SPATIOTEMPORAL PATTERNS OF AN IRRUPTION AND DECLINE OF SMALL MAMMALS IN NORTHCENTRAL CHILE

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During the austral winter of 1987 (June–August) at a semi-arid site in northcentral Chile, an outbreak of small mammals apparently was triggered by one episode of unusually high rainfall. From October 1987 to November 1990, we monitored the outbreak on a monthly basis on two equatorial- and two polar-facing slopes. Overall density on equatorial-facing slopes was 239 individuals/ha in spring 1987, increasing to a peak of 404/ha by summer 1988, and then steadily declining to a crash of 20/ha (5% of peak density) by spring 1990, with no signs of recovery. On polar-facing slopes, mammalian abundances were about one-half those of equatorial-facing slopes. There were 112 individuals/ha in spring 1987, increasing to a peak of 199/ha by summer 1988, and then steadily declining to a crash of 8/ha (4% of peak density) by spring 1989. Since then, mammal populations on polar-facing slopes have been slowly recovering, reaching 11% of their peak density by November 1990. Of the eight species monitored, only three irrupted: the granivorous cricetid *Phyllotis darwini*, the omnivorous cricetid *Akodon olivaceus*, and the insectivorous didelphid *Marmosa elegans*. These three irrupted and declined in phase, simultaneously on the two opposite-facing slopes, such that their relative frequencies did not shift markedly. Two of the three folivores (*Abrocoma bennettii, Octodon degus,* but not *Chinchilla lanigera*), one granivore (*Oryzomys longicaudatus*), and one insectivore (*Akodon longipilis*) disappeared from the site, persisting longer on equatorial-facing slopes.

Key words: spatiotemporal patterns, population density, Chile, Rodentia, *Marmosa*

Outbreaks of small mammals frequently have been reported in semi-arid regions of western South America (Hershkovitz, 1962). Pearson (1975), for example, documented a 1972–1973 outbreak in coastal Peru to which the cricetid *Phyllotis darwini* was the chief contributor. Fulk (1975), Glanz (1977), and Péfaur et al. (1979) reported on the 1972–1973 outbreak in northcentral Chile, where the cricetid *Oryzomys longicaudatus* irrupted in agricultural landscapes and where both *P. darwini* (the main component) and the cricetid *Akodon olivaceus* irrupted in arid native habitats. These studies were short-term; little is known about population trajectories of the mammals involved either before or after their peak abundance. One exception is the work of Meserve (Meserve, 1981*b*; Meserve and Le Boulengé, 1987). Between November 1973 and January 1975 he monitored the aftermath of the outbreak reported by Fulk (1975) in Fray Jorge National Park, Chile.

All authors concur that these mammal outbreaks are triggered by unusually high rainfall and subsequent pulses in plant

growth. Pearson (1975) showed that the Peruvian outbreak was associated with an unusual rainfall of 81 mm in a locality characterized by a mean annual rainfall of 32 mm. He hypothesized, though, that two consecutive years of high winter rainfall seemed necessary to actually trigger the outbreak. Péfaur et al. (1979) showed that 1972 was the wettest year in a series of 6 (1970–1975), but also implied that 2 consecutive years of heavy rainfall were necessary to produce an outbreak. Meserve and Le Boulengé (1987) reported that annual precipitation in Fray Jorge National Park averaged 69 mm between 1969 and 1976, but reached 255 mm during the peak outbreak year of 1972. They did not mention whether this precipitation was preceded by a higher-than-average rainfall the previous year. Summarizing various studies, Fuentes and Campusano (1985) found an overall significant association between high rainfall years and small-mammal outbreaks throughout northcentral Chile.

Because the winter of 1987 was unusually wet, we decided to begin monitoring densities of small mammals in a semi-arid locality of northcentral Chile. In Aucó, our chosen site, characterized by a mean annual rainfall of 206 mm (1980–1989), annual precipitation peaked at 513 mm in 1987, 56% falling during 2 weeks of July. During the 2 previous years annual precipitation had been less than average (56 mm in 1985 and 158 mm in 1986), and so we were not expecting a small-mammal outbreak until the next year. But a mammalian irruption was already underway by October 1987 when we started monitoring small-mammal populations. Unfortunately, we had not accumulated baseline data on mammal densities before the rainy winter. Nevertheless, we were able to monitor the increase phase (6 months) as well as 32 months of the decrease phase of the outbreak. Thus, here we can report both the maximum (peak) as well as the minimum (crash) densities of all species involved. In addition, our study gives simultaneous consideration to two typical habitat types in rugged areas of northcentral Chile: equatorial- and polar-facing slopes.

MATERIALS AND METHODS

The study site was Las Chinchillas National Reserve, at Aucó (31°30′S; 71°06′W), 300 km N of Santiago. Located in the coastal ranges, the Reserve has a rugged topography with numerous ridges dissected by deep ravines and an absence of flat areas. Elevations range from 400 to 1,700 m. The climate is semi-arid, with sparse rainfall concentrated in austral winter months (June–August). Mean annual precipitation is ca. 200 mm, but with high interannual variability (Fuentes et al., 1988). The vegetation is a thorn-scrub whose species composition depends on sun exposure (Durán et al., 1987; Gajardo, 1978). Slopes that face to the north (equatorial) receive higher solar radiation, and have sandy soils with scattered gravel patches and rock outcrops. Because of the xeric character of these slopes, grasses are scarce (mainly *Nassela* sp. and *Stipa* sp.), but cacti (*Trichocereus* sp., *Tephrocactus ovatus*), bromeliads (*Puya berteroniana*), and sclerophyllous shrubs (*Bahia ambrosioides, Cordia decandra, Bridgesia incisaefolia, Flourensia thurifera*) are abundant. In contrast, slopes that face to the south (polar) receive less radiation and are thus more mesic; grasses are more abundant, there are no cacti or bromeliads, and a different assemblage of shrubs prevails (*Adesmia* sp., *Porlieria chilensis, Colliguaya odorifera, Proustia* sp.). Thus, we designated equatorial- and polar-facing slopes as the two main habitat types for small mammals.

Through mark-recapture procedures, we monitored small mammal populations on two opposite-facing slopes in each of two ravines 2 km apart. Using live traps, we estimated the minimum number of mammals known alive on each grid during a particular trapping period (Krebs, 1966), a standard procedure for mammal studies in central and northcentral Chile (Iriarte et al., 1989; Jaksić et al., 1981; Meserve and Le Boulengé, 1987; Simonetti, 1989). The procedure is justified by the high trappabilities (>90%) demonstrated by Simonetti (1986) for the same mammals in the region to the south of our study site.

We used four trapping grids: two on opposite-facing slopes of the El Grillo ravine, and two in the El Cobre ravine. Each 7 by 7 trapping grid had stations separated by 15 m, thus covering an area of 105 by 105 m (including a boundary

strip of 7.5 m), or 1.1 ha. Grids were equipped with one Sherman trap (polar-facing slopes) or with one Sherman and one Tomahawk-like trap (equatorial-facing slopes). Sherman traps (8 by 10 by 23 cm) served to capture all small mammal species except for *Chinchilla lanigera* (Jiménez, 1987), the largest such species at the site, which we observed only on equatorial-facing slopes. Tomahawk-like traps (16 by 20 by 60 cm, mesh size 9 mm) served to capture *C. lanigera.* Trapping sessions occurred monthly, alternating between El Grillo and El Cobre ravines, with traps activated simultaneously on the equatorial- and polar-facing slopes of each ravine during the 1st week of the month for 5 consecutive nights (trapping effort = 735 trapnights/month). All traps were kept permanently in the field and closed when not in use. During trapping sessions, traps were baited with rolled oats (the most effective bait for local small mammals—Jiménez, 1989), then checked every morning. Each individual captured was marked with a metal ear tag. All small mammal species known to be present at the site were captured, except for the fossorial *Spalacopus cyanus* (Octodontidae), whose tunnels were evident on equatorial-facing slopes of El Cobre.

Although trapping effort was duplicated on equatorial-facing slopes by use of both Sherman and Tomahawk-like traps, potentially biasing our abundance estimates for opposite-facing slopes, we think that the bias was negligible. First, *C. lanigera* was present only on equatorial-facing slopes. Second, only the next two large rodent species at the site (*A. bennetti* and *O. degus*) were heavy enough to trigger Tomahawk-like traps. Third, mesh size was large enough to allow escape of small *A. bennetti, O. degus,* and all of the remaining local mammals. Fourth, Sherman traps did capture large (and of course small) *A. bennetti* and *O. degus.* Finally, even if all individuals of these two species would have been captured only in Tomahawk-like traps, thus underestimating their abundance on polar-facing slopes, only 110 different *O. degus* and 15 *A. bennetti* were captured, over a grand total of 2,369 different small mammals. That is, these two species together accounted for only 5.3% of all individuals captured.

For presentation here, we pooled data into austral seasons: spring (September through November); summer (December through February); autumn (March through May); and winter (June through August). Because population yields were more similar between the same slopes of El Cobre and El Grillo ravines, than between opposite slopes of either ravine, we pooled data from the same slopes of different ravines but not between different slopes of the same ravine. We follow nomenclature of Honacki et al. (1982) for names of mammalian species.

RESULTS

Equatorial-facing slopes. — In order of decreasing total abundance, the eight species we trapped were (Table 1): *Phyllotis darwini* (Cricetidae), *Akodon olivaceus* (Cricetidae), *Octodon degus* (Octodontidae), *Chinchilla lanigera* (Chinchillidae), *Marmosa elegans* (Didelphidae), *Oryzomys longicaudatus* (Cricetidae), *Abrocoma bennetti* (Abrocomidae), and *Akodon longipilis* (Cricetidae). Coefficients of variation for population densities were similar for all species (102–141%), except for *C. lanigera,* which had a surprisingly low population variability (49%). Total mammal density during our study period began with 239 individuals/ha in spring 1987, increased to a peak of 404/ha in summer 1988, and fell from 378/ha in autumn to 200/ha in winter of the same year. Then densities declined further to 193/ha in spring 1988, through 32/ha in spring 1989 and to 20/ha in spring 1990, when the study was terminated (Table 1). Thus, crash densities at the end of the study represented about 5% of those at peak. As of November 1990, overall densities had shown no clear signs of recovery, after 3 dry years (<105 mm precipitation).

Only three of the eight species monitored at equatorial-facing slopes clearly irrupted, i.e., displayed an increase phase from spring 1987, before a well-defined peak, and declined to less than one-half that peak abundance the following winter, thus completing an annual cycle (Table 1). Of the three, *P. darwini* was the most abundant, but sustained population loses that reduced its density to 6% of those at peak (305 to 17/ha). *A. olivaceus* declined to 2% of its peak density (from 56 to 1/ha), and *M. elegans* to

10% (from 21 to 2/ha). Note that *P. darwini* peaked earlier (summer 1988) than the two other species (autumn 1988).

Most of the less-common species for which we detected no clear irruption, nonetheless disappeared from the study site towards the latter phase of our study (Table 1). *A. longipilis* (peak density = 3/ha) was the first to disappear from the grids during winter 1989, *O. degus* (peak density = 23/ha) was last captured during autumn 1990, and both *A. bennetti* (peak density = 5/ha) and *O. longicaudatus* (peak density = 12/ha) were last captured during winter 1990. The apparent disappearance of *C. lanigera* (peak density = 14/ha) after autumn 1990 was not real; at the request of Reserve officials we shut down the Tomahawk-like traps in June 1990.

Polar-facing slopes.—Here we trapped the same species as before except for *C. lanigera* (Table 1), which does not inhabit polar-facing slopes at the site. The same sequence of decreasing total abundance as on equatorial-facing slopes was observed, except that *O. degus* ranked fifth instead of third. Coefficients of variation for population densities were higher here than on equatorial-facing slopes for all species except *M. elegans* and *P. darwini*.

Total density of mammals began with 112 individuals/ha in spring 1987, increased to a peak of 199/ha in summer 1988, and fell from 185/ha in autumn to 72/ha in winter of the same year. Densities increased to 97/ha in spring 1988, then steadily declined toward 8/ha in spring 1989, and again increased to 22/ha in spring 1990 (Table 1). Thus, crash densities did not persist here to the end of the study, but were reached 1 year before (spring 1989) and represented about 4% of those at peak (similar to the 5% observed on equatorial-facing slopes). Starting in December 1989, overall densities were showing signs of recovering on polar-facing slopes, unlike equatorial-facing slopes. Note that despite population densities following the same pattern here as on equatorial-facing slopes, total abundance was approximately one-half on polar-facing slopes.

The same three species as on equatorial-facing slopes irrupted on polar-facing slopes (Table 1). Again, *P. darwini* was the most abundant, and its crash density in spring 1989 was 3% that at peak (146 to 4/ha). *A. olivaceus* declined to 6% of its peak density (from 49 to 3/ha), and *M. elegans* to 9% (from 11 to 1/ha). Here, both *P. darwini* and *M. elegans* peaked earlier (summer 1988) than *A. olivaceus* (autumn 1988).

The remaining four species did not irrupt. *A. bennetti* (peak density = 1/ha) was not captured at all during the first 7 seasons of our study, and starting in winter 1989 it was captured only sporadically. *A. longipilis* (peak density = 1/ha) was captured only once (spring 1988). *O. degus* (peak density = 2/ha) was captured only during the first three field seasons. *O. longicaudatus* (peak density = 2/ha) showed the same pattern as *O. degus,* and was then captured during only 2 other seasons (Table 1). None of these species appear to have resided permanently on polar-facing slopes.

DISCUSSION

In agreement with marked physiognomic, vegetational, and microclimatic differences between equatorial- and polar-facing slopes, there were clear differences between the small-mammal assemblages at these two habitat types. Whereas *C. lanigera* was present only on equatorial-facing slopes, the remaining seven species were only one-half as abundant on polar- than on equatorial-facing slopes. The rarefaction effect of this overall halving in abundance resulted in the four least common species (*A. bennetti, A. longipilis, O. degus, O. longicaudatus*) being only sporadically trapped at polar-facing slopes. The three most common species (*P. darwini, A. olivaceus, M. elegans*) resided continually on both slopes, but reached double their density on equatorial-facing slopes. Perhaps the productivity of equatorial-facing slopes was substantially increased because of the unusual water input

TABLE 1.—Density (number/ha) and percent numerical composition, based on minimum number known alive, of small mammals on equatorial- and polar-facing slopes in Auco, Chile, by season.

Mammals	Spring 1987		Summer 1988		Autumn 1988		Winter 1988		Spring 1988		Summer 1989		Autumn 1989	
	No./ha	%	No./ha	%	No./ha	%	No./ha	%	No./ha	%	No./ha	%	No./ha	%
Equatorial-facing slopes														
Abrocoma bennetti	4.5	1.9	0.0	0.0	2.7	0.7	0.9	0.5	0.0	0.0	1.8	2.5	0.9	1.8
Akodon longipilis	2.7	1.1	2.7	0.7	0.0	0.0	1.8	0.9	2.7	1.4	0.0	0.0	0.9	1.8
Akodon olivaceus	21.8	9.1	54.5	13.5	55.5	14.7	24.5	12.3	27.3	14.2	9.1	12.5	3.6	7.3
Chinchilla lanigera	10.0	4.2	13.6	3.4	9.1	2.4	11.8	5.9	11.8	6.1	6.4	8.8	6.4	12.7
Marmosa elegans	8.2	3.4	3.6	0.9	20.9	5.5	7.3	3.6	11.8	6.1	1.8	2.5	6.4	12.7
Octodon degus	22.7	9.5	21.8	5.4	15.5	4.1	20.9	10.5	16.4	8.5	2.7	3.8	6.4	12.7
Oryzomys longicaudatus	0.9	0.4	3.6	0.9	11.8	3.1	10.0	5.0	5.5	2.8	0.0	0.0	0.9	1.8
Phyllotis darwini	168.2	70.4	304.5	75.2	262.7	69.5	122.7	61.3	117.3	60.9	50.9	69.9	24.5	49.2
Total	239.0	100.0	404.3	100.0	378.2	100.0	199.9	100.0	192.8	100.0	72.7	100.0	50.0	100.0
Polar-facing slopes														
Abrocoma bennetti	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Akodon longipilis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.9	0.0	0.0	0.0	0.0
Akodon olivaceus	11.8	10.6	40.0	20.1	49.1	26.6	21.8	30.4	17.3	17.9	4.5	14.7	3.6	15.4
Marmosa elegans	3.6	3.3	10.9	5.5	6.4	3.4	0.9	1.3	5.5	5.7	0.9	2.9	0.0	0.0
Octodon degus	1.8	1.6	0.9	0.5	0.9	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oryzomys longicaudatus	0.9	0.8	0.9	0.5	1.8	1.0	0.0	0.0	5.5	5.7	0.0	0.0	0.0	0.0
Phyllotis darwini	93.6	83.7	146.4	73.4	126.4	68.5	49.1	68.3	67.3	69.8	25.5	82.4	20.0	84.6
Total	111.7	100.0	199.1	100.0	184.6	100.0	71.8	100.0	96.5	100.0	30.9	100.0	23.6	100.0

TABLE 1.—*Extended.*

Mammals	Winter 1989 No./ha	%	Spring 1989 No./ha	%	Summer 1990 No./ha	%	Autumn 1990 No./ha	%	Winter 1990 No./ha	%	Spring 1990 No./ha	%	Overall $\bar{X}$	SD	CV (%)	n
Equatorial-facing slopes																
Abrocoma bennetti	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.7	13.0	0.0	0.0	1.0	1.5	140.8	13
Akodon longipilis	0.9	3.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	1.2	129.1	13
Akodon olivaceus	3.6	13.8	3.6	11.4	2.7	9.7	1.8	6.7	1.8	8.7	0.9	4.5	16.2	19.6	120.5	13
Chinchilla lanigera	3.6	13.8	3.6	11.4	3.6	12.9	4.5	16.7	nt*	0.0	nt*	0.0	7.7	3.7	48.6	11
Marmosa elegans	2.7	10.3	0.9	2.9	0.0	0.0	1.8	6.7	1.8	8.7	1.8	9.1	5.3	5.8	109.3	13
Octodon degus	3.6	13.8	3.6	11.4	0.9	3.2	0.9	3.3	0.0	0.0	0.0	0.0	8.9	9.1	102.1	13
Oryzomys longicaudatus	2.7	10.3	0.0	0.0	0.0	0.0	0.9	3.3	0.9	4.3	0.0	0.0	2.9	3.9	137.5	13
Phyllotis darwini	9.1	34.6	20.0	62.9	20.9	74.2	17.3	63.3	13.6	65.3	17.3	86.4	88.4	100.9	114.2	13
Total	26.2	100.0	31.7	100.0	28.1	100.0	27.2	100.0	20.8	100.0	20.0	100.0	130.1	139.2	107.0	13
Polar-facing slopes																
Abrocoma bennetti	0.9	4.3	0.9	11.1	0.0	0.0	0.0	0.0	0.9	5.0	0.0	0.0	0.2	0.4	190.0	13
Akodon longipilis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.3	360.6	13
Akodon olivaceus	2.7	13.0	2.7	33.3	0.9	3.0	0.0	0.0	2.7	15.0	0.9	4.2	12.2	16.0	131.2	13
Marmosa elegans	0.0	0.0	0.9	11.1	4.5	15.2	1.8	16.7	3.6	20.0	1.8	8.3	3.1	3.1	99.1	13
Octodon degus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6	204.9	13
Oryzomys longicaudatus	0.9	4.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	1.5	198.0	13
Phyllotis darwini	16.4	78.4	3.6	44.5	24.5	81.8	9.1	83.3	10.9	60.0	19.1	87.5	47.1	47.3	100.4	13
Total	20.9	100.0	8.1	100.0	29.9	100.0	10.9	100.0	18.1	100.0	21.8	100.0	63.7	65.7	103.1	13

* nt = Not trapped because Tomahawk-like traps were not operated this season.

to the soil matrix, which together with the higher solar radiation, allowed a flush of the dormant seed bank and of emergent vegetation as well. The small-mammal outbreak occurred almost simultaneously in both habitat types, led by *P. darwini,* and followed by *M. elegans* and *A. olivaceus.*

The rank order of numerical dominance at our study site (*P. darwini* followed by *A. olivaceus*) differed from that of an earlier outbreak in nearby agricultural habitats, where *O. longicaudatus* was the most irruptive small mammal (Péfaur et al., 1979), but agrees with data of Pearson (1975) for coastal Peru and those of Fulk (1975), Glanz (1977), and Meserve and Le Boulengé (1987) for arid native habitats of northcentral Chile. By comparison, the population increase we observed in *M. elegans* was rather modest, but in phase with the irruption and crash of the two previously mentioned species.

Judging from the follow-up study conducted by Meserve and Le Boulengé (1987) on the mammal outbreak in Fray Jorge National Park first reported by Fulk (1975), the Aucó irruption differed markedly. Meserve and Le Boulengé (1987) documented that in Fray Jorge National Park only *A. olivaceus* crashed, to about one-sixth its peak density over a 3-year period. *P. darwini* remained at rather stable density, while both *A. longipilis* and *O. degus* increased their initial densities by 4 and 6 times, respectively. The overall result was that absolute population density of all species combined remained stable, and only their relative frequencies changed. In fact, the crash of the most irruptive species (*A. olivaceus*) in Fray Jorge National Park actually may have released populations of two others (*A. longipilis* and *O. degus*).

At Aucó, however, relative frequencies of the three irruptive species remained stable throughout the study period (Table 1) despite the overall 20-fold difference between peak and crash densities. Their synchronized responses are surprising in light of their different food habits. Judging by Meserve's (1981*a*) data from a nearby site in

northcentral Chile, *P. darwini* and *O. longicaudatus* were the most granivorous species in our study site; *M. elegans* was insectivorous; *A. bennetti* and *O. degus* were folivorous; and both *A. longipilis* and *A. olivaceus* were omnivorous (the former more of an insectivore and the latter more of a granivore—Glanz, 1984). Although one granivore at the site (*P. darwini*) irrupted, another (*O. longicaudatus*) did not. The more granivorous of the two omnivores, *A. olivaceus,* irrupted but its congener, *A. longipilis* (the more insectivorous), did not, even though the insectivorous *M. elegans* also irrupted by our criterion. The disparate population responses by members of the same trophic guild were foreshadowed by Meserve (1981*b*:754). He stated that in northcentral Chile "two members of the same foraging guild are almost never found highly abundant in the same trapping site" implying that interspecific competition may be the ecological process underlying this pattern.

Why did three species with such divergent diets irrupt at all? We lack data on vegetation, seed, and insect productivity, but it is reasonable to expect that the heavy rainfall in winter 1987 resulted in unusually high production of foliage and (later) seeds, and, consequently, of herbivorous insects as well. Our anecdotal observations at the site corroborate this. Such a pulse in productivity can explain the irruptions and subsequent declines of all three species even though the failure of other species to irrupt is still unexplained. The years when the decline has been occurring are characterized by well-below-average rainfall (<105 mm). Whether the species have been declining owing to higher mortality, decreased or nil reproduction, or both, is unknown. That the decline was reversed first on the more mesic polar-facing slopes may speak to the role of a more sustained—if lower—primary productivity.

Phyllotis darwini, A. olivaceus, and *M. elegans* are the most ubiquitous small mammals in northcentral Chile (Meserve and Glanz, 1978). The first two demonstrate at

least some ability to tolerate water deprivation (Cortés et al., 1988; Meserve, 1978), and the third enters torpor facultatively when faced with low temperatures or a scarcity of food (Rosenmann et al., 1980). With their distinctive feeding specializations, these three species in Aucó apparently constitute a resilient core of small mammals that persists even under resource scarcity in temporarily harsh environments, and takes full advantage of resource flushes by irrupting in classic fashion. The evidence discussed herein—outbreaks apparently triggered by unusual high rains and subsequent increased productivity—speaks to a role of extrinsic factors in affecting the population dynamics of at least some small mammals in northcentral Chile.

LITERATURE CITED

CORTÉS, A., C. ZULETA, AND M. ROSENMANN. 1988. Comparative water economy of sympatric rodents in a Chilean semi-arid habitat. Comparative Biochemistry and Physiology, A. Comparative Physiology, 91:711–714.

DURÁN, J. C., P. E. CATTÁN, AND J. L. YÁÑEZ. 1987. Food habits of foxes (*Canis* sp.) in the Chilean National Chinchilla Reserve. Journal of Mammalogy, 68:179–181.

FUENTES, E. R., AND C. CAMPUSANO. 1985. Pest outbreaks and rainfall in the semi-arid region of Chile. Journal of Arid Environments, 8:67–72.

FUENTES, E. R., E. R. HAJEK, AND G. ESPINOZA. 1988. Some consequences of rainfall variability for mediterranean-type ecosystems in Chile. Pp. 342–360, *in* Proceedings of the 5th International Conference on Mediterranean Ecosystems: time scales and water stress (F. di Castri, C. Floret, S. Rambal, and J. Roy, eds.). International Union of Biological Sciences, Paris, 425 pp.

FULK, G. W. 1975. Population ecology of rodents in the semiarid shrublands of Chile. Occasional Papers, The Museum, Texas Tech University, 33:1–40.

GAJARDO, R. 1978. Antecedentes para la determinación de las comunidades vegetales de Aucó. (Illapel, IV Región). Ciencias Forestales (Chile), 1:19–27.

GLANZ, W. E. 1977. Comparative ecology of small mammal communities in California and Chile. Ph.D. dissert., University of California, Berkeley, 300 pp.

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

HERSHKOVITZ, P. 1962. Evolution of Neotropical cricetine rodents (Muridae), with special reference to the phyllotine group. Fieldiana: Zoology, 46:1–524.

HONACKI, J. H., K. E. KINMAN, AND J. W. KOEPPL (EDS.). 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press Inc. and The Association of Systematics Collections, Lawrence, Kansas, 694 pp.

IRIARTE, J. A., L. C. CONTRERAS, AND F. M. JAKSIĆ. 1989. A long-term study of a small-mammal assemblage in the central Chilean matorral. Journal of Mammalogy, 70:79–87.

JAKSIĆ, F. M., J. L. YÁÑEZ, AND E. R. FUENTES. 1981. Assessing a small mammal community in central Chile. Journal of Mammalogy, 62:391–396.

JIMÉNEZ, J. E. 1987. Eficiencia relativa de seis modelos de trampa para la captura viva de micromamíferos silvestres, con énfasis en *Chinchilla lanigera* (Molina, 1782). Medio Ambiente (Chile), 8:104–112.

———. 1989. Uso de la técnica de tarjetas ahumadas para evaluar la efectividad de cebos para micromamíferos silvestres, con énfasis en *Chinchilla lanigera*. Medio Ambiente (Chile), 10:84–91.

KREBS, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecological Monographs, 36:239–273.

MESERVE, P. L. 1978. Water dependence in some Chilean arid zone rodents. Journal of Mammalogy, 59:217–219.

———. 1981a. Trophic relationships among small mammals in a Chilean semiarid thorn scrub community. Journal of Mammalogy, 62:304–314.

———. 1981b. Resource partitioning in a Chilean semi-arid small mammal community. The Journal of Animal Ecology, 50:745–757.

MESERVE, P. L., AND W. E. GLANZ. 1978. Geographical ecology of small mammals in the northern Chilean arid zone. Journal of Biogeography, 5:135–148.

MESERVE, P. L., AND E. LE BOULENGÉ. 1987. Population dynamics and ecology of small mammals in

the northern Chilean semiarid region. Pp. 413–431, *in* Studies in Neotropical mammalogy: essays in honor of Philip Hershkovitz (B. D. Patterson and R. M. Timm, eds.). Fieldiana: Zoology, new series, 39: 1–506.

PEARSON, O. P. 1975. An outbreak of mice in the coastal desert of Peru. Mammalia, 39:375–386.

PÉFAUR, J. E., J. L. YÁÑEZ, AND F. M. JAKSIĆ. 1979. Biological and environmental aspects of a mouse outbreak in the semi-arid region of Chile. Mammalia, 43:313–322.

ROSENMANN, M., P. BARAHONA, AND L. C. CONTRERAS. 1980. Metabolismo energético y sopor en *Marmosa elegans.* Archivos de Biología y Medicina Experimentales (Chile), 13:R105.

SIMONETTI, J. A. 1986. Heterogeneity of recaptures in Chilean small mammals. Revista Chilena de Historia Natural, 59:59–63.

———. 1989. Microhabitat use by small mammals in central Chile. Oikos, 56:309–318.