

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/287515727>

Community structure and diversity of sigmodontine rodents (Muridae: Sigmodontinae) inhabiting maize and soybean fields i....

Article *in* *Interciencia* · November 2010

CITATIONS

3

READS

29

2 authors, including:



Maria Busch

University of Buenos Aires

23 PUBLICATIONS 315 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:

Project

Rodent ecology. Applications to control and prevention of diseases [View project](#)

Competitive interactions among rodents (*Akodon azarae*, *Calomys laucha*, *C. musculinus* and *Oligoryzomys flavescens*) in a two-habitat system. I. Spatial and numerical relationships

by M. BUSCH and F.O. KRAVETZ

*Departamento de Biología. Facultad de Ciencias Exactas y Naturales.
Universidad de Buenos Aires.*

*Av. Intendente Cantilo s/n. Ciudad Universitaria. Pab. II. 40 piso.
Lab. 104. Núñez. (CP 1428). Buenos Aires. Argentina*

Summary. — Interspecific relationships among cricetid rodents in agrarian ecosystems were studied. The principal rodent species found in these habitats are *Akodon azarae*, *Calomys laucha*, *Calomys musculinus* and *Oligoryzomys flavescens*. Fieldwork was carried out in D. Gaynor, Buenos Aires Province (Argentina), from 1979 to 1982. Spatial and numerical relations in a two-habitat system comprising croplands and their borders were analyzed. Asymmetrical interspecific competition for space was found mainly in summer with *A. azarae* being the dominant species. Individual differences in competitive ability were found. Females of *A. azarae* were more dominant than males, and juveniles of *C. laucha* were more segregated than adults. Coexistence mechanisms of different species in borders are discussed.

Résumé. — Les relations interspécifiques entre une série de rongeurs Cricétidés ont été étudiées dans des écosystèmes agraires de la province de Buenos-Aires de 1979 à 1982. Leurs relations spatiales et numériques ont été analysées dans un système de double habitat comprenant les champs cultivés et leurs bordures. Une compétition interspécifique asymétrique pour l'espace a été mise en évidence, surtout pendant l'été chez l'espèce dominante *Akodon azarae*, et on a constaté des différences individuelles dans l'aptitude à la compétition. Les femelles de cette espèce étaient plus dominantes que les mâles, et les juvéniles de *Calomys laucha* étaient plus dispersés que les adultes. Les mécanismes de coexistence d'espèces différentes dans les bordures sont discutées.

INTRODUCTION

Akodon azarae, *Calomys laucha*, *Calomys musculinus* and *Oligoryzomys flavescens* are cricetid rodents that inhabit pampean agrarian ecosystems. They are found in a variety of habitat including native grasslands, pastures, croplands and their borders (marginal areas below wire fences, where a weed community has developed), railway terraces and river embankments.

Previous data (Crespo 1966, Crespo *et al* 1970, Dalby 1975, de Villafañe *et al* 1977, Kravetz 1978, Kravetz *et al* 1975, Kravetz and de Villafañe 1981,

Kravetz *et al* 1982, Kravetz and Polop 1983, Busch *et al* 1984, de Villafañe and Bonaventura 1986) suggest that these species show a differential spatial distribution and rodent community composition varies according to the habitat. While the *Calomys* are dominant in cropfields, *A. azarae* is in general more abundant than *O. flavescens*, *C. laucha* and *C. musculus* in cropfield borders and less disturbed habitats.

Many authors have stressed the importance of interspecific competition in determining the distribution and abundance of small mammals (Brown 1970, Brown and Munger 1985, Grant 1969, 1970, 1971, 1972, Stoecker 1972, among others). Although the distribution of the rodent species studied herein can be attributed to the existence of interspecific competition (de Villafañe *et al* 1977, Kravetz 1978, Busch *et al* 1984) through habitat segregation, interspecific relationships in these species have not yet been studied.

The goal of this paper is to assess the role of interspecific competition in determining the spatial distribution and numerical relations of *Calomys laucha*, *Calomys musculus*, *Akodon azarae* and *Oligoryzomys flavescens* in agrarian habitats. In this work we attempt to analyze the effect of competitive interactions on community and population structure, taking into account spatial and temporal ambient variability as well as individual differences in competitive abilities.

METHODS

Study area

Fieldwork took place at D. Gaynor (34°8'S, 59°14'W), Exaltacion de la Cruz Department, Buenos Aires Province, Argentina. This area is a gently sloping plain in the pampean subregion. The climate is temperate, characterized by a winter having more than five days with frost per month, a figure considered critical for rodent survival (Crespo 1944).

The vegetation of this area features an absence of native trees, and has been drastically changed by human activity. Originally, the predominant plant community included matted grasses 0.5-1 m high, but this has been replaced by cropfields (corn, soya bean, sunflower, flax wheat) and pastures. Dominant species are *Stipa neesiana*, *S. papposa*, *S. brachichaeta*, *Bothriocloa laguroides*, *Paspalum dilatatum*, *Lolium multiflorum*, *Bromus unioloides*, *Carduus acanthoides*, *Cirsium vulgare* and *Cynara cardunculus*.

Crespo (1966) described the principal types of habitats present in pampean agrarian ecosystems and Bonaventura and Cagnoni (in press) provided a more detailed description of the vegetation.

Trapping methods, species identification and relative abundances

Fieldwork was carried out between November 1979 and June 1982 with multiple capture pitfall traps that were placed in cropfields and borders in different months of the year. Pitfalls had formaldehyde, so each animal died upon entering the trap. Traps were placed in lines of 8, spaced at 20 m intervals. They were

left active for a period of one week, after which all animals caught were collected. A total of 101 and 102 lines were placed in borders and fields, respectively (Table 1).

Rodents captured were identified to species and measured (total, tail, tarsus and ear lengths). Sex, breeding condition, trap location and date of capture were also recorded. Breeding condition of males was assessed by recording their testes position as either abdominal (not breeding) or scrotal (breeding). For females vaginal status (open or closed, and perforate or unperforate), pregnancies and number of embryos were recorded.

Relative abundances of different species were estimated by means of a relative density (RDI = number of rodents/number of traps x number of nights).

Continuous capture traps allowed different kinds of individuals to be caught in spite of their social status, because traps were automatically reset after each capture. Even if dominant individuals were caught first, subordinate ones could be captured later in the same trap.

TABLE 1. — Number of individuals of each rodent species caught in each month in field and border traplines.

A a : *Akodon azarae* ; C l : *Calomys laucha* ; C m : *Calomys musculus* ; O f : *Oligoryzomys flavescens*.

Year	Month	Field Lines					Border Lines							
		n	Aa	Cl	Cm	Of	Mm	n	Aa	Cl	Cm	Of	Mm	
1979	10	11	0	6	0	0	0	3	3	1	0	0	0	
	11	12	2	10	4	0	0	9	5	2	0	0	0	
	12	8	0	6	0	0	0	8	0	7	0	0	0	
1980	2	15	2	30	2	2	2	12	22	16	12	6	1	
	3	5	0	6	2	0	0	6	3	6	6	0	0	
	4	7	15	41	9	1	0	5	19	24	3	2	0	
	6	0	0	0	0	0	0	0	0	0	0	0	0	
	7	6	0	41	1	12	0	7	32	42	3	0	0	
	8	1	3	8	4	1	0	1	4	16	0	1	0	
	10	1	1	60	1	0	0	3	4	33	0	1	0	
	12	2	0	12	0	0	0	2	1	4	0	0	0	
	1981	3	3	0	10	0	0	0	3	0	8	0	0	1
		4	1	0	1	1	0	0	1	3	7	1	0	0
5		1	0	22	0	0	0	1	0	3	0	0	0	
6		6	1	115	3	0	0	4	11	25	2	0	0	
8		1	1	14	0	0	0	4	12	2	0	0	0	
9		0	0	0	0	0	0	3	6	1	0	0	0	
10		3	2	0	0	0	0	5	4	13	0	0	0	
11		3	0	4	0	0	0	6	0	3	0	0	0	
12		3	0	0	0	0	0	6	1	0	0	0	0	
1982		2	5	1	7	0	0	0	6	0	4	0	0	0
	3	1	1	1	0	0	0	1	1	0	0	0	0	
	4	2	0	9	0	0	0	0	0	0	0	0	0	
	5	3	0	8	0	0	0	4	3	2	0	0	0	

Spatial and numerical relations

The distribution of capture sites in field and border habitats was compared by a heterogeneity X² test (Lison 1976). Competition coefficients were estimated by means of the Pianka (1973) Overlap Index for each habitat and according to the degree of slope of the regression lines of the numbers of individuals captured per line for each pair of species (Hallett and Pimm 1979). Statistical significance of these two estimations were assessed in the first case by determining

a critical region by calculating the distribution of normal parameters for 1 000 overlap indices, generated by random permutations of the original capture matrix of captures (Cohen, pers. com.). For the regression method, linear correlation coefficients between captures of each pair of species were calculated. Multiple correlations were not used due to the lack of a multinormal capture distribution. Places with null captures were not included in pairwise comparisons.

Competition coefficients were also estimated according to the numbers of individuals of each species captured per trap station. In order to study the differences in interspecific roles between population components, a principal component analysis was performed. Variables were defined as species, sex and age class (the latter based on total length and breeding condition). The elements of the matrix were the capture units (traps with captures for each date) and the attributes were the individuals of each species and class captured. A Q analysis was performed with a covariance matrix.

RESULTS

Seasonal variations in rodent abundance

During the study period there was a strong seasonal variation in rodent abundance (Fig. 1), with a minimum in spring (when approximately 0.33 individuals per line were caught) and a maximum in winter (12 individuals per line), followed by a dramatic drop. This seasonal pattern of variation in density has been attributed to several factors, including seasonality in reproduction, climate and disturbance from agrarian labours. Densities were not strictly equal during successive years for the same month. Although this temporal series is too short to extrapolate patterns of variation in multiannual abundance, these data suggest that there is no unique point of density equilibrium and a stable limit cycle is unlikely.

Distribution between fields and borders

A. azarae and *O. flavescens* were captured 86 and 90 % of the time in borders, respectively, while the number of *Calomys* taken in cropfields was double that in borders (Table 1). These interspecific differences in distribution between habitats proved to be statistically significant (X^2 : 53.87, $P < 0.001$). As cropfields showed a low specific diversity, interspecific relationships could not be analyzed by the number of captures, so this method was used only in borders.

Population interactions (capture distribution per border line)

The sign and magnitude of interspecific relationships estimated by means of regression slopes of the regression curves and by overlap indices were similar. There were few statistically significant relationships. Competition coefficients were all negative in spring for all pairs of species, while for the other seasons these

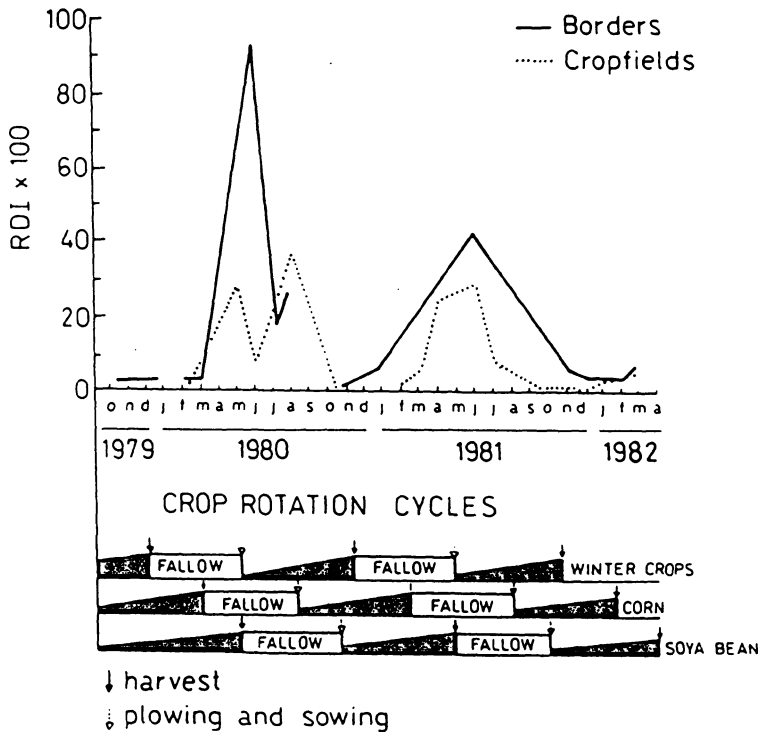


Fig. 1. — Rodent abundance as expressed as RDI in croppfields and borders during different months with concurrents crop rotation cycles.

values were variable (Table 2). The total number of *C. laucha*, *C. musculus* and *O. flavescens* captured per trap line was positively related to those of *A. azarae* up to a threshold value, above which captures of the former species were low (Fig. 2). These changes in curve slopes can explain the absence of statistically significant values for the regression equations.

For each species, the number of individuals captured in lines with low, medium and high values of each of the other species was compared with those

TABLE 2. — Competition coefficients estimated by the slope of the regression curves between the numbers of individuals captured per trap line for different pair of species.

* : statistically significant values ; $P < 0,05$ (—) : there are not enough numbers for estimating these coefficients.

	Aa-C1	Aa-Cm	Aa-Of	C1-Cm	C1-Of	Cm-Of
Spring	-0.35	-0.35*	-0.43	-0.10	-0.17	-
Summer	-0.17	0.13	1.04	-0.34	0.32	-0.35
Autumn	0.03	-0.05	0.02	0.17	0.35	1.64
Winter	0.38	0.03	-0.02	0.09	-0.04	-0.67

expected according to total capture and the number of trap lines in each class. The distribution of *O. flavescens* and *C. laucha* when compared to *A. azarae* showed a higher capture rate than expected for intermediate values, and lower than expected for low and high numbers of *A. azarae* ($X^2 : 30.6, P < 0.001$). *A. azarae* showed less captures than expected for low numbers of *C. laucha* but more than expected for high numbers of this latter species ($X^2 : 10.9, P < 0.001$). These relationships held for all trap lines and for each season when analyzed separately. Distributions with respect to *C. musculus* and *O. flavescens* could not be analyzed in a similar way because there were few captures per line of these species.

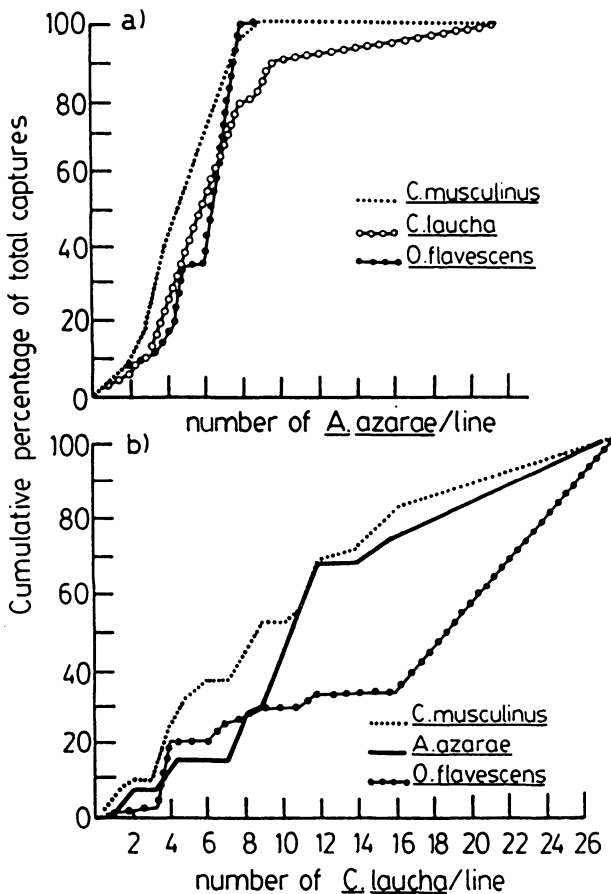


Fig. 2. — Capture distribution for each species as a function of the number of individuals of each other species present per line.

Individual interaction (capture distribution per trap)

At this level interactions were higher than at the population level. Interactions were high and negative in summer, moderate in spring, and low or mostly positive in autumn and winter. *A. azarae* was the species showing the highest number of negative interactions with the other species both at trap or individual and at line or population level (Tables 2 and 3).

TABLE 3. — Competition coefficients estimated by the slope of the regression curve for individual numbers of each species pair captured per trap station (cf. tables 2 and 3).

	Aa-C1	Aa-Cm	Aa-Of	C1-Cm	C1-Of	Cm-Of
Spring	-0.30*	-0.28*	-0.12	-0.15	-0.21	-
Summer	-0.81*	-0.43*	-0.44*	-0.29*	-0.02	-0.41*
Autumn	-0.17	-0.35*	-0.12	0.06	0.07	0.22
Winter	0.14	0.10	0.27	0.10	0.50*	0.21

Individual differences within populations were found as regards interspecific segregation. *A. azarae* females and *C. laucha* juveniles were the primary population components for determining the composition of capture groups, and as the variables that contributed most to define the first axis of variation in the principal component analysis, accounting for 47 % of total variance. According to this analysis, capture groups were characterized either by the presence of *A. azarae* females or by *C. laucha* juveniles. These variables showed a negative correlation when there were no significant relationships between the total populations of *A. azarae* and *C. laucha* or between other population components in autumn and winter (Table 4).

TABLE 4. — Competition coefficients for different population components of *A. azarae* and *C. laucha* (according to numbers captured per trap station) in Autumn and Winter (cf. tables 2 and 3).

t	t	t	j	f	t	f	j	m	t	m	j
Aa	C1	Aa	C1	Aa	C1	Aa	C1	Aa	C1	Aa	C1
-0.50		-0.65*		-0.51		-0.70*		-0.89		-1.11	

DISCUSSION

Akodon azarae, *O. flavescens*, *C. laucha* and *C. musculus* showed a differential distribution between cropfields and their borders. The first two species predominantly occupied borders, whereas both species of *Calomys* prevailed in cropfields (Table 1). On the basis of competition coefficient values, a negative interaction was detected, specially in summer and spring, which partly explains this segregation. The negative spatial association (according to the distribution of captures per trap) between species may be an expression of interference competition for space, which causes interspecific segregation at the individual level.

Analysis of captures at the population level reveals that competition is asymmetrical, *A. azarae* individuals affect *C. laucha*, *C. musculinus* and *O. flavescens* more than the reverse. Above a threshold number of *A. azarae* individuals per line, captures of the other species are reduced considerably (Fig. 2a). The distribution of captures of *A. azarae* seems to be independent of the abundance of *C. laucha* (Fig. 2b). The hypothesis of the dominance of *A. azarae* in borders has been previously mentioned (de Villafane *et al* 1973, Kravetz *et al* 1975, 1982) in order to explain the increase in captures of *Calomys* after the removal of *A. azarae* and/or *Bolomys obscurus*. According to Calhoun (1964), the order of capture may reveal the rank of individuals in an intra or interspecific hierarchy.

Seasonal variation in competition may be related to changes in reproductive and population structure : at the beginning of the breeding season, animals establish their territories (de Villafañe 1970), which could cause competition for space. Low densities in spring may prevent any expression of competition until summer, when abundance is significantly increased. A decrease in interspecific competition in autumn and winter may be related to changes in population structure, with the recruitment at this time of a large number of juveniles (Kravetz *et al* 1981). According to principal component analysis *A. azarae* juveniles would not be able to compete with *C. laucha* such as adults do (Table 4). Females of *A. azarae* also show an intraspecific dominance over males and they occupy the most favourable microhabitats (Zuleta *et al.* 1988, Bonaventura and Kravetz 1984). The greater territoriality of females with respect to males and their litters has been related to reproductive investments, which cause a higher demand for resources, specially for food (Ims 1987).

Individual differences in competition are also expressed in populations of *C. laucha* where juveniles are more segregated than adults by females of *A. azarae*. This is shown by the predominance of the segregation of these groups in captures.

The influence of individual differences on the regulation of numbers has been reported by Lomnicki (1978). For rodents Grant (1972) has stressed that social status influences the results of interspecific encounters. Juveniles, non resident and/or subordinate individuals would be more strongly affected by density than resident ones, so that the former are the first to disperse to areas less frequented by the species. Danielson and Gaines (1987) showed the effect of conspecific and heterospecific residents on colonization rates in *Microtus ochrogaster*, *Synaptomys cooperi* and *Sigmodon hispidus*.

Variations in the age structure of populations generate changes in competitive relationships in different months of the year, as well as a non-linear relationship between the abundance of different species. The existence of a threshold value (Fig. 2a) in the abundance of *A. azarae* beyond which there is a stronger effect on other species implies that competition coefficients are not constant for different values of population abundance.

Habitat heterogeneity may play an important role in the determination of abundance for the species studied, mainly for *C. laucha*, which is abundant in both habitats. The use of the border as an alternative habitat may be crucial for survival when existing conditions in cropfields are unfavourable, as during farming activities in the fields.

Why do different species persist in borders ?

Temporal and spatial ambient heterogeneity and non-linear relationships between species abundances may allow different species to coexist in borders even under strong competition, according to the hypothesis that temporal and spatial habitat heterogeneity promotes species coexistence, originally advanced by Hutchinson (1961) and developed in greater detail by several authors (Levin 1974, Yodzis 1978, Levins 1979, Goh 1980, Dale 1978, Chesson and Warner 1981, Chesson 1986). Fig. 3 shows the hypothetical relations between the equilibrium densities of *A. azarae* and those of *O. flavescens* and *C. laucha*. A negative relationship was assumed for all values of the abundance of *A. azarae*, with a slope change above a threshold value. The equilibrium density of *A. azarae* was assumed to be independent of those of *C. laucha* and *O. flavescens* (Fig. 2). The abundance of *A. azarae* remains constant in spite of changes in the numbers of *C. laucha* or *O. flavescens*, and the value depends on the ambient carrying capacity (K) for *A. azarae*. If this ordinate is greater than the value at which *C. laucha* and *O. flavescens* disappear (Fig. 3a), system dynamics leads to the extinction of these species. Ambient variability causes a seasonal return to initial

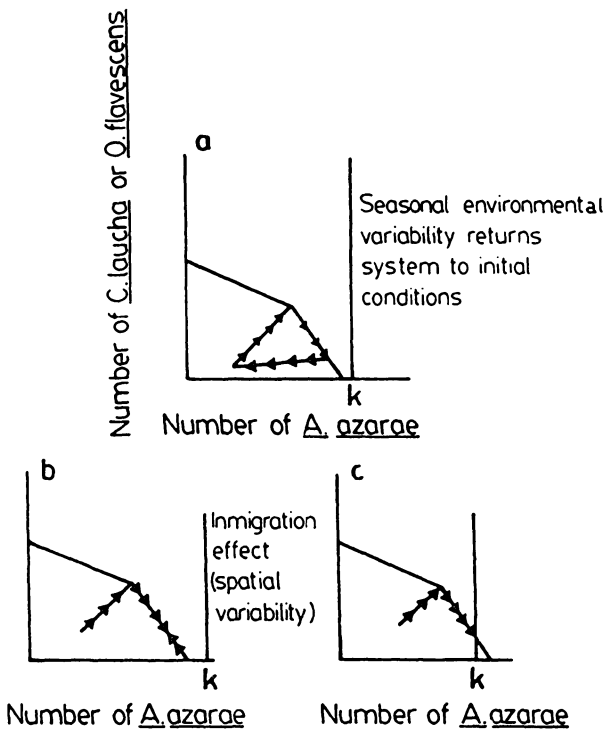


Fig. 3. — Hypothetical relationships for the abundance of *C. laucha*, *O. flavescens* and *A. azarae* and possible mechanisms that allow coexistence. In a) and b) the carrying capacity (K) for *A. azarae* is assumed higher than the value where there are no individuals of *C. laucha* and *O. flavescens*, while in c) it is lower.

conditions when all species undergo a winter drop in abundance. This prevents the total disappearance of *C. laucha* and *O. flavescens* (Fig. 3a). An alternative is the persistence of different species in borders by means of emigration from cropfields, specially for *C. laucha*, which maintains a large population pool in this latter habitat (Fig. 3b). If a lower value of K for *A. azarae* is assumed (Fig. 3c), all species can persist without immigration or ambient variability. We conclude that both *C. laucha* emigration from cropfield to borders and seasonal variation in habitat conditions and densities are essential to maintain rodent diversity in cropfield borders. Rodent communities in natural grasslands or fallow pastures in this area show a greater dominance of *A. azarae* and an absence of *C. laucha*.

ACKNOWLEDGMENTS

We thank D. Gaynor people, for their assistance in the field work. We also thank M.I. Bellocq, who helped in field work and manuscript discussion. Dr. J. Cohen, G. Zuleta and D. Bilenca critically read the manuscript. J. Marcenaro and P. de Carli gave us assistance in computational work. We also thank an anonymous reviewer for his suggestions. This study was funded by grants from CONICET and F.O. Ocampo.

BIBLIOGRAPHY

- BONAVENTURA, S.M. and M. CAGNONI (in press). — La vegetación de los bordes de caminos de la pampa ondulada, Pcia de Buenos Aires. (Argentina). *Parodiana*.
- BONAVENTURA, S.M. and F.O. KRAVETZ, 1984. — Relación roedor-vegetación : estudio preliminar. *Rev. Mus. arg. Cs. Nat. « Bernardino Rivadavia » (Zool)*, XIII : 445-451.
- BROWN, J.H., 1970. — Mechanisms of competitive exclusion between two species of chipmunk. *Ecology*, 52, (2) : 305-311.
- BROWN, J.H. and J.C. MUNGER, 1985. — Experimental manipulation of a desert rodent community : food addition and species removal. *Ecology*, 66 : 1545-1563.
- BUSCH, M., F.O. KRAVETZ, R.E. PERCICH and G.A. ZULETA, 1984. — Propuestas para un control ecológico de la FHA a través del manejo del habitat. *Medicina*, 44 : 34-40.
- CALHOUN, J.B., 1964. — The social use of space. In : *Physiological Mammalogy* (Eds W. Majer and R. van Gelder). Vol. 1. Academic Press, New York.
- CHESSON, P.L., 1986. — Environmental variation and the coexistence of species. In : *Community Ecology* (Eds J. Diamond and T.J. Case. pp. 240-256. Harper and Row, New York.
- CHESSON, P.L. and WARNER, 1981. — Environmental variability promotes coexistence in lottery competitive systems. *Am. Nat.*, 117 : 923-943.
- CRESPO, J.A., 1944. — Relaciones entre estados climáticos y la ecología de algunos roedores de campo (Cricetidae). *Rev. Mus. Arg. de Zoogeografía*, IV (3) : 137-144.
- CRESPO, J.A., 1966. — Ecología de una comunidad de roedores silvestres en el Partido de Rojas, Pcia de Buenos Aires. *Rev. Museo Arg. de Ciencias Naturales*, I (3) : 79-134.
- CRESPO, J.A., M.S. SABATTINI, M.J. PANTANIDA y G. DE VILLAFANE, 1970. — Estudio ecológico sobre roedores silvestres. Observaciones sobre densidad, reproducción y estructura de la comunidad de roedores silvestres en el Sur de la Pcia de Córdoba. *Min. Bienestar Social. Soc. Est. de Salud Publ.* : 1-45.

- DALBY, D.E., 1975. — Biology of pampa rodents. Balcarce area. Argentina. *Publ. Museum Michigan State Univ. Biol., Series 5*, (3) : 153-271.
- DALE, G., 1978. — Money in the bank : a model for coral reef fish coexistence. *Environ. Biol. Fishes.*, 3 : 103-108.
- DANIELSON, B.J. and M.S. GAINES, 1986. — The influences of conspecific and heterospecific residents on colonization. *Ecology*, 68 (6) : 1778-1884.
- DE VILLAFANE, G., 1970. — *Ecología de roedores silvestres (Cricetidae) en el sur de la Provincia de Córdoba, completada con observaciones sobre reproducción y desarrollo obtenidas por cría experimental*. Tesis Doctoral. Univ. Nac. de Córdoba.
- DE VILLAFANE, G., F.O. KRAVETZ, M.J. PIANTANIDA and J.A. CRESPO, 1973. — Dominancia, densidad e invasión en una comunidad de roedores en la localidad de Pergamino (Provincia de Buenos Aires). *Physis., seccion C*, 32 (84) : 47-59.
- DE VILLAFANE, G., F.O. KRAVETZ, O. DONADÍO, R.E. PERCICH, L.E. KNECHER and M.P. TORRES, 1977. — Dinámica de las comunidades de roedores en agroecosistemas pampásicos. *Medicina*, 37 : 128-138.
- DE VILLAFANE, G. and S.M. BONAVENTURA, 1986. — Ecological studies in cropfields of the endemic area of Argentine Hemorrhagic Fever. *Calomys musculinus* movements in relations to habitat and abundance. *Mammalia*, 51 : 233-248.
- GOH, B.S., 1980. — *Management and the analysis of biological populations*. Elsevier. New York.
- GRANT, P.R., 1969. — Experimental studies of competitive interactions in a two-species system. I. *Microtus* and *Clethrionomys* species in enclosures. *Can. J. Zool.*, 47 : 1059-1082.
- GRANT, P.R., 1970. — Experimental studies of competitive interaction in a two-species system. II. The behavior of *Microtus*, *Peromyscus* and *Clethrionomys* species. *An. Behav.*, 18 : 411-426.
- GRANT, P.R., 1971. — Experimental studies of competitive interaction in a two-species system. III. *Microtus* and *Peromyscus* species in enclosures. *J. An. Ecol.*, 40 : 323-350.
- GRANT, P.R., 1972. — Interspecific competition among rodents. *Ann. Rev. Ecol. Syst.*, 3 : 79-106.
- HALLETT, J.G. and S.L. PIMM, 1979. — Direct estimation of competition. *Am. Nat.*, 113 (4) : 593-600.
- HUTCHINSON, G.E., 1961. — The paradox of the plankton. *Am. Nat.*, 95 : 137-145.
- IMS, R.A., 1987. — Male spacing systems in microtine rodents. *Am. Nat.*, 130 (4) : 575-484.
- KRAVETZ, F.O., 1978. — *Dinámica de las comunidades de roedores involucradas en la Fiebre Hemorrágica Argentina*. Tesis Doctoral. Universidad de Buenos Aires. Argentina.
- KRAVETZ, F.O., G. DE VILLAFANE, M.P. TORRES and M.J. PIANTANIDA, 1975. — Poblaciones de roedores en un campo de trigo. *Physis. Sección C*, 31 (89) : 187-197.
- KRAVETZ, F.O. and G. DE VILLAFANE, 1981. — Poblaciones de roedores en cultivo de maíz durante las etapas de madurez y rastrojo. Mendoza. Argentina. *Hist. Nat.*, 1, (31) : 213-232.
- KRAVETZ, F.O., M.C. MANJÓN, M. BUSCH, R.E. PERCICH, P.N. MARCONI and M.P. TORRES, 1981. — Ecología de *Calomys laucha* (Rodentia, Cricetidae) en el Depto de Río Cuarto (Córdoba). I. Dinámica de población. *Ecología*, 6 : 15-22.
- KRAVETZ, J.O., M. BUSCH, J. GOBBI, J.M. MARCENARO, R.E. PERCICH and G.A. ZULETA, 1982. — Dinámica de especies de roedores cricétidos en la localidad de D. Gaynor. Com. IX Congreso Latinoamericano de Zoología. Perú.
- KRAVETZ, F.O. and J.J. POLOP, 1983. — Comunidades de roedores en agroecosistemas del Depto de Río Cuarto, Córdoba. *Ecosur*, 10 : 1-10.

- LEVIN, S.A., 1974. — Dispersion and population interactions. *Am. Nat.*, 108 : 207-228.
- LEVINS, R., 1979. — Coexistence in a variable environment. *Am. Nat.*, 114 (6) : 765-783.
- LISON, L., 1976. — *Estatística aplicada a la biología experimental*. Editorial Universitaria de Buenos Aires. (EUDEBA). Original version in French. Gauthier-Villars, Paris, 1968.
- LOMNICKI, A., 1978. — Individual differences between animals and the natural regulation of their numbers. *Blackwell Sci. Publ.* : 461-475.
- PIANKA, P.R., 1973. — The structure of lizard communities. *Ann. Rev. Ecol. Syst.*, 4 : 53-74.
- STOECKER, R.E., 1972. — Competitive relations between sympatric populations of voles (*Microtus montanus* and *M. pennsylvanicus*). *J. An. Ecol.*, 41 : 311-329.
- YODZIS, P., 1978. — *Competition for space and the structure of ecological communities*. Springer Verlag. Berlin. West Germany.
- ZULETA, G.A., F.O. KRAVETZ, M. BUSCH and R.E. PERCICH, 1988. — Dinámica poblacional del ratón del pastizal pampeano (*Akodon azarae*) en ecistemas agrarios de Argentina. *Revista Chilena de Historia Natural*, 61 : 231-244.