Competitive interactions among rodents (Akodon azarae, Calomys laucha, Calomys musculinus and Oligoryzomys flavescens) ....

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Competitive interactions among rodents *(Akodon azarae, Calomys laucha, Calomys musculinus* and *Oligoryzomys flavescens)* in a two-habitat system. II. Effect of species removal.

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Summary. — Competitive relationships between rodent species were studied in pampean agrosystems. *Akodon azarae, Calomys laucha, Calomys musculinus* and *Oligoryzomys flavescens* show a differential spatial distribution between cropfields and their borders in this system. The goal of this paper was to assess the role of competition in determining spatial distributions and relative abundances of these species. A removal experiment in border habitats showed that the removal of *A. azarae* causes an increase in captures, survival and residency time in *C. laucha* and *O. flavescens* (as compared to control areas). Removal of *C. laucha* didn't cause any change in the remaining species. Results showed that competition with *A. azarae* limits the use of field borders by *C. laucha* and *O. flavescens*. Presence of *A. azarae* in border habitats prevents the establishment of residents of *C. laucha* and *O. flavescens*, thereby causing also higher mortality and lower reproductive rates in these two species than those registered when *A. azarae* is removed. Interspecific encounters in a test arena showed that behavioral interactions are contributing to spatial segregation, with *A. azarae* becoming dominant over *C. laucha*.

Résumé. — La compétition entre les espèces de rongeurs a été étudiée dans les agrosystèmes de la pampa. *Akodon azarae, Calomys laucha, C. musculinus* et *Oligoryzomys flavescens* y montrent des différences de répartition dans les cultures et leurs bordures. Le but de ce travail a été de déterminer le rôle de la compétition dans la distribution spatiale et l'abondance relative de ces espèces. En retirant du terrain une espèce après l'autre on constate que les autres espèces modifient leur occupation du sol et que la mortalité et la reproduction de chacune sont affectées. Des rencontres expérimentales en captivité mettent en évidence les modifications comportementales responsables de la ségrégation spatiale, *A. azarae* devenant dominant sur *C. laucha*.

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INTRODUCTION

The role of competition in determining community structure has been the subject of considerable discussion in the last 10 years. Many authors have studied competitive relationships among rodents and its consequences on resource exploitation and relative abundance (Grant 1972 a, b, Brown 1972, Brown *et al.* 1985, Joule and Jameson 1972, among others), thus showing that competition is contributing in some degree to the structure of rodent communities.

In a previous work (Busch and Kravetz 1992) we studied the spatial relationships between *Akodon azarae, Oligoryzomys flavescens, Calomys laucha* and *Calomys musculinus* in pampean agrarian systems where these four species inhabit two main habitats : cropfields (consisting of corn, soya bean, flax and wheat) and their immediate borders or fence rows, a marginal habitat with spontaneous vegetation that is little disturbed by farming activities. Most of the study area is covered by cropfields of approximately 25 hectares each, while the marginal borders and natural pastures are very reduced in size. It was observed previously that in the latter habitats *A. azarae* is more abundant than *C. laucha* and *C. musculinus,* while in cropfields essentially only *C. laucha* or *C. musculinus* are present. This spatial distribution was attributed to habitat segregation due to competition. Border habitats are more suitable for rodents than cropfields, at least during sowing and harvesting periods, because of the absence of farming activities which may cause rodent mortality (de Villafañe *et al.* 1988) and they offer a more constant plant cover than cropfields. Negative spatial relationships between *A. azarae* and the other species were recorded in field borders, and found to be related to interspecific competition (Busch and Kravetz 1992). Species diversity, high population densities, small area and overall shape may enhance competition for space in these kind of habitats. Peak densities of about 1200 rodent/ha were registered in borders, while those of fields attained 300 rodents/ha.

The goal of this present study was to analyze whether the negative spatial relationships between *A azarae* and the other species are due to interspecific competition or to different habitat preferences. In order to discriminate between these alternatives, a manipulative experiment involving the removal of *A. azarae* from one border and *C. laucha* from another was done. This experiment was based on the hypothesis that if competition was determining spatial relationships, a decrease in the density of a competitor in the field border habitat would cause an increase in density or a change in habitat use for the other species.

STUDY AREA

Fieldwork took place at D. Gaynor (34° 8' S, 59° 14' W), Exaltación de la Cruz Department, Buenos Aires Province, Argentina. This site is the pampean region and experience a temperate climate that has a winter season affecting rodent survival (Crespo 1966). Originally trees were absent and the principal plant species were matted grasses of 0.5-1 m height. This condition has been replaced by cropfields and pastures, in which other types of grasses were favoured and where trees were planted.

Dominant plant species are now *Stipa neesiana, S. brachychaeta, S. papposa, S. hyalina, Paspalum dilatatum, Bromus unioloides, Lolium multiflorum, Briza minor, Sporobolus indicus, Steraria geniculata, Ranunculus platensis, Veronica persica, Videns sp, Taraxacum officinale, Coniza bonariensis, Brassica campestris, Raphanus sp, Wedelia glauca, Solidago chilensis, Senecio grisebachii, Foeniculum vulgare, Conium maculatum* and the thistles *Cynara cardunculus, Cirsium vulgare, Carduus acantoides* and *Centaurea calcitrapa*. A more detailed description of these habitats can be found in Crespo (1966) and Bonaventura and Cagnoni (in press).

Rodent populations in this area show seasonal variation in density, with minimum numbers in spring when reproduction begins after the winter interruption and a maximum in fall followed by a great decline in numbers during winter.

MATERIALS AND METHODS

A removal experiment was carried out from March 1984 until February 1985. The cropfields studied were the object of farming activities, while field borders were influenced to a lesser degree by the passage of cattle during grazing and walking. These activities were not under our control, since farmers allowed us to work in their farms but did not change their activities. The experiment consisted of a preliminary trapping period during which study plots were chosen according to their similar floristic and rodent community composition followed by 12 capture-mark-recapture trapping periods involving the removal of individuals of *A. azarae* or *C. laucha* depending on the specific trap site.

Sherman live traps baited with peanut butter were used. Trapping periods of four days duration each month were conducted. Figure 1 shows the location

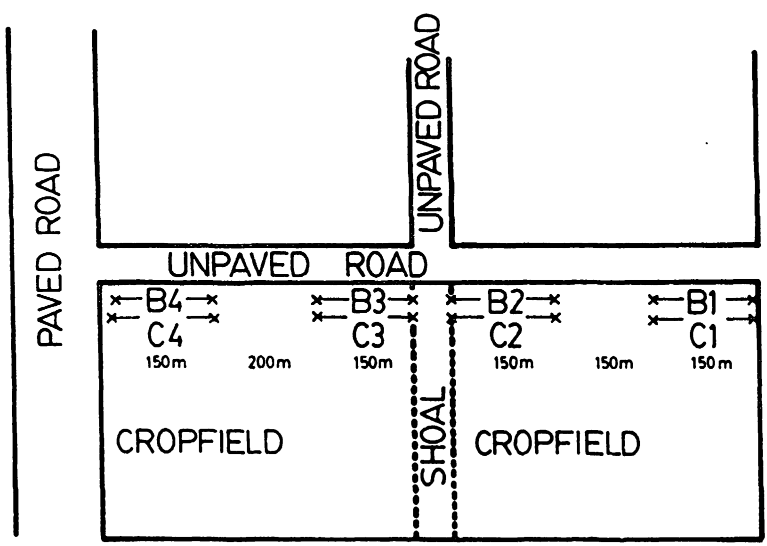

Fig. 1. — Diagram of experimental and control trap lines. B1 : *C. laucha* removal border, B2 : control of B1, B4 : *A. azarae* removal border, B3 : control of B4. C1, C2, C3 and C4 are the adjacent trap lines in cropfields.

of traplines and the relative sizes of cropfields and fields borders. The study area included two blocks, each consisting of an experimental and a control plot. The distance between plots was 150-200 meters. At each plot field borders and adjacent cropfields were studied. In each field border habitat one trapline of 30 traps each was set at 15 trap stations (two traps per station) spaced at 10 m intervals. In order to assess the cropfield rodent abundance and any movements between fields and their borders, four parallel traplines with 20 traps spaced at 20 meter intervals were set in adjacent cropfields. Different trap spacing was used in fields and their borders because of respective size differences; the total area of fields is approximately 20 times larger than those of field borders.

For one field border (trapline B4) all individuals of *A. azarae* that were captured were removed and for another field border (B1), all *C. laucha* were removed. The other two field border traplines were controls (B3 of B4 and B2 of B1). Each block was considered separately (B3-B4 and B2-B1) because although initially all fields were planted with soya bean, then they experienced different levels of farming activities. The soya crop adjacent to blocks B1 and B2 was harvested and the field was maintained as a fallow condition with grazing cattle whereas wheat was planted in the cropfield next to B3 and B4 after harvesting.

All animals captured were ear tagged with fingerling fish tags. Species identification, tag number, sex, breeding condition, body weight, total and tail length, trap location, and date were recorded for each animal. Animals were grouped in size classes according to length (head plus body). The first class included individuals measuring 140 mm or less, the second class grouped those rodents between 141 and 170 mm, and to the last class belonged those animals larger than 170 mm. Breeding condition of males was assessed according to the position of testes: abdominal (not breeding) or scrotal (breeding). For females we recorded the vaginal condition (open or closed, and perforate or unperforate). Only obvious pregnancies were detected by palpation. Animals were released in the site of capture, except those that were removed. Relative abundances of different species were estimated by means of the Minimal Number Known to be Alive method (MNKA, Krebs 1966). These MNKA numbers must be refered to an area of 320 square meters, according to trap line length, habitat dimensions and rodent home ranges.

A comparison of numbers of individuals caught throughout the year in different field borders was done by a X^2 test. A time-period analysis by a G-test for goodness of fit was also used to test for differences in the number of individuals of *O. flavescens* in field borders (Sokal and Rohlf, 1969). The components of the G-statistics that were calculated were the test of heterogeneity (Gh), the test of pooled trends (Gp), and the total goodness of fit (Gt). While Gh examines variation between time periods, Gp tests for differences between subgrids. For *C. laucha,* comparisons were made also by a Wilcoxon rank test because of the low number of capture of this species.

We considered as resident, individuals that were captured at least two times. Disappearance percentages between months were estimated according to the percentage of individuals tagged in any month that were not recaptured the following month and included factors of both emigration and mortality.

The area covered by each species was estimated by the percentage of trap stations that were visited by each species in relation to total trap stations visited by rodents of any species (according to Gliwicz 1981).

Movements between cropfields and their borders were estimated from the percentage of *C. laucha* individuals that moved between them. The relationships between the numbers of resident and colonizing individuals was studied by means of the method of Danielson *et al.* (1986).

Behavioral interactions were studied by means of individual encounters in a test arena. Animals were brought from the field and after a period of acclimation to laboratory conditions, they were placed in a glass cage (120 × 70 × 70 cm dimensions), into which had been placed some sod taken from field borders in the area where experimental animals had been caught. Animals were introduced simultaneously in different corners of the cage, thereby allowing them to perform some exploratory movements without seeing each other. Their behavior was observed during 1/2 hour interval under illumination by low levels of yellow light, thus avoiding interference with their normal nocturnal behavior. Observations were conducted between 18.00 h and 10.00 h, the time period during which the two species had been observed to be active. A total of 14 trials were done; 5 for *C. laucha* × *C. laucha*, 4 for *Akodon azarae* × *Akodon azarae* and 5 for *C. laucha* × *A. azarae*. Each individual was matched only once since the results of a previous encounter might influence the results in a subsequent one. Aggressive behavior, fights, avoidance, inhibition, retreats, and amicable behavior were recorded. We considered dominant the individual who caused the retreat of the other animal, even without a fight. These behavioral experiments are part of a larger series that are still being conducted. We present here only some preliminary results.

RESULTS

During the trapping year we recorded a total of 936 captures of 564 different *Akodon azarae,* 47 captures of 40 different *Calomys laucha,* 93 captures of 78 different *Oligoryzomys flavescens* and 17 captures of 16 different *Calomys musculinus* during a total trapping effort of 1880 trap-nights. *Mus musculus* was also captured, but un very low numbers and therefore was not included in the analysis.

Effect of *A. azarae* removal

Effectiveness of A. azarae *removal.* Although the number of individuals of *A. azarae* caught in the removal field border trapline and its control did not differ significantly (Fig. 2), the number of captures during the three day period of trapping showed a significant decrease in numbers in the removal border trapline for each trapping period, as compared with the distribution of captures in the control border trappline ($X^2 = 18$, $P < 0.001$). In addition, the percentage of colonizing individuals in the removal border was higher than for the control trapline, especially during high density months (Table 1). Therefore, the recovery of numbers between months in the removal border trapline might have been due to immigration from adjacent areas.

Changes in abundance in the remaining species. By comparing the captures of *A. azarae* removal trapline (B4) and its control trapline (B3), it can be seen that *C. laucha* showed a significantly higher number of individuals where *A.*

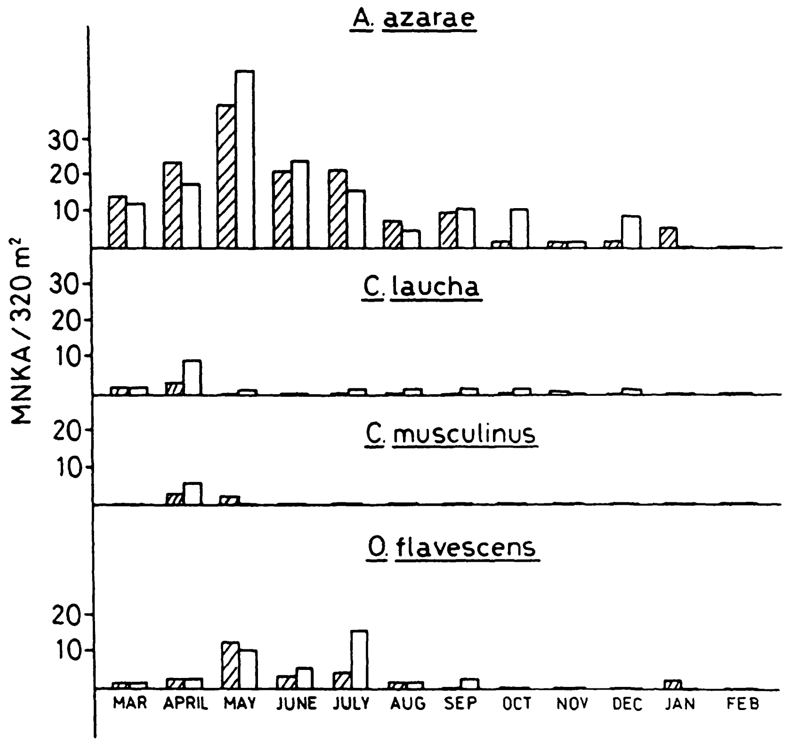

Fig. 2. — Number of individuals (MNKA) of each species in the border trapline with *A. azarae* removed (white) and comparable control traplines (hatching).

TABLE 1. — Percentages of colonist in different months of the year for *A. azarae* (a) and *O. flavescens* (b) in *A. azarae* removal border and control border traplines.

a)

	Month										
	A	M	J	J	A	S	O	N	D	J	F
Control border	48	44	19	46	38	0	0	0	100	67	-
Removal border	65	58	79	64	0	90	89	100	75	-	-

b)

	A	M	J	J	A	S	O	N	D	J	F
Control border	0	67	-	25	0	-	-	-	-	50	-
Removal border	4	100	50	38	35	0	-	100	-	-	-

azarae was removed with respect to the control (Wilcoxon rank signed test, $P < 0.05$) (Fig. 2). At the same time *O. flavescens* showed a statistically significant higher number of individuals in the removal border trapline only in June and July (20 versus 7 individuals, $X^2 = 4.61$, $P < 0.05$), months of high density. *C. musculinus* didn't show any differences in *A. azarae* removal border trapline with respect to control border ones.

Residency and survival. Although *O. flavescens* failed to show a significant numerical response to *A. azarae* removal, it showed a high number of resident individuals (Table 2), where recapture rates for *A. azarae* in removal border traplines are higher than those of control border ones (Exact Fisher Test, $P < 0.01$). *C. laucha* and *C. musculinus* didn't show any difference in their recapture rates between control and removal border traplines.

TABLE 2. — Percentages of residents and residency time ($\bar{x} \pm$ SE) for *A. azarae (a), C. laucha* (b) and *O. flavescens* (c) in control and experimental border traplines with *A. azarae* removed and in adjacent fields.

a) A. azarae

		Control		Removal	
		Border	Field	Border	Field
Percentage of resident individuals.		54.6	--	--	--
Mean residency time	$\bar{x}$	15.04			
	SE	0.28	--	--	--
	n	102			

b) C. laucha

		Control		Removal	
		Border	Field	Border	Field
Percentage of resident individuals.		0.0	--	--	--
Mean residency time	$\bar{x}$	1.00	7.03	4.88	10.39
	SE	0.00	0.39	3.68	0.75
	n	6	39	16	41

c) O. flavescens

		Control		Removal	
		Border	Field	Border	Field
Percentage of resident individuals.		4	--	32.4	--
Mean residency time	$\bar{x}$	1.04	--	5.68	--
	SE	0.08	--	3.09	--
	n	24	--	34	--

$\bar{x}$: Mean number of days. SE: Standard Error. n: number of individuals used for this calculus.

Low disappearance percentage (Fig. 3) and high residency times (Table 2) were obtained in the removal border traplines with respect to the control for both *C. laucha* and *O. flavescens*. For *C. laucha* a lower disappearance rate and high residency times were recorded in the field adjacent to the removal border trapline with respect to the field trapline adjacent to the control border one.

Area covered by each species. A. azarae showed the highest values of habitat occupancy in both the removal and control border traplines, occupying 82 % and 97 % of the trap stations, respectively. *C. laucha* occupied the border habitats when rodent abundance in fields was high (May-June, Fig. 4). Percentage occupancies for *C. laucha* and *O. flavescens* were higher (17.11 % versus 3.5 % for the former and 21.3 % versus 13.5 % for the latter) in the removal border trapline than in the control ($X^2 = 18.8$, $P < 0.01$ for *C. laucha* and $X^2 = 3.82$, $p < 0.1$ for *O. flavescens*).

Calomys laucha showed and increase in movement between the removal border and its adjacent field with respect to the control border and adjacent field habitats, but this difference was not statistically significant (11 % versus 3 %, $X^2 = 2.66$, $0.05 < P < 0.1$).

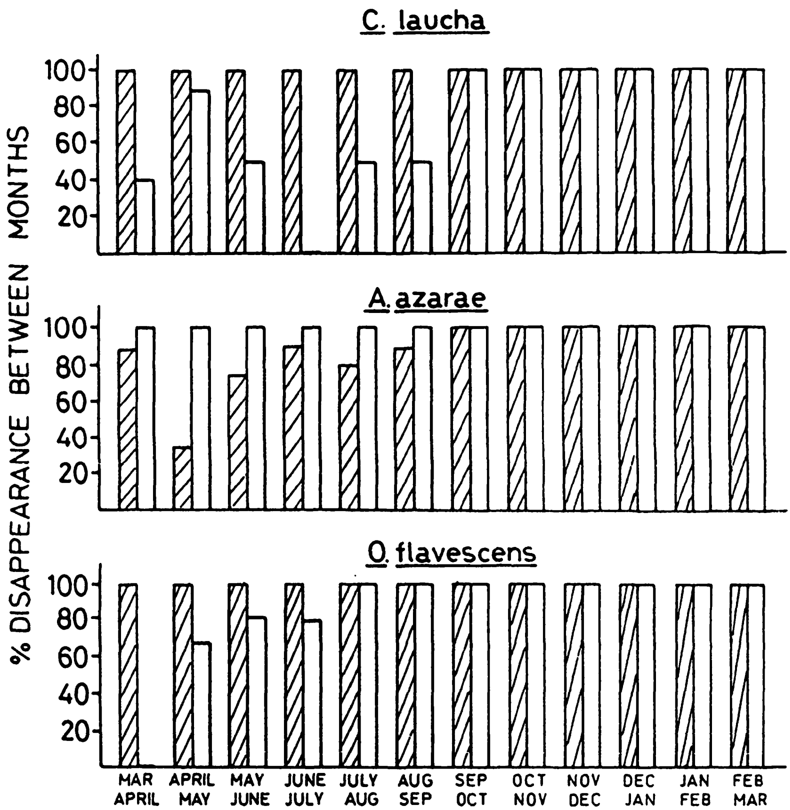

Fig. 3. — Disappearance percentages between months in the control border trapline (hatching) and the border trapline with *A. azarae* removed (white).

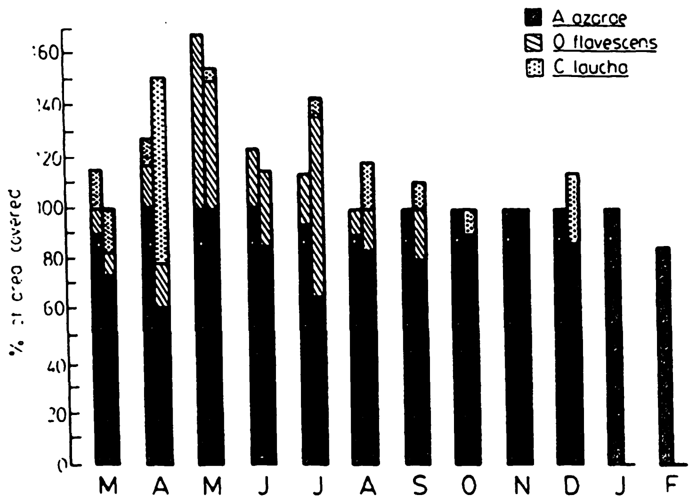

Fig. 4. — Percent of study area covered by each species during different months of the year. Occupancy was estimated by the ratio between trap stations visited by each species compared to the total trap stations visited by any rodent species (right, border trapline with *A. azarae* removed, left, control border trapline).

Reproduction and population structure. A. azarae showed a significantly lower number of large sized individuals in the removal trapline compared to the control border one (Table 3). There were no significant differences between removal and control border traplines in either *sex ratios* or breeding activity

TABLE 3. — Age structure, *sex ratio* and reproductive activity in populations of *A. azarae* in control and experimental border traplines with *A. azarae* removed.

		CONTROL	REMOVAL
Percent composition of age classes	I	4	0
	II	52	100
	III	44	0
	n	115	134
Sex ratio (males/total)		0.44	0.43
	n	133	148
scrotal males	%	8.6	12.7
	n	58	63
open vagina	%	34.7	44.7
	n	75	85
pregnancy	%	2.7	8.1
	n	133	148
breeding individuals	%	23.3	31.1
	n	133	148

for this species. There were no significant differences in the age structure of population or in the proportion of breeding individuals between the control and *A. azarae* removal border traplines for *C. laucha* and *O. flavescens* (Tables 4 and 5). However, *C. laucha* showed differences between field and border traplines in both *sex ratios* and age structure (Table 4). In the border traplines, the numerical dominance of males of intermediate size for *C. laucha* was higher than in the field traplines ($P < 0.01$, Exact Fisher Test).

Effect of removal of *C. laucha*

The number of individuals and total captures of *A. azarae* and *O. flavescens* did not differ significantly in the *C. laucha* removal border and control border traplines (Fig. 5). *C. laucha* was not captured in the removal border trapline after the second trapping session, whereas in the control border it was taken for five months. This difference may not be attributed to differences in the density of populations in the cropfields, because in both neighbor fields, 27 individuals of this species were captured. Removal of *C. laucha* was only expressed through its own density, as they failed to recolonize the area after the removal of resident individuals.

Behavioral encounters

Animals did exhibit exploratory movements after their release in the cage where they slowly left the place where they were placed initially. The vegetation on the cage bottom did not allow the individuals to see each other until they were close, almost physically in contact.

Fights were not observed in interspecific or intraspecific encounters. The presence of *A. azarae* caused an inhibition in exploratory movements in *C. laucha*, but there was no inhibition of movement when individuals of the same species were matched (Table 6). Dominant individuals (those who caused an inhibition in movement or retreat of the alternate animal) were in all occasions those of large body weight. In cases of similar weight between the paired animals there was no evident dominance expressed.

DISCUSSION

Changes in the population of *C. laucha* and *O. flavescens* in the *A. azarae* removal plots of the border traplines when compared to the control traplines are in agreement with the negative spatial relationships found for these species previously (Busch and Kravetz 1992). The changes were attributed to competitive relationships. *C. laucha* increased in numbers when resident *A. azarae* were removed, thus confirming the hypothesis that *A. azarae* is limiting the use of border habitats by *C. laucha*. The spatial segregation observed between cropfield and border habitats and within border habitats themselves is therefore a result of competitive interactions and not due only to different habitat preferences.

The positive numerical response of *C. laucha* to the removal of *A. azarae* was probably possible because of the large population of *C. laucha* present in the cropfields and which serve to recolonize the border habitats when conditions

TABLE 4. — Age structure, *sex ratio* and reproductive activity in populations of *C. laucha* in control and experimental border traplines with *A. azarae* removal and in adjacent fields.

		CONTROL		REMOVAL	
		Border	Field	Border	Field
Percent composition of age classes	I	0	9	0	10
	II	100	77	91	66
	III	0	14	9	24
	n	3	24	12	29
Sex ratio (males/total)		0.83	0.23	0.77	0.44
	n	6	24	13	29
scrotal males	%	20	--	60	--
	n	5	--	10	--
open vagina	%	0	--	33	--
		1	--	3	--
pregnancy	%	0	--	33.3	--
	n	1	--	3	--
breeding individuals	%	16.7	--	53.84	--
	n	6	--	13	--

TABLE 5. — Age structure, *sex ratio* and reproductive activity in populations of *O. flavescens* in control and experimental (*A. azarae* removal) border traplines with *A. azarae* removed.

		CONTROL	REMOVAL
Percent composition of age classes	I	20	6
	II	40	44
	III	40	50
	n	15	32
Sex ratio (males/total)		0.52	0.38
	n	23	32
scrotal males	%	0.0	8.3
	n	8	12
open vagina	%	3	9.1
	n	13	11
pregnancy	%	0.0	14.2
	n	23	21
breeding individuals	%	8.7	19
	n	21	23

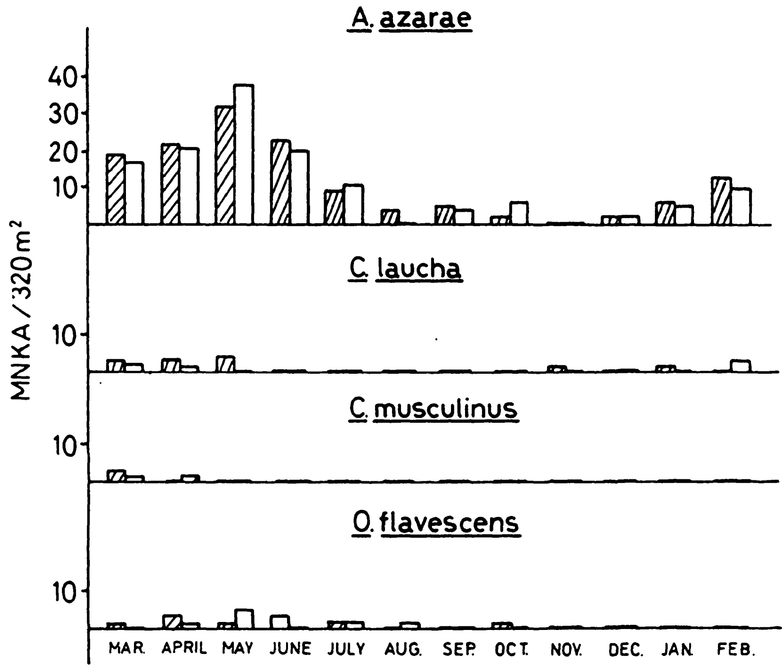

Fig. 5. — Number of individuals of each species (MNKA) in the border trapline with *C. laucha* removed (white) and its comparable control (hatching).

TABLE 6. — Results of behavioral encounters between *A. azarae* and *C. laucha* in a test arena duplicating a border habitat.

	Inhibition of movement	No inhibition
C. laucha x C. laucha	0	5
C. laucha x A. azarae	4	1
A. azarae x A. azarae	0	4

became comparatively better there than in the fields. Movement of individuals between cropfield and border habitats may enhance survival by lessening the negative effect of farming activities and at the same time providing an escape route for animals under competitive pressure. Human activities in agrosystems might have been indirectly contributing to an increase in the densities of *Calomys* in past years by increasing areas under cultivation. These areas provide good habitats for populations of *Calomys*, whereas individuals of *A. azarae* are practically absent in them. In natural pastures this latter species was dominant numerically over *Calomys*. The overall increase in densities of *Calomys* has been related to a spread of Argentina Hemorrhaghic Fever (AHF) since the 1950 s because species of this genus are reservoirs of Junin virus, the ethiological agent of AHF.

O. flavescens responded to the removal of *A. azarae*, by showing an increase in survivorship and subsequent resident numbers but without a significant change in overall numbers. However it showed higher numbers in the *A. azarae* removal border traplines than in the comparable control ones (Fig. 2).

In general *A. azarae* is more abundant than is *O. flavescens* in agrarian systems, with both species occupying the same kind of habitats (pastures, cropfield borders). *Oligoryzomys* is an opportunistic genus with a wide distribution in Argentina where it occupies a great variety of habitats. In the Pampean region, however, it is restricted to specific habitats which have a well structured plant cover and low levels of human disturbance. In these habitats it is competitively inferior to *Akodon azarae*. Whether the limited use of cropfields by *O. flavescens* in order to escape from competition with *A. azarae* is due to habitat selection or to competition with *Calomys* is a matter for future research. In a previous study (Busch and Kravetz 1992) we found insignificant or positive spatial associations between *C. laucha* and *O. flavescens* in similar borders and cropfield habitats.

The lack of a significant numerical response in *O. flavescens* can be attributed to a number of different factors. One is that if individuals of *A. azarae* were preventing the establishment of resident individuals of *O. flavescens*, the removal of the former should cause an immediate increase in resident *O. flavescens* without changing overall numbers. The condition of residency should enhance survival. Another possibility is that recolonization by *A. azarae* prevented a greater number increase in *O. flavescens*. Hence we think that if provided with sufficient time and a prevention of recolonization by *A. azarae*, a greater numerical response in *O. flavescens* would have been found.

This experiment showed the importance of displacement of individuals in the regulation of rodent populations. There was a high recolonization rate of empty areas by *A. azarae* of intermediate size. These are probably transient individuals in their original areas from which they migrate to the removal areas where they become residents. The response of *A. azarae* to its own removal by colonization of empty areas indicates that field borders are habitats with high intraspecific as well as interspecific competitive pressures. In these habitats the condition of residency is an important feature with respect to interspecific dominance. The removal of resident *A. azarae* caused an invasion of *A. azarae* from other places, but it also enhanced the possibility of colonization by *Calomys laucha* and resulted in an increase in resident numbers of *O. flavescens*. The further results show that the effect of social status over interspecific competition are reinforcing those results obtained by Busch and Kravetz (1992). We found that negative spatial relationships were detected between adult females of *A. azarae* and juveniles of *C. laucha* in a period of the year when there was no detectable negative spatial relationships between populations as a whole.

The results of the behavioral encounters carried out during this study showed that competitive interference between *A. azarae* and *C. laucha* may be expressed in spatial segregation produced from individual interactions.

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