

Regulation of numbers in two Neotropical rodent species in southern Chile

Regulación de los números en dos especies de roedores neotropicales en el sur de Chile

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ABSTRACT

The two co-dominant small mammal species in a southern Chilean rain forest community. *Akodon olivaceus brachiotis* and *Oryzomys longicaudatus philippii* showed density patterns with both betweenyears and seasonal fluctuations. *Akodon olivaceus* exhibited a four -or five- year cycle and *O. longicaudatus* a two-year cycle. Despite the complexity of factors involved in the regulation of numbers of these species, some can be recognized. For *A. olivaceus* these factors are: the age composition of the breeding stock, the differential survival of cohorts, and presaturation dispersal. Environmental heterogeneity provides a dispersal sink that can be colonized every year. In *O. longicaudatus* two factors are important: saturation and presaturation dispersal, and the seed availability in the habitat.

Key words: Neotropical mammals, cricetid rodents, population cycles, population regulation, *Akodon olivaceus*, *Oryzomys longicaudatus*.

RESUMEN

Las dos especies de pequeños mamíferos codominantes en la comunidad de bosque higrófilo templado, *Akodon olivaceus brachiotis* y *Oryzomys longicaudatus philippii*, presentan fluctuaciones en su densidad tanto estacionales como multianuales. *Akodon olivaceus* muestra un ciclo de mayor abundancia cada cinco años, mientras que este ciclo es cada dos años en *O. longicaudatus*. Es posible reconocer algunos factores asociados a la regulación de los números de estas especies. En *A. olivaceus* son importantes la composición de edades de los individuos que inician la reproducción del año, la sobrevivencia diferencial de las cohortes y la dispersión de presaturación. La heterogeneidad ambiental proporciona áreas de dispersión (dispersal sink) que son colonizadas anualmente. En *O. longicaudatus* son importantes la dispersión tanto de saturación como de presaturación y la cantidad de semillas disponibles cada año en el hábitat.

Palabras claves: mamíferos neotropicales, roedores cricétidos, ciclos poblacionales, regulación poblacional, *Akodon olivaceus* y *Oryzomys longicaudatus*.

INTRODUCTION

The distribution of the southern temperate rain forest in Chile is between approximately 38° S and 42° S. In this forest, there are up to ten species of small mammals in two orders, Rodentia and Marsupialia. The most diverse rodent family is the Cricetidae, which includes two abundant species, *Akodon olivaceus brachiotis* and *Oryzomys longicaudatus philippii*. These are the typical co-dominant species during most of the year, particularly in secondary growth forests (Murúa *et al.* 1982). Both

species have been thoroughly studied since 1978, considering several ecological attributes that include food habits, habitat characteristics, temporal activity and population dynamics.

The results have shown marked differences in three niche dimensions of *A. olivaceus* and *O. longicaudatus*. Regarding habitat, the former species prefers patches with dense herb cover whereas *O. longicaudatus* is associated with high foliage density at 15 cm (Murúa & González 1982). Food habits in both cafeteria tests and in the field show a clear tendency

for *Oryzomys* to be granivorous, whereas *Akodon* appears to be omnivorous (Murúa *et al.* 1980, Murúa & González 1981). With regard to temporal activity, *A. olivaceus* is a crepuscular and nocturnal species whereas *O. longicaudatus* is strictly nocturnal (Murúa *et al.* 1982, Feito & Ortega 1981). Additional differences have been found in their spatial distributions and home ranges. *Akodon* shows an aggregated distribution throughout the year suggesting a colonial social organization whereas *Oryzomys* shows aggregations only during spring, with solitary individuals moving extensively the rest of the year (Murúa & González 1979, Murúa & González 1982).

Density estimates for the two species have also shown important differences when population fluctuations are followed in successive years. Although both species show a multi-year cycle, *Oryzomys* has a two-year cycle of abundance (Murúa *et al.* 1986) and *A. olivaceus* a four-to five-year cycle (Murúa & González 1985a).

If every species is unique in its relationship with the environment it should be expected that most of the regulatory forces acting upon them are different. Because multiple factors could be acting on the regulation of numbers of the two species, an holistic view should allow us to visualize the behavior of the population as a product of the total network of interacting components (Lidicker 1978).

Given that *A. olivaceus* and *O. longicaudatus* show different demographic attributes and life history patterns, the present paper attempts to detect some factors involved in the population regulation process to find out whether similar regulatory mechanisms operate in the two species.

MATERIAL AND METHODS

The study area is located in the San Martin Experimental Preserve, 74 km by road from Valdivia, Chile (39° 38'S, 73° 7'W). The mean annual precipitation is 2,472 mm with 75% of it falling from April

to September. Ambient temperature is moderate, due to the oceanic influence, with a mean monthly maximum of 15°C in summer and a minimum of 8°C in winter (Huber 1975).

Two plots were established, one in an early successional stage (produced after the forest was cut approximately eighty years ago), composed of graminoid species such as *Holcus lanatus*, *Dactylis glomerata*, *Agrostis tenuis*, *Bromus unioloides*, and patches of shrubs including *Greigia sphacelata*, *Rubus constrictus*, and *Rosa moschata*. The second plot was in a late stage of secondary growth forest dominated by *Aextoxicon punctatum* and *Gevuina avellana*, and containing components of primary growth forest including *Nothofagus obliqua*, *Eucryphia cordifolia*, *Myrceugenella apiculata*, *Laurelia sempervirens*, *Laurelia philippiana*, and *Drimys winteri*. The understory is dominated by *Chusquea quila* and *Luzuriaga radicans* with the ground covered by a thick layer of bryophytes, ferns and fungi.

A 1.2 ha live-trap grid with 12x12 configuration, (10 m interval between traps) was located in each of the plots described above. Small-mammal trapping began in 1978 (with one medium Sherman trap baited with oats at each trap station) on a seasonal basis, and in subsequent years on a monthly basis. Trapping sessions ranged from four to eleven nights each and standard mark and recapture techniques were used. Additional trapping details are given elsewhere (Murúa & González 1985a, Murúa *et al.* 1986).

For comparison of trapping results the coefficient of fluctuations, C.F. was used (Whittaker 1975). This coefficient is expressed as 10^{D^1} , where D^1 represents the standard deviation as calculated for the logarithms of populations numbers over the 7 years study, and depicts the relative stability of monthly densities in successive years. A Kruskal Wallis test was performed between the highest monthly densities of different years. The Spearman correlation test between monthly densities and dispersal was also performed.

RESULTS AND DISCUSSION

An annual cycle in both species has been previously reported (González *et al.* 1982, Murúa 1983, Murúa and González 1985a, Murúa *et al.* 1986) and was confirmed when monthly densities were grouped in the seven years studied for both species and habitats (Fig. 1a, b). *Akodon olivaceus* and *O. longicaudatus* exhibit a limited reproductive period from November to April, which results in their annual cycle of abundance (González and Murúa 1985), with marked seasonal fluctuations due to a concentrated period of high recruitment (Fall). In addition, there are two other factors, high mortality and dispersal, which are involved in the pronounced decrease in numbers thereafter.

Populations of several species of temperate North American rodents have annual cycles with peaks during the Fall (Petticrew & Sadleir 1974, Gaines Rose 1976, Joule Cameron 1975). One species of deer mice (*Peromyscus maniculatus*) exhibit the same annual cycle (Taitt 1981) as the two Chilean rodents. A similar annual cycle has been described in *Calomys musculus*, *Akodon azarae*, and *Mus musculus* in three different habitats studied in Córdoba Province, Argentina, during three successive years (Crespo *et al.* 1970).

The annual cycle of *A. olivaceus* in grassland-shrubland habitat is characterized by two small peaks in February and November, and a large one in April followed by a decline in numbers (Fig. 1a). The coefficient of fluctuations (C.F.) based on censuses during the same season in consecutive years, reveals a seasonal regularity during winter in grassland-shrubland and forest (C.F. = 1.494, 1.443, 2.047 for grassland-shrubland, and 1.483, 1.591, 2.017 for forest). The highest values were observed in summer and fall (C.F. = 2.679 in December, 2.708 in January, 2.350 in March, and 2.325 in April) in grassland-shrubland, and in forest as well (C.F. = 5.050 in December, 4.130 in January, 4.540 in March, and 7.010 in April). Bujalska (1985), also using C.F., found higher values in spring (April) and

smaller during fall (Sept-Oct) in *Clethrionomys glareolus* in Poland.

The numerical variation observed in the C.F. during summer and fall are produced by dispersal processes involving immigrants and/or emigrants, and recruitment of animals born *in situ*. During this period of the year, successive waves of colonizing animals enter this habitat. This also explains the variation between years (Murúa 1983).

Oryzomys longicaudatus differs from *A. olivaceus* in its patterns of density changes in the grassland-shrubland ha-

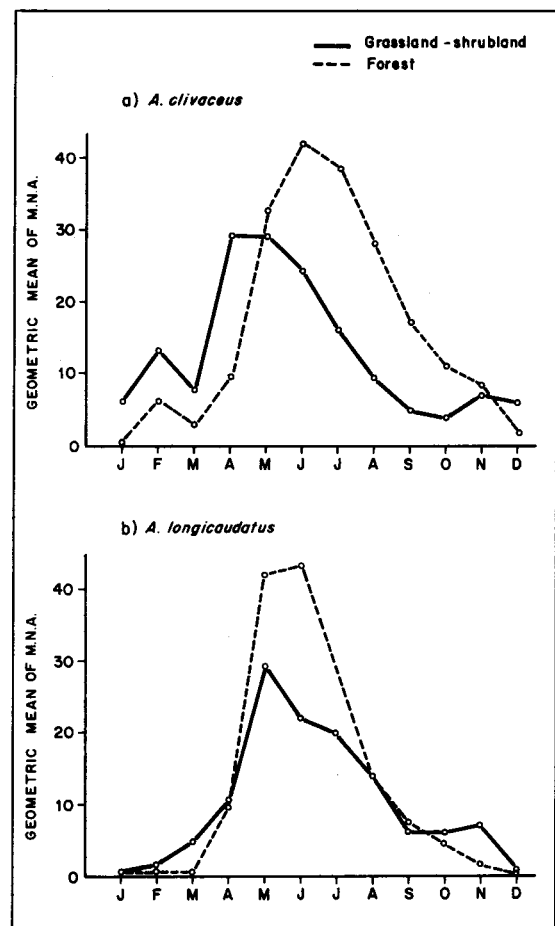


Fig. 1: Monthly geometric mean of the minimum number of individuals known to be alive (M.N.A.), for seven successive years in two different habitats, for a) *Akodon olivaceus* and b) *Oryzomys longicaudatus*.

Valores mensuales de los promedios geométricos del número mínimo de individuos supuestos vivos en siete años consecutivos en dos hábitats diferentes para a) *Akodon olivaceus* y b) *Oryzomys longicaudatus*.

bitat. The former species is characterized by a rapid increase in numbers by late fall, a peak in winter, and a declining population throughout the remainder of the year (Fig. 1b). A similar pattern is observed in the forest habitat with high numbers in June, declining rapidly through December (Fig. 1b). During the summer the population shows the lowest numbers, even disappearing from the trapping grid. The scansorial habits of *Oryzomys* (Pearson 1983, Murúa *et al.* 1986) may explain their disappearance at that time of the year.

The monthly C.F. values were low in a few months: 1.494 in May, 1.443 in June, and 1.598 in August, in grassland-shrubland, and 1.584 in May and 1.483 in June, in the forest. Other months showed higher values of the C.F., ranging from 1.729 to 2.746 in grassland-shrubland, and from 1.675 to 5.030 in the forest. The highly mobile population, comprising movements of immigrants and emigrants (Murúa *et al.* 1986) seems to explain the rapid simultaneous increase in numbers observed during late summer and autumn in both habitats, and also their continuous decrease during the rest of the year.

Both rodent species showed a long term cycle. In *O. longicaudatus* the significance of differences between years of high and low density was established in the two habitats when a Kruskal Wallis test was performed (grassland-shrubland: $X^2 = 15.57$, d.f. = 6, $P < 0.05$; forest: $X^2 = 23.27$, d.f. = 6, $P < 0.01$). In *A. olivaceus*, however, no statistical differences were found in the forest, although the Kruskal-Wallis statistic ($H = 11.78$) was close to the significant level

($X^2_{0.05 [6]} = 12.59$).

Only one year of high numbers (1983) was considered in the analysis (1978 was discarded due to the trapping schedule). In Fig. 2 it can be observed that the other years are of population low levels. The peak years of 1978 and 1983 showed an increase of 37% and 49% in numbers with respect to the other years.

Table 1 shows the factors involved in the regulatory process of both rodent

species. Dispersal has been postulated by several workers as the mechanism of population regulation both in multiannual and annual cycling species in the northern hemisphere (Gaines & Rose 1976, and references therein). Dispersal is also a principal factor involved either in the annual or multiannual fluctuations of the two Chilean cricetids rodents.

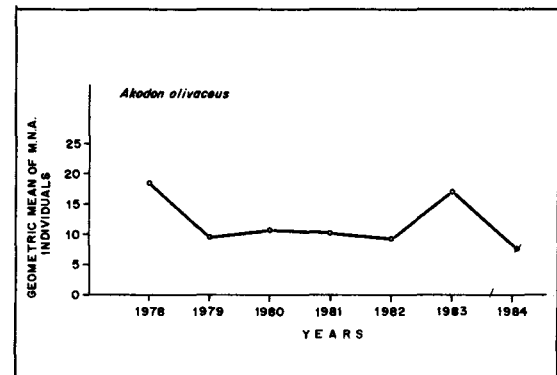


Fig. 2: Annual geometric mean of the minimum number of individuals known to be alive (M.N.A.) for *Akodon olivaceus*.

Valores anuales de los promedios geométricos de densidad en *Akodon olivaceus*.

TABLE 1

Main regulating factors of populations of *A. olivaceus* and *O. longicaudatus*

Principales factores reguladores de las poblaciones de *A. olivaceus* y *O. longicaudatus*.

INTRINSIC FACTORS	<i>A. olivaceus</i>	<i>O. longicaudatus</i>
-Dispersal		
-saturation	-	+
-presaturation	+	+
-Age structure of the stock		
breeding	+	-
-Cohort survival	+	+
-Agonistic behavior	+	?
EXTRINSIC FACTORS		
-Climate	+	+
-Seed availability	-	+
-Survival habitat, and colonizing habitat	+	?

In *A. olivaceus* an association between dispersal and density was found during the increase phase in a year of high numbers: 1983 ($r_s = 0.884$, $P < 0.05$). This means that the animals leave the population during the increase period before the population reaches a saturation level. This is a typical pre-saturation dispersal *sensu* Lidicker (1975). The animals moved from grassland-shrubland to the forest by the end of the summer. They were not surplus individuals, aged or weakened, but rather belonged to all age classes. They represented a good sample of the cohorts present in grassland-shrubland (Murúa 1983).

Oryzomys longicaudatus exhibited a close association between density and dispersal both in the increase and decrease phase of the annual cycle during the year of high numbers: 1983 (increase, $r_s = 0.850$, $P < 0.05$; decrease, $r_s = 0.832$, $P < 0.05$). These correlations indicate the existence of pre-saturation and saturation dispersal (Lidicker 1975) in this species. During the decline, the population losses (mortality or dispersal) affected mainly

old and very young animals (K_1 and K_4 cohorts).

Age structure was another factor involved in the regulation of numbers in both species. In *A. olivaceus* the age structure varied during the multiannual cycle due to a differential pattern of cohort survival (Murúa & González 1985a). This pattern was characterized by three general trends: 1) An improvement in the survival of the summer or $K_1 + K_2$ cohorts (animals born in December, January, and February) starting in 1979 to a maximum during summer-autumn 1981-1982 (Fig. 3). 2) A good survival of the K_3 cohort during much of the year, with high values during the period when the older ($K_1 + K_2$) cohorts showed lowest survival (1979-1980). 3) The appearance of a K_4 cohort in winter in those years when the survival of summer cohorts was also low.

In *O. longicaudatus* the age structure showed seasonal fluctuation with no evident changes in successive years. The intermediate cohorts K_2 and K_3 were well represented in both habitats in different years (Murúa *et al.* 1986).

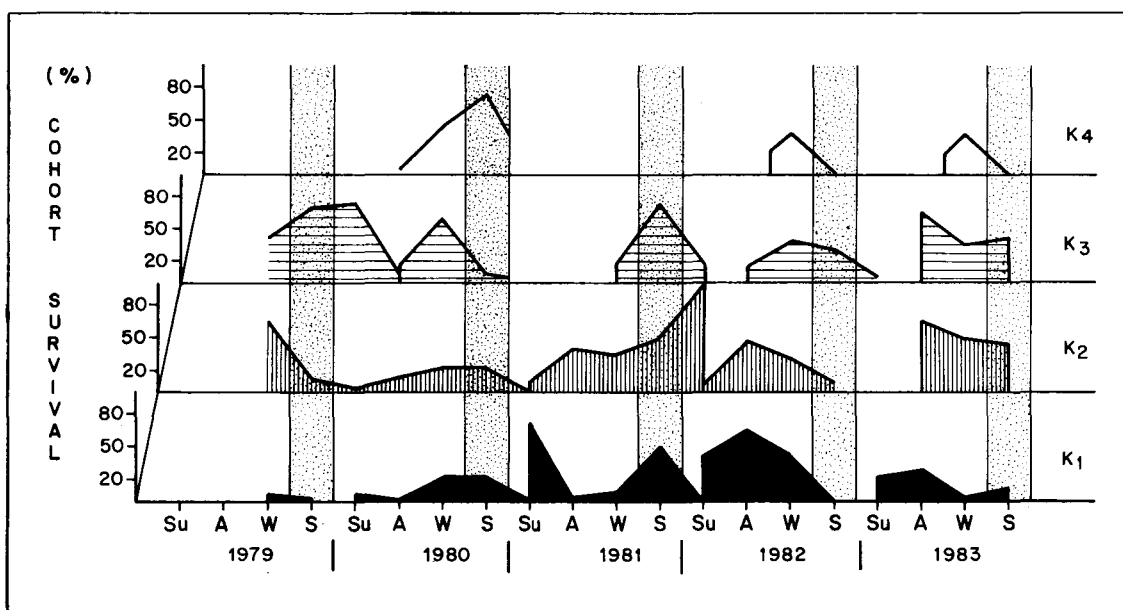


Fig. 3: Seasonal values of cohort survival in *Akodon olivaceus* (K_1 and K_2 = summer cohorts, K_3 and K_4 = fall cohorts) [dotted] = spring season.

Valores estacionales de la sobrevivencia de las cohortes en *A. olivaceus* K_1 y K_2 = cohortes de verano, K_3 y K_4 = cohortes de otoño. [dotted] = primavera.

The age composition of the overwintering animals that formed the breeding stock (*sensu* Gliwicz 1975) was also a relevant factor in the regulation of numbers in *A. olivaceus*. The breeding stock may be relatively old when it is dominated by members of the previous summer cohorts, or relatively young, when the autumn cohorts dominate. The crucial factor affecting population fluctuations seemed to be the age of the animals that were going to begin the breeding season. A dramatic change in the age composition of the breeding stock was observed during the spring previous to the year of the peak, 1983 (Fig. 4). Animals born during the fall did not reproduce during the same season (González & Murúa 1985) and this accounted for the better survival of fall cohorts. This situation has also been observed in *Microtus oeconomus* where fall-born non-reproducing individuals survive better through the winter (Stenseth 1985). In fact, the first-born of the year were initially trapped in November 1982, the spring previous to the year of peak, 1983. In all previous years, the first animals born in the season were not trapped until December or January. This also happened in 1981, when a spring breeding stock with a high ratio of fall-cohort individuals (60: 40), was present. An analysis of this stock showed that it was formed mainly by individuals of the K_4 cohort, which despite showing the best overwinter survival, did not gain enough weight during winter to reproduce immediately. This was reflected by their low spring weights in spite of the abundant amount of seeds available (Murúa & González 1985a, b). Consequently, their reproduction was delayed and population increase was small. This delay in reproduction may explain the low numbers of animals and lower instantaneous growth rates observed despite the high seed availability. Whether this delay was due to physiological factors such as reproductive inhibition, or to intrinsic processes, or to plant secondary compounds, or to behavioral changes, is an open question.

On the other hand, in *O. longicaudatus* the composition of the breeding stock did

not change during the years studied and it was formed mainly by K_2 and K_3 cohorts (Murúa *et al.* 1986).

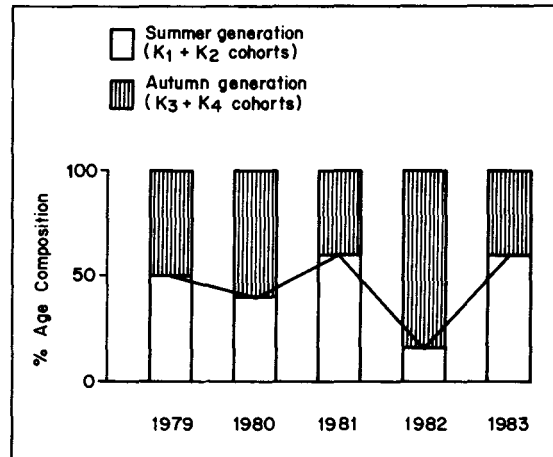


Fig. 4: Age composition of *A. olivaceus* during the spring months of five years, 1979-1983.

Composición por edades de *A. olivaceus* durante los meses de primavera de cinco años, 1979 a 1983.

Laboratory encounters between male individuals of *A. olivaceus* collected during fall and spring showed the existence of agonistic behavior in both groups of animals (unpublished results). This finding, together with field evidence that males increase the size of their home range in spring and summer (González *et al.* 1982), indicates that this type of behavior was also affecting the rodent population. This aspect has not been fully studied and research is on the way to visualize the role of agonistic behavior as a regulatory mechanism in *A. olivaceus*, as it has been postulated for northern hemisphere rodents (Krebs 1979).

Seed availability may be an extrinsic factor of importance in the population regulation of the granivorous species *Oryzomys*. Studies conducted on seed production of trees in the trapping grid as evaluated with wooden boxes placed on the forest floor showed a seasonal fluctuation with seed crops concentrated in summer and fall. Some tree species (*Gevuina avellana*, *Aextoxicum punctatum*) showed an alteration of years of high

(1981-1983) and low (1980-1982) crops (Murúa & González 1985b).

Oryzomys longicaudatus showed a two-year cycle with an alternation of years of high and low numbers which were coincident with peak and low years of seed production. Thus, a food limitation hypothesis could account for an association between density and seed production (Murúa *et al.* 1986).

The climate is an extrinsic factor that could be acting directly or indirectly, through the ripening of seeds or growth of herbs, on the rodent populations. It is known that high temperatures and precipitation during summer affect the seed production of the following year (Holmsgaard & Olsen 1960). These aspects have not been analyzed in detail in the study area but they will be considered in future studies.

Both of the rodent species at San Martin appeared to use the two available habitats, grassland-shrubland and forest, and these provided a mosaic of resources in time and space, so that animals could alternate between patches according to their requirements. Forbs and grasses provided adequate protection from predators as well as food for summer populations during the reproductive period, and the forest harbored sufficient food resources at the end of the summer. It has been suggested that only species which choose between patches should be cyclic (Stenseth 1985). By late spring animals disappeared almost completely from the forest habitat, moving to the open patches of grassland-shrubland, where both species reproduced at that time (González & Murúa 1985). Thus, two types of habitats were recognized, a survival one where animals reproduced annually, and a colonizing one. The two species could choose alternative patches of habitat during their life cycle. The existence of survival and colonizing habitats and their relative availability to the species have been considered as an important regulation mechanism in species with multiannual cycle (Lidicker 1983).

The multi-factorial model used in the analysis of the regulation mechanism of both rodents, has been useful to show

several interactive factors that may produce the observed cyclic fluctuations. There are extrinsic factors (climate, seed availability, survival and colonizing habitats), and intrinsic factors (dispersal, agonistic behavior, age structure, and age structure of the breeding stock). From the knowledge gathered since 1978 on both species, it is possible to seek generality about their regulatory machinery based on field observations. Dispersal (especially pre-saturation dispersal) is a general factor acting on both populations, which has also been reported in other unrelated species such as *Lepus americanus* and *Microtus californicus* (Lidicker 1978). The cohort survival showed changes that follow a multiannual or an annual pattern in successive years. There are other factors about which presently is no information, but which could be important, such as agonistic behavior, predation, and the existence of survival and colonizing habitats.

A better understanding of the regulatory processes involved will depend on the feasibility of carrying out long term studies on the target populations. It would also be necessary to subject the hypothesized regulatory mechanisms to rigorous experimental tests.

ACKNOWLEDGMENTS

The work was partially funded by Projects Nº S-81-17, RS-81-17 and S-83-50 of the Dirección de Investigación, Universidad Austral de Chile. We are grateful for the comments and suggestions made by Dr. Eduardo del Solar, to Dr. Peter Meserve for critical revision of the manuscript, to Dr. C. Cox for his assistance in language correction, to Cecilia Jofré for her technical assistance, and to Pedro Muñoz, caretaker at San Martin Experimental Preserve, Universidad Austral de Chile.

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