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Characteristics of a terrestrial small mammal assemblage in a temperate rainforest in Chile

Características de un ensamble de micromamíferos terrestres en un bosque higrófilo templado de Chile

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ABSTRACT

Small mammal population fluctuations and aspects of demography were studied over more than 4 years on two 0.81 ha live–trapping grids in a precordilleran primary growth temperate rainforest in southern Chile. Seven species of sigmodontine rodents plus a putative hybrid, and two marsupials were trapped; the majority of recaptures were of four sigmodontine species: *Akodon olivaceus, A. longipilis, A. sanborni,* and *Oryzomys longicaudatus.* Maximum numbers occurred in January-July (late summer to winter months) and minimum in August-December (late winter to early summer months). Annual *A. olivaceus* numbers fluctuated strongly whereas *A. longipilis* and *A. sanborni* remained relatively stable. Numbers of *O. longicaudatus* were sporadic and irruptive. Reproduction was predominantly seasonal, in spring to fall months (September-April) for all species; most recruitment of young occurred in January-May for *Akodon*, but was apparently unrelated to reproduction in *O. longicaudatus. Akodon* had high 30-day survival rates and some individuals lived over two years; survival rates were generally low for *O. longicaudatus.* Additional live-trapping on peripheral lines suggested that movements of *A. olivaceus* during a period of population decline were predominantly unidirectional, but bidirectional for *A. longipilis* when their numbers were relatively stable. Comparisons with precordilleran Argentine forest sharing principal small mammal and dominant tree species indicates that both assemblages are similar in species diversity, densities, and in the chronology of reproduction and population change, but Chilean forests are dissimilar in being dominated by omnivorous *Akodon,* and *O. longicaudatus.* Historically, immigration from nearby forest areas may have resulted in greater homogeneity of small mammal assemblages in Chilean rainforests than in Argentine forests where immigrations from adjacent forests have been more restricted. Compositional differences in the faunas of the two forest regions appear to have been present over at least the last 10,000 yr.

Key words: Small mammals, temperate rainforests, community ecology, Chile, South America.

RESUMEN

Durante un período de más de 4 años se estudiaron las fluctuaciones poblacionales de pequeños mamíferos y los aspectos de demografía, en dos grillas de trampeo vivo de 0.81 ha, en un bosque templado lluvioso de crecimiento primario en el sur de Chile. Se atraparon siete especies de roedores sigmodóntidos más un híbrido putativo, y dos marsupiales; la mayoría de las recapturas fue de cuatro especies de sigmodóntidos: *Akodon olivaceus, A. longipilis, A. sanborni,* y *Oryzomys longicaudatus.* El número más alto se presentó en enero-julio (meses tardíos del verano hasta los de invierno) y el mínimo en agosto-diciembre (meses tardíos del invierno hasta comienzos de verano). Los números anuales de *A. olivaceus* fluctuaron fuertemente, mientras que *A. longipilis* y *A. sanborni* se mantenían relativamente estables. Los números de *O. longicaudatus* eran esporádicos e irruptivos. La reproducción fue estacional, en los meses de primavera hasta los de otoño (septiembre-abril), para todas las especies; la mayor parte del reclutamiento de los jóvenes ocurrió en enero-mayo para *Akodon*, y no estaba relacionado con la reproducción en *O. longicaudatus. Akodon* mostró altas tasas de sobrevivencia de 30 días y algunos individuos vivieron sobre los dos años; la sobrevivencia fue baja para *O. longicaudatus.* Los trampeos vivos sobre líneas periféricas insinuaron que los movimientos de *A. olivaceus* durante el período de declinación poblacional fueron predominantemente unidireccionales, pero bidireccionales para *A. longipilis* cuando sus números fueron relativamente estables. Las comparaciones con bosques precordilleranos de Argentina que comparten los principales mamíferos y especies arbóreas dominantes, indican que ambos ensambles son similares en cuanto a diversidad de especies, densidades, y en la cronología de reproducción y el cambio poblacional, pero los bosques chilenos son disímiles en cuanto a la dominancia del onmívoro *Akodon* y *O. longicaudatus.* Históricamente, la inmigración desde áreas boscosas cercanas puede haber resultado en una mayor homogeneidad de los ensambles de pequeños mamíferos en los bosques lluviosos de Chile que en los bosques de Argentina, donde las inmigraciones desde áreas adyacentes han sido más restringidas. Las diferencias en cuanto a composición en las faunas de las dos regiones forestales parecen haber estado presentes por al menos los últimos 10.000 años.

Palabras claves: Pequeños mamíferos, bosques templados lluviosos, ecología de comunidades, Chile, Sudamérica.

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INTRODUCTION

Quantitative descriptions of small mammal demography and dynamics are lacking for most Neotropical rainforests. However, recent studies of indigenous small mammal faunas inhabiting undisturbed primary growth temperate rainforests in southern South America have shown a surprising diversity and abundance (Meserve *et al.*, 1982, Pearson & Pearson 1982, Pearson 1983, Patterson *et al.*, 1989). Up to two species of marsupials and seven species of rodents have been found in forests on opposite sides of the Andes at approximately 41°S latitude in Chile and Argentina. Precordilleran forests between 100-1,000 m elevation in this region have high annual rainfall [2,000-3,000 mm with approximately two thirds in cooler fall to winter months (April-September)], and moderate temperatures with only occasional snow cover (Dimitri 1972, Heusser 1974, di Castri & Hajek 1976, Pearson & Pearson 1982, Pearson 1983). Vegetative cover is dominated by tall (up to 30 m) overstory trees with a dense understory layer, and a diverse groundstory flora of shrubs, lianas, herbaceous plants, mosses, ferns and fungi. Major plant species shared on both sides of the Andes include coihue (*Nothofagus dombeyi* Blume 1850), and mañio (*Saxegothaea conspicua* Lindl. 1851), as well as many overstory and understory trees, shrubs and lianas. These forests are classified as temperate broad-leaved rainforests with conifers admixed (Veblen *et al.*, 1983). Small mammal species shared between Chilean and Argentine forests include the marsupial *Dromiciops australis* (Philippi 1894), and the sigmodontine rodents *Akodon olivaceus* (Waterhouse 1837), *A. longipilis* (Waterhouse 1837), *Oryzomys longicaudatus* (Bennett 1832), *Geoxus valdivianus* (Philippi 1858), *Chelemys macronyx* (Thomas 1894), *Auliscomys micropus* (Waterhouse 1837), and *Irenomys tarsalis* (Philippi 1900). Argentine forests however appear to lack the marsupial *Rhyncholestes raphanurus* Osgood 1924 (although present 15 km W Argentina at Peulla, Chile; Kelt & Martínez 1989), and the rodent *Akodon sanborni* Osgood 1943 (although recorded at Lago Quillen, Argentina; O.P. Pearson, pers. comm.).

The strong similarities between primary growth forests on opposite sides of the intervening Andes offers opportunities for comparison of small mammal ecological relationships and demographic characteristics. The questions addressed here are: to what extent do small mammal faunas in relatively undisturbed rainforests show similar characteristics in their abundances, demography, reproductive patterns, and other ecological aspects? If major differences exist, are they attributable to historical factors resulting from different opportunities for local colonization, or perhaps to different resource levels? Herein, we report the general features of small mammal population dynamics obtained through four years of sampling in an undisturbed primary growth rainforest in southern Chile and make comparisons with results from neighboring Argentine forests.

MATERIALS AND METHODS

Between December 1980 and May 1985, live-trapping studies were conducted in the precordilleran Andes (Parque Nacional Vicente Pérez Rosales, NW Volcan Osorno; 41°02'S, 72°30'W; 84 km ESE Osorno, X Región, Chile). The locality ("La Picada") contains virtually undisturbed Valdivian temperate rainforest between the lower park boundary (400 m) to tree line (1,100 m). The vegetation has been qualitatively described (Meserve *et al.*, 1982), 1988; Patterson *et al.*, 1989). The two sites (Plots 1 and 2, respectively) fall approximately into Type 6 and Type 7 categories of *Nothofagus dombeyi*-dominated Valdivian forests in the mid-elevational (400-950 m) precordilleran Andes of the Chilean Lake District (Veblen *et al.*, 1983). Quantitative vegetation analysis was conducted in summer (January-March) 1984, and repeated for certain components in winter (July-August) 1984 using point-centered quarter quadrats at each trap station (Mueller-Dombois & Ellenberg 1974). Measurements included canopy cover (using vertical photographs taken with a 35 mm camera and 35 mm lens measuring a 63° field), number of fallen logs (⩾ 7.2 cm diameter), estimations and tabulations of shrub cover, ground cover, number of shrub and tree species, and number of individual trees within a 5 m radius of each station, soil hardness (with a soil penetrometer; Soiltest Inc., Chicago, IL), and distance, diameter, and species of the nearest tree (⩾ 7.2 cm dbh) within 5 m of the stations in each 90° quadrat.

Live-trapping was initiated on a 10 x 10 grid (Plot 1; 10 m interval; total area = 0.81 ha) located at 445 m elevation in December 1980. A single medium Sherman trap was placed within 1 m of each station, covered by a wooden board, and baited with rolled oats. Traps were checked twice daily, and animals marked by toe-clipping or ear-tagging. Standard data were taken from each animal during handling; age was based on body weight following Murúa & González (1985, 1986) and Murúa *et al.* (1987). For *Akodon olivaceus*, juveniles were < 12.0 g, subadults 12.0-17.9 g, and adults ⩾ 18.0 g; for *A. longipilis, A. sanborni,* and *Oryzomys longicaudatus*, juveniles were < 14.0 g, subadults 14.0-19.9 g, and adults ⩾ 20.0 g. Observations on sexual/reproductive condition included for males: scrotal or abdominal testes; and for females: perforate or imperforate; pregnant or lactating status. Until August 1983, census intervals varied from 2 to 7 months and duration from 4 to 6 consecutive nights; thereafter, census intervals were 30 days through January 1985 consisting of 6 consecutive nights/census; a final census occurred in May 1985. In November 1983, trapping was initiated on a second 10 x 10-0.81 ha grid (595 m; Plot 2) 2.4 km SE Plot 1, with identical chronology, duration, and procedures as on Plot 1 thereafter.

Although the results of Patterson *et al.* (1989) suggested potential bias using live-traps vs. Museum Special snap-traps in assessing small mammal abundance and diversity, comparison of results here with those from simultaneous snap trapping on nearby (0.3-2.0 km) lines showed no significant differences between different trap results for *Akodon* and *O. longicaudatus* on/near Plot 1 (all $X^2 < 2.91$, $p > 0.05$); small sample sizes for other species precluded use of X^2 tests. Although most comparisons were significant for results from on/near Plot 2 with snap-traps capturing higher numbers of small mammal species (all $X^2 > 4.29$, $p < 0.05$; *Akodon longipilis, A. sanborni, Oryzomys longicaudatus,* and *Dromiciops australis*: $X^2 > 11.55$, $p < 0.001$), this could reflect significant faunal changes known to occur above Plot 2 (about 700 m; Patterson *et al.*, 1989) where snap–traps may have been sampling compositionally different mammal assemblages. Although we recognize that live-trapping methods may possess inherent biases with respect to sampling some species in these forests, it is the only way to collect information on critical demographic parameters (e.g., reproduction, survival rates, recruitment) without altering the assemblage composition through removal.

Demographic analyses of live-trap data were conducted with the CMR package on the NIU, and Université Catholique de Louvain, Louvain-la-Neuve, Belgium, computer facilities (Le Boulengé 1985: Meserve & Le Boulengé 1987). These programs yield computational analyses of mark-recapture data such as the Calender of Captures (Petrusewicz & Andrzejewski 1962), minimum number known alive tabulations (Krebs 1966), reproductive condition, survivorship, and body weight trends. For purposes of population estimation, the minimum number known alive was used since an average 84% or more of the individuals of the four major small mammal species were caught each census (Hilborn *et al.*, 1976). Reproductive trends were based on proportions of scrotal vs. abdominal males, and pregnant or lactating females. Thirty-day survivorship rates were determined by the proportion of individuals surviving between consecutive censuses; period analyzed was August 1983-January 1985 when censuses were at uniform intervals. Animals dying in traps were excluded from survivorship tabulations. During September-December 1984, peripheral line live-trapping was conducted at varying distances (0.1-0.7 km) from plots in similar forest habitat, and significant movements documented for some species.

Pearson & Pearson (1982)'s Table 1 was utilized to compare small mammal data for corresponding time periods at two Argentine sites, Puerto Blest (770 m) and Rio Castaño Overo (950 m). These sites are dominated by *Nothofagus dombeyi* similar to La Picada, but are in Type 8 and 10, respectively, of mid –to high– elevational Valdivian forest categories (Veblen *et al.*, 1983). We followed the procedure of Pearson & Pearson (1982) of adding a boundary area to each grid perimeter equal to the mean maximum distance between captures to determine the effective trapping area. These were calculated separately for *A. olivaceus*, all other *Akodon* sp., *O. longicaudatus*, and the remaining species (mean of above estimates) for each period.

RESULTS

Vegetation

Table 1 presents vegetation analysis results (nomenclature follows Muñoz 1980, and Hoffmann 1982). Both plots were similar in canopy and shrub cover, numbers of shrub and tree species, and tree density. Despite this, Plot 2 had almost twice the total basal area of trees indicating dominance by larger, older individuals. Two species (*Nothofagus dombeyi* and *Weinmannia trichosperma* Cav. 1759) accounted for 67.3% and 74.9% of the basal area, and 42.3% and 43.8% of all individuals, on Plots 1 and 2, respectively. *Saxegothaea conspicua* Lindl. 1851 and *Amomyrtus meli* (Phil. 1856) were important overstory, and understory trees, respectively, on Plot

TABLE 1

Vegetation characteristics of two live-trapping grids in La Picada, Chile during summer and winter 1984

Características de la vegetación de dos grillas de trampas vivas en La Picada, Chile durante el verano e invierno de 1984

	Plot 1		Plot 2	
	Summer	Winter	Summer	Winter
Canopy cover, %	88.7	87.3	88.6	89.8
Number of fallen logs, 5 m radius	8.6	–	10.5	–
Shrub cover, %, 5 m radius	48.8	–	50.4	–
Number of shrub species, 5 m radius	8.5	10.6	9.5	10.6
%Ground cover (2 and 4 m radius) Bare ground	39.2	33.6	48.5	40.3
Herbaceous	39.9	43.3	30.6	35.2
Trunk and fallen logs	20.9	23.1	20.9	24.5
Soil hardness	0.73	–	0.42	–
Tree density (5 m radius)	7.9	–	8.2	–
Number of tree species (5 m radius)	3.5	–	3.6	–
Basal area of trees ($cm^2/100\ m^2$)	4,584.2	–	8,790.0	–

2; *Eucryphia cordifolia* Cav. 1797, and *Drimys winteri* J.R. et G. Forster 1776 were similarily important on Plot 1. At least 12 tree species were present on each plot. Important shrub species and lianas on both plots included *Berberis* spp. Linn. 1737, *Pernettya* spp. Gaudich 1825, *Gaultheria* spp. Kalm 1751, *Griselinia racemosa* (Phil 1856), *Luzuriaga* spp. Ruiz et Pav. 1802, and *Philesia magellanica* J.F. Gmel. 1789. Bamboo (*Chusquea* spp. Kunth 1822) is an important groundstory species forming dense thickets in many Argentine and Chilean forests, but was only moderately abundant in the heavily shaded forest interior. Plot 2 had a higher proportion of bare ground cover relative to herbaceous cover, and more fallen logs although trunk/log cover was similar. Soils in Plot 2 were generally softer probably reflecting a higher organic content in the thin A horizon (25-50 cm) overlying the B horizon consisting of granular pumice. Herbaceous cover and fallen debris increased in winter months on both plots relative to bare ground probably due to increased windfall, precipitation, and soil decomposition. The increase in shrub species number in winter may reflect a deciduous tendency for some shrubs in summer.

Small mammal diversity

25,400 trap-nights of effort yielded 4675 captures (18.4% success) of 647 individuals of nine small mammal species plus putative *Akodon longipilis* X *A. sanborni* hybrids. *A. longipilis and A. sanborni* are considered by Reig (1987) to be in the subgenus *Abrothrix*, and *A. olivaceus* in the subgenus *Akodon*; however, A. Spotorno (pers. comm.) considers all of three species to be in the genus/subgenus *Abrothrix*. Putative hybrids comprised 17.8% and 10.2% of all *Abrothrix* (*sensu* Reig 1987) on Plots 1 and 2, respectively. Trapping success was higher on Plot 2 than Plot 1 ($\overline{X}$ = 22.0% versus 16.2%, respectively) due to higher numbers of captures/individual (Plot 2: $\overline{X}$ = 9.26, Plot 1: $\overline{X}$ = 6.12). There was a tendency for more diurnal captures during warmer summer months (November-February) than in winter months (May-August) although the shorter daylength in the latter period may have influence capture rates. Excluding hybrids, Plots 1 and 2 had similar numbers of species/census ($\overline{X}$ = 4.37 ± 1.08, 1SD versus $\overline{X}$ = 4.56 ± 0.63, respectively) although one species (*Auliscomys micropus*) was absent from Plot 1. The Shannon diversity index (Brower & Zar 1984; $\log_e$) indicated higher species diversity for Plot 1 than for Plot 2 (H' = 1.134 vs. 0.988, respectively) due partially to species evenness (J' = 0.52, and 0.45 for Plot 1, and 2, respectively) and more captures of rarer species (i.e., *Irenomys tarsalis, Geoxus valdivianus*, and *Rhyncholestes raphanurus*) on Plot 1. *R. raphanurus* was the fourth most abundant species in numbers after *A. olivaceus, A. longipilis*, and *O. longicaudatus* (40 individuals); but only 3 recaptures were recorded in more than four years. Only 23 individuals were captured of *Dromiciops australis, Geoxus valdivianus, Auliscomys micropus*, and *Irenomys tarsalis*, and only the latter species recaptured. While this may reflect a trapping bias (i.e., *D. australis*; Patterson *et al.*, 1989), other species (i.e., *A. micropus*) may also be scarce in dense forest.

Population trends

Population trends for all species are shown in Fig. 1. Typically, increases in populations occurred in late summer to winter months (January-July), and decreases in late winter to early summer months (August-December). Excluding putative hybrids, 88.8%, and 93.2% of the individuals captured on Plots 1, and 2, respectively, consisted of four species: *Akodon olivaceus, A. longipilis, A. sanborni*, and *Oryzomys longicaudatus*. Fig. 2 presents the minimum number known alive numbers for these species during 1980-1985. Although *A. olivaceus* and *A. longipilis* were continually resident on both plots, demographic trends were distinct. *A. olivaceus* populations had large increases in summer and early winter, and sharp declines in late winter to sping. In contrast, *A. longipilis* had relatively stable numbers of individuals with only gradual increases and declines. *A. sanborni* was

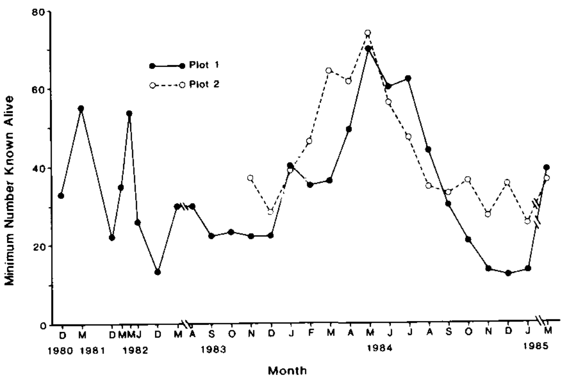

Fig. 1: Minimum number known alive trends for all small mammal species on Plots 1 and 2 at La Picada during December 1980-May 1985. Letters on abcissa indicate month of the census; time scales have been truncated prior to August 1983, and following January 1985 due to irregular census intervals.

Tendencias de número mínimo conocido vivo para todas las especies de micromamíferos en Grillas 1 y 2 en La Picada durante diciembre 1980-mayo 1985. Letras sobre la abscisa indican mes del censo; las escalas de tiempo han sido truncadas antes de agosto 1983, y después de enero 1985 debido a los intervalos irregulares entre censos.

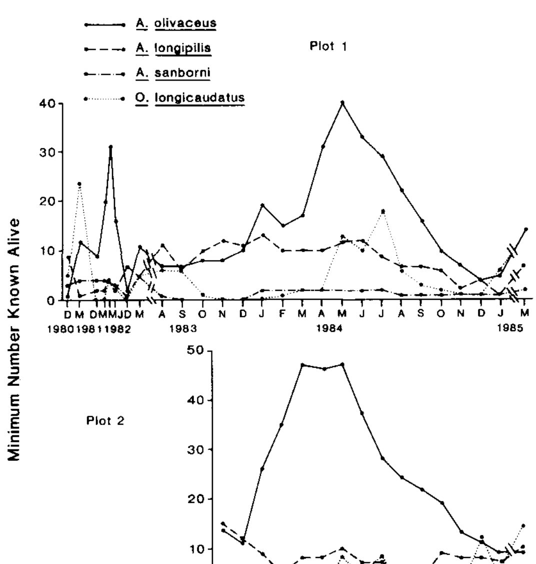

Fig. 2: Minimum number known alive trends for the four principal small mammal species on Plots 1 and 2 at La Picada during December 1980-May 1985. Explanation of letters on abcissa, and scaling are as in Fig. 1.

Tendencias de número mínimo conocido vivo para las cuatro especies principales de micromamíferos en Grillas 1 y 2 en La Picada durante diciembre 1980-mayo 1985. La explicación de las letras sobre la abscisa, y la escala son como en la Fig. 1.

continually resident fluctuating between one and five individuals except for September-December 1983 on Plot 1 when it was absent. Numbers of *O. longicaudatus* were extremely variable, and this species was absent from Plots 1 and 2 for 6/27, and 5/16 censuses, respectively.

Thirty-day survival rates and longevity

Thirty-day survival rates for the period of September 1983 through January 1985 are shown in Fig. 3. Although *A. olivaceus* maintained high 30-day survival rates (Plot 1: $\overline{X} = 69.5 \pm 18.4\%$, 1SD; Plot 2: $\overline{X} = 75.9 \pm 11.8\%$), lower rates were present in summer months (December-Febru-

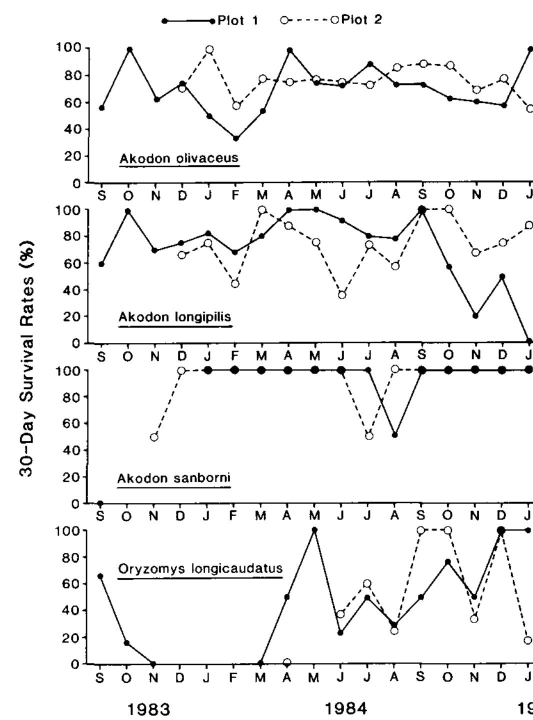

Fig. 3: Thirty-day survival rates for the four principal small mammal species on Plots 1 and 2 at La Picada during September 1983-January 1985. The single point for *O. longicaudatus* in April 1984 on Grid 2 indicates a 30 survivorship rate of 0% for individuals captured in March 1984; no new individuals were captured until May 1984 on Grid 2.

Tasas de sobrevivencia de treinta días para las cuatro especies principales de micromamíferos en Grillas 1 y 2 en La Picada durante septiembre 1983-enero 1985. El punto solitario para *O. longicaudatus* en abril 1984 en la Grilla 2 indica una tasa de sobrevivencia de treinta días de 0% para individuos capturados en marzo de 1984; no hubo capturas de nuevos individuos hasta mayo de 1984 en Grilla 2.

ary) when populations were lowest indicating high turnover of individuals. In contrast, although mean 30-day survival rates for *A. longipilis* were about the same (Plot 1: $\overline{X}$ = 71.3 ± 28.0%; Plot 2: $\overline{X}$ = 74.6 ± 19.6%), rates as low as those of *A. olivaceus* were present only towards the end of the study on Plot 1 (Fig. 3). *A. sanborni* had high 30-day survival rates (Plot 1: $\overline{X}$ = 95.8 ± 14.4%; Plot 2: $\overline{X}$ = 92.9 ± 18.2%); in 11/13, and 12/14 months, respectively, 30 day survival rates were 100%. Finally, *O. longicaudatus* had low and highly variable survival rates (Plot 1: $\overline{X}$ = 50.1 ± 34.4%; Plot 2: $\overline{X}$ = 53.0 ± 39.1%) with no consistent seasonal pattern (Fig. 3).

Some individual *Akodon* had unusual longevity. Ten *A. olivaceus* (4.6%) were caught over 12 + months ($\overline{X}$ = 13.8 ± 1.8 [1SD] months; maximum = 18 months); six *A. longipilis* (5.2%) survived 12 + months ($\overline{X}$ = 16.8 ± 4.3 months; maximum = 25 months), and five *A. sanborni* (22.7%) survived 12 + months ($\overline{X}$ = 15.6 ± 1.9 months; maximum = 18 months). Six putative *A. longipilis* X *A. sanborni* hybrids (24.0%) survived 12 + months ($\overline{X}$ = 14.3 ± 2.6 months; maximum = 18 months). Since most *Akodon* spp. were adults at first capture, field longevity may be as long as 26-28 months in this genus. In contrast, only two of 148 *O. longicaudatus* individuals were captured over more than 5 months (both for 8 months).

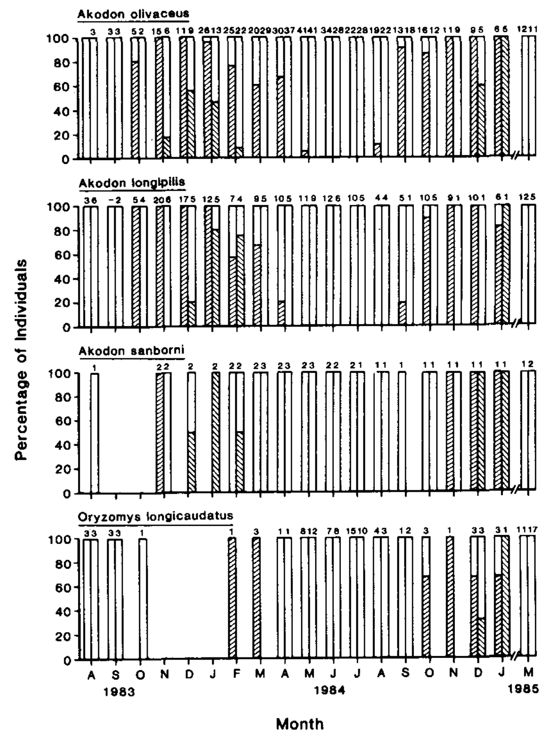

Fig. 4: Percentages of reproductive individuals for the four principal small mammal species for both plots combined at La Picada during August 1983-May 1985. Hatched columns to left of months are percentages of scrotal males, and those to the right are percentages of pregnant/lactating females. Sample sizes are indicated by numbers over respective columns.

Porcentajes de individuos reproductivos para las cuatro especies principales de micromamíferos en las dos grillas combinadas en La Picada durante agosto 1983-mayo 1985. Las columnas con achurado a la izquierda de los meses corresponden a porcentajes de machos escrotales, y a la derecha a porcentajes de hembras preñadas/lactantes. El tamaño de las muestras se indica sobre las columnas respectivas.

Reproductive trends, age structure, and movements

Reproductive trends for the four major small mammal species on the live trap grids are presented in Fig. 4. *A. olivaceus* had the broadest period of sexual and reproductive activity with scrotal males between October and May, and pregnant or lactating females between November and April; however, snap-trap results indicated the presence of pregnant females also in October 1984. *A. longipilis* has a narrower period of reproduction on the grids with scrotal males between October and April, and pregnant or lactating females between December and February; however, snap-trap results showed the presence of pregnant females in March, and October 1984. *A. sanborni* also had a narrower reproductive period than *A. olivaceus* on the grids with scrotal males between November and February, and pregnant or lactating females between November and January; again, snap-trap results indicated that scrotal males were present in October 1984, and reproduction continued into March 1984 for both sexes. The onset of sexual competency for male *A. olivaceus* and *A. longipilis* was advanced by one to two months in 1984 compared to 1983 suggesting yearly reproductive variation; however, pregnant or lactating females did not appear earlier on the grids in 1984. *O. longicaudatus* had scrotal males in February, March and October 1984; pregnant or lactating females were recorded in December-January 1984-85 on the grids, but also in February-April 1984 as determined by snap-trapping. Estimates of litter size for these species from irregular snap-trapping efforts indicate that *A. olivaceus* had a mean placental scar/embryo count of 5.00 ± 1.51 (1SD, N = 8) versus 2.75 ± 1.06 (N = 16) for *A. longipilis*, and 2.75 ± 0.96 (N = 4) for *A. sanborni*. *O. longicaudatus* had a mean placental scar/embryo count of 4.00 ± 1.91 (N = 7), and was the only species with recent scars in winter months (May-August) suggesting the presence of a less pronounced seasonal reproductive pattern than *Akodon* spp.

Body weight was only an approximate indicator of age, as many *Akodon* individuals initially caught at subadult weights in April-May did not show significant weight gains until the following spring months (September-October); chronologically, these were considered adults in their third month of residence. *A. olivaceus* males as small as 9.5 gm were detected with scrotal testes. Juvenile *A. olivaceus* were trapped in January-April 1984, and April 1984. Juvenile *A. longipilis* and *A. sanborni* were present only in January 1984, and new subadults between January and July. In contrast, *Q. longicaudatus* juveniles and new subadults were trapped sporadically in virtually all seasons. Thus, there is an unclear relationship between recruitment and reproduction in this species.

A trapping effort of 1640 trap-nights on peripheral live-trap lines yielded 259 captures (15.8% success) including 14 previously marked *A. olivaceus*, 8 *A. longipilis*, and 1 *O. longicaudatus* at distances up to 0.7 km from the plots in similar, but not always contiguous forest habitat. Some individuals were live-trapped up to one year after their last grid capture indicating that they had shifted residence. Of animals that had been previously resident on the grid within one to two months, 4/11 *A. olivaceus*, and 5/6 *A. longipilis* returned to the live-trap grids in the same or following months. One *A. longipilis* male moved 0.7 km from the grid to a peripheral trap line and back again within 48 hr. Thus, a much lower proportion of *A. olivaceus* individuals made return movements to the grid in the September-December 1984 period as compared to *A. longipilis*, and some *Akodon* individuals possessed high vagility.

Comparison of Argentine and Chilean Forest Assemblages

Based on comparisons of the data of Pearson & Pearson (1982) with those here for similar months (November and May 1983-1985 which are approximately the periods of minimum and maximum numbers and biomass; Table 2), it is notable that Chilean and Argentine forests support similar species numbers (total of 9 including *Dromiciops australis*, an abundant species in La Picada; Patterson *et al.*, 1989), diversities ($\overline{X}$ = 1.096 in Chile vs. 1.087 in Argentina), and total densities.

DISCUSSION

Primary growth temperate rainforests of southern Chile are characterized by a diverse small mammal fauna of up to nine species, but the majority of individuals are *Akodon* and *O. longicaudatus*. *A. olivaceus* is numerically the most important, but shows strong seasonal fluctuations such that in summer months, other *Akodon* species with higher survival rates and more stable numbers are often more abundant. The fluctuations of *A. olivaceus* suggets an intrinsic annual cycle similar to populations in secondary growth rainforests near the Chilean coast (i.e., San Martín; Murúa & González 1985, 1986). Peripheral live-trapping indicated that net movement by this species was predominantly unidirectional in September-December 1984 emphasizing the role of dispersal. In contrast, *A. longipilis* individuals had fewer unidirectional movements from trapping grids to peripheral forest habitat. In San Martín, *A. olivaceus* may disappear entirely in summer

TABLE 2

Density and biomass of small mammals at forest sites in Argentina and Chile during April-May and November

Densidad y biomasa de micromamíferos en sitios de bosque en Argentina y Chile durante abril-mayo y noviembre

	La Picada								Argentina							
	Nov. 1983 Plot 1	Nov. 1983 Plot 2	May 1984 Plot 1	May 1984 Plot 2	Nov. 1984 Plot 1	Nov. 1984 Plot 2	May 1985 Plot 1	May 1985 Plot 2	May 1978 Pto. Blest	May 1978 R.C. Overo	Nov. 1978 Pto. Blest	Nov. 1978 R.C. Overo	Nov. 1979 Pto. Blest	Nov. 1979 R.C. Overo	Apr. 1980 Pto. Blest	Apr. 1980 R.C. Overo
Thyncholestes raphanurus																
Density				0.8			0.7	0.3								
Biomass				28			15	9								
Dromiciops australis																
Density	a	a	a	a	a	a	a	a			0.2	0.5			0.5	
Biomasss											5	12			9	
Akodon olivaceus																
Density	2.5	4.0	15.7	17.5	2.7	3.8	3.7	2.7		7.2		1.2				4.2
Biomass	65	104	324	373	61	97	92	63		191		39				104
Akodon longipilis																
Density	2.9	5.3	4.8	3.1	0.7	1.8	2.5	4.1	2.8	4.9	2.9	3.1		4.8	3.9	9.4
Biomass	93	173	104	76	22	57	60	125	87	168	106	111		186	115	296
Akodon sanborni																
Density		1.4	0.8	0.9	0.4	0.2	0.7	0.4								
Biomass		45	17	24	11	8	20	12								
Akodon sp.																
Density	0.5	0.7	1.2	1.2	0.4	0.7		0.4								
Biomass	14	24	29	29	10	21		10								
Oryzomys longicaudatus																
Density			6.1	3.6	0.4	0.6	6.7	4.0	0.3	0.3					5.4	
Biomass			133	74	12	18	179	94	15	10					115	
Irenomys tarsalis																
Density		0.3							5.1		1.4				2.1	
Biomass		14							209		79				76	
Geoxus valdivianus																
Density					0.4					0.4		0.4			0.4	
Biomass					11					9		10			11	
Chelemys macronyx																
Density										14.7		1.1		1.5		3.8
Biomass										903		84		110		207
Autiscomys micropus																
Density		0.3								0.9		1.1				4.1
Biomass		18								56		91				238
Rattus sp.																
Density											0.2					
Biomass											10					
Number of Species	2	5	4	5	5	4	5	5	3	6	4	6	–	2	5	4
Total Density	5.9	12.0	28.6	27.1	5.0	7.1	14.3	11.9	8.2	28.4	8.6	7.4	–	6.3	12.3	21.5
Total Biomass	172	378	607	604	127	201	366	313	311	1,337	200	347	–	296	326	845
Diversity, H', ln	0.69	1.17	1.06	1.02	1.24	0.99	1.31	1.29	0.78	1.21	0.93	1.57	–	0.55	1.27	1.30

[a] Species known to be common from snap trapping (Patterson *et al.*, 1989)

months although they persist at low numbers in adjacent shrubland-grassland habitats; *A. longipilis* numbers are generally very low in San Martín, however. *O. longicaudatus* also has strong annual cycles in these coastal forests (Murúa & González 1986; Murúa *et al.*, 1986); those in La Picada were highly sporadic and irruptive with an unclear relationship between *in situ* reproduction and recruitment. For *Akodon*, reproduction is strongly seasonal in all forests compared here. Recruitment of younger individuals into trappable populations occurs earlier in Argentine forests than in Chilean ones (cf. Pearson 1983). In La Picada, population increases often occur in wetter, cooler late fall to winter months after reproduction has ceased. Hence, there is a time lag between reproduction and the largest numerical changes in the populations, particularly those of *Akodon.* The appearance of new adult and subadult individuals on the La Picada grids in May-July implicates a major role for immigration at that season.

Argentine and Chilean primary growth forests dominated by *Nothofagus dombeyi* in the Andean precordilleran region have been extensively glaciated as recently as 10-11,000 yr. B.P. (Huesser 1981; Porter 1981). The higher elevation of Argentine forests studied by Pearson & Pearson (1982) and Pearson (1983) reflects a rain shadow effect created by the intervening cordillera (Dimitri 1972). The areas have similar amounts of precipitation predominantly in winter months; mean temperatures are somewhat lower in Argentine forests with longer snowfall persistence. Visual comparison of the sites suggests that the canopy of Argentine forests are more open with relatively dense shrubby undergrowth; this is similar to conditions at higher La Picada elevations (above 700 m) where persistent snow cover influences the development of groundstory vegetation (Veblen *et al.*, 1977).

The pattern of *Akodon* spp. and *O. longicaudatus* being the more abundant small mammals in the La Picada forests is repeated throughout southern Chile in coastal secondary growth forests as well as other primary growth forests N of La Picada (Parque Nacional Puyehue) and S through the continental Chile Chico region to Coyhaique (Murúa & González 1985, 1986; Murúa *et al.*, 1986; Meserve *et al.*, 1991). The higher biomass of Argentine forest is due principally to *Chelemys macronyx* (known from higher and lower elevations elsewhere in Chile; Greer 1965; D.R. Martínez, pers. comm.), *Auliscomys micropus*, and *Irenomys tarsalis.* Patterson *et al.* (1989) found that *A. micropus* as well as *Dromiciops australis*, and *Akodon longipilis* were more abundant at higher elevations (above 700 m) in La Picada. *Geoxus valdivianus* appears to be ubiquitous in both Argentine and Chilean forests although nowhere common. The absence of *A. sanborni* and *Rhyncholestes raphanurus* from Argentine forests seems unexplained by the elevational differences since they have been caught at 1,100 m near Lago Quillen, Argentina (first species), and at 1,135 m at La Picada (second species; Patterson *et al.*, 1989).

The role of resource availability and historical factors in affecting demographic changes and faunal composition of the small mammal assemblage in the La Picada rainforest is intriguing. Although climatic conditions are more severe in winter due to occasional snowfall, hailstorms, and generally cooler, wetter conditions, groundstory herbaceous cover and shrub diversity increases in La Picada in those months (Table 1). Phenological observations indicated the presence of fruit and seed-bearing plants in the forest during most months of the year. Pearson and Pearson (1982) commented on the scarcity of mast seeds in Argentine forests; the paucity of tree species on their sites may account for this; only four, and two species are present in Puerto Blest and Rio Castaño Overo, respectively. Qualitative observations of seed and fruit availability in La Picada suggested a fairly constant level of seeds and fruits of overstory and understory trees such as *N. dombeyi, W. trichosperma, Caldcluvia paniculata* (Cav. 1830), *Tepualia stipularis* (H. et A. 1854), *Dasyphyllum diacanthoides* Less. 1959, and *Azara lanceolata* Hook. 1799 in forest litter throughout the year. Armesto *et al.* (1987) emphasized the apparent high availability of seeds and fruits in Chilean temperate rainforests, but suggested that birds and larger mammals (i.e., *Pudu pudu* (Molina, 1782) and omnivorous carnivores) may be more important consumers than small mammals. Additionally, Murúa & González (1981) and Rau *et al.* (1981) noted the failure of many rainforest seeds to be utilized by *Akodon* and *O. longicaudatus* in laboratory feeding trials and in the field. *O. longicaudatus* is highly granivorous in all habitats examined (Meserve 1981, Meserve *et al.*, 1988, Murúa & González 1981), and its unstable demography and residence in La Picada populations may reflect the low availability of certain highly utilized seeds in these forest.

Consumption of arthropods by *Akodon* decreased in fall to winter months (Meserve *et al.*, 1988), but increased rapidly afterwards. Higher arthropod consumption in spring to summer months especially by the more omnivorous *A. olivaceus* during periods of population declines does not implicate resource availability as a limiting factor. The more mycophagous *Akodon*, especially *A. longipilis* and *A. sanborni*, shifted to larger amounts of fungi in winter months when that resource probably increases (Meserve *et al.*, 1988); yet, the latter two species did not demonstrate large increases then. In summer months, *D. australis* and *A. micropus* are predominantly animalivorous, and granivorous-frugivorous, respectively, and these resources may be more abundant in open, scrubby habitats where they tend to occur. Meserve *et al.* (1988) noted both *Rhyncholestes raphanurus* and *G. valdivianus* to be relatively animalivorous although also consuming fungi and herbaceous material, and *Chelemys* appears to be primarily frugivorous-omnivorous (Pearson 1983, 1984).

Other major differences between Argentine and Chilean forests are in the proportions of small mammal biomass composed of various consumer groups. Following the above designations, a mean 80.0% of the biomass of small mammals in Table 2 was omnivorous at La Picada; only 17.5%, and 2.5% were granivorous-frugivorous/herbivorous, and animalivorous, respectively. In contrast, in Argentine coihue forests (Table 2) a mean 65.0% of the small mammal biomass was omnivorous in contrast to 32.8%, and 2.2% granivorous-frugivorous/herbivorous, and animalivorous species' biomasses, respectively. Much of the omnivore biomass in Argentine forests is due to the relatively large bodied *Chelemys*. Similarly, larger and more stenophagic frugivorous/granivorous forms such as *Irenomys* and *Auliscomys* make a bigger contribution to Argentine forest small mammal biomass. Interestingly, based on detailed dietary analyses at La Picada (Meserve *et al.*, 1988), if the om--nivorous species' diets there are partitioned into granivorous/frugivorous/herbivorous, and animalivorous components, proportions of Chilean small mammal biomass are allocated more similarly to respective dietary categories in Argentine forests. Thus, differences between Argentine and Chilean rainforest small mammal assemblages reflect the greater importance of more omnivorous *Akodon* in the latter versus a greater contribution by more stenophagic and/or larger non-*Akodon* species in the former.

Biogeographically, the greater proximity of precordilleran Valdivian forests in Chile to historically contiguous forests in the central valley and coast ranges may have resulted in a more homogeneous mixture of species; in contrast, Argentine forests are climatically restricted to a narrow band along the eastern side of the Andes bordered by the arid Patagonian steppes. Hence, recent dispersal of typically forest forms into Argentine forests has had to occur along or across the Andes whereas Chilean forests have probably had more frequent entries of small mammals via the Andes, and Chilean central valley plus coastal regions. Argentine forests seem to contain a more heterogeneous assemblage of consumer groups and taxa; in contrast, Chilean forests are characterized by a more homogeneous group of widespread, and predominantly omnivorous species such as *Akodon* plus the granivorous *O. longicaudatus*. Argentine forests have had little immigration from adjacent steppe regions;

rather, a spillover of forest species into shrub-steppe habitats occurs (Pearson & Pearson 1982, Pearson 1987). In contrast, Chilean forests have had little contact with steppe species except in the extreme southern Patagonian region. Analyses of mammal remains in the Traful Valley, Neuquen Province NE of the Argentine forests indicate a very stable composition of small mammal assemblages for the last 10,000 yr (Pearson & Pearson 1982, Pearson 1987). Thus, the factors that have led to the present compositional differences between Chilean and Argentine forests have been fairly long-term.

The interplay between such historical factors appears to have had major consequences for the relative contribution of various trophic groups and taxa to the small mammal assemblages on opposite sides of the Andes. Despite this, however, forest communities support similar densities and diversities of small mammals and contain representatives of most of the same species.

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