

# Predation upon small mammals in shrublands and grasslands of southern South America: ecological correlates and presumable consequences

Depredación sobre micromamíferos en matorrales y praderas del cono  
sur sudamericano: correlaciones ecológicas y presuntas consecuencias

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## ABSTRACT

I made a selective review of studies conducted in shrublands and grasslands of Chile, Argentina, and Uruguay, in which population levels of small mammals had been assessed, information on the diet of local predators had been reported, and/or presumed effects of predation had been discussed. The information available supports the following generalizations: 1) Predators seem to concentrate on the most abundant native rodents (e.g., *Octodon degus* in Chile; *Microcavia australis*, *Cavia aperea*, and *Akodon azarae* in Argentina; and *Cavia aperea* in Uruguay), consuming the remaining mammal species about in proportion to their relative abundances, but sometimes "ignoring" abundant introduced lagomorphs (e.g., *Oryctolagus cuniculus*). 2) The most preyed-upon rodents tend to be of large size (>200 g) and usually are diurnal folivores. 3) Population levels of these rodents are sometimes depressed by predation but predators do not seem capable of driving them to extinction, except in very small habitat patches, and perhaps only temporarily. 4) Predators seem effective in restricting the spatial activity patterns of their main prey to the vicinity of protective cover (e.g., bushes, burrows, rock piles), which usually are interconnected by tunnels, galleries, and/or runways. 5) Intensive removal of herbs caused by rodent foraging in the periphery of cover or shelter generates characteristic bare zones. 6) Low predation upon introduced lagomorphs (e.g., *Oryctolagus cuniculus* in Chile) has resulted in the expansion of their habitat use, which has affected the physiognomy and vegetational composition of the areas invaded. 7) In general, the different predation pressures upon small mammals directly affect their spatial activities, and indirectly, their impact on the habitats they occupy.

Key words: Native rodents, introduced rabbits, vertebrate predators, predation effects, refuging behavior, grazing effects.

## RESUMEN

Efectué una revisión selectiva de estudios realizados en matorrales y praderas de Chile, Argentina y Uruguay, en los cuales los niveles poblacionales de micromamíferos hubieran sido evaluados, y en que existiera información sobre la dieta de los predadores locales, o que los presuntos efectos de la depredación hubieran sido al menos discutidos. La información disponible permite las siguientes generalizaciones: 1) Los predadores parecen concentrar su caza sobre los roedores nativos localmente más abundantes (e.g., *Octodon degus* en Chile; *Microcavia australis*, *Cavia aperea*, o *Akodon azarae* en Argentina; *Cavia aperea* en Uruguay), consumiendo las restantes especies de micromamíferos en el orden aproximado de sus abundancias relativas, pero a veces "ignorando" densas poblaciones de lagomorfos introducidos (e.g., *Oryctolagus cuniculus*). 2) Los roedores más predados tienden a ser de tamaño grande (> 200 g) y usualmente son folívoros de hábitos diurnos. 3) Los niveles poblacionales de dichos roedores son a veces reducidos por acción de la depredación, pero los predadores no parecen ser capaces de llevarlos a la extinción, excepto en parches de hábitat muy pequeños y tal vez sólo en forma temporaria. 4) Los predadores sí parecen ser efectivos en restringir los patrones de actividad espacial de sus principales presas a la cercanía de refugios potenciales (e.g., arbustos, cuevas, pilas de rocas), los cuales usualmente aparecen interconectados por túneles, galerías o corredores superficiales. 5) La intensa remoción de hierbas que efectúan los roedores al alimentarse en la periferia de sus refugios antidepredación genera a su alrededor característicos anillos de suelo desnudo. 6) La baja depredación sobre lagomorfos introducidos (e.g., *Oryctolagus cuniculus* en Chile) resulta en una expansión de su uso del espacio, que afecta la fisonomía y la composición vegetacional de las áreas que ellos han invadido. 7) En general, las diferentes presiones de depredación sobre micromamíferos afectan directamente sus actividades espaciales e indirectamente su impacto sobre los hábitats que ocupan.

Palabras claves: Roedores nativos, conejos introducidos, depredadores vertebrados, efectos de depredación, conducta de refugio, efectos de pastoreo.

## INTRODUCTION

Direct predation upon small mammals is rarely seen. However, because predation eliminates particular prey phenotypes, it could be expected to be an important selective force acting on small mammals. The question is: What does predation select for, and how is an investigator to evaluate its ecological consequences for small mammals (Pearson 1985)?

Although ideally the investigator should use direct experimentation to disentangle causality among processes, this method is of limited applicability in field studies of vertebrate predation. For example, experimental additions of predators to a study area in order to increase predation pressure on resident small mammals requires first capturing the predators and then preventing their emigration once released. Conversely, the capture and removal of predators from an experimental area in order to decrease predation pressure on small mammals usually results in their quick replacement by immigrants from the periphery (see Taylor 1984, and references herein).

For these and other reasons, most experimental field studies of predation upon small mammals are based on indirect manipulations and assessment of its impact on prey populations. For example, by manipulating the number or distribution of potential refuges for resident small mammals, one can presumably alter their vulnerability to predation (Thompson 1982a, 1982b). Alternatively, one can manipulate the amount of illumination in the small mammals' habitat, and thus study their avoidance behavior to nocturnal predators (Kotler 1984a, 1984b).

No such experimental studies have been conducted in southern South America, and consequently the assessment of the potential effects of predation upon small mammals has to be done with a different approach: the observational/comparative method. In this case, the investigator does not manipulate the system under study, but derives conclusions based on correlations (Jaksić 1985). There is risk in using correlations to assign causal relationships, but I think that at the present state of knowledge in South America, it is justifiable to use this method in an attempt to detect general patterns of predation upon small mammals. In pointing to recurrent

patterns, and proposing causal mechanisms, some heuristic avenues of inquiry may be opened for future and more detailed scrutiny by other scientists using more powerful techniques.

## METHODS

Under the general assumption that predation is a major selective agent for small mammals, I made a selective but not exhaustive review of studies conducted in shrublands and grasslands of Chile, Argentina, and Uruguay. My criteria of selection considered only those studies in which the population levels of small mammals had been assessed, information on the food habits of the local predators had been reported, and/or the presumed effects of predation had at least been discussed on reasonable grounds.

Most of these studies had as a main focus the population ecology of small mammals, and predation was usually discussed as a mortality factor rather than as a selective agent capable of modifying the behavior of the survivors. Consequently, I reinterpreted results that were often unplanned byproducts of the main research thrust, and in the process of making comparisons I may have forced those results into a framework biased toward the detection of predation as a major selective force. However, because the investigators who did the original research were presumably unbiased toward predation, they at least provide a neutral data source and the best presently available. In an attempt to evaluate any possible bias, I offer a critique of my own analysis at the end of this paper.

The literature sources on which I based my conclusions are listed below for each country. For the nomenclature of small mammals I followed the designations of Honacki *et al.* (1982).

## RESULTS

*Chile*

For several years, my colleagues and I have evaluated the densities of small mammals in our main study area in central Chile, Los Domínicos/La Dehesa, a mediterranean-type shrubland located ca. 20 km NE of Santiago. The results have been consistent

year after year, despite use of different types of traps (Table 1). The most abundant small mammal in the area is the rodent *Octodon degus* (mean weight = 230 g), a diurnal folivore. The densities documented for this species in Table 1 are low in comparison to those obtained by other researchers in the same study area. Le Boulenge & Fuentes (1978) also trapping in Los Dominicos found maximum densities to be between 39 and 73 *Octodon* per hectare in patches of intermediate shrub cover, and between 192 and 159 per hectare in more open patches. Meserve *et al.* (1984) trapping in dense patches of La Dehesa documented maximum densities of 59-65 *Octodon* per hectare. Other density estimates for small mammals in central

Chilean shrublands elsewhere can be found in Fulk (1975), Glanz (1977a, 1977b), and Meserve (1981).

Concomitantly with the trapping studies, we have collected information on the diets of all the local predators (Table 2). It is clear that *Octodon* is one of the most-preyed upon small mammals in the area. In fact, using the data provided in Table 2 it can be shown that the numerical incidence of different small mammals in the field and in the diet of the local predators is significantly (or nearly so) correlated in five out of the nine cases analyzed (Table 3). In addition, the joint correlation pattern for the entire set of predators is highly significant (Table 3). Based on this information it can be concluded that in general the pre-

TABLE 1

Density of small mammals (individuals per hectare) in sparse shrubland of Los Dominicos, Chile, as estimated by mark/recapture live trapping (medium Sherman traps) during 1976, and by removal (snap) trapping (Victor four-way rat traps) during 1978. The species captured were the rodents *Abrocoma bennetti*, *Akodon olivaceus*, *Octodon degus*, *Oryzomys longicaudatus* and *Phyllotis darwini*, and the marsupial *Marmosa elegans*. Data based on Tables 1 and 2 of Jaksic *et al.* (1981b: 393 & 394).

Densidad de micromamíferos (individuos por hectárea) en matorral ralo de Los Dominicos, Chile, estimada por trampeo con recaptura (trampas Sherman) durante 1976 y por trampeo con remoción (trampas Víctor) durante 1978. Las especies capturadas fueron los roedores *Abrocoma bennetti*, *Akodon olivaceus*, *Octodon degus*, *Oryzomys longicaudatus* y *Phyllotis darwini*, y el marsupial *Marmosa elegans*. Datos basados en Tablas 1 y 2 de Jaksic *et al.* (1981b: 393 & 394).

Mammals	Jan	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Mean
<i>Abrocoma</i>											
live	—	—	—	—	—	0.7	0.7	0.7	0.7	0.7	0.4
snap	—	—	—	—	—	—	1.1	—	—	—	0.3
<i>Akodon</i>											
live	—	—	—	0.7	0.7	0.7	16.2	0.7	—	—	1.9
snap	—	—	—	—	—	—	4.4	—	—	1.1	1.4
<i>Marmosa</i>											
live	0.7	—	—	—	—	—	—	1.3	—	—	0.2
snap	—	—	—	—	—	—	—	—	—	1.1	0.3
<i>Octodon</i>											
live	18.2	9.4	8.8	10.1	11.4	10.1	10.1	29.6	29.0	23.6	16.0
snap	—	22.2	—	17.8	—	—	12.2	—	—	21.1	18.3
<i>Oryzomys</i>											
live	—	—	—	—	—	—	4.7	—	—	—	0.5
snap	—	—	—	—	—	—	2.2	—	—	—	0.6
<i>Phyllotis</i>											
live	0.7	—	—	—	1.3	2.7	4.0	2.7	0.7	0.7	1.3
snap	—	—	—	—	—	—	1.1	—	—	2.2	0.8

TABLE 2

Numerical incidence (expressed as percentage) of different prey in the diet of 12 predators in Los Dominicos/La Dehesa, Chile. Species names are as in Table 1, and additional small mammals not previously mentioned correspond to the rodents *Akodon longipilis*, *Rattus rattus*, *Spalacopus cyanus*, and to the lagomorph *Oryctolagus cuniculus*. Data based on Appendix 1 of Jaksic *et al.* (1981a: 27), on Yañez *et al.* (1982) and on Greene & Jaksic (unpublished). Higher values of the abundance rank (= AR, see Jaksic *et al.* 1981a: 27) indicate correspondingly higher densities of those small mammals in the field.

Species names of the predators are in Table 3.

Incidencia numérica (expresada en porcentaje) de distintas presas en la dieta de 12 predadores en Los Dominicos/La Dehesa, Chile. Nombres específicos de micromamíferos no mencionados ya en Tabla 1 corresponden a los roedores *Akodon longipilis*, *Rattus rattus*, *Spalacopus cyanus*, y al lagomorfo *Oryctolagus cuniculus*. Datos basados en Apéndice 1 de Jaksic *et al.* (1981a: 27), en Yañez *et al.* (1982) y en Greene & Jaksic (no publicado). Valores mayores del rango de abundancia (= AR, véase Jaksic *et al.* 1981a: 27) indican densidades mayores de los correspondientes micromamíferos en el terreno. Los nombres específicos de los predadores pueden consultarse en la Tabla 3.

Prey	Wt (g)	AR	Fsp	Mch	Ele	Pun	Bpo	Gme	Acu	Tal	Bvi	Dcu	Tpe	Pch
Mammalia														
<i>Abrocoma</i>	219	5	0.0	0.0	0.0	12.8	12.0	7.6	0.3	18.5	18.4	11.6	0.0	0.0
<i>Akodon l.</i>	76	1.5	0.0	0.0	10.0	1.2	0.0	0.0	0.7	4.8	16.7	0.0	0.0	0.0
<i>Akodon o.</i>	40	8	1.1	0.0	34.4	1.2	2.6	0.0	3.5	6.0	0.8	4.1	0.0	2.9
<i>Marmosa</i>	40	4	0.0	0.0	0.0	0.0	1.0	0.0	0.4	6.7	3.5	0.0	0.0	0.0
<i>Octodon</i>	230	10	1.8	0.0	8.6	64.5	57.6	57.7	3.2	12.0	0.0	41.2	0.0	0.0
<i>Oryctolagus</i>	1300	9	0.0	0.0	0.0	1.2	6.1	18.8	0.1	0.0	15.8	19.7	0.0	2.9
<i>Oryzomys</i>	45	6	2.4	0.1	37.1	0.0	1.8	0.6	2.8	16.4	4.4	0.0	0.0	0.0
<i>Phyllotis</i>	66	7	0.0	0.0	1.3	7.0	14.3	2.9	4.0	32.7	4.4	5.3	0.0	0.0
<i>Rattus</i>	158	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	19.3	0.0	0.0	0.0
<i>Spalacopus</i>	112	3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
Unidentified	—	—	5.8	1.4	6.6	5.1	1.0	7.1	1.6	0.7	5.3	7.8	0.0	5.7
Aves	—	—	12.7	0.7	2.0	1.8	3.3	1.2	1.0	2.0	11.4	5.6	0.0	8.6
Reptilia	—	—	9.3	1.9	0.0	5.2	0.3	4.1	tr*	0.0	0.0	4.7	72.7	45.6
Amphibia	—	—	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	27.3	34.3
Invertebrates	—	—	66.9	95.9	0.0	0.0	0.0	0.0	79.2	0.0	0.0	0.0	0.0	0.0
Total sample:			378	1068	151	172	391	164	3038	729	114	319	22	35

\* tr = < 0.1%.

dator species in the area capture small mammals about in proportion to their relative abundances in the field.

It is interesting to note that in spite of the high removal effected by the predators, *Octodon* maintains its high densities year after year (Le Boulengé & Fuentes 1978, Jaksic *et al.*, 1981b, Meserve *et al.* 1984). Apparently, the local predators are not capable of producing even local extinctions of *Octodon*. Removal trapping conducted in Los Dominicos (Jaksic & Yañez, unpublished data) indicates that immigration from peripheral habitat patches into the trapping plots is sufficiently high so as to compensate for intense artificial removal (from trapping), and therefore by analogy for natural mortality (from predation).

Apparently due to the high predation pressure it experiences, *Octodon* restricts its activities to the vicinity of potential protective cover or shelters (bushes, burrows, rock piles; see Woods & Boraker 1975, Fulk 1976, Glanz 1977a, Fig. 1 in Jaksic *et al.* 1979: 208, Meserve *et al.* 1984). Perhaps as a consequence, it effects an intense removal of the peripheral herbs on which it feeds (Fuentes & Le Boulengé 1977, Le Boulengé & Fuentes 1978). This removal in turn generates characteristic zones of bare ground around *Octodon* habitat or shelters (see photograph in Le Boulengé & Fuentes 1978: 339). Perhaps as a means of reducing predation risk, *Octodon* moves between neighboring cover or shelters minimizing the distance transited (and presumably the time spent) in

TABLE 3

Correlations (Spearman's Rho) between abundance of small mammals in the field, and their numerical incidence in the diet of nine local predators in Los Dominicos/La Dehesa, Chile. The snakes are not included in the table due to their low (*Philodryas chamissonis*) or null (*Tachymenis peruviana*) consumption of small mammals. The same applies to the falconiform *Milvago chimango*. Data based on Table 2 of Jaksic *et al.* (1981a: 24).

Correlaciones (Rho de Spearman) entre abundancia de micromamíferos en el terreno y su incidencia numérica en la dieta de nueve predadores locales en Los Dominicos/La Dehesa, Chile. Las serpientes no están incluidas en la Tabla debido a su bajo (*Philodryas chamissonis*) o nulo (*Tachymenis peruviana*) consumo de micromamíferos. Lo mismo ocurre con la falconiforme *Milvago chimango*. Datos basados en Tabla 2 de Jaksic *et al.* (1981a: 24).

Predators	Rho	P (bilateral)*
<b>Falconiformes</b>		
<i>Falco sparverius</i>	0.603	< 0.07
<i>Elanus leucurus</i>	0.318	> 0.34
<i>Parabuteo unicinctus</i>	0.600	< 0.07
<i>Buteo polyosoma</i>	0.761	< 0.03
<i>Geranoaetus melanoleucus</i>	0.858	< 0.01
<b>Strigiformes</b>		
<i>Athene cunicularia</i>	0.439	> 0.18
<i>Tyto alba</i>	0.312	> 0.34
<i>Bubo virginianus</i>	- 0.433	> 0.19
<b>Carnivora</b>		
<i>Dusicyon culpaeus</i>	0.833	< 0.02

\* Combining the probabilities of the nine independent statistics (Sokal & Rohlf 1981: 780) results in  $X^2 = 39.1$ , d.f. = 18, P (unilateral) < 0.005 for the joint correlation pattern.

\* Combinando las probabilidades de los nueve estadígrafos independientes (Sokal & Rohlf 1981: 780) resulta en  $X^2 = 39.1$ , g.l. = 18, P (unilateral) < 0.005 para el patrón de correlación conjunto.

open areas, and generating conspicuous, straightline surface runways (Fulk 1976, Yáñez & Jaksic 1978; also noticeable in Le Boulengé & Fuentes' photograph 1978: 339). Apparently, when the distance between two neighboring patches of habitat or shelters is too long, *Octodon* builds short, shallow underground tunnels for use as intermediate, temporary refuges (see sketches in Yáñez 1976, and further descriptions in Yáñez & Jaksic 1978).

Observations similar to those documented above for *Octodon* (in terms of restricted habitat use associated with predation) have been reported by Simonetti *et al.* (1985) for two montane rodents of central Chile, *Akodon andinus* and *Phyllotis xanthopygus* (*sensu* Walker *et al.* 1984 = *P. darwini vaccarum* in Honacki *et al.* 1982).

### Argentina

The Argentine studies I re-analyzed were conducted in Buenos Aires Province. Rood (1970) studied the ecology and behavior of

the rodents *Microcavia australis* (mean weight = 250 g) and *Galea musteloides* (mean weight = 220 g) in a desert scrub community at "La Cristina" Ranch. *Microcavia*, a diurnal folivore, was the most abundant species in the area (Table 4), and was subject to high predation pressure, judging from population losses recorded between consecutive trapping periods (Table 4). Rood documented that a population of *Microcavia* living in a scrub patch was completely eliminated by a pair plus offspring of grisons (*Galictis cuja*), but that about 1 km away another local population of *Microcavia* was thriving and may have been a source of immigrants. Similar to *Octodon* in Chile, *Microcavia* concentrates its activities near cover or shelters (mainly bushes), intensely removing the surrounding herbs, and thus generating zones of bare ground around those sites (see photographs in Rood 1970: 418 and 419). Also, *Microcavia* develops straightline runways between potential cover or shelters and excavates short, shallow tunnels (see figure in Rood 1970: 420).

TABLE 4

Density of *Microcavia australis* and *Galea musteloides* (individuals per hectare, including both adults and juveniles) in "La Cristina" Ranch, Argentina. Population losses of adult *Microcavia* are also reported, based on number present in previous trapping sessions. Data are from Tables 2 and 3 of Rood (1970: 424, 425). n/a = not applicable.

Densidad de *Microcavia australis* y *Galea musteloides* (individuos por hectárea, incluyendo adultos y juveniles) en hacienda "La Cristina", Argentina. También se presenta la pérdida poblacional de *Microcavia* adultos en relación al número presente en trampeos previos. Datos basados en Tablas 2 y 3 de Rood (1970: 424, 425). n/a = no aplicable.

	1966						1967		Mean
	Apr	May	Jul	Sep	Oct	Dec	Feb	Sep	
Total densities:									
<i>Galea</i>	4.4	5.0	3.9	4.4	5.6	3.3	0.0	0.0	3.3
<i>Microcavia</i>	24.4	25.6	22.2	33.3	25.6	25.6	8.3	1.1	20.8
Adult losses:									
Nr. <i>Microcavia</i> in previous trapping:	n/a	42	40	32	42	37	39	13	n/a
Numerical loss during period:	n/a	14	11	12	12	11	28	11	n/a
Percent loss during period:	n/a	33	28	38	29	30	72	85	n/a

Dalby (1975) conducted a population study of the small mammals present in a grassland in Balcarce area near Buenos Aires. He initially found that the most abundant rodent was *Akodon azarae*, with *Oryzomys nigripes* and *Oxymycterus rutilans* being much less abundant (Table 5). Later during the study, however, *Akodon* declined markedly in one population (starting with trapping session # 11 in April 1969; Dalby 1975: 171), concomitant with the invasion of the area by substantial numbers of cavies: *Cavia aperea*. In spite of his efforts to extirpate *Cavia* from the study plots, Dalby did not succeed; the immigration was so massive that he (Dalby 1975: 226) mentions having removed 110 cavies in 140 trapping days from an area of only 0.13 hectares! According to Dalby, *Cavia* (mean weight = 400 g), a diurnal folivore, destroyed the vegetation cover to such an extent as to render the habitat inadequate for the requirements of *Akodon*. The negative association of *Cavia* and *Akodon* is clearly reflected in the diet of the local predators (Table 6). In this case, similarly as in Chile, the predators tended to consume the small mammal populations in proportion to their respective abundance (Rho's in Table 6), and did not appear to

be capable of reducing those populations to any important extent, much less to the verge of extinction.

An interesting consequence of high predation upon *Cavia* can be inferred from a study by Crespo (1966) in a grassland of Partido de Rojas. According to him, the density of *Cavia aperea* (= *C. pamparum* in Crespo 1966) was sometimes so high that the local predators killed the cavies without even attempting to eat them (Crespo 1966: 125 and plate V-2). Similar to *Octodon* and *Microcavia*, *Cavia* restricts its activities close to potential cover or shelters (terrain taluses, vegetation clumps) and causes extensive modification of the surrounding vegetation (see plates IV-1 and V-1 in Crespo 1966 and plate 3-b in Dalby 1975). *Cavia* also builds short underground tunnels, surface galleries through dense vegetation, and surface runways (Crespo 1966, Dalby 1975).

Observations similar to those described above in terms of restricted habitat use and important habitat modification have been reported for the nocturnal folivore *Lagostomus maximus* (mean weight = 3,300 g), by Llanos and Crespo (1952) in Entre Ríos Province, and by Mares *et al.* (1981) in Salta Province.

TABLE 5

Density of rodents (individuals per hectare) in Balcarce, Argentina. Densities of *Akodon azarae*, *Oryzomys nigripes*, *Oxymycterus rutilans*, *Mus musculus*, *Calomys musculinus*, *Holochilus brasiliensis* and *Reithrodon auritus* (= *R. physodes*) are based on total daily captures (averaged on a monthly basis) documented in Table 40 of Dalby (1975: 219), including only data from "Plot I" (except for *Reithrodon*, based only on data from "Hill Plot"). *Cavia aperea* invaded the study area in May 1969

Densidad de roedores (individuos por hectárea) en Balcarce, Argentina. Densidades de *Akodon azarae*, *Oryzomys nigripes*, *Oxymycterus rutilans*, *Mus musculus*, *Calomys musculinus*, *Holochilus brasiliensis* y *Reithrodon auritus* (= *R. physodes*) están basadas en capturas totales diarias (promediadas para el mes) documentadas en Tabla 40 de Dalby (1975: 219), incluyendo sólo datos del "Plot I" (excepto para *Reithrodon*, basadas sólo en datos de "Hill Plot"). *Cavia aperea* invadió el área de estudio en mayo 1969.

Rodents: Weight (g):	Akodon 28.9	Oryzomys 19.4	Oxymycterus 84.3	Mus 13.8	Calomys 10.9	Holochilus 157.9	Reithrodon 71.3
Dec 68	45.8	0.8	2.5	0.0	1.7	0.8	0.0
Jan 69	79.2	1.7	3.3	0.0	0.8	0.0	0.0
Feb 69	100.8	0.8	3.3	1.7	0.0	0.8	0.0
Mar 69	115.0	10.0	0.8	2.5	0.8	8.3	0.0
Apr 69	114.2	14.2	0.8	5.8	1.7	4.2	0.0
May 69	81.7	32.5	0.8	7.5	5.0	5.0	0.0
Jun 69	87.5	15.8	0.8	3.3	2.5	8.3	0.0
Jul 69	80.0	25.0	2.5	1.7	1.7	5.8	0.0
Aug 69	87.5	7.5	4.2	0.8	0.0	2.5	0.0
Sep 69	55.0	1.7	4.2	0.8	0.0	0.8	0.8
Oct 69	65.0	1.7	5.0	0.0	0.0	0.0	0.0
Nov. 69	57.5	0.8	0.8	0.0	0.0	0.0	0.0
Dec 69	40.8	0.0	6.7	0.0	0.0	0.0	0.0
Jan 70	30.0	0.0	8.3	0.8	0.0	0.0	0.0
Feb 70	39.2	0.0	6.7	0.8	0.0	0.0	0.0
Mar 70	66.7	0.0	4.2	0.8	0.0	0.0	0.8
Apr 70	64.2	0.0	4.2	1.7	0.0	0.0	0.0
Mean:	71.2	6.6	3.5	1.7	0.8	2.1	0.1

*Uruguay*

Information from Uruguay is not as well documented as that from Chile and Argentina. I have based my conclusions only on the findings reported by Barlow (1969). According to Barlow (1969: 43) *Cavia pamparum* (= *C. aperea* in Honacki *et al.* 1982) is: "...the most abundant rodent in Uruguay. Cavies are often so abundant locally that they severely deplete herbs and other plants" and that: "*Cavia pamparum* [= *Cavia aperea*] does not excavate tunnels but builds galleries and interconnected surface runways..." and that: "...typically remains close to shelters of some kind..." Although I am not aware of the existence of quantitative data on the incidence of *Cavia* in the diet of Uruguayan predators (there are a few records in Aplin 1894, Barlow 1969, and Mones *et al.* 1973), it seems reasonable that predation is a likely

cause behind the activity pattern of this rodent.

*An attempt at validation*

Based on the evidence collected in Chile, Argentina, and Uruguay, it is logical to conclude that predation upon some folivorous small mammals results in the restriction of their activities to the vicinity of cover or shelters, in the generation of bare zones devoid of herbs around those sites, and in the making of underground tunnels and surface runways that connect neighboring sites. If this is a general pattern observable among the most preyed-upon small mammals, by symmetry it should be expected that the least preyed-upon folivores may behave differently in their use of habitat and in their effects on the vegetation. As a case study, in what follows, I shall report some findings that my co-

Ileagues and I have documented in central Chile.

The European rabbit, *Oryctolagus cuniculus*, a crepuscular folivore, was introduced in central Chile during the mid-1800's, but it did not become abundant until the 1960's, when it reached the status of an agricultural pest (Jaksic & Soriguer 1981, Jaksic & Ostfeld 1983). In contrast to *Octodon*, *Oryctolagus* is scarcely preyed upon, and then mostly on its juvenile cohorts (Table 7). Low predation on adult rabbits has been attributed to the lack of behavioral adaptation of native predators to hunt for this historically recent prey (Jaksic & Soriguer 1981), although the fact that adult rabbits (mean weight = 1,300 g) are among the largest mammal prey in central Chile may suggest an "escape in size". However, this does not explain why juvenile rabbits (mean weight = 300 g), although killed by native predators, are infrequent prey in comparison to the similarly-sized *Octodon degus* (Table

7). Simultaneous trapping with Tomahawk traps between May 1984 – May 1985 in Los Dominicos indicates an annual mean density of 7.2 degus/ha versus 2.8 juvenile rabbits/ha. Thus, the latter reach 39% of the abundance of the former, but the incidence of juvenile rabbits in the predators' diets averages only 18% of that of degus (Table 7). Apparently, size *per se* does not explain low predation on rabbits.

At any rate, the different predation pressure on these two small mammals is clearly reflected in their respective patterns of habitat use: whereas *Octodon* of all ages concentrate their activities close to shrubs, adult *Oryctolagus* are found in the open areas between shrubs (see Fig. 1 in Jaksic *et al.* 1979: 208). In Spain, the place of origin of the rabbits introduced in central Chile, *Oryctolagus* is strongly preyed-upon and behaves similar to *Octodon* in its use of cover and shelters (Jaksic & Soriguer 1981, Jaksic & Ostfeld 1983).

TABLE 6

Abundance in the field (individuals per hectare) and numerical incidence (expressed as percentage) of different rodents in the diet of three local predators in Balcarce, Argentina (only "Crovetto Pasture", which comprises "Plot I"). The densities of rodents during each of the three periods were calculated on the basis of data in Table 40 of Dalby (1975: 219). Dietary data were based on the analysis of 308 feces of the carnivore *Galictis cuja* and of the marsupial *Lutreolina crassicaudata*, and on 18 pellets of the strigiform *Asio flammeus*, as documented in Table 23 of Dalby (1975: 200). *Cavia aperea* invaded the study area in May 1969.

Abundancia en el terreno (individuos por hectárea) e incidencia numérica (expresada en porcentaje) de distintos roedores en la dieta de tres predadores locales en Balcarce, Argentina (sólo "Crovetto Pasture", que incluye "Plot I"). Las densidades de roedores en los tres períodos fueron calculadas en base a datos de la Tabla 40 de Dalby (1975: 219). Los datos dietarios basados en el análisis de 308 fecas del carnívoro *Galictis cuja* y del marsupial *Lutreolina crassicaudata*, y de 18 egagrópias de la strigiforme *Asio flammeus*, están documentados en Tabla 23 de Dalby (1975: 200). *Cavia aperea* invadió el área de estudio en mayo 1969.

	SUMMER		WINTER		SUMMER	
	Dec 68 – Apr 69		May 69 – Oct 69		Nov 69 – Apr 70	
	#/ha	% diet	#/ha	% diet	#/ha	% diet
<i>Akodon</i>	91.0	48.2	76.1	34.2	49.7	5.1
<i>Cavia</i>	0.0	0.0	>76.1 ?	47.8	>> 76.1?	89.7
<i>Oryzomys</i>	5.5	10.3	14.0	7.1	0.1	2.6
<i>Oxymycterus</i>	2.1	3.5	2.9	3.2	5.2	2.6
<i>Calomys</i>	1.0	34.5	1.5	5.8	0.0	0.0
<i>Reithrodon</i>	0.0	3.5	0.1	1.9	0.1	0.0
Total Sample	–	29	–	155	–	39
Rho	0.750		0.943		0.925	
P (bilateral)*	<0.20		<0.01		<0.02	

\* Combining the probabilities of the three independent statistics (Sokal & Rohlf 1981: 780) results in  $X^2 = 20.3$ , d.f. = 6, P (unilateral) < 0.005 for the joint correlation pattern.

\* Combinando las probabilidades de los tres estadígrafos independientes (Sokal & Rohlf 1981: 780) resulta en  $X^2 = 20.3$ , g.l. = 6, P (unilateral) < 0.005 para el patrón de correlación conjunto.

TABLE 7

Numerical incidence (expressed as percentage) of juvenile and adult *Oryctolagus*, in comparison to *Octodon*, in the diet of 13 common predators in shrublands of central Chile. Data based on Table 1 of Simonetti & Fuentes (1982: 56), except for predators' weights, which are based on data from Jaksic (unpublished).

Incidencia numérica (expresada en porcentaje) de *Oryctolagus* juveniles y adultos en comparación a *Octodon*, en la dieta de 13 predadores comunes en matorrales de Chile central. Datos basados en Tabla 1 de Simonetti & Fuentes (1982: 56), excepto por los pesos de los predadores, que están basados en datos de Jaksic (no publicados).

Predators	Weight (g)	<i>Oryctolagus</i>		<i>Octodon</i>	Other Verts	Inverts	Total Sample
		Juv	Adu	Juv+Adu			
<b>Falconiformes</b>							
<i>Falco sparverius</i>	116	0.0	0.0	1.6	35.7	62.7	442
<i>Milvago chimango</i>	296	0.0	0.0	0.0	11.8	88.2	374
<i>Elanus leucurus</i>	302	0.0	0.0	8.6	91.4	0.0	869
<i>Parabuteo unicinctus</i>	876	1.2	0.0	64.5	34.3	0.0	172
<i>Buteo polyosoma</i>	975	6.1	0.0	57.6	36.3	0.0	391
<i>Geranoaetus melanooleucus</i>	2,378	16.5	2.4	57.6	23.5	0.0	164
<b>Strigiformes</b>							
<i>Athene cunicularia</i>	247	0.1	0.0	3.2	17.5	79.2	3,038
<i>Tyto alba</i>	307	0.0	0.0	12.0	88.0	0.0	1,348
<i>Bubo virginianus</i>	1,227	9.7	6.1	0.0	84.2	0.0	114
<b>Carnivora</b>							
<i>Dusicyon griseus</i>	3,807	3.3	0.0	39.8	56.9	0.0	211
<i>Dusicyon culpaeus</i>	7,367	12.8	5.5	39.1	42.6	0.0	343
<b>Serpentes</b>							
<i>Tachymenis peruviana</i>	22	0.0	0.0	0.0	100.0	0.0	46
<i>Philodryas chamissonis</i>	96	2.7	0.0	8.1	89.2	0.0	37
Mean consumption/ predator:	—	4.0	1.1	22.5	54.7	17.7	—

It is interesting to note that in Chile juvenile *Oryctolagus*, which are more strongly preyed-upon than are adults, also restrict their activities to the vicinity of shrubs (see Fig. 1 in Simonetti & Fuentes 1982: 55). Consequently, juvenile *Oryctolagus* may contribute with *Octodon* to the generation of bare zones devoid of vegetation around shrubs, but adult *Oryctolagus* may have a less restricted effect by virtue of their broader spatial activity. This does not mean, however, that adult *Oryctolagus* do not affect the vegetation of the habitats they occupy. Using a methodology of experimental exclusions, Jaksic & Fuentes (1980) showed that the restricted distribution of native perennial herbs underneath bushes can be attributed to their extirpation from open areas by the foraging *Oryctolagus*. With the same methodology, Fuentes *et al.* (1983) also showed that *Oryctolagus* causes high mortality among shrub seedlings, and concluded that *Oryctolagus* may be halting the process of

secondary succession in central Chilean shrublands, causing them to become sparser in cover, and/or altering their composition with an increase of unpalatable (to the rabbits) shrub species.

This case study supports the conclusion that the different predation pressures experienced by small mammals directly affect their spatial activity patterns, and indirectly modulate their effects on the physiognomy and vegetational composition of the habitats they occupy. Although the information is scanty, some reports (e.g., Howard & Amaya 1975, Amaya & Bonino 1980, Jaksic & Yáñez 1983, Bonino & Amaya 1984) indicate that this conclusion also applies to *Oryctolagus* in Argentina.

#### CONCLUSIONS

The information available on small mammal predation in shrublands and grasslands of southern South America supports the

following generalizations (Table 8): 1) Predators seem to concentrate their hunting on the locally most abundant native rodents (e.g., *Octodon degus* in Chile; *Microcavia australis*, *Cavia aperea*, or *Akodon azarae* in Argentina; and *Cavia aperea* in Uruguay), consuming the remaining mammal species about in proportion to their relative abundance in the field, but sometimes "ignoring" dense populations of introduced lagomorphs (e.g., *Oryctolagus cuniculus* in Chile). 2) The most-preyed upon rodents tend to be of large size (> 200 g) and usually are folivores of diurnal habits. 3) Population levels of those rodents are sometimes reduced by predation, but predators do not seem capable of driving them to extinction, except in very small habitat patches, and perhaps only temporarily. 4) Predators seem effective, however, in restricting the spatial activity patterns of their main prey to the vicinity of potential cover or shelters (e.g., bushes, burrows, rock piles), which usually are interconnected by underground tunnels, surface galleries, and/or runways made by the rodents themselves. 5) Intensive removal of herbs effected by rodents foraging in

the periphery of their shelters generates characteristic zones of bare ground. 6) Low predation upon introduced lagomorphs in Chile (*Oryctolagus cuniculus*) results in the expansion of their habitat use, which affects the physiognomy and vegetational composition of the areas that they have invaded. 7) In general, the different predation pressures upon small mammals seem to affect directly their spatial activities, and indirectly their impact on the habitats they occupy.

#### A CRITIQUE AND SUGGESTIONS FOR FURTHER RESEARCH

I cautioned that this review was biased toward considering predation as a major selective agent for small mammals. I should like now to address some potential shortcomings of my analysis and explore some alternative hypotheses that may account for the reported patterns.

1) It is remarkable that the small mammals in which strong predation effects have been shown are not only predominantly large, diurnal, and folivorous, but also colonial and

TABLE 8

Ecological correlates of predation upon small mammals native to shrublands and grasslands of southern South America. See the text for discussion of the consequences of low predation pressure upon introduced small mammals.

Correlaciones ecológicas de la predación sobre micromamíferos nativos de matorrales y praderas del cono sur sudamericano. Véase el texto para discusión de las consecuencias de baja presión de predación sobre micromamíferos introducidos.

CARACTERISTICAS	CHILE	ARGENTINA	URUGUAY
Predation correlated with small mammal abundance?	positive	positive	unknown
Most abundant rodent (most preyed upon)?	<i>O. degus</i>	<i>M. australis</i> <i>C. aperea</i> *	<i>C. aperea</i>
Food habits?	folivorous	folivorous*	folivorous
Activity period?	diurnal	diurnal*	diurnal
Makes runways?	yes	yes*	yes
Builds underground tunnels and/or surface galleries?	yes	yes*	yes
Concentrates activity to vicinity of shelters?	yes	yes*	yes
Generates bare zones around shelters?	yes	yes*	yes

\* Apparently in detriment of *Akodon azarae*, which is omnivorous, active all day, uses runways and galleries made by other rodents, and concentrates its activities to zones of high herbaceous cover, but does not generate areas devoid of herbs.

\* Aparentemente en desmedro de *Akodon azarae*, quien es omnívoro, activo todo el día, usa corredores y galerías de otros roedores y concentra su actividad en zonas de alta cobertura herbácea, pero no genera áreas desnudas de hierbas.

hystricognathous. Whether high predation pressure favors colonial behavior (warning calls against predators have been described for *Octodon degus*, see Fulk 1976), and/or colonial species attract predators (because they represent concentrated, conspicuous sources of food) cannot be determined. However, hystricognaths are generally larger than the native cricetids, tend to be more colonial and social, and have been present much longer in South America (Eisenberg 1981). Perhaps the observed patterns apply only to small mammal assemblages with hystricognaths present, and not to other small mammal-predator systems. However, the fact that similar observations of restricted small mammal spatial activity, and bare zones devoid of herbs and grass have also been made in California (Bartholomew 1970), where hystricognath rodents are not present, suggest the generality of the observations reported here.

2) Alternatively, the bare zones devoid of herbaceous plants around shrubs may have nothing to do with grazing by small mammals but rather with the effect of shrub allelochemicals (allelotoxins) on herbs (Mueller *et al.* 1968). However, this was not the case in the California chaparral, as shown by Bartholomew (1970), and Chilean shrubs have been shown not to affect surrounding herbs via allelopathy (Montenegro *et al.* 1978). To clarify further this aspect, experimental studies similar to Bartholomew's (1970) would be welcome in this and other South American shrublands and grasslands.

3) Construction of burrows and galleries may not be entirely in response to predators, but also to thermoregulatory constraints of the small mammals themselves. For example, *Octodon degus* has been shown to be stenothermic and to have little tolerance to high temperatures (Rosenmann 1977). However, if temperature is a limiting factor, it is surprising that *O. degus* is not nocturnal. The presence of territoriality and/or coloniality also confounds the adaptive value of excavating behavior. I was not implying that burrows and galleries only served the purpose of reducing predation risk; perhaps several needs are met with this behavior.

This summary of the ecological correlates and presumable consequences of predation upon small mammals in southern

South America does not mean that the underlying mechanism (predation as a major selective force) has been unequivocally demonstrated. Rather, I propose a plausible working hypothesis that may help orient further research on the topic. In this light, more studies are needed in which populations levels of small mammals are assessed simultaneously with the food habits of sympatric predators. Are large, diurnal, folivorous, colonial, hystricognathous rodents, always the main prey base? What happens in places where these rodents are absent (e.g., temperate rain forests)? How universal is the generalization that sympatric predators feed on different prey species about in proportion to their respective abundance in the field? If my inferences are correct, predation studies on different small mammal prey bases (e.g., small, nocturnal, granivorous, solitary, and/or cricetid rodents) should still have predictable results, perhaps based again on relative abundance.

Predation studies in South America are still in the descriptive stage, and field experiments may have to wait until enough case studies accumulate. When this new phase is reached, perhaps more meaningful comparisons will be made, and an evaluation of the importance of specific mechanisms underlying observed community patterns will become possible.

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