Food habits of Akodon azarae and Calomys laucha (Cricetidae, Rodentia) in agroecosystems of central Argentina

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*(Cricetidae, Rodentia)*  
in agroecosystems of central Argentina

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Summary. — We report results of dietary analyses of *Akodon azarae* and *Calomys laucha* and of food availability in corn fields and their borders in the Pampean region of central Argentina. Sampling was conducted at different developmental crop stages, in order to assess the influence of food availability on diet and reproductive performance. Both species were generalistic and opportunistic feeders, but differed in food habits and nutritional requirements for reproduction: *A. azarae* had omnivorous diets and its breeding activity was related to high requirements of insects, whereas *C. laucha* was mainly an herbivorous-granivorous feeder and required high amounts of green forage to improve its reproductive performance. We discuss the role that food availability may play as a potential factor for competitive interactions at the different crop stages, regarding the changes in abundance of both species and their differences in diet, competitive ability, habitat preferences and colonizing potential.

Résumé. — Le régime alimentaire d'*Akodon azarae* et de *Calomys laucha* a fait l'objet d'une étude dans les champs de maïs et leurs abords, dans la pampa d'Argentine centrale. Un échantillonnage à différents stades de développement des cultures a permis de déterminer l'influence de la disponibilité de la nourriture sur le régime alimentaire et sur la reproduction. Pour se nourrir, les deux espèces sont généralistes et opportunistes, mais elles diffèrent dans leurs habitudes alimentaires et dans leurs besoins pour la reproduction. *A. azarae* est omnivore et la reproduction est liée à des besoins élevés en insectes. *C. laucha* est un herbivore-granivore et a besoin de beaucoup de nourriture pour se reproduire. La disponibilité de la nourriture verte pourrait être un facteur de la compétition à différents stades des cultures, en modifiant l'abondance relative des deux espèces, du fait de leur différence de régime alimentaire, de leur aptitude à la compétition, de leurs habitats préférentiels et de leurs aptitudes à coloniser.

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INTRODUCTION

*Calomys laucha* and *Akodon azarae* are two of the most abundant rodent species inhabiting agroecosystems of the Pampa region in central Argentina. *Calomys* is numerically dominant in crop areas, whereas *Akodon* is more abundant in less disturbed habitats including cropfield edges, fencerows, roadsides, railroad rights-of-way and grasslands (Crespo et al. 1970, Dalby 1975, Busch et al. 1984, Mills et al. 1991, Busch and Kravetz 1992). Habitat segregation of these species among crop areas and borders is related to negative interspecific interactions (Busch 1987, Busch and Kravetz 1992 and in press).

Cropfields and their adjacent borders have seasonal variations of plant composition, coverage and food availability, characteristic for areas with farm labours in temperate zones (Bonaventura and Kravetz 1984, de Villafañe et al. 1988, Mills et al. 1991, Bonaventura et al. in press). There are many examples in rodents species showing that the use of food resources is largely related to their availability (Reichman 1975, Gebczynska 1976, Glanz 1982, 1984, Meserve et al. 1988, Martino and Aguilera 1989). Moreover, food habits may vary according to sex (Watts 1968, Holisova 1971, Gebczynska 1983) and reproductive condition (Batzli 1986, Martino and Aguilera 1989, Norrie and Millar 1990).

Despite both *C. laucha* and *A. azarae* have been indicated as agricultural pests on cropfields and pastures (Quintanilla et al. 1973, Massoia 1984) food habits of these species are poorly known and largely based on qualitative information (Barlow 1969, Quintanilla et al. 1973). Quantitative information on diets is lacking and there are no studies considering the influence of food availability on diet composition. In this paper we report results of dietary analyses of *C. laucha* and *A. azarae* and of food availability in corn fields and borders at different developmental crop stages, in order to analyze the role of food availability on diet composition, reproductive performance and potential for competitive interactions among these species.

STUDY AREA AND METHODS

The study area is located in an agricultural plain with a gently slope in D. Gaynor (34°8'S, 59°14'W, Buenos Aires province) in the Pampean region of central Argentina. The range of the mean annual temperature in the region is 11-22°C, and annual precipitation averages 1000 mm (Papadakis 1974). Originally, trees were absent and the predominant plant species were matted grasses of 0,5-1,0m high, which were replaced by cropfields (corn, soybeans, wheat and sunflower) and pastures due to anthropogenic alterations of the habitat. Nowadays, most of the native plant species are restricted to linear habitats such as cropfield edges, roadsides, fencerows and railroad rights-of-way (Bonaventura and Kravetz 1984, Bonaventura and Cagnoni in press), typically known as 'borders’ (Busch et al. 1984, Busch and Kravetz 1992 and in press), and little areas of grasslands that still remain in the Pampas (Dalby 1975).
### Table 1

| Crop Phase | I   | II  | III | IV  |
|------------|-----|-----|-----|-----|
| Stipa hymala | 4 D | 4 D | 4 V | 4 V |
| Baccharis minima | 3 V:F | 3 V:F | 2 F | 2 D |
| Cyperus decipiens | 2 V | 2 V | 3 V | 2 V |
| Sorghum halapncea | 2 F | 2 D | --- | --- |
| Phylia canescens | 1 F | --- | --- | --- |
| Paniculus dillatatus | 1 F | --- | --- | 3 S |
| Verbena intermedia | 1 F | 1 F | --- | --- |
| Juncus lubricatus | --- | 1 D | --- | --- |
| Tastena minuta | --- | --- | --- | 1 S |
| Sida rhombifolia | --- | --- | --- | 1 Fr |
| Salidago chilensis | --- | --- | --- | 1 V:F |
| Bidens subalternana | --- | --- | --- | 1 S |

| Maximum height (cm) | 120 | 95 | 85 | 90 |
| Seed availability |  |
| (Number of seeds/sample, n=6) | X | 100 | 90 | 94 | 100 * |
| Invertebrates | (mg dry matter/sample, n=8) | X | 506 | 318 | 44 * |

| No trap-nights | 231.5 | 90.5 | 115 | 111 |
| Trap success (%) | 5.6 | 8.8 | 7.0 | 21.6 |
| C. laucha (%) | 3.9 | 8.8 | 6.1 | 21.6 |

Sampling was conducted between November 1986 and May 1987, in 4 different corn fields and adjacent borders, including the different developmental stages of the crop (Table 1). Snap traps were placed in pairs at 10 m intervals along lines including both types of habitats. Traps were baited with peanut butter and fat mix, and checked daily for the next 3 nights. Fifteen individuals caught in corn fields during phases I and II in 1988-89 (12 *C. laucha* and 3 *A. azarae*) were also included in this study. Since capture effort differed among samplings, trap success of each species was calculated as number of captures/number of trap-nights × 100. Trap-nights is the number of traps/night × the number of nights in the field minus half of the number of sprung-but-empty traps encountered (Mills *et al.* 1991).

Standard autopsy data (species, weight, sex, reproductive condition) were recorded. Individuals were classified as active (males: scrotal testes; females: pregnant or lactating) or inactive (males: abdominal testes; females: non pregnant and non lactating). Stomachs were removed and fixed in 70% alcohol. Procedures followed those of Taylor and Green (1976) and Pelz (1987); stomach contents
were boiled for 5 minutes, cleared in 50 % Sodium hipochlorite for 3 minutes, then washed, filtered and spread on microscope slides. The contents were examined at 12 × and 50 ×, and visual assessment was made of the relative (volumetric) quantities of seeds, invertebrates (mostly insects) and green parts of plants; bait was removed and not counted in the measurements.

Vegetation was analyzed in 10 random plots of 1 m² each in each habitat type. The percentage of ground cover was considered as a measure of the amount of forage available (Gebczynska 1976). Seed availability was estimated by counting the number of seeds in 6 random soil samples of 35 cm³ each. The abundance of invertebrates was estimated by the dried weight of samples collected with 9 Barbour traps (80 cm²) which were randomly placed at ground level for 20 days.

Statistical tests used in this study include ANOVA F-test, Friedman and Kruskall-Wallis (K-W) non parametric tests, Scheffe and Student-Neuman-Keuls (SNK) paired comparisons tests and Spearman's rank correlation coefficient, as described in Sokal and Rohlf (1979).

RESULTS

Vegetation, food availability and abundance of rodents (Tables 1 and 2).

The percentage of ground cover varied according to the type of habitat and the crop phase (Friedman test : comparison among habitats = 34.11 P < 0.001; comparison among crop phases = 18.52; P < 0.001). In the borders (Table 1) there was a higher and more constant abundance of vegetation than in the crop areas; the grasses Stipa hyalina and Cynodon dactylon and the shrub Baccharis pingraea were the dominant species, and there was a slightly but significantly higher ground cover in phases I and IV. At the beginning of this study, most of the dominant plant species were flowering or disseminating, and gradually they turned to vegetative or senescent stages. Into the crop areas (Table 2), maize (Zea mays) was the dominant species in phase I, and ground cover was at its minimum (12 %). During phases II and III the crop reached its maximum coverage, and Digitaria sanguinalis was the dominant weed. During the stubble (phase IV), ground cover was at its peak, since maize had been harvested and species such as Dichondra sp. and Paspalum distichum emerged. Most of the species in the crop areas were usually in vegetative stage.

Seed availability in the borders was higher than in the corn fields (Friedman test : 4.17 P < 0.05; Tables 1 and 2). The peak of seeds was in phase I (85.5 seeds per soil sample) and the minimum in phase IV (7.5) (Table 1). In the crop areas seed availability in phase IV was lower than in the other crop stages (Table 2). In contrast, invertebrates were more abundant in the crop areas than in the borders (Friedman test : 13.37; P < 0.001; phase I excluded; Tables 1 and 2). Both types of habitats had the minimum in phase IV, and the peak occurred in phase II.

Trap success in borders was higher than in crop areas. A azarae was more abundant in the borders, whereas most of individuals of Calomys were caught in the corn fields. Both species had low abundances in crop stage I, increasing to relatively high values at the end of the study period.
### TABLE 2. — Plant composition, food availability and trap success of *A. azarae* and *C. laucha* in corn fields at different developmental stages of the crop, November 1986 - May 1987 (Same legend as Table 1).

| CROP PHASE | I | II | III | IV |
|------------|---|----|-----|----|
| *Zea mays* | 3 F | 3 F | 3 F | --- |
| *Raphanus sativus* | 2 F | --- | --- | --- |
| *Sonchus haladana* | 1 F | --- | --- | --- |
| *Colutea ar. | 1 V | --- | --- | --- |
| *Digitaria sanguinalis* | --- | 4 F | 3 D:Fr | 3 S |
| *Sida rhombifolia* | --- | 2 V | --- | 2 Fr |
| *Tagetes minuta* | --- | 2 V | --- | --- |
| *Paniceae ar. | --- | 2 V | --- | --- |
| *Chenopodium album* | --- | 1 V | --- | --- |
| *Borrelia incana* | --- | 3 V | --- | --- |
| *Portulaca oleracea* | --- | 2 V | --- | --- |
| *Glicinta ar. | --- | --- | --- | 3 V |
| *Allberanterea ar. | --- | --- | 2 V:F | --- |
| *Paspalium distichum* | --- | --- | 2 V:F | --- |
| *Setaria granulata* | --- | --- | 1 D | --- |
| Maximum height (cm) | 80 | 205 | 140 | 50 |

1 Green ground cover (n=10) x

| | a | b | c | R-W |
| | 12 | 56 | 35 | 84 |
| S.D. | 4.7 | 30.6 | 25.1 | 14.4 |

Seed availability (Number of seeds/sample, n=8)

| | a | b | SNK |
| | 28.0 | 35.0 | 27.3 | 8.7 |
| S.D. | 13.2 | 10.7 | 11.8 | 3.1 |

Invertebrates (mg dry matter/sample, n=9)

| | a | b | a | a | SNK |
| | 434 | 1139 | 494 | 318 | *
| S.D. | 364 | 597 | 368 | 203 |

No. trap-nights 408.5 718.5 110.5 117.5

Trap success (x) 2.1 2.4 7.2 5.1

*A. azarae* (x) 0.2 1.3 1.0 0.0

*C. laucha* (x) 1.9 1.1 5.4 5.1

### TABLE 3. — Total diet composition of *Akodon azarae* and *Calomys laucha* in agroecosystems near Diego Gaynor, Buenos Aires province, Argentina. November 1986 - May 1987. Results are expressed in volume percentage with standard deviation (S.D.), and percentage frequency of occurrence by food item. (1): data were arcsin transformed.

| SPECIES | *A. azarae* (n=60) | *C. laucha* (n=34) | F (1) |
|---------|-------------------|-------------------|-----|
| SEEDS   | 35.7 (25.2)       | 44.8 (30.3)       | 2.13 |
| Frequency | 98.3             | 94.1              | P > 0.1 |
| INVERTEBRATES | 34.3 (24.8) | 13.6 (19.3) | 24.92 |
| Frequency | 98.7             | 81.8              | P < 0.0001 |
| VEGETATION | 29.5 (25.4) | 40.5 (32.3) | 3.68 |
| Frequency | 100              | 97.1              | P = 0.058 |
Diet of Akodon azarae and Calomys laucha.

a. Total (Table 3).

Both species had above 90% of occurrence of the three food categories (seeds, invertebrates and vegetation) except a lower occurrence of invertebrates in the stomach contents of C. laucha. However, species differed in the percentages of the items ingested: overall individuals of A. azarae consumed approximately equal proportions of seeds (35.7%), invertebrates (34.3%) and vegetal material (29.5%), whereas C. laucha was mainly a granivorous-herbivorous species, with moderate amounts of invertebrates in its diet (seeds and greenery comprised about 85% of the stomach contents). A. azarae was more insectivorous (P < 0.0001) and less herbivorous (P = 0.058) than C. laucha. The remainder of the stomach contents in both species (about 1.5%) comprised unidentified material, mosses and anthers.

b. Temporal fluctuations in diet and breeding activity.

A. azarae (Table 4) consumed more seeds in phase I (57.3%) than in phase IV (26.4%). In contrast, green parts of plants were more consumed during phase IV (49.5%) than in the other crop stages. The species also showed significant shifts in the amount of invertebrates consumed; the peak of ingestion occurred in phase II (54.4%), and the minimum in phase IV (23.3%). Breeding activity of A. azarae gradually increased between phases I and III (55.5% - 85.7%), and dropped drastically during the fall in phase IV (29.2%).

**TABLE 4. — Temporal variations of food habits and breeding activity in A. azarae inhabiting in cropfield borders. Results are expressed in volume percentage with standard deviation (S.D.). Values followed by the same superscript letter represent homogeneous subsets (Scheffe paired comparison test and K-W test; P = < 0.05). (1): data were arcsin transformed.**

| CROP PHASE | I  | II | III | IV  |
|------------|----|----|-----|-----|
| SEEDS      |    |    |     |     |
| (n=9)      |    |    |     |     |
| 57.3       | ab | ab | abc | abc |
| (18.7)     | (23.5) | (23.1) | (21.8) | 4.48 |
| INVERTEBRATES |    |     |     |     |
| (n=8)      |    |    |     |     |
| 28.4       | ab | b  | abc | a  |
| (10.5)     | (21.8) | (23.8) | (18.1) | 4.84 |
| VEGETATION |    |    |     |     |
| (n=7)      |    |    |     |     |
| 12.5       | a  | a  | a   | b   |
| (10.9)     | (5.1) | (12.5) | (23.5) | 25.20 |
| Breeding activity. |
| (1 Active Ind.) | 55.5 | 82.5 | 85.7 | 28.2 |

In C. laucha (Table 5), seeds comprised about 50%-60% of the stomach contents in crop phases I and II and dropped to 11.7% in phase IV, while in the same period green forage rose up to 84.2%, doubling the amount consumed in the other crop stages. This species consumed little amount of invertebrates (about 4%-10%) except in sampling period III (31.3%), but no significant tempo-
TABLE 5. — Temporal variations of food habits and breeding activity in *C. laucha* inhabiting in corn fields. (Same legend as Table 4). (1): data were arcsin transformed.

| CROP PHASE | SEEDS | INVERTEBRATES | VEGETATION |
|------------|-------|---------------|------------|
|            | (n=9) | (n=8)         | (n=6)      | (n=8)     |
| I          | a 59.7 | 10.1 | 28.9 | a 26.8 | 8 31.3 | 40.0 | a 28.6 |
| II         | (25.8) | (10.8) | (28.5) | (17.4) | (28.9) | (32.0) | (21.5) |
| III        | a 49.7 | 8.9  | 36.8 | a 40.0 | 100 | 84.2 | 68.7 |
| IV         | (30.8) | (17.4) | (28.9) | (21.5) | (19.1) | (32.0) | (21.5) |

Breeding activity:
(1 Active Ind.) 68.7 87.5 100 100

TABLE 6. — Results of the analyses of variance for *A. azarae* and *C. laucha* between food items ingested and habitat. Results are expressed in volume percentage with standard deviation (S.D.). K-W: Kruskal-Wallis test. (1): data were arcsin transformed.

|              | *A. azarae* | *C. laucha* |
|--------------|-------------|-------------|
|              | CROP PHASE II | CROP PHASE I |
|              | CORN BORDER | CORN BORDER | CORN BORDER | CORN BORDER |
|              | (n=8) | (n=8) | (n=5) | (n=8) |
| CROP PHASE II | F (1) | F (1) | F (1) | F (1) |
| SEEDS        | 29.6 39.4 | 50.7 88.2 | 25.8 23.2 | 0.05 0.36 | 0.21 0.66 |
| INVERTEBRATES| 49.7 54.4 | 10.1 17.3 | 37.3 21.8 | 0.18 0.70 | 0.13 0.73 |
| VEGETATION   | 20.6 0.3 | 28.9 14.3 | 20.8 5.1 | 5.18 0.02 | 0.68 0.43 |

TABLE 7. — Results of the analyses of variances for *A. azarae* between sexes, reproductive conditions and food items ingested. Results are expressed in volume percentage with standard deviation (S.D.). NON ACT: non active individuals; ACT: active individuals. (1): data were arcsin transformed.

|              | MALES | FEMALES | NON ACT | ACT. |
|--------------|-------|---------|---------|------|
|              | (n=30) | (n=30)  | (n=27)  | (n=33) |
| CROP PHASE II | F (1) | F (1) | F (1) | F (1) |
| SEEDS        | 39.1 32.2 | 1.48 1.48 | 35.0 38.3 | 0.16 0.16 |
|              | (25.9) | (24.4) | (25.8) | (25.4) |
| INVERTEBRATES| 32.8 35.6 | 0.48 0.48 | 25.6 41.8 | 4.34 4.34 |
|              | (25.5) | (24.4) | (25.8) | (25.8) |
| VEGETATION   | 27.3 31.7 | 0.48 0.48 | 38.8 21.4 | 4.21 4.21 |
|              | (24.7) | (26.2) | (27.5) | (21.7) |
eral differences were found in the amount ingested. Breeding activity of *C. laucha* was higher than in *A. azarae* and remained high even during the fall (100% in phase IV).

c. Differences according to habitat (Table 6).

In two sampling periods both species were caught simultaneously in corn fields and borders (very few individuals of *Akodon* and *Calomys* were caught in other crop phases, Tables 1 and 2). There were no significant differences in the amount of the items ingested among habitat types, except *A. azarae* ate more vegetal material in the corn fields.

d. Differences according to the sexes and reproductive conditions.

There were no significant differences between the diets of males and females neither in *A. azarae* (Table 7) nor in *C. laucha* (Table 8). However, diet composition varied with reproductive condition. Active individuals of *A. azarae* consumed more invertebrates and less vegetal material than inactive ones (Table 7). In *C. laucha*, comparisons in diet according to reproductive conditions were only performed among females, since all males had scrotal testis (active condition) during the study period. Pregnant and lactating females were more herbivorous and less granivorous than females in inactive condition (Table 8).

e. Diet of *C. laucha* and *A. azarae* according to available food in crop areas and borders.

To evaluate variation in diet with available food, Spearman's ordinate correlation coefficients were performed (Table 9). Categories of periods with similar food availability were ranked accordingly with the different homogeneous subsets obtained by the paired comparisons performed for each food category in crop fields and borders (Tables 1 and 2). The proportions of the food items in the stomach...
TABLE 9. — Spearman’s correlation coefficients between the food available in borders and corn fields with the volume percentage of the items ingested by *A. azarae* and *C. laucha* (*P = <0,01*). (1): individuals caught in 1988-89 were excluded, since food availability was not measured.

| SPECIES | *A. azarae* (n=48) | *C. laucha* (n=17) |
|---------|-------------------|-------------------|
| SEEDS   | 0.473 *           | 0.631 *           |
| INVERTEBRATES | 0.425 *         | -0.189            |
| VEGETATION | 0.414 *       | 0.620 *           |

Contents of these species were positively correlated with the availability of each food category, except that invertebrates consumed by *C. laucha* did not show any correlation with the amount offered in the cropfields.

**DISCUSSION**

Our results support that there is a great temporal variation in food availability in corn fields and borders (Tables 1 and 2), and also show a sequence in the peaks of the different food categories: first, there is a peak of seeds during crop phases I and II, then a peak of invertebrates occurs during phases II and III, and finally the highest availability of green parts of plants occurs in phase IV (Tables 1 and 2).

Fluctuations in available food were followed by similar trends of changes in both diet composition and breeding activity of *A. azarae* and *C. laucha* (Tables 4, 5 and 9). These patterns suggest that each species has to satisfy specific nutritional requirements to improve its reproductive performance (Tables 7 and 8), and that food availability, as well as other correlated factors (weather conditions) may influence on breeding activity and duration of the breeding season of these species (Mills *et al.*, in press), as observed in North American microtines (Batzli 1986). Likewise, reproductive performance of females of *C. laucha* was related to herbivorous diets (Table 8), and in general breeding activity and green foraging increased as the amount of ground cover increased in the crop areas (Tables 2 and 5). With regard to *A. azarae*, reproductive performance was related to high consumptions of insects (Table 7). In particular, all pregnant females had more than 20% of insects in their stomach contents (Bilenca, personal observations). Proteins are highly required for reproduction in the formation of new tissues and may be easily obtained from animal material (Clark 1981). Breeding activity of *A. azarae* was high when insects were more available (and consumed) in the borders (sampling periods II and III), and dropped drastically in crop phase IV, when insects were scarce and less consumed (Tables 1 and 4).

We did not find any relation between seed consumption and reproductive performance (Tables 7 and 8), although seeds provide high quantities of carbohydrates (energy) in an easily digestible form (Mc Donald *et al.* 1969, Batzli 1986). We consider that this food category should contribute mainly for maintenance, and probably as a complement in the diets of active individuals of these species.
(Tables 7 and 8). The moderate amount of invertebrates in the stomach contents of *C. laucha* (Table 3), although is not accidental, suggests that animal food is only an occasional complement in the diet of this species as for numerous herbivorous rodents (Landry 1970).

Previous investigations of small mammals communities in grasslands emphasized the importance of strong interactions of habitat and food preferences in relation to their availability and of densities of competing species in determining the structure of these communities (Batzli 1985). In grasslands and agroecosystems of central Argentina densities of rodent species have seasonal fluctuations with a minimum in spring, a peak in late fall, and a drastic crash in late winter (Crespo 1966, Crespo *et al.* 1970, Dalby 1975, Kravetz *et al.* 1981, Zuleta *et al.* 1988, Mills *et al.* 1991, Tables 1 and 2). Habitat use in borders is related to coverage, phenology and composition of plant communities (Bonaventura and Kravetz 1984, Bonaventura *et al.* in press), whereas habitat suitability and abundance of rodents in cropfields are affected by farming alterations (Kravetz *et al.* 1981, de Villafañe *et al.* 1988, Mills *et al.* 1991, Table 2). Busch and Kravetz (1992 and in press) showed that spatial segregation of *A. azarae* and *C. laucha* among bordres and cropfields was partially due to competitive interactions, *Akodon* being the dominant species. Food supplementation experiments carried out in cropfield borders supported that at least during winter and early spring food shortage was a limiting factor for rodents, and *Akodon* excluded *Calomys* from the baiting points (A. Cittadino, unpublished data). These findings suggest that seasonal changes in habitat may be crucial for the persistence of *Calomys* in the community (de Villafañe *et al.* 1977, Kravetz 1977), and that spatial segregation at high population densities (Tables 1 and 2) may relax potential exploitative competition for food (Rosenzweig 1974).

However, there are some periods that favor the coexistence of *A. azarae* and *C. laucha* in the same type of habitat (Table 6). *C. laucha* was in the borders during crop stage I, when vegetal food and cover in the crop areas were in short supply (Table 2); coincidently, most of rodent damage in corn fields occurs during this crop stage (Bilenca and Kravetz, unpublished data). The coexistence of both species in the borders during period I should be possible due to relatively higher food and cover supplies (Table 1), and because rodents are in low densities (Table 1) and segregated at microhabitat (individual) level (Busch and Kravetz, 1992). *A. azarae*, on the other hand, appeared in the crop areas during period II (and III), when rodents had intermediate densities (Table 2) and corn fields reached their maximum coverage and food supply, mainly insects (Table 2), which are required for reproduction (Table 7). Therefore, space overlap in cropfields could be tolerable during this crop stage and each species could satisfy its food demands (Table 6); *A. azarae* ate more vegetal material in the corn fields than in borders (Table 6), probably because during crop stage II most of plant species in the corn fields were in early vegetative stage, being more palatable than dominant grasses in disemminating stage in the borders (Tables 1 and 2).
CONCLUSIONS

Summarizing, *C. laucha* and *A. azarae* are generalistic feeders (Table 3), and also show a high plasticity in switching to those food items which are more abundant at a particular time (Tables 4, 5 and 9). These findings are in agreement with the general pattern that small mammals are characterized broadly as opportunistic and omnivorous (Landry 1970). However, both species differ in diet, competitive ability and other features of their niches, reflecting different adaptations to grassland habitats (Hershkovitz 1962, Reig 1981, 1984). *Akodon* is a successful competitor, limited to stable habitats (de Villafane et al. 1977, Kravetz 1977, Zuleta et al. 1988, Mills et al. 1991), and all the species within the genus are considered as omnivorous or insectivorous (Meserve 1981, Reig 1981, Murúa et al. 1982, Glanz 1984, Meserve et al. 1988, Martinez et al. 1990, Table 3). *Calomys*, on the other hand, has a relative higher colonizing potential, taking advantage of unstable, temporarily suitable habitat for its rapid reproduction (de Villafane et al. 1977, Kravetz et al. 1981, Mills et al. 1991) and many species within the genus and other phyllotines seem to be granivorous-herbivorous (Reig 1981, 1984, Meserve et al. 1988; Table 3). Finally, we found that these species also differ in their food requirements for reproduction (Tables 7 and 8), suggesting that even if the food habits of *Akodon* and *Calomys* comprise the same set of food categories, the availabilities of insects and green vegetation play different roles on their reproductive success, and consequently, on the population dynamics of these species.

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