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SPATIAL ECOLOGY OF SMALL MAMMALS IN NORTH-CENTRAL CHILE: ROLE OF PRECIPITATION AND REFUGES

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Lower-elevation habitats of north-central Chile are characterized by semiarid vegetation that is strongly influenced by rainfall related to El Niño Southern Oscillation (ENSO) events. During the ENSO warm phase (i.e., El Niño), heavy rains occur resulting in small mammal irruptions or ratadas. During prevailing drier periods, pronounced droughts result in reductions in small mammal densities and local extinctions of some species. Within the dominant thorn-scrub habitat of a national park, we identified 2 other habitat types, aguadas (riverine shrublands) and fog-forest patches that serve as refuges for small mammals during dry years. We divide small mammal species of the thorn scrub into 2 groups: core species (*Octodon degus*, *Phyllotis darwini*, *Abrothrix olivaceus*, and *Thylamys elegans*) maintain populations at all times, whereas opportunistic species (*Oligoryzomys longicaudatus* and *A. longipilis*) are present only after rains. The latter group appears to maintain refuge populations in aguadas and fog forests and to opportunistically exploit the thorn scrub when conditions are favorable. Aguadas also may play an important role in the persistence of less-common species, such as *Octodon lunatus* and *Abrocoma bennetti*. Despite being small and patchily distributed, aguadas are important for the maintenance of regional biodiversity.

Key words: Chile, El Niño, El Niño Southern Oscillation (ENSO), irruptions, refuges, semiarid zone, small mammals

Spatial and temporal variations have important implications for population and community structure and ecological processes (Kareiva and Wennergren 1995). However, study of such variation has proven problematic because most theoretical and empirical treatments are constrained to emphasize either space or time but not both aspects. Further, logistical considerations often force ecologists to concentrate on variation that occurs at small spatial scales over short time scales (e.g., M'Closkey 1972, 1976; Meserve 1981a; Meserve and Le Boulengé 1987; Schamberger and Fulk 1974; Smith and Vrieze 1979), large spatial scales over short time scales (e.g., Brown 1975; Ernest et al. 2000; Marquet 1994; Meserve and Glanz 1978), or temporal variation at reduced spatial scale (e.g., Brown and Heske 1990; Getz and Hofmann 1999; Meserve et al. 1995, 1999). However, studies at broader spatial and temporal scales (e.g., Beatley 1976) may sacrifice the ability to detect subtle changes in spatial and demographic structure at the local level.

Since 1989, we have conducted a long-term experimental manipulation at a thorn-scrub site in north-central Chile (Meserve et al. 1995, 1996, 1999, 2003). This region (the ''Norte Chico'') has a semiarid Mediterranean climate strongly influenced by El Niño Southern Oscillation (ENSO) events. During such periods, warming of the equatorial surface waters of the Pacific (the ENSO warm phase or El Niño) causes heavy winter rains in northern Chile, whereas surface cooling (the ENSO cold phase or La Niña) results in severe droughts (Allan et al. 1996). Rains trigger mass germination of herbaceous

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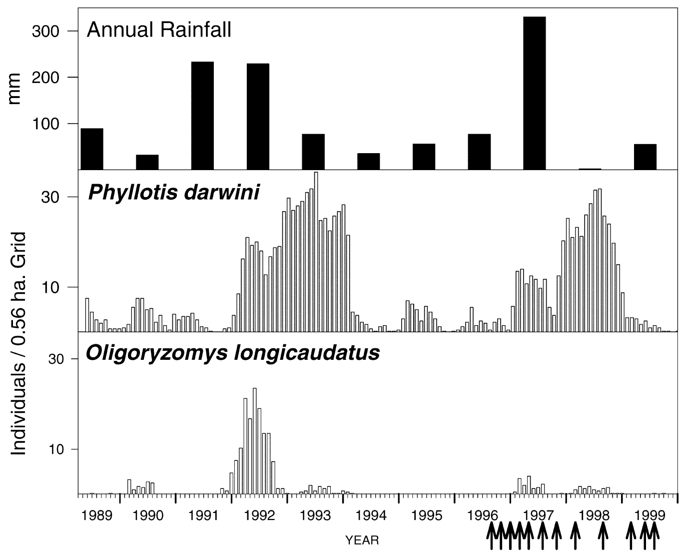

FIG. 1.—Annual precipitation (mm) and abundance patterns for a core species (*Phyllotis darwini*) and an opportunistic species (*Oligoryzomys longicaudatus*). Data are from Meserve et al. (2003). Arrows indicate sampling periods for this study.

plants leading to synchronous flowering (Armesto et al. 1993; Gutiérrez et al. 1993, 1997). Small mammal populations respond to the increased primary production with dramatic irruptions (Fuentes and Campusano 1985; Gilmore 1947; Jiménez et al. 1992; Lima et al. 1999; Meserve et al. 1995; Pearson 1975; Péfaur et al. 1979) known as ratadas (Hershkovitz 1962). After outbreaks, populations crash dramatically and many species become locally extinct. During dry periods, some of the most irruptive small mammal species are completely absent from the thorn scrub (Meserve et al. 1995).

Because numerous local extinctions and recolonizations of small mammals have been observed in the thorn scrub since 1989 (Meserve et al. 1995), it is clear that species disappearance does not represent regional extinction and that refuge habitats must play a role in the maintenance of populations of all small mammals. Thus, their regional persistence results from differential and temporally variable habitat use in a spatially heterogeneous landscape. The goals of this study were to verify the existence of refuges for small mammals, to understand the role of refuges in the development of small mammal assemblage structure in thorn-scrub habitats, and to examine the importance of spatial heterogeneity in the maintenance of regional biodiversity.

MATERIALS AND METHODS

Study site description.—The study site was in Parque Nacional Bosque Fray Jorge (71°40′W, 30°38′S), a 10,000-ha park located on the Pacific coast approximately 50 km west of Ovalle in north-central Chile. Although the area has had a long history of human habitation resulting in widespread habitat degradation (Bahre 1979), the park has been spared the effects of grazing by goats and dryland farming since establishment in 1941 (Muñoz and Pisano 1947). It now contains the largest area of minimally disturbed native thorn-scrub habitat in Chile's Region IV, and as a result was designated a World Biosphere Reserve in 1977.

Mean precipitation in Fray Jorge from 1989 to 1999 was 110 mm ($SD = 105.0$ mm) with 95% falling during the winter months (May–August). During this 10-year period, 2 major El Niño events occurred, in 1991–1992 and in 1997. Precipitation was well above average in all 3 years (233, 229, and 330 mm, respectively; see Fig. 1). One of the largest recorded La Niña events occurred during 1998 with only 11 mm precipitation in the park (ENSO data from the National Oceanographic and Atmospheric Administration (2007).

Most of the habitat in the park is thorn-scrub vegetation dominated by spiny, woody perennial shrubs including *Porliera chilensis*, *Adesmia bedwellii*, and *Proustia pungens* (Muñoz and Pisano 1947). After winter rains, a diverse assemblage of native and introduced ephemeral plants may also be present (Gutiérrez et al. 1993, 1997). Although the thorn-scrub matrix is relatively homogeneous, local variation in slope, aspect, hydrology, and topography leads to the presence of other minor habitat types. Preliminary surveys and trapping resulted in identification of 2 habitats important to small mammals—fog forest and aguadas. These habitats represent approximately 2% (aguadas) and 13% (fog forest) of the study area shown in Fig. 2 (W. B. Milstead, in litt.).

Fog forest occurs in patches ranging from <1 ha to about 10 ha in size, on the summits of coastal ridges near the western boundary of the park (Fig. 2). Patches are maintained by moisture-laden fog that blows in from the ocean and ameliorates arid conditions (Bahre 1979; Kummerow 1966; Philippi 1884). Forest vegetation is dominated by the trees *Aextoxicon punctatum*, *Drimys winteri*, and *Myrceugenia correaefolia* plus numerous understory shrubs, herbaceous plants, and vines that form a nearly impenetrable thicket (Muñoz and Pisano 1947).

Aguada habitats are patchily distributed in the riparian areas of a valley (Quebrada de las Vacas), and the arroyos that intersect it (Fig. 2). Subsurface waters and seeps in these areas allow the establishment of riverine shrublands. Aguada habitats are characterized by a diverse assemblage of plants that includes both generalized thorn-scrub as well as drought-intolerant species. The dominant plants are *Schinus*, *Baccharis*, and *Senecio murorum* (Milstead 2000).

These 3 habitats—thorn scrub, aguadas, and fog forest—are the dominant vegetative zones of the interior portion of the park, and representative sites for each were sampled extensively during this project.

Study animals.—We documented 10 small mammal species during this study. With the exception of a small marsupial, the elegant mouse opossum (*Thylamys elegans*; 22 ± 8 g [$\bar{X}$ ± 1 *SD* throughout]), all species studied were rodents. Four of these are sigmodontines, including Darwin's leaf-eared mouse (*Phyllotis darwini*; 54 ± 14 g), the olive grass mouse (*Abrothrix olivaceus*; 28 ± 6 g), the long-haired grass mouse (*Abrothrix longipilis*; 47 ± 9 g), and the long-tailed rice rat (*Oligoryzomys longicaudatus*; 27 ± 7 g). Three species are hystricomorphs (i.e., the degu [*Octodon degus*; 128 ± 29 g], the moon-toothed degu [*O. lunatus* Osgood; 156 ± 36 g], and

Bennett's chinchilla-rat [*Abrocoma bennetti*; 171 ± 65 g]). The remaining 2 species are introduced murines, the black rat (*Rattus rattus*; 110 ± 50 g) and the Norway rat (*R. norvegicus*; 128 ± 44 g). Although rats (*Rattus*) are common near human settlements in the park they have limited occurrence in natural habitats. In native habitats, both species of *Rattus* are mostly confined to the fog forest and for purposes of analysis are treated together.

Procedures.—To quantify habitat-specific demography, standard sampling grids (60 × 60 m, 5 × 5 array of trap stations, 15 m apart) were established in 2 fog-forest and 4 aguada areas in early 1996 (Fig. 2). Data from thorn-scrub sites were available for the same time period from 4 control grids that form part of a larger, long-term experimental study in progress since March 1989 (see Meserve et al. 1996, 1999, 2003; Fig. 2). Grid layout and methodology were the same at all sites.

Twelve trapping sessions were conducted at all sites between August 1996 and July 1999 (Fig. 1). Except for October 1997, censuses were 4 nights and 3 days in duration; in the latter period, they were 3 nights for the fog-forest and aguada sites. Animals were captured with 2 Sherman-type live traps (10.0 × 11.5 × 30.0 cm) per trap station baited with rolled oats. Traps were checked once to twice daily (early morning and late afternoon). All animals captured were identified to species, given a unique mark (ear tag or leg band), and released. Sex, weight, and reproductive condition were recorded each time an animal was captured. All trapping procedures and protocol were approved by the Institutional Animal Use and Care committee at Northern Illinois University, and met guidelines recommended by the American Society of Mammalogists (Gannon et al. 2007).

Abundance was estimated as the number of individuals (NI) captured per grid during each trapping session (effective trapping area = 0.56 ha; 60 × 60 m with a 7.5-m buffer). Most species exhibited high capture probabilities (in declining order, *P. darwini* and *T. elegans*, 1.00; *A. olivaceus*, 0.92; *O. degus*, 0.83; *A. bennetti* and *O. longicaudatus*, 0.50; *A. longipilis*, 0.42; see also Meserve et al. 1995, 1999), justifying the use of this metric of abundance. To confirm this, estimates of abundance based on number of individuals were compared to estimates based on the minimum number known alive from 10 years of monthly trapping records for the control grids of the main study site in the thorn scrub. For the 6 most common species, number of individuals closely tracked minimum number known alive, with regression slopes ranging from 0.82 to 0.94; all Pearson's correlation coefficients were highly significant ($P < 0.001$; all $r > 0.90$).

Data analysis.—Spatial and temporal variations in small mammal assemblages were analyzed with repeated-measures analysis of variance (rmANOVA—von Ende 2001). Mixed-model ANOVA (Wolfinger and Chang 1995), a procedure with specific application to rmANOVA, was used for all calculations. Mixed-model ANOVA allows for unequal replication, missing data, and the testing and specification of the covariance structure. Pairwise tests of the influence of habitat, time, and their interaction were performed on log-transformed abundance estimates ($\log_{10}(\text{NI} + 1)$) by habitat type (aguada, fog forest, and thorn scrub). Comparisons were made only between pairs of habitats in which a species was present in both. Residuals from all analyses were tested for normality. Departures from normality were analyzed graphically to verify the ANOVA assumption of homoscedasticity (Stevens 1992).

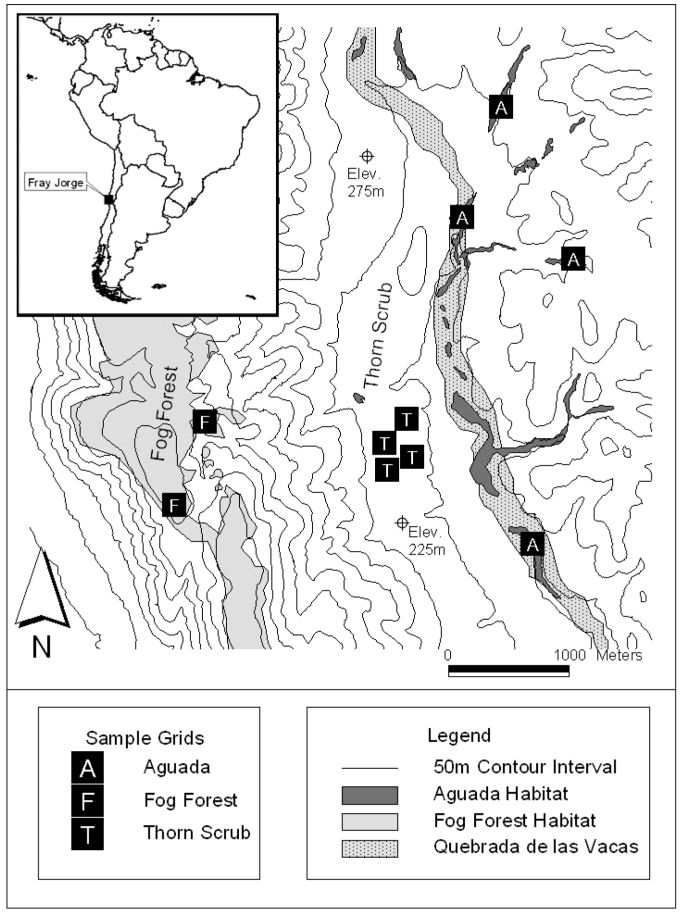

Fig. 2.—Map of the study site showing the location of sample grids. Letters indicate the habitat type: A = aguada grids; F = fog-forest grids; and T = thorn-scrub grids. Solid lines indicate 50-m contour lines. For reference, Quebrada de las Vacas, a dry river valley, also is indicated.

Results

Abundances.—Small mammal abundance fluctuated over time and across habitats (Fig. 3). For most ANOVA comparisons, both time and time × habitat interaction terms were significant ($P < 0.05$, Huyhn-Feldt adjusted—von Ende 2001) indicating that abundance varied over time (as documented by (Meserve et al. [1995]) but that the response was not consistent among habitat types.

The 3 dominant small mammal species in the thorn scrub, *A. olivaceus* (AO), *O. degus* (OD), and *P. darwini* (PD), showed consistent temporal and spatial patterns. Generally, densities were slightly but not significantly higher in the thorn scrub compared to the aguadas (all $d.f. = 1, 6$; $P_{AO} = 0.1975$;

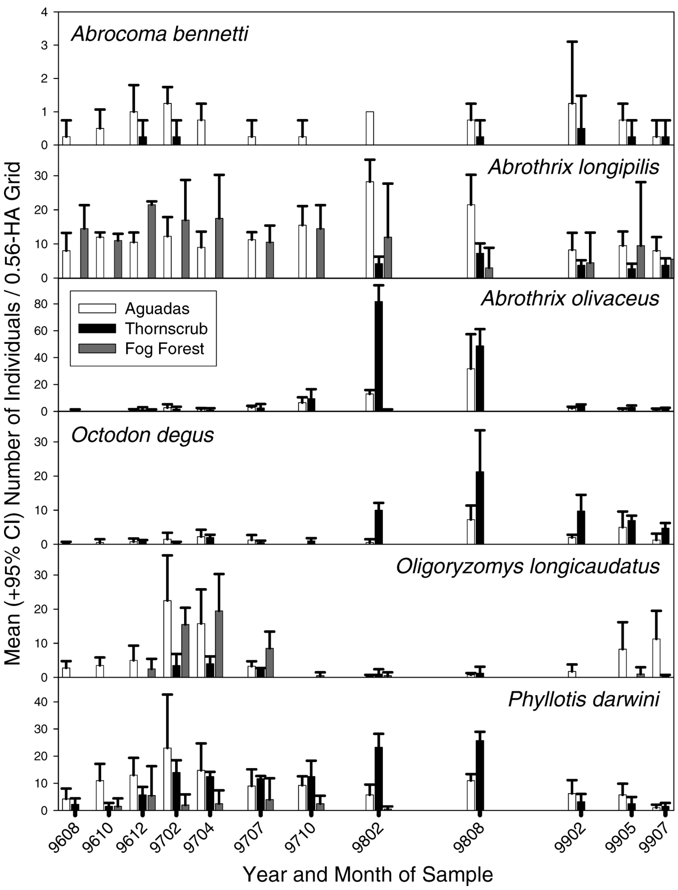

FIG. 3.—Mean abundance with 95% confidence interval for 6 small mammal species in 3 habitats in Fray Jorge Forest National Park between August 1996 and July 1999. Abundance in aguada, thorn-scrub, and fog-forest habitats is represented by open, black, and gray bars, respectively.

$P_{OD} = 0.1084$; $P_{PD} = 0.6547$; Fig. 3). Only 1 *A. olivaceus* and no *O. degus* were captured in the fog forest. *P. darwini* was recorded in the fog forest, but population size was always lower than in other sites (*d.f.* = 1, 6, $P = 0.0083$; Fig. 3). All 3 species reached peak densities in 1998 after the wet (El Niño) year of 1997. The increase was most pronounced for *A. olivaceus* and *O. degus*, but also evident for *P. darwini* (Fig. 3).

Both *A. bennetti* and *Octodon lunatus* were rare in all habitats. One individual of each species was captured in the fog forest. Only the aguada and thorn scrub were compared for *A. bennetti*; aguadas had significantly more individuals of this species (*d.f.* = 1, 4, $P = 0.0067$). No *O. lunatus* were found in the thorn scrub.

Oligoryzomys longicaudatus, well known for its irruptive demographics (Gilmore 1947; Meserve et al. 1995; Péfaur et al. 1979), disappeared from the thorn-scrub habitat for varying lengths of time before and after the 1997 El Niño (Fig. 1). It was always found in aguadas (Fig. 3), albeit at low densities. Overall, there were no significant differences in small mammal abundance between aguadas and the fog forest (*d.f.* = 1, 4, $P = 0.2718$), but examination of the significant time × habitat interaction showed aguada densities to be consistently higher when population levels were low elsewhere (Fig. 3).

Abrothrix longipilis was the dominant species in the fog forest, although densities were equivalent to those in the aguadas (*d.f.* = 1, 4, $P = 0.1537$; Fig. 3). Populations of this species were significantly lower in the thorn-scrub habitat compared both to aguadas (*d.f.* = 1, 6, $P = 0.0001$) and the fog forest (*d.f.* = 1, 4, $P = 0.0002$), but this difference was most notable before the 1997 rains, when individuals were completely restricted to mesic habitats. Temporal variation in abundance was evident for all sites (Fig. 3); however, marked differences were seen only in the thorn scrub.

Introduced rats (*R. norvegicus* and *R. rattus*) were present, although not abundant, in the fog forest and were virtually absent from other habitat types. Only 2 individuals (both *R. norvegicus*) were captured in arid habitats (1 each in an aguada and an ecotonal area), and none were recorded in the thorn-scrub habitat. All of the individuals in the forest were captured at a single grid (lower left F grid in Fig. 2) leading to large within-habitat variability. Although the vegetation and appearance of the 2 forest grids was similar, they differed in slope, aspect, and patch size. Further, this grid was located in a larger, mostly contiguous patch of forest on the western slope, whereas the other forest grid was smaller, more isolated, and located on the eastern slope (Fig. 2).

Thylamys elegans was cosmopolitan in its distribution and found equally in all habitats (all $P > 0.05$). We observed slightly higher population sizes in the thorn-scrub habitat compared to the aguadas during the last 3 sampling periods, but all other comparisons among sites were not significant. In general, numbers of *T. elegans* were low and temporally variable.

DISCUSSION

Our results reveal important qualitative and quantitative differences between habitats within the Fray Jorge landscape. The thorn scrub exhibited the greatest temporal variation in small mammal assemblage membership. Core and quasicore species (*P. darwini*, *O. degus*, *T. elegans*, and *A. olivaceus*) maintained persistent populations during both wet and dry years. All 4 species reproduce during wet years, yet only *P. darwini* is known to reproduce consistently during dry years (Meserve et al. 1995). Rainfall appears to improve the quality of lower-elevation habitats (i.e., thorn scrub and aquadas) for *P. darwini* such that their densities actually decrease in the fog forest in El Niño years; whether this is due to migration or increased mortality is unknown. *O. degus* is long-lived and may defer reproduction during 1 or even 2 unfavorable years; as a result it may be buffered from short-term environmental variation. Interestingly, *O. degus* showed a much longer delay between precipitation and responses in the 1991–1992 El Niño (e.g., Meserve et al. 1995; Milstead 2000) than we documented for the 1997 event. This suggests that *O. degus* has a complicated demography. It is possible that *A. olivaceus* and *T. elegans* remain reproductive during all years, but their exact status is unknown. *P. darwini* and *O. degus* always maintain populations in the thorn scrub, whereas *A. olivaceus* and *T. elegans* maintain populations during most, but not all, years. Migration into the thorn scrub from the aguadas may help to stabilize these populations, especially during dry years.

Opportunistic species comprised the 2nd major component of the thorn-scrub small mammal assemblage. During wet years, *A. longipilis* and *O. longicaudatus* colonized the thorn scrub, but we saw little evidence of successful reproduction there. Individuals of *A. longipilis* persisted for many months or years, whereas individuals of *O. longicaudatus* always had short residence times. Despite their transient nature, population size of *O. longicaudatus* in thorn scrub was predictable from rainfall history (Milstead 2000), although minor irruptions occurred in 1990 and 1997 before onset of rainfall (Fig. 1). Other researchers (e.g., Murúa et al. 1986) have noted the vagile nature of *O. longicaudatus*, and this may result from its dependence on a spatially and temporally variable food resource (i.e., seeds—Meserve 1981b). The remaining 2 thorn-scrub opportunists, *A. bennetti* and *O. lunatus*, were captured intermittently during both wet and dry years, but neither species persisted in the thorn scrub. This suggests that the thorn scrub represented marginal habitat and that the primary habitat for these species in the park is aguadas. These species also did not show any rainfall-related increases, although analysis of a longer temporal sequence indicated that *A. bennetti* displayed a delayed response to precipitation in the thorn scrub (Milstead 2000). Persistence of *A. bennetti* in aguadas probably explains why this species was overrepresented in predator diets when compared to density estimates from the thorn scrub (Jaksic et al. 1997).

The fog forest had the lowest numbers of small mammals species; *A. longipilis* and *Rattus* were the only species to maintain populations in this habitat although all species except *O. degus* was occasionally recorded in some grids. Whether the fog forest was important in the regional dynamics of the native species is unknown because *A. longipilis* maintained populations in aguadas as well. *T. elegans* appeared not to breed in the fog forest but larger individuals may colonize or forage there. Larger body size could also be favored in wet, cool fog forests.

The presence of *Rattus* in the fog forest is disturbing. These introduced murines are active predators and strong competitors, and are associated with declines in biodiversity worldwide (Towns et al. 2006). They nest arboreally, which may explain the frequent extinctions and reduced breeding success there of *O. longicaudatus*, another arboreal nester (Redford and Eisenberg 1992). In nearby Colina Talinay where a 10-ha isolated forest patch exists at approximately 600-m elevation 40 km south of the park, a trapping session in September 1996 (2 grids, same trapping methodology as this study) yielded captures of 16 *Rattus* and only 4 *A. longipilis*. These rats were almost certainly introduced after construction of a microwave station around 1995, and the lack of other species there suggests that *Rattus* may have a devastating effect on the native small mammal fauna; whether this is due to competition or direct predation is unknown and merits further study. Captures of *Rattus* in Fray Jorge decreased over the course of the study, reaching their lowest point after the 1997 rains. They may emigrate from forest patches when conditions are favorable, occupying nearby ecotonal areas.

All native small mammal species were captured consistently in aguadas (Fig. 3). If local extinction did occur, recolonization was rapid and species rarely were absent from aguada grids for long. Thus, aguadas appear to play a crucial role in the regional dynamics of small mammals in north-central Chile.

Intensive mining, dry-land farming, and livestock grazing during the last 300 years have led to serious degradation of the natural habitat of north-central Chile (Bahre 1979). An assessment of the conservation status and priorities for Chilean mammals (Cofré and Marquet 1999) stressed the high levels of endemism characterizing north-central Chile; yet $<1\%$ of the habitat is protected in reserves or national parks. Dias (1996) argued for the importance of identifying refuge habitats for conservation purposes, regardless of their spatial extent; aguadas in north-central Chile appear to meet this criterion, although more detailed demographic study is called for to further document local dynamics in this habitat.

Aguadas serve as important habitats for most of the native small mammal species and for some they appear to provide refuges enhancing regional persistence during recurring dry periods. Two of the species primarily restricted to aguadas are endangered (*O. lunatus*) or vulnerable (*A. bennetti*; Cofré and Marquet 1999). In addition to small mammals, aguadas also support diverse assemblages of native plants, invertebrates, birds, and amphibians, and, therefore, are important for regional biodiversity. Traditionally, aguadas have been protected by local tenant farmers who believed that removal of vegetation would cause the water to dry up (Bahre 1979). However, corporate farms are rapidly replacing locally owned farms, and the protection of existing aquadas should be a major conservation objective in long-term planning for the region.

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Literature Cited

Allan, R., J. Lindesay, and D. Parker. 1996. El Niño Southern Oscillation and climatic variability. CSIRO Publishing, Collinwood, Australia.

Armesto, J. J., P. E. Vidiella, and J. R. Gutiérrez. 1993. Plant communities of the fog-free coastal desert of Chile: plant strategies in a fluctuating environment. Revista Chilena de Historia Natural 66:271–282.

Bahre, C. J. 1979. Destruction of the natural vegetation of north-central Chile. University of California Publications in Geography 23:1–118.

Beatley, J. C. 1976. Rainfall and fluctuating plant populations in relation to distributions and numbers of desert rodents in southern Nevada. Oecologia 24:21–42.

Brown, J. H. 1975. Geographical ecology of desert rodents. Pp. 315–341 in Ecology and evolution of communities (M. L. Cody and J. M. Diamond, eds.). Harvard University Press, Belknap Press, Cambridge, Massachusetts.

Brown, J. H., and E. J. Heske. 1990. Temporal changes in a Chihuahuan Desert rodent community. Oikos 59:290–302.

Cofré, H., and P. Marquet. 1999. Conservation status, rarity, and geographic priorities for conservation of Chilean mammals: an assessment. Biological Conservation 88:53–68.

Dias, P. C. 1996. Sources and sinks in population biology. Trends in Ecology and Evolution 11:326–330.

Ernest, S. K. M., J. H. Brown, and R. R. Parmenter. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. Oikos 88:470–482.

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.

Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88: 809–823.

Getz, L. L., and J. E. Hofmann. 1999. Diversity and stability of small mammals in tallgrass prairie habitat in central Illinois, USA. Oikos 85:356–363.

Gilmore, R. R. 1947. Cyclic behavior and economic importance of the rata-muca (*Oryzomys*) in Peru. Journal of Mammalogy 28: 231–241.

Gutiérrez, J. R., P. L. Meserve, S. Herrera, L. C. Contreras, and F. M. Jaksic. 1997. Effects of small mammals and vertebrate predators on vegetation in the Chilean semiarid zone. Oecologia 109:398–406.

Gutiérrez, J. R., P. L. Meserve, F. M. Jaksic, L. C. Contreras, S. Herrera, and H. Vásquez. 1993. Dynamics and structure of vegetation in a Chilean semiarid thorn scrub community. Acta Oecologia 14:271–285.

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

Jaksic, F. M., S. I. Silva, P. L. Meserve, and J. R. Gutiérrez. 1997. A long-term study of vertebrate predator responses to an El Niño (ENSO) disturbance in western South America. Oikos 78:341–354.

Jiménez, J. E., P. Feinsinger, and F. M. Jaksic. 1992. Spatiotemporal patterns of an irruption and decline of small mammals in northcentral Chile. Journal of Mammalogy 73:356–364.

Kareiva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373:299–302.

Kummerow, J. 1966. Aporte al conocimiento de los condiciones climáticas de bosque de Fray Jorge. Boletín Técnico, Facultad de Agronomía, Universidad de Chile 24:21–28.

Lima, M., P. Marquet, and F. Jaksic. 1999. El Niño events, precipitation patterns, and rodent outbreaks are statistically associated in semiarid Chile. Ecography 22:213–218.

Marquet, P. A. 1994. Diversity of small mammals in the Pacific Coastal Desert of Peru and Chile and in the adjacent Andean area: biogeography and community structure. Australian Journal of Zoology 42:527–542.

M'Closkey, R. T. 1972. Temporal changes in populations and species diversity in a California rodent community. Journal of Mammalogy 53:657–676.

M'Closkey, R. T. 1976. Community structure in sympatric rodents. Ecology 57:728–739.

Meserve, P. L. 1981a. Resource partitioning in a Chilean semi-arid small mammal community. Journal of Animal Ecology 50: 745–757.

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

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., J. R. Gutiérrez, J. A. Yunger, L. C. Contreras, and F. M. Jaksic. 1996. Role of biotic interactions in a small mammal assemblage in semiarid Chile. Ecology 77:133–148.

Meserve, P. L., D. A. Kelt, W. B. Milstead, and J. R. Gutiérrez. 2003. Thirteen years of shifting top-down and bottom-up control. BioScience 53:633–646.

Meserve, P. L., and E. R. 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.

Meserve, P. L., W. B. Milstead, J. R. Gutiérrez, and F. M. Jaksic. 1999. The interplay of biotic and abiotic factors in a semiarid Chilean mammal assemblage: results of a long-term experiment. Oikos 85:372–374.

Meserve, P. L., et al. 1995. Heterogeneous responses of small mammals to an El Niño Southern Oscillation event in northcentral semiarid Chile and the importance of ecological scale. Journal of Mammalogy 76:580–595.

Milstead, W. B. 2000. The demographic and genetic structure of arid-land small mammal populations in north-central Chile: rainfall, refuges and ratadas. Ph.D. dissertation, Northern Illinois University, DeKalb.

Muñoz, C. P., and E. V. Pisano. 1947. Estudio de la vegetación y flora de los Parques Nacionales de Fray Jorge y Talinay. Agricultura Técnica 7:71–190.

Murúa, R., L. A. González, and P. L. Meserve. 1986. Population ecology of *Oryzomys longicaudatus* Philippii (Rodentia: Cricetidae) in southern Chile. Journal of Animal Ecology 55:281–293.

National Oceanographic and Atmospheric Administration. 2007. Cold and warm episodes by season. www.noaa.gov/products/analysis_monitoring/ensostuff/enoyears.shtml. Accessed 18 October 2007.

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

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

Philippi, F. 1884. A visit to the northernmost forest of Chile. Journal of Botany 22:201–211.

Redford, K. H., and J. F. Eisenberg. 1992. Mammals of the Neotropics: the southern cone. The University of Chicago Press, Chicago, Illinois.

Schamberger, M., and G. Fulk. 1974. Mamíferos del Parque Nacional Fray Jorge. Idesia (Chile) 3:167–179.

Smith, A. T., and J. M. Vrieze. 1979. Population structure of Everglades rodents: responses to a patchy environment. Journal of Mammalogy 60:778–794.

Stevens, J. 1992. Applied multivariate statistics for the social sciences. Lawrence Erlbaum, Hillsdale, New Jersey.

Towns, D. R., I. A. E. Atkinson, and C. H. Daugherty. 2006. Have the harmful effects of introduced rats on islands been exaggerated? Biological Invasions 8:863–891.

von Ende, C. E. 2001. Repeated-measures analysis: growth and other time-dependent measures. Pp. 134–157 in Design and analysis of ecological experiments (S. M. Scheiner and J. Gurevitch, eds.). 2nd ed. Oxford University Press, New York.

Wolfinger, R., and M. Chang. 1995. Comparing the SAS® GLM and mixed procedures for repeated measures. SUGI Proceedings 1995:1–11.

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