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Oikos, Vol. 74, No. 2. (Nov., 1995), pp. 259-264.

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Lagos, V. O., Contreras, L. C., Meserve, P. L., Gutiérrez, J. R. and Jaksic, F. M. 1995. Effects of predation risk on space use by small mammals: a field experiment with a Neotropical rodent. – *Oikos* 74: 259–264

Predation is often implicated as the most important factor determining differential microhabitat use by small mammals, particularly in desert ecosystems. This generalization, however, is based primarily on observational and correlational approaches and only a few field experimental studies. In a large-scale, long-term experimental manipulation of predators in semiarid north-central Chile, we studied the effects of excluding vertebrate predators on the space use of a small mammal species. We used three different techniques to determine space use under and away from shrubs by the diurnal, herbivorous rodent *Octodon degus*. These included smoked tiles, fluorescent pigment tracking, and tabulation of numbers of runways among shrubs. Results show that *O. degus* used spaces away from shrubs more often, made more (and less straight) runways between shrubs and had smaller daily home ranges in grids where predators were excluded. Thus, besides the well known predator effects of density depression and survival reduction of their prey, our study demonstrates experimentally that prey respond behaviorally to perceived predation risks.

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There is considerable empirical support indicating that small mammals preferentially use certain microhabitats, especially in desert ecosystems (e.g., Rosenzweig 1973, Price 1978, Thompson 1982, Kotler and Brown 1988). However, the presumable causes of differential space use have only recently been studied (Schroder 1987 and references therein, Brown 1992, Brown et al. 1992, Cassini and Galante 1992, Kotler et al. 1992). Hypotheses explaining how this phenomenon may have evolved consider factors such as predation risk, food distribution, vegetation structure, body size, and locomotion mode (Reichman and Oberstein 1977, Price 1983, Kotler 1984, Kotler and Brown 1988, Simonetti 1989, Desy et al. 1990, Longland and Price 1991, Brown 1992). Of these, predation has been suggested as the major factor influen-

cing space use, yet relatively few experimental studies have been conducted in the field to evaluate its effect (Sih et al. 1985).

Predation may influence population abundance and age/size structure by removing individual prey and/or by affecting prey behavior (Brown et al. 1988, Kotler et al. 1991, 1992, Brown 1992). Behavioral responses of prey include different spatial and temporal use of microhabitats, to reduce predation risk and/or maximize the difference between benefits and costs associated with the use of available patches (Lima et al. 1985, Brown et al. 1988, Kotler et al. 1992). Studies of predation effects on small mammals have ranged from correlational approaches relating changes in predator and prey numbers (e.g., Pearson 1964, Fitzgerald 1977, Erlinge et al. 1983, Pech et al.

Accepted 3 April 1995

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ISSN 0030-1299

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1992) to experiments in small aviaries or enclosures controlling factors such as light intensity, vegetation cover, food distribution, prey size, and prey density (Kotler 1984, Podolsky and Price 1990, Brillhart and Kaufman 1991, Kotler et al. 1991). Other studies have assessed the behavioral responses of small mammals to introduced predators in enclosures (Brown et al. 1988, Kotler et al. 1988). Few studies have evaluated the effect of predation on prey behavior by excluding predators under natural conditions (Desy and Batzli 1989, Newsome et al. 1989, Desy et al. 1990), and none has assessed its effect on prey microhabitat use under these conditions.

In arid mediterranean ecosystems of central Chile, the landscape is composed of a mosaic of patches of evergreen shrubs structurally varied at a broad spatial scale (Fuentes et al. 1984). In this type of environment, small mammals may potentially specialize in the use of different microhabitats (e.g., underneath or away from shrubs), thus enabling their coexistence by avoiding direct interference. However, except for the herbivorous subterranean rodent *Spalacopus cyanus* (Contreras et al. 1993), there are no native small mammals specialized in the use of open habitats. The activity of most species occurs mainly underneath shrub canopies and near potential shelters, such as crevices and burrows (Glanz 1977, Meserve 1981, Jaksic 1986). Studies of factors determining the differential use of microhabitats in this geographic area have been mostly descriptive and inferential (see review of Jaksic and Simonetti 1987). Nevertheless, all of them attribute an important role of predation.

Octodon degu (Octodontidae), henceforth degu, is one of the most conspicuous and common components of small mammal assemblages in mediterranean Chile, and has been well studied (e.g., Woods and Boraker 1975, Meserve et al. 1984). The degu is a 184 ± 9 g (SD) diurnal herbivorous rodent, that builds burrows in shrubby patches and generates conspicuous runways by frequently moving between neighboring shrubs (Yañez and Jaksic 1978). The intensive use of spaces under and around shrubs by degu has been determined by direct observation as well as by noting their foraging effect on annual vegetation around shrubs (Yañez and Jaksic 1978, Jaksic 1986). The degu is among the most common prey items in the diets of local predators in this ecosystem (Jaksic et al. 1981, 1993, Jaksic 1986). In apparent response to predation risk the degu constrains its activities close to potential shelters, and moves quickly between neighboring shrubs in straight lines in an apparent effort to minimize transit distance and time spent in open areas (Yañez and Jaksic 1978, Jaksic 1986).

The aim of this paper is to investigate in further detail the effects of predation on microhabitat use by degu, using three different techniques to quantify spatial use in two field experimental conditions: large experimental enclosures with and without predators. If predation is an important factor influencing restricted space use by degu, then we should observe a number of interrelated effects, including changes in microhabitat use, in daily

home ranges, and in number and geometry of degu runways as responses to the absence of predation.

Methods

Study site

The study area is located in Fray Jorge National Park ($30^{\circ}38'S$, $71^{\circ}40'W$), 400 km north of Santiago, Chile. The park is near the Pacific coastline, and comprises 10 000 ha of arid mediterranean thorn-scrub vegetation, and some remnants of fog forest at higher elevations along the coastal range (Meserve and Le Boulengé 1987). Mean annual precipitation is 85 mm, and occurs mostly (90%) during the austral winter (May-September). Summer is warm and dry, although frequent fog contributes to high relative humidity. Work took place from June 1991 to May 1992 in "Quebrada de las Vacas", a broad valley with relatively homogenous vegetation, dominated by drought-deciduous and evergreen shrubs including *Porlieria chilensis*, *Adesmia bedwellii*, and *Proustia pungens* (Gutiérrez et al. 1993). Besides degus, the small mammal assemblage included the sigmodontine rodents *Abrothrix olivaceus* (olivaceous field mouse), *Abrothrix longipilis* (long-haired field mouse), and *Phyllotis darwini* (leaf-eared mouse). Other species such as *Oligoryzomys longicaudatus* (long-tailed rice rat), *Octodon lunatus* (coastal degu), *Abrocoma bennetti* (chinchilla rat), *Chelemys megalonyx* (mole-mouse), and *Thylamys elegans* (mouse opossum) were rare and/or highly localized (Meserve and Le Boulengé 1987). The commonest predators were the culpeo fox *Pseudalopex culpaeus* and the owls *Athene cunicularia*, *Bubo virginianus* and *Tyto alba* (Jaksic et al. 1993).

Experimental design

This work is part of a large scale long-term experimental study to evaluate the role of biotic interactions, including predation, competition, and herbivory in this ecosystem (for further details see Meserve et al. 1993a). Four 75×75 m (0.56 ha) experimental grids allowing access to all small mammals and predators served as controls; they were surrounded by 1.0 m high chicken wire fencing, of which 40 cm was buried in the ground and with enlargements of 2.5 cm mesh cut in the chicken wire (yielding an approximately 5 cm diameter hole) at ground level every 2 m (total = 159 five-cm holes for each grid). The five-cm diameter holes in the fencing allowed free movement of degu through the holes at ground level in both treatments (see following). Foxes were able to jump the short fencing, and were regularly seen inside the control grids. Four other experimental grids of equal dimensions allowed access to all small mammals but excluded foxes and raptors by using high (1.8 m high) fencing buried 40 cm and a ca 10-cm diameter mesh polyethylene netting sus-

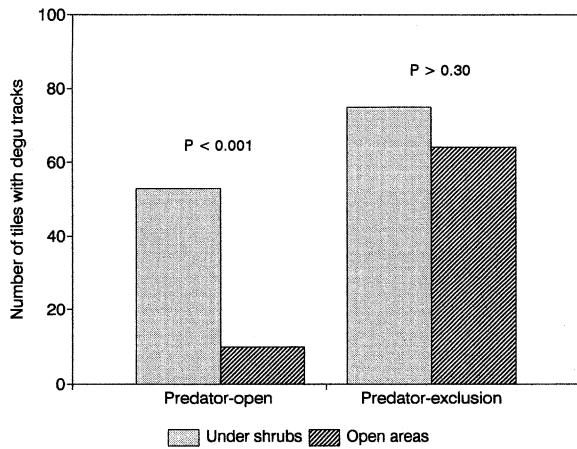


Fig. 1. Number of smoked tiles underneath shrubs and in open areas, with tracks of *Octodon degus* in predator-open (control) and predator-exclusion grids. P's are probability values of X^2 goodness-of-fit tests.

pended overhead. Experimental and control grids were randomly distributed in a ca 50-ha area, separated by about 200 m from each other (Meserve et al. 1993a).

Shrub cover and distances between shrubs were measured in all grids to assess possible differences among them. Shrub cover was estimated by the point-intercept method (Mueller-Dombois and Ellenberg 1974) along four parallel lines spaced 15 m apart in each grid. Distance between shrubs was measured along the same parallel lines.

Three techniques were used to evaluate space use by degus in grids with and without predators. (a) The frequency of space use underneath and away from shrubs was estimated by recording the presence of degu tracks on smoked tiles (Justice 1961). Formica tiles 25 × 25 cm in size were smoked on the glossy side, and placed in three pairs of grids with and without predators for two days/month from June 1991 to May 1992. Five stations were permanently positioned about 20 m apart along a diagonal line connecting two opposing corners of each grid. Each station had two tiles, one under and one away from a shrub, yielding a total of 60 tile-days/month under (30) and away from (30) shrubs in each treatment (with and without predators). A total of 720 tile-days underneath (360) and away from (360) shrubs were examined for each treatment during the study period. Tiles away from shrubs were located midway between a shrub with a smoked tile and the nearest neighboring shrub. The distance from the canopy's edge to these tiles varied from 0.5 to 1.4 m ($\bar{X} = 0.9 \pm 0.2$ SD). Tiles were checked twice daily for tracks, in early morning and late afternoon, and all results pooled because there were no differences between periods. Tiles with tracks were replaced with new smoked tiles during each inspection. If degus reduce predation risk by staying under or close to shelters, we expected that in predator-exclusion grids there would be

relatively more tracks in tiles placed in open spaces than in predator-open grids.

(b) From May 1991 to June 1992, 48 different adult degus (> 90 g) were live-trapped early in the evening, marked with differently colored fluorescent pigment the following morning from 08.00 to 11.00, and then released in the same spots where they had been captured. Two h after dusk of the same day, trails left by marked individuals were recorded by activating fluorescent pigments with a U.V. lamp (Lemen and Freeman 1985, McShea and Gilles 1992). For each animal, the number and length of segments traversed along trails in the open was recorded. The sum of these segments yielded the total length of trails traversed in the open. Trails with total lengths less than 1.5 m were omitted from analysis. The daily home range of degus was estimated as a circle with a radius equal to the mean length of eight trails from the release points to the farthest points with detectable pigments. To estimate how straight the trails were connecting shrubs, the number of turns with angles less than 135° was counted, and standardized by the total length of trails between shrubs. If degus minimized the time spent in the open we expected to find straighter trails in predator-open grids.

(c) Because of frequent movement among shrubs, degus generate conspicuous runways on the annual herbaceous layer that extends among shrubs (Yañez and Jakšic 1978). They are the only small mammals in the area known to generate and use these runways. Fifteen shrub patches were randomly chosen in three grids each with and without predators, and the number and length of runways exceeding 1-m long were recorded. Because runways were less clearly distinguishable during the period of annual vegetative growth, runways were measured before and after that period (i.e., in May and December 1991). If predation is a significant factor reducing the use of open spaces by degus we expected shorter runways in predator-open grids and/or longer runways in predator-exclusion grids.

Degu tracks on smoked tiles and number of degu runways were absolute frequencies and were thus analyzed with X^2 tests (Steel and Torrie 1980). The results of fluorescent tracking were expressed as meters traversed, and were thus analyzed with Mann-Whitney tests (SAS 1985).

Results

We found no significant difference in shrub cover ($F_{1,6} = 0.01$, $P > 0.99$), or in distances between shrubs ($F_{1,22} = 0.75$, $P > 0.39$) among grids with and without predators. During the study period densities of degu were $10.5/\text{ha} \pm 1.2$ SD ($n = 12$ months) in predator-exclusion grids and 5.0 ± 1.2 (12) in predator-open grids.

Results obtained with smoked tiles showed that degus used spaces underneath shrubs more frequently in those

Table 1. Mean, standard deviation, range, and sample size of daily home range in m², number of trails between shrubs, total length of trails between shrubs in m, and number of turns on trails between shrubs standardized by length of trails, for *Octodon degus*.

Treatments	Activ. range	No. trails	Length trails	No. turns
With predators ($\bar{X}\pm SD$)	369±148	9.8±3.3	24.8±9.7	0.14±0.06
Range (n)	70-748 (20)	8-26 (17)	11.9-50.4 (20)	0.08-0.25 (20)
Without predators ($\bar{X}\pm SD$)	163±102	11.1±4.9	25.5±8.3	0.30±0.09
Range (n)	26-599 (25)	2-25 (25)	2.7-70.3 (28)	0.16-0.88 (28)
Mann Whitney z	-3.42	1.23	-0.11	-3.30
P	0.0006	0.2206	0.9121	0.0007

grids with predators ($X^2 = 30.8$, $P < 0.001$, Fig. 1). In contrast, in grids without predators, there was no significant difference between use of these two microhabitats ($X^2 = 0.97$, $P > 0.30$, Fig. 1). Therefore, where predators were absent, degus expanded their activity to open microhabitats.

Fluorescent tracking results showed that the number of trails among shrubs and their total length did not differ significantly between grids with and without predators (Table 1). Degus, however, had significantly smaller daily home ranges in predator-exclusion than in predator-open grids (Table 1). These results indicate that in grids without predators, degus traveled more frequently in the open, but concurrently contracted their spatial home range. The number of turns relative to the total length of trails was significantly higher in predator-exclusion grids (Table 1). Thus, trails were straighter in grids with predators than in those without.

The total number of runways longer than 1-m was not significantly different between grids with and without predators ($X^2 = 0.96$, $P > 0.30$, Fig. 2). However, short runways (1–2 m) were significantly more frequent in grids with predators, whereas longer runways were sig-

nificantly more frequent in grids without predators (Fig. 2).

Discussion

Our results are consistent with previous reports that degus use space under shrubs more frequently than space away from them (Jaksic 1986). They also demonstrate that in experimental exclusions of predators, degus increase their use of open spaces. Further, in these predator-exclusion grids degus generate longer and more winding runways between shrubs, thus indicating that they move through open spaces more freely.

Empirical and theoretical studies conducted in the Northern Hemisphere point out that small mammals perceive microhabitats underneath and away from shrub canopies as qualitatively different with regard to predation risks (Longland and Price 1991, Brown 1992, Kotler et al. 1992). Our experimental results support the hypothesis that predation is an important factor influencing space use by at least one Southern Hemisphere rodent. Perceived risk of predation may promote changes in microhabitat use. A selective mechanism that may apply in this case is the field-experimental demonstration in the same study site, that predation reduces the survival and density of degus (Meserve et al. 1993b).

Although there is a lack of quantitative information relating predation intensity to activity area in small mammals, it might be expected that predators restrict the prey's daily home range (Peterson and Batzli 1975, Kaufman and Kaufman 1982, Desy et al. 1990). Our results were counter to this expectation, but may be explained by patch use theory, which predicts that under predation, small mammals deplete their food sources less thoroughly and thus need more area to obtain sufficient food (Morris 1987, Rosenzweig 1989). Small mammals freed from predation may thus concentrate in smaller, food-rich patches, and exploit them more thoroughly.

The most obvious effect of predation on small mammals should be a depression in their densities and survival. In a parallel study at the same site, Meserve et al. (1993b) showed that both effects were detected on degus subjected to the same treatments used here. During this study, degu densities in predator-exclusion grids were

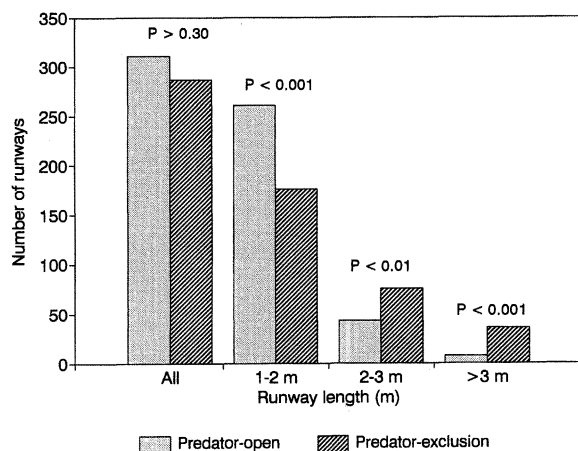


Fig. 2. Number of runways (and their length) generated by *Octodon degus* traffic between shrubs in predator-open (control) and predator-exclusion grids. P's are probability values of X^2 goodness-of-fit tests.

twice (10 vs 5/ha) those in predator-open grids. The major contribution of this study is to demonstrate a third, behavioral effect of predation. Degus released from predators use non-sheltered patches more thoroughly than their conspecifics subjected to predation risk. Whether predation alone, or increased density brought about by lack of predation, are the ultimate factors explaining our findings, we cannot tell. There is not enough variance among our four experimental treatments and four controls to test for the separate effect of lack of predation or of increased degu abundance. What is clear, however, is that predation directly (perceived risk) or indirectly (increased density) affects patch use by degus.

The behavioral effect documented here may be pervasive among other small mammals, but it has not received much attention. Perhaps even a low predation risk may be enough to alter small mammals' assessment of habitat quality and resource heterogeneity, and thus, their patterns of microhabitat use.

Acknowledgements. – We appreciate the comments and field assistance of S. Herrera, B. Milstead, V. Valverde, S. Silva, and H. Vasquez. A. Levican and M. A. Vergara helped with the field work. Special recognition goes to F. Bozinovic for his role as Lagos' co-advisor during his M.Sc. thesis (Universidad de Chile). CONAF-IV Region provided authorization and facilities to work in Fray Jorge National Park. This study was supported by grants FONDECYT 90-0930, 193-1150, DIULS 120-2-33, and BSR 90-20047. Joel S. Brown made cogent criticisms that helped improve our presentation of results.

References

- Brillhart, D. B. and Kaufman, D. W. 1991. Influence of illumination and surface structure on space use by prairie deer mice (*Peromyscus maniculatus bairdi*). – *J. Mammal.* 72: 764-768.
- Brown, J. S. 1992. Patch use under predation risk: I. Models and predictions. – *Ann. Zool. Fenn.* 29: 301-309.
- , Kotler, B. P., Smith, R. J. and Wirtz II, W. O. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. – *Oecologia* 76: 408-415.
- , Morgan, R. A. and Dow, B. D. 1992. Path use under predation risk: II. A test with fox squirrels, *Sciurus niger*. – *Ann. Zool. Fenn.* 29: 311-318.
- Cassini, M. H. and Galante, M. L. 1992. Foraging under predation risk in the wild guinea pig: The effect of vegetation height on habitat utilization. – *Ann. Zool. Fenn.* 29: 285-290.
- Contreras, L. C., Gutiérrez, J. R., Valverde, V. and Cox, G. W. 1993. Ecological relevance of subterranean herbivorous rodents in arid coastal Chile. – *Rev. Chil. Hist. Nat.* 66: 357-368.
- Desy, E. A. and Batzli, G. O. 1989. Effect of food availability and predation on prairie vole demography: a field experiment. – *Ecology* 70: 411-421.
- , Batzli, G. O. and Liu, J. 1990. Effects of food and predation on behavior of prairie voles: a field experiment. – *Oikos* 58: 159-168.
- Erlinge, S., Göransson, G., Hansson, L., Högstedt, G., Liberg, O., Nilsson, I.N., von Schantz, T. and Silvé, M. 1983. Predation as a regulating factor on small rodent populations in southern Sweden. – *Oikos* 40: 36-52.
- Fitzgerald, B. M. 1977. Weasel predation on a cyclic population of the montane vole (*Microtus montanus*) in California. – *J. Anim. Ecol.* 46: 367-397.
- Fuentes, E. R., Otaíza, R. D., Alliende, M. C., Hoffmann, A. and Poiani, A. 1984. Shrub clumps of the Chilean matorral vegetation: structure and possible maintenance mechanisms. – *Oecologia* 62: 405-411.
- Glanz, W. E. 1977. Comparative ecology of small mammal communities in California and Chile. – Ph.D. dissertation, Univ. of California, Berkeley.
- Gutiérrez, J. R., Meserve, P. L., Jaksic, F. M., Contreras, L. C., Herrera, S. and Vásquez, H. 1993. Structure and dynamics of vegetation in a Chilean arid thorn scrub community. – *Acta Oecol.* 14: 271-285.
- Jaksic, F. M. 1986. Predation upon small mammals in shrublands and grasslands of southern South America: ecological correlates and presumable consequences. – *Rev. Chil. Hist. Nat.* 59: 209-221.
- and Simonetti, J. 1987. Predator/prey relationships among terrestrial vertebrates: an exhaustive review of studies conducted in southern South America. – *Rev. Chil. Hist. Nat.* 60: 221-244.
- , Greene, H. W. and Yañez, J. L. 1981. Guild structure of a community of predatory vertebrates in central Chile. – *Oecologia* 49: 21-28.
- , Meserve, P. L., Gutiérrez, J. R. and Tabilo, E. 1993. The components of predation on small mammals in semiarid Chile: preliminary results. – *Rev. Chil. Hist. Nat.* 66: 305-321.
- Justice, K. E. 1961. A new method for measuring home ranges of small mammals. – *J. Mammal.* 42: 462-470.
- Kaufman, D. W. and Kaufman, G. A. 1982. Effect of moonlight on activity and microhabitat use by Ord's kangaroo rat (*Dipodomys ordii*). – *J. Mammal.* 63: 309-312.
- Kotler, B. P. 1984. Risk of predation and the structure of desert rodent communities. – *Ecology* 65: 689-701.
- and Brown, J. S. 1988. Environmental heterogeneity and the coexistence of desert rodents. – *Annu. Rev. Ecol. Syst.* 19: 281-307.
- , Brown, J. S., Smith, R. J. and Wirtz II, W. O. 1988. The effects of morphology and body size on rates of owl predation on desert rodents. – *Oikos* 53: 145-152.
- , Brown, J. S. and Hasson, O. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. – *Ecology* 72: 2249-2260.
- , Blaustein, L. and Brown, J. S. 1992. Predation facilitation: The combined effect of snakes and owls on the foraging behavior of gerbils. – *Ann. Zool. Fenn.* 29: 199-206.
- Lemen, C. A. and Freeman, P. W. 1985. Tracking mammals with fluorescent pigments: a new technique. – *J. Mammal.* 66: 134-136.
- Lima, S. L., Valone, T. J. and Caraco, T. 1985. Foraging efficiency-predation risk tradeoff in the gray squirrel. – *Anim. Behav.* 33: 115-165.
- Longland, W. S. and Price, M. V. 1991. Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? – *Ecology* 72: 2261-2273.
- McShea, W. J. and Gilles, A. B. 1992. A comparison of traps and fluorescent powder to describe foraging for mast by *Peromyscus leucopus*. – *J. Mammal.* 73: 218-222.
- Meserve, P. L. 1981. Resource partitioning in a Chilean semiarid small mammal community. – *J. Anim. Ecol.* 50: 745-757.
- and Le Boulengé, E. 1987. Population dynamics and ecology of small mammals in the northern Chilean semiarid region. – *Fieldiana Zool.* 39: 413-431.
- , Martin, R. E. and Rodríguez, J. 1984. Comparative ecology of the caviomorph rodent *Octodon degus* in two Chilean mediterranean-type communities. – *Rev. Chil. Hist. Nat.* 57: 79-89.
- , Gutiérrez, J. R., Contreras, L. C. and Jaksic, F. M. 1993a. Role of biotic interactions in a semiarid scrub community in northcentral Chile. – *Rev. Chil. Hist. Nat.* 66: 225-241.
- , Gutiérrez, J. R. and Jaksic, F. M. 1993b. Effects of ver-

- tebrate predation on a caviomorph rodent (*Octodon degus*), in a semiarid thorn scrub community in Chile. – *Oecologia* 94: 153–158.
- Morris, D. W. 1987. Ecological scale and habitat use. – *Ecology* 68: 362–369.
- Mueller-Dombois, D. and Ellenberg, H. 1974. Aims and methods of vegetation ecology. – Wiley, New York.
- Newsome, A. E., Parer, I. and Catling, P. C. 1989. Prolonged prey suppression by carnivore-predator-removal experiments. – *Oecologia* 78: 458–467.
- Pearson, O. P. 1964. Carnivore-mouse predation: an example of its intensity and bioenergetics. – *J. Mammal.* 45: 177–188.
- Pech, R. P., Sinclair, A. R. E., Newsome, A. E. and Catling, P. C. 1992. Limits to predator regulation of rabbits in Australia: Evidence from predator-removal experiments. – *Oecologia* 89: 102–112.
- Peterson, R. M. and Batzli, G. O. 1975. Activity patterns in natural population of the brown lemming (*Lemus trimocronatus*). – *J. Mammal.* 56: 718–720.
- Podolsky, R. H. and Price, M. V. 1990. Patch use by *Dipodomys deserti* (Rodentia: Heteromyidae): profitability, preference, and depleting dynamics. – *Oecologia* 83: 83–90.
- Price, M. V. 1978. The role of microhabitat in structuring desert rodent communities. – *Ecology* 59: 910–921.
- 1983. Ecological consequences of body size: a model for patch choice in desert rodents. – *Oecologia* 59: 384–392.
- Reichman, O. J. and Oberstein, D. 1977. Selection of seed distribution types by *Dipodomys merriami* and *Perognathus amplus*. – *Ecology* 58: 636–643.
- Rosenzweig, M. L. 1973. Habitat selection experiments with a pair of coexisting heteromyid species. – *Ecology* 54: 111–117.
- 1989. Habitat selection, community organization, and small mammal studies. – In: Morris, D. W., Abramsky, Z., Fox, B. J. and Willig, M. R. (eds), *Patterns in the mammalian communities*. Texas Tech Univ. Press, Lubbock, TX, pp. 5–21.
- SAS. 1985. Introductory guide for personal computers, Version 6. – SAS Institute Inc., Cary, NC.
- Schroder, G. D. 1987. Mechanisms for coexistence among three species of *Dipodomys*: habitat selection and an alternative. – *Ecology* 68: 1071–1083.
- Sih, A., Crowley, P., McPeck, M., Petranka, J. and Strohmeier, K. 1985. Predation, competition, and prey communities: a review of field experiments. – *Annu. Rev. Ecol. Syst.* 16: 269–311.
- Simonetti, J. A. 1989. Microhabitat use by small mammals in central Chile. – *Oikos* 56: 309–318.
- Steel, R. G. D. and Torrie, J. H. 1980. Principles and procedures of statistics. A biometrical approach. 2nd. ed. – McGraw-Hill, New York.
- Thompson, S. D. 1982. Microhabitat utilization and foraging behavior of bipedal and quadrupedal heteromyid rodents. – *Ecology* 63: 1303–1312.
- Woods, C. A. and Boraker, D. K. 1975. *Octodon degus*. – *Mamm. Species* 67: 1–5.
- Yañez, J. L. and Jaksic, F. M. 1978. Historia natural de *Octodon degus* (Molina) (Rodentia, Octodontidae). – *Publ. Ocas. Mus. Nac. Hist. Nat. (Chile)* 27: 1–11.