant preference for food plant; - = significantly avoided; + = significantly preferred item, as measured by 95% CI).

Plant species	Habitat	Autumn						Winter						Spring						Summer					
		CM	CL	AA	OF	BO	UBIQ	CM	CL	AA	OF	BO	UBIQ	CM	CL	AA	OF	BO	UBIQ	CM	CL	AA	OF	BO	UBIQ
Annual dicot																									
<i>Amaranthus</i>	Crop	0	0	0	0	0	0	0	0	0	0	0	0	-	0	-	0	-	0	-	0	-	0	-	0
<i>Ammi majus</i>	Border	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Artemisia annua</i>	Border	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bidens</i>	Border	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	-	0	0	0	-	0	-	0
<i>Bowlesia incana</i>	Border	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Brassica</i>	Border	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Capsella bursa-pastoris</i>	Border	0	-	-	-	-	-	-	-	-	-	-	-	0	0	-	0	-	0	0	0	-	0	-	0
<i>Carduus</i>	Border	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Coryza</i>	Border	-	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-
<i>Coronopus didymus</i>	Crop	-	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-
<i>Datura ferox</i>	Ubiq	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Gainsoga parviflora</i>	Crop	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Glycine max</i>	Crop	-	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lamium amplexicaule</i>	Crop	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Oxalis</i>	Border	-	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-
<i>Portulaca oleracea</i>	Crop	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Solanum</i>	Border	-	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sonchus</i>	Border	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Stellaria media</i>	Ubiq	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Tagetes minuta</i>	Border	-	0	0	0	0	0	0	0	0	0	0	0	0	0	+	0	0	0	0	0	+	0	0	0
<i>Urtica urens</i>	Border	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Veronica</i>	Crop	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Annual monocot																									
<i>Brachiaria</i>	Crop	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bromus unioloides</i>	Border	0	0	0	0	0	0	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	-	-	-
<i>Digitaria</i>	Ubiq	-	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	-	0	0	0	-	0	-	0
<i>Echinochloa cruzgalli</i>	Crop	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lotium multiflorum</i>	Border	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

tumn; *Brachiaria* was a favorite food item of *A. azarae* in autumn.

DISCUSSION

Our results show clearly that the five species of rodents studied were omnivores; however, differences in the proportion of both major food groups and specific plant species consumed varied temporally and spatially for each rodent species. Among the five species, *A. azarae* and *B. obscurus* were relatively entomophagous. This tendency was most pronounced in autumn and winter when all other species tended to specialize on seeds. The two species of *Calomys* had nearly identical diets (in terms of major diet categories) throughout the year. This extensive dietary overlap may be possible because of pronounced spatial segregation between the two congeners, with *C. musculinus* inhabiting border habitats and *C. laucha* predominantly in crops (Mills et al., 1992). Although *O. flavescens* has been categorized in the literature as spermophilous (Dalby, 1975; O'Connell, 1982), our data do not support that characterization. Although sample sizes for this species were not as large as for the other species, *O. flavescens* did not consume larger quantities of seed than *C. musculinus* or *C. laucha*. Given the high degree of dietary overlap with the two species of *Calomys*, it may be important that *O. flavescens* is very restricted to border habitats (Mills et al., 1992). It was the only species that did not consume appreciably higher quantities of crop than border species during at least one season of the year.

Bilenca et al. (1992) also observed differences in the amount of major food groups consumed by *A. azarae* and *C. laucha* in late spring through autumn. As in our study, those researchers found *A. azarae* consumed arthropods in higher quantities than seeds or foliage compared with *C. laucha*, which showed the reverse pattern (Fig. 1, Table 2). Our failure to find statistically significant differences in consumption of the major food items between sexes also corroborates findings of Bilenca et al. (1992).

Food plants were classified as crop, border, or ubiquitous based on their frequencies of occurrences in the transects. Although some crop plants occurred primarily in crop habitats, these species also may have occurred in a much lower frequency in border habitats, and vice versa. Given this caveat, classification of plant food items by habitat type suggests a seasonal pattern of habitat utilization. All five species consumed more plants from crop habitats in autumn, concomitant with corn and soybean maturity and increasing cover and maximum height found in these fields (Ellis et al., in litt.). Lowest utilization of crop plants for all species was in summer, except *C. laucha*, which was in spring. This may be due to the lower cover and species diversity of plants seen in crop fields during this time, non-availability of corn and soybean grain, and increased availability of grass seed in border habitats. *C. laucha* consumed less plants from border habitats during winter ($P = 0.06$, not corrected for experiment-wise error rate; Table 6) when cover in crop fields was lowest and rodent density in border habitats was highest (Mills et al., 1992). This finding might be explained by competitive exclusion of *C. laucha* from border habitats by larger more dominant species. In laboratory experiments, *Akodon* is dominant over *C. laucha* (Cueto et al., 1995), and evidence from food supplementation experiments suggests that food may be a limiting factor for these rodents in winter (Cittadino et al., 1994).

For most species pairs, highest dietary overlap occurred in winter when rodents were forced to share a relatively narrow resource pool. During winter, all five rodent species ate large amounts of soybean grain (11% for *B. obscurus* to 27% for *C. laucha*). We found ≤ 50 g of soybean grain within 1-m² quadrats in stubble fields at the post-harvest sites where small-mammal trapping was done. That grain is eaten by all five rodent species in winter. In contrast, highest overlap for *A. azarae* with *C. musculinus*, *C. laucha*, and *O. flavescens* occurred in summer when *A. azarae* had the widest dietary breadth.

During this time of abundant resource availability, high dietary overlap of *A. azarae* with the other rodent species appears sustainable.

Akodon azarae had the lowest dietary breadth compared with the other four species. However, caution should be used when interpreting dietary breadth based on a few broad categories of food items. Levin's breadth statistic, like the Simpson diversity measure on which it is based (Ludwig and Reynolds, 1988), is sensitive to both richness and evenness. In this case, because all species consumed all seven diet categories, their richness values are equal, and differences in breadth reflect only the differences in evenness of dietary components among rodent species.

The pattern of plant preference indices indicates that there exists a large subset of plants that are not considered food items (the significantly "avoided" species) and a large suite of plants that are considered food items and are consumed in the proportion in which they occur in the environment (those for which no significant avoidance was seen; Table 7). Apparently very few plant species are actively sought in preference to other species that also are considered acceptable food plants.

The high preference index for corn by *C. musculinus* and *A. azarae* in autumn represents grain consumed from post-harvest corn fields where grain is abundant, but the coverage by corn plants was relatively low. We recorded an average of 126 g of corn grain/1-m² quadrat in stubble fields where animals were captured, representing a significant resource for species that enter post-harvest crop fields.

Several sources of error with our method of establishing food preference can result in either over- or underestimation of taxa consumed (Holechek et al., 1984; Westoby et al., 1976). Those sources include: 1) methods of processing samples that may result in differences of ratios of identifiable to non-identifiable fragments between plant species; 2) differential digestion of taxa so that stom-

achs contain different proportions of tissues that are identifiable (only the epidermis of non-woody tissue is identifiable); 3) an item may occur several times before the observer acquires a "search image" for it; 4) identifiable material may vary among taxa in ease of recognition; and 5) problems in identification of taxa, including misidentification of all particles of an identifiable material, inability to name material that was identifiable, and missing material entirely. Any analysis of diet based on stomach content is subject to potential bias, including differential digestive rates of food items and problems associated with identification and quantification of fragmented dietary items (Rosenberg and Cooper, 1990). An additional potential source of bias in this study was the lack of specific identifications of arthropods consumed. We do not know the range of arthropods or seasonal variations in their consumption. This limitation must be considered when interpreting our results of dietary breadth measurements for the largely insectivorous *A. azarae*. If arthropods had been classified into several categories and all plant items lumped into a single category, our results would have been quite different. Finally, difficulties associated with quantification of available resources (plant species) in a particularly heterogeneous environment are another source of potential bias. It is unknown if our sampling design of assessing availability of food items at a 5-m transect actually reflects availability of those items within the home ranges of these rodent species. In addition, quantification of percent cover by these items does not necessarily reflect availability to the rodent, as access is affected by height, location, and density of plants and human activity.

Observed variation in dietary choice of major food groups and specific plant species with season and rodent species underscores the importance of scale at the level of food-item identification and appropriate time intervals for assessment when designing studies of small mammals. Studies that do not span all seasons do not provide results that

are generalizable. This study, conducted over a 15-month period, is the most complete study to date of the dietary habits of these five rodents, but it still is based on a single complete annual cycle.

A variety of factors may result in differences in rodent diets among seasons and years, species, or other subgroups of rodents. Although these were outside the scope of this work, it is important to consider them. Tardiff and Gray (1978) have shown that for a population of *Peromyscus leucopus*, immigrants are food generalists, while residents are food specialists. Furthermore, dietary specialization of resident *P. leucopus* may undergo daily changes. Effects of stochastic events such as aberrant climatic patterns, or deterministic events such as crop phenology and land use management techniques, affect population dynamics of the small-mammal assemblage in central Argentina (Bonaventura et al., 1991; Crespo, 1944; Mills et al., 1992). Flexibility of selection in dietary items among Pampa rodents in response to these events remains unknown. We cannot address year-to-year variation but speculate that as year-to-year climatic conditions vary, they will result in different availabilities of food resources and different densities of rodents and patterns of competition. These different patterns in biotic and abiotic environmental conditions may translate into different dietary patterns.

Bilenca and Kravetz (1995) found that *C. laucha* reduced density and ear production of corn plants by 3.1% and 4.6%, respectively, and suggested that a rodenticide application would offer a high benefit-to-cost ratio. Our study suggests that this rodent-control strategy may not necessarily be the most prudent approach. Application of rodenticides would result in decreased populations of other non-target rodents, such as *A. azarae*, which consumes large quantities of insects that may destroy substantial quantities of insect pests of crops. While it is not possible for us to address numbers and kinds of insects that these rodent species consume,

further studies should be done to quantify this aspect of these rodents' diets.

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LITERATURE CITED

- ABRAMS, P. 1980. Some comments on measuring niche overlap. *Ecology*, 61:44-49.
- BARLOW, J. C. 1969. Observations on the biology of rodents in Uruguay. *Life Sciences Contributions, Royal Ontario Museum, Toronto, Ontario, Canada*, 75:1-59.
- BAUMGARTNER, L. L., AND A. C. MARTIN. 1939. Plant histology as an aid in squirrel food-habitat studies. *The Journal of Wildlife Management*, 3:266-268.
- BILENCA, D. N., AND F. O. KRAVETZ. 1995. Danos a maiz por roedores en la region pampeana (Argentina) y un plan para su control. *Vida Silvestre Neotropical*, 4: 51-57.
- BILENCA, D. N., F. O. KRAVETZ, AND G. A. ZULETA. 1992. Food habits of *Akodon azarae* and *Calomys laucha* (Cricetidae, Rodentia) in agroecosystems of central Argentina. *Mammalia*, 56:371-383.
- BONAVENTURA, S. M., M. J. PANTANIDA, L. GURINI, AND M. I. SANCHEZ LOPEZ. 1991. Habitat selection in population of cricetine rodents in the region Delta (Argentina). *Mammalia*, 55:339-354.
- BROWN, J. H., AND J. C. MUNGER. 1985. Experimental manipulation of a desert rodent community: food addition and species removal. *Ecology*, 66:1545-1563.
- BROWN, J. S., B. P. KOTLER, R. J. SMITH, AND W. O. WIRTZ. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia*, 76: 408-415.
- CITTADINO, E. A., P. DE CARLI, M. BUSCH, AND F. O.

- KRAVETZ. 1994. Effects of food supplementation on rodents in winter. *Journal of Mammalogy*, 75:446–453.
- COX, G. W. 1980. *Laboratory manual of general ecology*. William C. Brown Company, Dubuque, Iowa, 237 pp.
- CRESPO, J. A. 1944. Relaciones entre estados climaticos y la ecologia de algunos roedores de campo (Cricetidae). *Revista Argentina de Zoogeografia*, 4:137–144.
- CUETO, G. R., D. N. BILENCA, AND F. O. KRAVETZ. 1995. Interspecific social relationships in three murid rodent species of central Argentina, after fasting and unlimited food. *Behaviour*, 132:811–820.
- DALBY, P. L. 1975. *Biology of Pampa rodents*. Publications of the Museum, Michigan State University, Biological Series, 5:149–272.
- DEARDEN, B. L., R. E. PEGAU, AND R. M. HANSEN. 1975. Precision of microhistological estimates of ruminant food habits. *The Journal of Wildlife Management*, 39:402–407.
- DESY, E. A., AND G. O. BATZLI. 1989. Effects of food availability and predation on prairie vole demography: a field experiment. *Ecology*, 70:411–421.
- DESY, E. A., G. O. BATZLI, AND J. LUI. 1990. Effects of food and predation on behaviour of prairie voles: a field experiment. *Oikos*, 58:159–168.
- ELLIS, B. A., J. N. MILLS, E. J. T. KENNEDY, J. I. MAIZTEGUI, AND J. E. CHILDS. 1994. The relationship among diet, alimentary tract morphology, and life history for five species of rodents from the central Argentine pampa. *Acta Theriologica*, 39:345–355.
- GIRAUDOUX, P., P. DELATTRE, J.-P. QUERE, AND J.-P. DAMANGE. 1994. Structure and kinetics of rodent populations, in a region under agricultural land abandonment. *Acta Oecologica*, 15:385–400.
- HALL, A. J., C. M. REBELLA, C. M. GHERSA, AND J. P. CULOT. 1992. Field-crop systems of the Pampas. Pp. 413–450, *in* *Field crop ecosystems* (C. J. Pearson, ed.). Elsevier, Amsterdam, The Netherlands, 576 pp.
- HOLECHEK, J. L. 1982. Sample preparation techniques for microhistological analysis. *Journal of Range Management*, 35:267–268.
- HOLECHEK, J. L., AND B. D. GROSS. 1982a. Evaluation of different calculation procedures for microhistological analysis. *Journal of Range Management*, 35:721–723.
- . 1982b. Training needed for quantifying simulated diets from fragmented range plants. *Journal of Range Management*, 35:644–647.
- HOLECHEK, J. L., AND M. VAVRA. 1981. The effect of slide and frequency observation numbers on the precision of microhistological analysis. *Journal of Range Management*, 34:337–338.
- HOLECHEK, J. L., M. VAVRA, AND R. D. PIEPER. 1982. Botanical composition determination of range herbivore diets: a review. *Journal of Range Management*, 35:309–317.
- . 1984. Methods for determining the botanical composition, similarity, and overlap of range herbivore diets. Pp. 425–471, *in* *Developing strategies for rangeland management* (G. M. Van Dyne, J. Brotmov, B. Burch, S. Fairfax, and B. Huey, eds.). Westview Press, Boulder, Colorado, 2,022 pp.
- HORNFELDT, B. 1994. Delayed density dependence as a determinant of vole cycles. *Ecology*, 75:791–806.
- IVLEV, V. S. 1961. *Experimental ecology of the feeding of fishes*. Yale University Press, New Haven, Connecticut, 302 pp.
- JACOBS, J. 1974. Quantitative measurement of food selection. A modification of the forage ratio and Ivlev's electivity index. *Oecologia*, 14:413–417.
- KAUFMAN, D. W., AND G. A. KAUFMAN. 1989. Nongame wildlife management in central Kansas: implications of small mammal use of fencerows, fields and prairie. *Transactions of the Kansas Academy of Science*, 92:198–205.
- LEVINS, R. 1968. *Evolution in changing environments*. Princeton University Press, Princeton, New Jersey, 120 pp.
- LUDWIG, J. A., AND J. F. REYNOLDS. 1988. *Statistical ecology*. John Wiley & Sons, New York, 337 pp.
- MARTINEZ, R. L. 1985. *Preferencias alimentarias de Akodon dolores (Thomas) durante la estacion invernal*. M.S. thesis, National University of Rio Cuarto, Rio Cuarto, Argentina, 65 pp.
- MILLS, J. N., B. A. ELLIS, K. T. MCKEE, J. I. MAIZTEGUI, AND J. E. CHILDS. 1991. Habitat associations and relative densities of rodent populations in cultivated areas of central Argentina. *Journal of Mammalogy*, 72:470–479.
- MILLS, J. N., ET AL. 1992. A longitudinal study of Junin virus activity in the rodent reservoir of Argentine hemorrhagic fever. *American Journal of Tropical Medicine and Hygiene*, 47:749–763.
- MOEN, J., H. GARDFIJELL, L. OKSANEN, L. ERICSON, AND P. EKERHOLM. 1993. Grazing by food-limited microtine rodents on a productive experimental plant community: does the "green desert" exist? *Oikos*, 68:401–413.
- NORUSIS, M. J. 1993. *SPSS for Windows*. Release 6.0. SPSS Inc., Chicago, Illinois, 828 pp.
- O'CONNELL, M. A. 1982. Population biology of North and South American grassland rodents: a comparative review. Pp. 167–185, *in* *Mammalian biology in South America* (M. A. Mares and H. H. Genoways, eds.). Special Publications Series, Pymatuning Laboratory of Ecology, University of Pittsburgh, 6:1–539.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, 43:223–225.
- ROSENBERG, K. V., AND R. J. COOPER. 1990. Approaches to avian diet analysis. *Studies in Avian Biology*, 13:80–90.
- SAS INSTITUTE INC. 1988. *SAS/STAT user's guide*, release 6.03 edition. SAS Institute, Inc. Cary, North Carolina, 1,028 pp.
- SCHOENER, T. W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology*, 51:408–418.
- SINGLETON, G. R. 1985. Population dynamics of *Mus musculus* and its parasites in mallee wheatlands in Victoria during and after drought. *Australian Wildlife Resources*, 12:437–445.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry: the principles and practice of statistics in biological research*, Second ed. W. H. Freeman & Co., San Francisco, California, 776 pp.
- SORIANO, A., ET AL. 1991. Temperate subhumid grasslands of South America. Pp. 367–407, *in* *Natural*

- grasslands (R. T. Coupland, ed.). Volume 8A. Elsevier, Amsterdam, The Netherlands, 469 pp.
- SPARKS, D. R., AND J. C. MALECHEK. 1968. Estimating percentage dry weight in diet using a microscope technique. *Journal of Range Management*, 21:264–265.
- TAITT, M. J. 1981. The effect of extra food on small rodent populations. I. Deermice (*Peromyscus maniculatus*). *The Journal of Animal Ecology*, 50:111–124.
- TAITT, M. J., AND C. J. KREBS. 1981. The effect of extra food on small rodent populations. II. Voles (*Microtus pennsylvanicus*). *The Journal of Animal Ecology*, 50:125–137.
- TARDIFF, R. R., AND L. GRAY. 1978. Feeding diversity in resident and immigrant *Peromyscus leucopus*. *Journal of Mammalogy*, 59:559–562.
- UPTON, M. S. 1993. Aqueous gum-chloral slide mounting media: an historical review. *Bulletin of Entomological Research*, 83:267–274.
- WESTOBY, M., G. R. ROST, AND J. A. WEIS. 1976. Problems with estimating herbivore diets by microscopically identifying plant fragments from stomachs. *Journal of Mammalogy*, 57:167–172.

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APPENDIX I

Food plants consumed by rodent species collected from August 1989 through October 1990 from agroecosystems in central Argentina. Average percent aerial coverage by each plant species as measured from 5-m transects in crops (percent crop; primarily soybeans, corn, wheat) and weedy habitats which border crop fields (percent border; primarily roadside, fence line, railroad rights of way) is given, along with percent volume of the item observed in stomach contents from each of five rodent species. Percentages from the stomachs that were $\leq 1\%$ are listed as trace (T; NP = not present in transects but present in rodent stomachs; CM = C. musculus; CL = C. laucha; AA = A. azarae; BO = B. obscurus; OF = O. flavescens).

Plant family	Plant species	% crop	% border	CM	CL	AA	BO	OF
Aizoaceae	<i>Molluga verticillata</i>	<0.1	<0.1	T	1	T		
Amaranthaceae	<i>Alternanthera philoxeroides</i>	<0.1	0.2					
Amaranthaceae	<i>Amaranthus</i>	2.4	1.8	9	5	5	4	7
Amaranthaceae	<i>Iresine diffusa</i>	<0.1	0.1					
Apiaceae	<i>Ammi majus</i>	<0.1	2.1					
Apiaceae	<i>Bowlesia incana</i>	0.4	3.8	T	T	1	T	T
Apiaceae	<i>Conium maculatum</i>	NP	NP	T				
Apiaceae	<i>Eryngium</i>	<0.1	2.8					
Asclepiadaceae	<i>Morrenia</i>	<0.1	<0.1					
Asteraceae	<i>Ambrosia tenuifolia</i>	<0.1	1.1	T	T	T		T
Asteraceae	<i>Anthemis cotula</i>	<0.1	<0.1					
Asteraceae	<i>Artemisia annua</i>	0.2	5	1		1	T	T
Asteraceae	<i>Baccharis</i>	<0.1	3.1			T		
Asteraceae	<i>Bidens</i>	<0.1	4.3	1	1	1	1	T
Asteraceae	<i>Carduus</i>	0.3	9.2	T		T		
Asteraceae	<i>Chrysanthemum</i>	<0.1	<0.1					
Asteraceae	<i>Cichorium intybus</i>	0.1	1					
Asteraceae	<i>Conyza</i>	<0.1	1.9	T	T	T		
Asteraceae	<i>Cotula australis</i>	NP	NP	T	T	T		
Asteraceae	<i>Gaillardia</i>	<0.1	<0.1					
Asteraceae	<i>Galinsoga parviflora</i>	5	0.2	1	T	T		T
Asteraceae	<i>Gamochaeta falcata</i>	<0.1	<0.1					
Asteraceae	<i>Gnaphalium</i>	<0.1	0.5					
Asteraceae	<i>Helianthus annuus</i>	<0.1	0.9					
Asteraceae	<i>Lactuca</i>	<0.1	0.6					
Asteraceae	<i>Matricaria chamomilla</i>	<0.1	<0.1	T	T	T		
Asteraceae	<i>Schkuhria pinnata</i>	<0.1	<0.1					
Asteraceae	<i>Senecio</i>	<0.1	2					

APPENDIX I—Continued.

Plant family	Plant species	% crop	% border	CM	CL	AA	BO	OF
Asteraceae	<i>Solidago chilensis</i>	<0.1	1.2					
Asteraceae	<i>Sonchus</i>	0.1	0.2	T	T	T	T	T
Asteraceae	<i>Tagetes minuta</i>	0.5	0.8	T	T	T		
Asteraceae	<i>Taraxacum officinale</i>	0.2	0.1					
Asteraceae	<i>Wedelia glauca</i>	2.5	0.3	1	T		T	T
Boraginaceae	<i>Echium plantagineum</i>	<0.1	<0.1					
Brassicaceae	<i>Brassica</i>	<0.1	1.2	1	T	1		
Brassicaceae	<i>Capsella bursa-pastoris</i>	<0.1	0.1	1	1	T	T	1
Brassicaceae	<i>Coronopus didymus</i>	2.1	0.2	1	2	2	T	
Campanulaceae	<i>Triodanis biflora</i>	NP	NP	T		T		
Caryophyllaceae	<i>Silene</i>	<0.1	<0.1					
Caryophyllaceae	<i>Stellaria media</i>	6.2	1.9	5	12	2	1	8
Chenopodiaceae	<i>Chenopodium</i>	2.1	1.3	T	1	T		
Commelinaceae	<i>Commelina diffusa</i>	<0.1	<0.1		T			
Convolvulaceae	<i>Convolvulus arvensis</i>	<0.1	0.1	T	T			
Convolvulaceae	<i>Dichondra</i>	0.1	0.2	T		T		T
Convolvulaceae	<i>Ipomoea</i>	<0.1	0.1					
Cyperaceae	<i>Cyperus</i>	7.9	3.1	T	T		T	T
Euphorbiaceae	<i>Euphorbia serpens</i>	0.3	0.1	T	T	T		
Euphorbiaceae	<i>Tragia</i>	<0.1	<0.1	T			T	
Fabaceae	<i>Glycine max</i>	40.1	1.5	7	13	11	11	8
Fabaceae	<i>Lens culinaris</i>	<0.1	0.1					
Fabaceae	<i>Medicago</i>	<0.1	0.1	1	T	T		T
Fabaceae	<i>Pisum sativum</i>	NP	NP		1			
Fabaceae	<i>Rhynchosia</i>	<0.1	<0.1					
Fabaceae	<i>Trifolium</i>	<0.1	0.1	1	T	T		T
Fumariaceae	<i>Fumaria</i>	<0.1	0.4					
Geraniaceae	<i>Geranium</i>	<0.1	0.1			T		
Juncaceae	<i>Juncus</i>	<0.1	<0.1					
Labiatae	<i>Lamium amplexicaule</i>	1.1	0.2	T		1	2	
Liliaceae	<i>Nothoscordum inodorum</i>	0.1	<0.1					
Malvaceae	<i>Anoda cristata</i>	<0.1	<0.1					
Malvaceae	<i>Malva parviflora</i>	<0.1	<0.1	T		T		
Malvaceae	<i>Modiolastrum</i>	<0.1	0.6	1	T	T	2	T
Malvaceae	<i>Sida rhombifolia</i>	<0.1	1	1	1	2	2	3
Melicaceae	<i>Melia azedarach</i>	<0.1	<0.1					
Moraceae	<i>Broussonetia papyrifera</i>	<0.1	0.3		T		T	
Nyctaginaceae	<i>Mirabilis jalapa</i>	<0.1	<0.1					
Onagraceae	<i>Oenothera officinalis</i>	<0.1	0.3	T				T
Oxalidaceae	<i>Oxalis</i>	<0.1	0.3		T			T
Passifloraceae	<i>Passiflora coerulea</i>	<0.1	0.1					
Plantaginaceae	<i>Plantago</i>	<0.1	0.1				T	
Poaceae	<i>Avena</i>	<0.1	0.7	T	T	T		
Poaceae	<i>Botriochloa</i>	<0.1	1.2					
Poaceae	<i>Brachiaria</i>	1.2	<0.1	1	T	1		
Poaceae	<i>Briza</i>	<0.1	0.3	T				
Poaceae	<i>Bromus unioloides</i>	<0.1	6.8	1	T	T	3	T
Poaceae	<i>Calamagrostis</i>	<0.1	1.4			T		
Poaceae	<i>Cenchrus</i>	<0.1	0.3					
Poaceae	<i>Cynodon</i>	18.7	19.5	1	2	1	3	T
Poaceae	<i>Digitaria</i>	9.2	3.7	1	3	2	2	T
Poaceae	<i>Echinochloa cruzgalli</i>	9.5	<0.1	1	4		1	T
Poaceae	<i>Eleusine</i>	0.1	0.1	1	1	1	4	2

APPENDIX I—*Continued.*

Plant family	Plant species	% crop	% border	CM	CL	AA	BO	OF
Poaceae	<i>Eragrostis</i>	<0.1	0.2	T	1			
Poaceae	<i>Hordeum</i>	<0.1	0.2	T		T		
Poaceae	<i>Lolium multiflorum</i>	<0.1	8.9	T	T	2	T	T
Poaceae	<i>Panicum</i>	0.2	0.9	T	T		T	
Poaceae	<i>Paspalum</i>	0.8	2.8	T			T	
Poaceae	<i>Phalaris</i>	<0.1	<0.1					
Poaceae	<i>Physalis mendocina</i>	NP	NP			T		1
Poaceae	<i>Poa</i>	0.1	<0.1					
Poaceae	<i>Schizachyrium</i>	0.4	1.1	1	T		T	
Poaceae	<i>Setaria</i>	0.2	7.4	T				
Poaceae	<i>Sorghum halepense</i>	6	22.2	9	1	2	2	12
Poaceae	<i>Sporobolus</i>	<0.1	<0.1					
Poaceae	<i>Stipa</i>	<0.1	30.3	1	T	T	T	T
Poaceae	<i>Triticum aestivum</i>	10.8	0.4	1	2	1	3	3
Poaceae	<i>Zea mays</i>	9.3	0.1	4	5	T	13	1
Polygonaceae	<i>Polygonum</i>	<0.1	0.2			T		
Polygonaceae	<i>Rumex</i>	<0.1	0.7					
Portulacaceae	<i>Portulaca oleracea</i>	0.1	<0.1	T	T			
Primulaceae	<i>Anagallis arvensis</i>	0.2	<0.1		1		2	T
Rubiaceae	<i>Galium</i>	<0.1	0.6				T	
Scrophulariaceae	<i>Veronica</i>	1	<0.1					
Solanaceae	<i>Datura ferox</i>	0.2	0.2	T		T		
Solanaceae	<i>Salpichroa organifolia</i>	NP	NP	T	T	T		
Solanaceae	<i>Solanum</i>	0.1	1	T	T	1	T	T
Urticaceae	<i>Urtica urens</i>	0.1	0.6		T	T		
Verbenaceae	<i>Verbena</i>	<0.1	1.1					
	<i>Moss</i>	0.3	0.5	T	T	T	T	3