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Food habits of *Akodon azarae* and *Calomys laucha* *(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 0,5-1,0 m 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. — Plant composition, food availability and trap success of *A. azarae* and *C. laucha* in cropfield borders at different developmental stages of corn fields, November 1986 - May 1987. Crop phase I : vegetative stage (November, December) ; II : flowering (January) ; III : ripening of the corn grain (March), and IV : stubble (May). Values followed by the same superscript letter represent homogeneous subsets (SNK test ; K-W test ; * P = < 0.05). 1 : scarce ; 2 : common ; 3 : abundant ; 4 : very abundant ; V : vegetative stage ; F : flowering ; Fr : fructifying ; D : disseminating ; S : senescent.

CROP PHASE		I	II	III	IV	
Stipa hyalina		4 D	4 D;V	4 V	4 V	
Baccharis pingraea		3 V;F	3 V;F	2 F	2 D	
Cynodon dactylon		2 V	2 V	3 V	2 V	
Sorghum halepense		2 F	2 D	---	---	
Phyla canescens		1 F	---	---	---	
Paspalum dilatatum		1 F	---	---	3 S	
Verbena intermedia		1 F	1 F	---	---	
Juncus imbricatus		---	1 D	---	---	
Tagetes minuta		---	---	---	1 S	
Sida rhombifolia		---	---	---	1 Fr	
Solidago chilensis		---	---	---	1 V;F	
Bidens subalternans		---	---	---	1 S	
Maximum height (cm)		120	85	85	90	
% Green ground cover (n=10)	$\bar{x}$	100^a	80^b	94^b	100^a	K-W *
	S.D.	0	10.6	2.1	0	
Seed availability (Number of seeds/sample, n=6)						
	$\bar{x}$	65.5^a	46.0^b	47.0^b	7.5^c	SNK *
	S.D.	31.2	28.5	29.2	4.3	
Invertebrates (mg dry matter/sample, n=9)						
	$\bar{x}$	---	506^a	316^a	44^b	SNK *
	S.D	---	302	133	29	
No trap-nights		231.5	90.5	115	111	
Trap success (%)		5.6	8.8	7.0	21.6	
A. azarae (%)		3.9	8.8	6.1	21.8	
C. laucha (%)		1.7	0.0	0.9	0.0	

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 testii ; females : pregnant or lactating) or inactive (males : abdominal testii ; 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 m^2 each in each habitat type. The percentage of green 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 cm^3 each. The abundance of invertebrates was estimated by the dried weight of samples collected with 9 Barbour traps (80 cm^2) 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 V	3 F	3 Fr	---	
Raphanus sativus	2 F	---	---	---	
Sorghum halepense	1 F	---	---	---	
Solanum sp.	1 V	---	---	---	
Digitaria sanguinalis	---	4 F	3 D;Fr	3 S	
Sida rhombifolia	---	2 V	---	2 Fr	
Tagetes minuta	---	2 V	---	---	
Panicum sp.	---	2 V	---	---	
Chenopodium album	---	1 V	---	---	
Bowlesia incana	---	---	3 V	---	
Portulaca oleracea	---	---	2 V	---	
Dichondra sp.	---	---	---	3 V	
Althernantera sp.	---	---	---	2 V;F	
Paspalum distichum	---	---	---	2 V;F	
Setaria geniculata	---	---	---	1 D	
Maximum height (cm)	80	205	140	50	
% Green ground cover (n=10) $\bar{x}$	12 [a]	56 [b]	35 [b]	84 [c]	K-W *
S.D.	4.7	30.6	25.1	14.4	
Seed availability (Number of seeds/sample, n=6)					
$\bar{x}$	28,8 [a]	35,0 [a]	27,3 [a]	6,7 [b]	SNK *
S.D.	13,2	10,7	11,8	3,1	
Invertebrates (mg dry matter/sample, n=9)					
$\bar{x}$	434 [a]	1139 [b]	494 [a]	318 [a]	SNK *
S.D.	364	597	368	203	
No. trap-nights	488.5	718.5	110.5	117.5	
Trap success (%)	2.1	2.4	7.2	5.1	
A. azarae (%)	0.2	1.3	1.8	0.0	
C. laucha (%)	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 P > 0.1
Frequency %	98.3	94.1	
INVERTEBRATES	34.3 (24.8)	13.6 (19.3)	24.92 P < 0.0001
Frequency %	96.7	61.8	
VEGETATION	29.5 (25.4)	40,5 (32.3)	3.68 P = 0.058
Frequency %	100	97.1	

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 (n=9)	II (n=8)	III (n=7)	IV (n=24)	F (1)
SEEDS	57.3^{a} (18.7)	39.4^{ab} (23.5)	42.5^{ab} (23.1)	26.4^{b} (21.8)	4.48 P = 0.008
INVERTEBRATES	28.4^{ab} (19.5)	54.4^{b} (21.8)	33.8^{ab} (23.8)	23.3^{a} (16.1)	4.84 P = 0.005
VEGETATION	12.5^{a} (18.9)	6.3^{a} (5.1)	21.4^{a} (12.5)	49.5^{b} (23.5)	25.20 (K-W) P = 0.00001
Breeding activity. (% Active Ind.)	55.5	82.5	85.7	29.2	

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	I	II	III	IV	
	(n=9)	(n=8)	(n=6)	(n=6)	F (1)
SEEDS	59.7 [a] (25.8)	49.7 [a] (30.9)	28.6 [ab] (18.8)	11.7 [b] (15.7)	5.82 P = 0.004
INVERTEBRATES	10.1 (10.9)	8.9 (17.4)	31.3 (28.5)	4.2 (6.6)	2.86 P = 0.08
VEGETATION	28.9 [a] (28.1)	40.0 [a] (32.0)	36.8 [a] (21.5)	84.2 [b] (19.1)	6.55 P = 0.002
Breeding activity.					
(% Active Ind.)	66.7	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 CROP PHASE II			C. laucha CROP PHASE I		
	CORN FIELD (n=9)	BORDER (n=8)	F (1)	CORN FIELD (n=9)	BORDER (n=5)	F (1)
SEEDS	29.6 (32.5)	39.4 (23.5)	0.85 P = 0.38	59.7 (25.8)	68.2 (23.2)	0.21 P = 0.66
INVERTEBRATES	49.7 (37.3)	54.4 (21.8)	0.16 P = 0.70	10.1 (10.9)	17.3 (23.6)	0.13 P = 0.73
VEGETATION	20.6 (20.9)	6.3 (5.1)	5.18 K-W P = 0.02	28.9 (28.1)	14.3 (11.9)	0.69 P = 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)	F (1)	(n=27)	(n=33)	F (1)
SEEDS	39.1 (25.9)	32.2 (24.4)	1.48 P = 0.23	35.0 (25.7)	36.3 (25.4)	0.16 P = 0.70
INVERTEBRATES	32.8 (25.5)	35.8 (24.4)	0.48 P = 0.51	25.6 (20.9)	41.8 (25.9)	4.54 P = 0.04
VEGETATION	27.3 (24.7)	31.7 (28.2)	0.48 P = 0.50	38.8 (27.5)	21.4 (21.7)	4.21 P = 0.04

ral 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

TABLE 8. — Results of the analyses of variance for *C. laucha* between sexes, reproductive conditions (only for females) 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.

				FEMALES		
	MALES	FEMALES		NON ACT.	ACT.	
	(n=20)	(n=14)	F (1)	(n=5)	(n=9)	F (1)
SEEDS	40.3 (32.6)	42.2 (27.8)	0.20 P = 0.67	73.0 (11.7)	38.7 (29.9)	21.06 P = 0.0006
INVERTEBRATES	11.8 (19.6)	16.0 (19.4)	0.25 P = 0.62	11.7 (14.7)	13.9 (20.2)	0.16 P = 0.70
VEGETATION	40.7 (31.7)	40.3 (34.2)	0.00 P = 0.99	13.5 (12.9)	45.2 (32.4)	6.77 P = 0.02

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 testii (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 cropfields 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 / ITEM	A. azarae (n=48)	C. laucha (n=17) (1)
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 mays be crucial for the persistence of *Calomys* in the community (de Villafãne *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 spécies 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 disseminating 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 Villafañe *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 Villafañe *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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BIBLIOGRAPHY

Barlow, J.C., 1969. — Observations on the biology of rodents in Uruguay, *Life Sci. Contr., R. Ont. Mus.,* 75 : 1-59.

Batzli, G.O., 1985. — Small mammal communities in North American grasslands. *Austr. Mamm.,* 8 : 145-152.

Batzli, G.O., 1986. — Nutritional ecology of the California vole : effects of food quality on reproduction. *Ecology,* 67 : 406-412.

Bonaventura, S.M. and F.O. Kravetz, 1984. — Relación roedor - vegetación : estudio preliminar. *Rev. Mus. Arg. Cs. Nats., Zool.,* 13 : 445-451.

Bonaventura, S.M. and M. Cagnoni, in press. — La vegetación de los bordes de caminos en la Pampa Ondulada, Provincia de Buenos Aires (Argentina). *Parodiana* (Argentina).

Bonaventura, S.M., F.O. Kravetz and O.V. Suarez, in press. — The relationship between food availability, space use and territoriality in *Akodon azarae. Mammalia.*

BUSCH, M., F.O. KRAVETZ, R.E. PERCICH and G.A. ZULETA, 1984. — Propuestas para un control ecológico de la Fiebre Hemorrágica Argentina a través del manejo del habitat. *Medicina (Buenos Aires),* 44 : 34-40.

BUSCH, M. and F.O. KRAVETZ, 1992. — Competitive interactions among rodents *(Akodon azarae, Calomys laucha, C. musculinus* and *Oligoryzomys flavescens)* in a two-habitat system. I. Spatial and numerical relationships, *Mammalia,* 56 : 45-56.

BUSCH, M. and F.O. KRAVETZ, in press. — Competitive interactions among rodents *(Akodon azarae, Calomys laucha, C. musculinus* and *Oligoryzomys flavescens)* in a two-habitat system. II. Effect of species removal. *Mammalia.*

CLARK, D.A., 1981. — Foraging patterns of Black rats across a Desert-Montane forest gradient in the Galápagos Islands. *Biotropica,* 13 : 182-194.

CRESPO, J., 1966. — Ecología de una comunidad de roedores silvestres en el Partido de Rojas, Provincia de Buenos Aires. *Rev. Mus. Cs. Nat., Ecol.,* 1 : 79-134.

CRESPO, J.A., M.S. SABATTINI, M.J. PIANTANIDA and G. DE VILLAFAÑE, 1970. — *Estudios ecológicos sobre roedores silvestres.* Publicación especial de la Secretaría de Estado de Salud Pública. Buenos Aires, Argentina.

DALBY, P., 1975. — Biology of Pampa rodents. *Publ. Mus. Michigan, Biol. Ser.,* 5 : 149-272.

DE VILLAFAÑE, G., F.O. KRAVETZ, O. DONADIO, R.E. PERCICH, L. KNECHER, M.P. TORRES and N. FERNANDEZ, 1977. — Dinámica de las comunidades de roedores en agroecosistemas pampásicos. *Medicina (Argentina),* 37 : 128-140.

DE VILLAFAÑE, G., S.M. BONAVENTURA, M.I. BELLOCQ and R.E. PERCICH, 1988. — Habitat selection, social strusture, density and predation in populations of Cricetine rodents in the pampa region of Argentina and the effects of agricultural practices on them. *Mammalia,* 52 : 339-359.

GEBCZYNSKA, Z., 1976. — Food habits of the bank vole and phenological phases of plants in an oak hornbeam forest. *Acta Theriol.,* 21 : 223-236.

GEBCZYNSKA, Z., 1983. — Feeding habits. Pp 40-49 *in : Ecology of the bank vole.* Ed. K. Petrusiewicz, *Acta Theriol.,* 28, Suppl. n° 1.

GLANZ, W.E., 1982. — Adaptative zones of Neotropical mammals : a comparison of some temperate and tropical patterns. Pp. 95-110 *in : Mammalian biology in South America.* Eds. Mares and Genoways, Spec. Publ. Pymatuning Lab. Ecol., Univ. Pittsburgh.

GLANZ, W.E., 1984. — Ecological relationships of two species of *Akodon* in central Chile. *Journal of Mammalogy,* 65 : 433-441.

HERSHKOVITZ, Ph., 1962. — Evolution of Neotropical Cricetine rodents (Muridae), with special reference to the Phyllotine group. *Fieldiana,* 46 : 1-525.

HOLISOVA, V., 1971. — The food of *Clethrionomys glareolus* at different population densities. *Acta Sc. Nat. Brno,* 5 : 1-43.

KRAVETZ, F.O., 1977. — Ecología y control de reservorios. *Ciencia e Investigación (Argentina),* 33 : 235-242.

KRAVETZ, F.O., M. BUSCH, R.E. PERCICH, M.C. MANJON and P.N. MARCONI, 1981. — Ecología de *Calomys laucha* (Rodentia, Cricetidae) en el departamento de Río Cuarto (Córdoba). I. Dinámica de la población. *Ecología (Argentina),* 1 : 15-22.

LANDRY, S.O., 1970. — The Rodentia as omnivorous. *Quart. Rev. Biol.,* 45 : 351-372.

MARTINEZ, R.L., M.E. BOCCO, N. MONACO and J.J. POLOP, 1990. — Winter diet in *Akodon dolores* Thomas, 1916. *Mammalia,* 54 : 197-205.

MARTINO, A.M.G. and M. AGUILERA, 1989. — Food habits of *Holochilus venezuelae* in rice fields. *Mammalia,* 53 : 545-561.

MC DONALD, P., R.A. EDWARDS and J.F.D. GREENHALL, 1969. — *Animal Nutrition.* Olwer and Boyd Ltd. Edinburg.

MESERVE, P.L., 1981. — Trophic relationships among small mammals in a Chilean semiarid thorn scrub community. *Journal of Mammalogy,* 62 : 304-314.

MESERVE, P.L., B.K. LANG and B.D. PATTERSON, 1988. — Trophic relationships among small mammals in a Chilean temperate forest. *Journal of Mammalogy,* 69 : 721-730.

MILLS, J.N., B.A. ELLIS, K.T. MCKEE Jr, 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., B.A. ELLIS, K.T. MCKEE Jr, J.I. MAIZTEGUI and J.E. CHILDS, in press. — Reproductive characteristics of the rodent community in cultivated areas of central Argentina. *Journal of Mammalogy.*

MURUA, R., L. GONZALEZ and C. JOFRE, 1982. — Estudios ecológicos de roedores silvestres en los bosques templados fríos de Chile. *Publicación Ocasional No. 38. Mus. Nac. de Hist. Nat. Chile.*

NORRIE, M.B. and J.S. MILLAR, 1990. — Food resources and reproduction in four microtine rodents. *Can. J. Zool.,* 68 : 641-650.

PAPADAKIS, J., 1974. — Posibilidades agropecuarias de las provincias argentinas. *Enciclop. Arg. de Agricultura y Jardinería.* Tomo II : 1-86.

PELZ, H.J., 1987. — Damage by wood mice *(Apodemus sylvaticus)* to sugarbeet seeds in relation to food availability. Pp. 5-14 *in : Control of mammal pests.* Eds. Richards and Ku. Taylor and Francis, London.

QUINTANILLA, R.H., H.F. RIZZO and C.P. FRAGA, 1973. — *Roedores perjudiciales para el agro en la República Argentina.* Eudeba, Buenos Aires.

REICHMAN, O.J., 1975. — Relation of desert rodent diets to available resources. *Journal of Mammalogy,* 56 : 731-751.

REIG, O.A., 1981. — Teoría del origen y desarrollo de los mamíferos de America del Sur. *Monografie Naturae, Mus. Cs. Nats. Mar del Plata,* 1 : 1-161.

REIG, O.A., 1984. — Distribucao geografica e historia evolutiva dos roedores muroideos sulamericanos (Cricetidae : Sigmodontinae). *Rev. Brasil. Genet.,* 7 : 333-365.

ROSENZWEIG, M.L., 1974. — On the evolution of habitat selection. *Proc. 1st. Int. Congr. Ecol.* : 401-414.

SOKAL, R.R. and F.J. ROHLF, 1979. — *Biometría.* Blume, Madrid.

TAYLOR, K.D. and M.G. GREEN, 1976. — The influence of rainfall on diet and reproduction in four African rodent species. *J. Zool. Lond.,* 180 : 367-389.

WATTS, C.H.S., 1968. — The foods eaten by wood mice *(Apodemus sylvaticus)* and bank voles *(Clethrionomys glareolus)* in Wytham woods, Berkshire. *J. Anim. Ecol.,* 37 : 25-41.

ZULETA, G.A., F.O. KRAVETZ, M. BUSCH and R.E. PERCICH, 1988. — Dinámica poblacional del ratón del pastizal pampeano *(Akodon azarae),* en ecosistemas agrarios de Argentina. *Rev. Chil. His. Nat.,* 61 : 231-244.