

Habitat utilization of two muroid species in relation to population outbreaks in southern temperate forests of Chile

Uso del hábitat por dos especies de múridos en respuesta a un aumento poblacional (ratada) en los bosques templados del sur de Chile

LUZ A GONZALEZ^{1,2}, ROBERTO MURUA¹ & CECILIA JOFRE¹

¹Instituto de Ecología y Evolución, Facultad de Ciencias, Universidad Austral de Chile, Casilla 567, Valdivia, Chile, e-mail: ²lgonzale@valdivia.uach.uca.cl

ABSTRACT

Large-scale outbreaks of two species of rodents (*Oligoryzomys longicaudatus* and *Abrothrix olivaceus*) in response to a large increase in food resources in San Martín Experimental Preserve and in the Peulla area of the Vicente Pérez Rosales National Park, were observed during fruiting and seedling of arborescent bamboo (*Chusquea* spp.). This unique phenomenon enabled the analysis of the effect of increased density on patterns of habitat use by these rodent species with mark-recapture grids in each area. Vegetation analysis was performed at three strata at each capture site. Associations between habitat variables and rodents presence or absence was assessed by using a logistic regressions. Habitat preference was strongly influenced by population density. Vegetation variables were important predictors for the presence of these rodent species only in years of low numbers. The results corroborate the predictions of the Fretwell-Lucas model of habitat selection.

Key words: rodent outbreak, habitat selection, *Chusquea* flowering, temperate forests, Chile.

RESUMEN

En respuesta a la enorme cantidad de recursos alimentarios producto de la fructificación y semillación de la bambúcea *Chusquea quila*, grandes ratadas de dos especies de roedores, *Oligoryzomys longicaudatus* y *Abrothrix olivaceus*, se observaron en la Reserva Experimental San Martín y en el sector de Peulla en el Parque Nacional Vicente Pérez Rosales. Este fenómeno único nos permitió analizar el efecto del aumento de la densidad sobre los patrones de uso del hábitat de estos roedores dominantes. Dos retículos de trapeo utilizando el método de captura, marcaje y recaptura se establecieron en los dos hábitat mencionados anteriormente. Los análisis vegetacionales se efectuaron en los tres estrata en cada sitio de captura. Se realizaron asociaciones entre variables del hábitat y la presencia/ ausencia de roedores mediante una regresión logística. La preferencia de hábitat estuvo fuertemente influida por la densidad poblacional. Las variables de vegetación fueron importantes predictores para la presencia de estas especies de roedores sólo en los años de bajos números. Los resultados corroboran lo predecido por el modelo de Fretwell-Lucas sobre la selección de hábitat y distribución de la población.

Palabras clave: ratada, selección de hábitat, florecimiento de *Chusquea* spp., bosques templados, Chile.

INTRODUCTION

The arborescent bamboo (*Chusquea* spp.) known as “quila” or “colihue” is an important component of southern temperate rainforests, especially in areas where forest has been opened by disturbances such as tree falls or logging. Fruiting and flowering of the species occurs every 10-20 years, and soon after fruiting the plant senesces and dies over the course of one or two years. The more

recent *Chusquea* die-off in the southern part of Chile covered most of the 10th Region, affecting nearly a million ha from 1991 to 1995 (CONAF 1993). *Chusquea* spp. may produce large seed crops estimated to be 51.3 million/ha in San Martín Experimental Preserve in 1994 (Murua et al. 1996). Seeds are consumed by many granivorous rodents and birds, including finch-like species *Carduelis barbata* (jilguero), *Phrygilus patagonicus* (cometocino) and the large pigeon or

torcaza, *Columba araucana* (Wilson & Armesto 1996). The flowering and seeding of quila is followed by large outbreaks of rodents known as "ratadas" (Hershkovitz 1962).

Oligoryzomys longicaudatus (Benett 1832) and *Abrothrix olivaceus* (Waterhouse 1837) are two co-dominant rodent species that inhabit southern temperate rain forests. During quila fruiting, these species showed a large numerical response to increased availability of food resources (Murua et al. 1996). The outbreaks in the San Martín Experimental Preserve and in the Peulla sector of the Vicente Pérez Rosales National Park (Murua et al. 1996) provided the opportunity to analyse the effect of increased density on patterns of habitat use. Microhabitat selection in these two species was studied by Murua & Gonzalez (1982). *Oligoryzomys longicaudatus* was found to select microsites with high foliage density and thick understory, which offer protection from horizontal view of predators. In contrast, *A. olivaceus* was associated with vegetation attributes that provided greater cover from above. According to the Fretwell-Lucas model however, it is expected that with high population densities, species occurrence will show no correlation with habitat type, as a result of a relaxation of habitat selection (Wiens 1976).

MATERIAL AND METHODS

Study Area

The study was carried out previous and during the fruiting of *Chusquea* spp. in San Martín Experimental Preserve, 78 km northwest of Valdivia (39°38'S, 73°07'W) and in the Peulla sector of Vicente Pérez Rosales National Park (41°06'S, 72°02'W).

San Martín Experimental Preserve is an area of 160 ha of secondary growth forest with multiaged trees from 15 to 300 years old. It is located at 60 m above sea level and the vegetation has been described by Cárdenas (1976) and it is dominated by evergreen trees including *Aextoxicon punctatum*, *Gevuina avellana*, *Nothofagus obliqua*, *Eucryphia cordifolia*, *Laurelia sempervirens*, *Laurelopsis phillippiana*, *Persea lingue* and a thick *Chusquea quila* under story. Peulla is located at 500 m above sea level, is less dense forest with thick shrubs strata where *Chusquea* spp. is a disseminated species. An evergreen forest dominated by trees as *Eucryphia cordifolia*, *Laurelia phillippiana*, *Nothofagus dombeyi* and *Aextoxicon punctatum*, *Saxegothea conspicua*, *Weinmannia trichosperma* characterizes it.

Methods

Rodent populations have been sampled continuously in San Martín Preserve since 1979 so that animals collected only the year previous to the outbreak (1993) and at the outbreak year (1994) were considered in this study. The mark-recapture grid at Peulla was sampled once during July 1995 (an outbreak year), then again in September 1995 and July 1996. Trapping grids at San Martín had 144 and Peulla 100 trap stations in 12x12 and 10x10 arrays, respectively. A Sherman live trap was placed at each capture point (10 m intervals). As sample periods were six days each a closed population model was used, because, these methods are generally conducted over relatively short period of time (5-10 days) (Lancia et al. 1996); traps were checked once each day and animals were marked with a uniquely numbered leg band. Traps were baited with rolled oats. Standard measurements such as mass, body and tail length were taken during handling. Animals were later released at the site of capture. Number of animals collected at each site during the outbreak and during previous or following years was estimated with CAPTURE (White et al. 1982). This computer program utilizes Jackknife techniques to estimate the standard error of density values; the heterogeneity model which includes variation in capture probabilities associated with unrecognized sources of variation that vary among individuals (M_h) was selected. The model assumes each animal has a unique capture probability that remains constant over the trapping period. Furthermore the capture probabilities are assumed to be a random sample of individuals in the population (Lancia et al. 1996). In order to analyse traps saturation we determined a quotient between the number of traps occupied and the total numbers of traps available during the sample period of six days (864 traps) each month.

A vegetation analysis was performed at each trap station based on the capture frequency of small mammals species. Habitat features were recorded during autumn in 1983 (low numbers) and 1994 at San Martín and in winter 1995 (high numbers) and 1996 in Peulla, simultaneously with trapping at each capture site. Vegetation variables were measured for three strata in 5 and 10 m radius circular plots centred on each trap site. Vegetation variables included: a) tree and shrub density (average distance from the centre to the five nearest trees or shrubs); b) shrub cover (ground area covered by the foliage projection calculated by πr^2 from the mean of the five nearest shrubs); c) number of tree species and shrubs in 10 m radius circular plots; d) number of herba-

ceous species present in 1 m² plots; e) ground cover, percentage of the area in 1m² plots covered by herbaceous vegetation; and f) foliage density measured using the profile board technique (MacArthur & MacArthur 1961, Rosenzweig & Winakur 1969) at heights of 0.15 m, 0.30 m, 0.50 m, and 1.00 m. In Peulla, aerial ground cover by quila and litter was also measured. Variables expressed in percentages were arc sine transformed (Sokal & Rohlf 1981). In order to establish an association between the vegetation variables and absence or presence of captures, vegetation variables and the presence/absence at a particular trapping site were analysed by using logistic regression techniques (Statistics 4.2, stepwise model) for years of high and low numbers. The convex polygon method (Jennrich & Turner 1969) was used to estimate the individuals home range in both rodent species of years with high and low numbers. All values are shown as arithmetic mean $\pm$ 1 SD (standard deviation).

RESULTS

Densities of *O. longicaudatus* and *A. olivaceus* during 1993 and 1994 in San Martín and 1995-1996 in Peulla are shown in Fig. 1. The numerical response to the large amount of "quila" seeds available was strong for *O. longicaudatus* with density increasing from 61 ± 12 animals/ha in May 1993 to 422 ± 33 animals/ha during April 1994 (Fig. 1). The numbers of *A. olivaceus* also showed a moderate increase during April 1994 (Fig. 1). In Peulla, *A. olivaceus* populations in July 1995 were 337 ± 28 individuals/ha during the outbreak, and <1 individual/ha two months later (September). In July 1996 the populations showed some recovery with 26 individuals/ha. In 1995 *O. longicaudatus* showed low abundance in Peulla with $n = 45 \pm 8.98$ while in 1996 only one animal was collected. It is interesting to note that the bulk of population is 91% of *O. longicaudatus* in San Martín and 93% of *A. olivaceus* in Peulla.

The analysis of the total number of occupied traps versus the total numbers of traps available in the grids (864) during April, May and June the year previous and during the outbreak did not show evidence of saturation. In the year of the outbreak it was observed higher values of traps occupancies (Fig. 2). In spite of the large number of captures during the outbreak animals showed a clear tendency to use the same traps in the different day of the trapping period. This comportment could explain the low values of traps occupancy found, which is a 12% in April, the month of highest density. The animal's captures at low

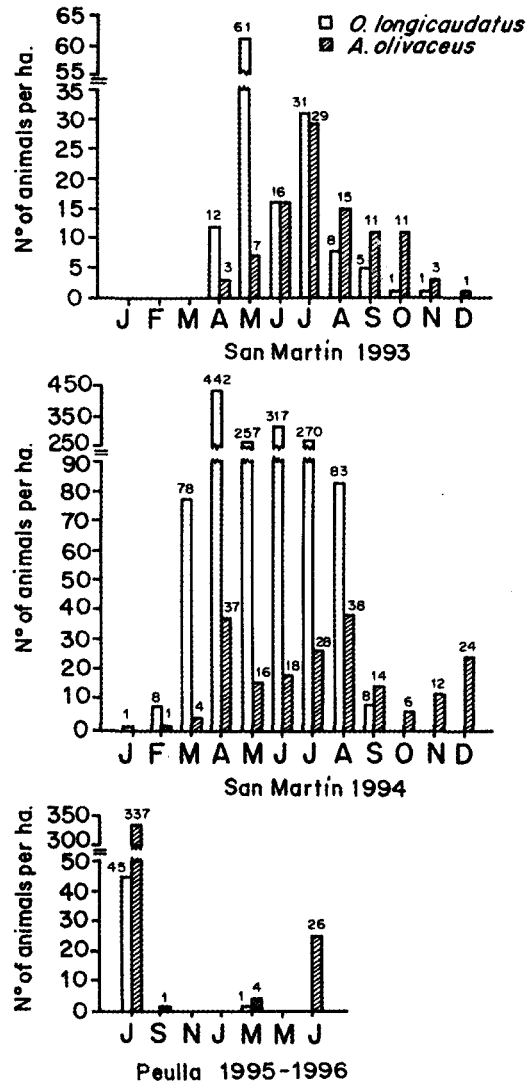


Fig. 1. Densities per ha as estimated by CAPTURE of *O. longicaudatus* and *A. olivaceus* at San Martín during 1993-1994 and Peulla during 1995-1996.

Densidad estimada por CAPTURE para *O. longicaudatus* y *A. olivaceus* en San Martín durante 1993-1994 y Peulla durante 1995 y 1996.

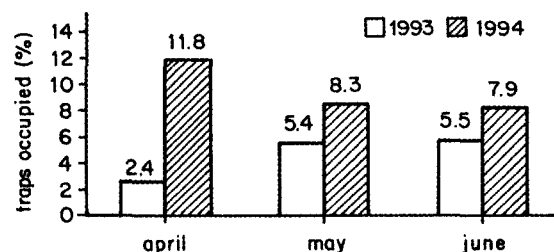


Fig. 2. Trap occupancy in San Martín during 1993 and 1994 of *O. longicaudatus* and *A. olivaceus*.

Trampas ocupadas en San Martín durante 1993 y 1994 por *O. longicaudatus* y *A. olivaceus*.

densities occurred in few traps presumably located in favourable habitats characteristics. In fact, the logistic regression indicated that there was a statistically significant association between certain habitat variables during years with low numbers of captures in both species of small mammals (Table 1). Only in years of low numbers in *O. longicaudatus* (1993 in San Martín and 1996 in Peulla), significant associations were found with foliage density (0.15 m, 0.30 m and 1.00 m) and number of shrubs (χ^2 , $P = 0.019$, 0.029, 0.048 and 0.050 respectively), whereas in *A. olivaceus* a significant association was found with herbaceous cover ($P < 0.006$) for low density years. These relationships disappeared in the years with high numbers of both species of small mammals.

Home range size varied between years of high and low numbers. *Akodon olivaceus* showed home range sizes (m^2) larger in years of low numbers (mean = 1007.8 ± 137.9 , $n = 26$) in San Martín during 1993, while the sizes were smaller (mean = 442.5 ± 169.9 , $n = 21$) in years of high numbers in Peulla (1995). The difference found was significant ($t = 11.69$, $P < 0.05$, $n = 14$). *Oligoryzomys longicaudatus* showed a similar tendency in the home ranges in the San Martín area, in 1993 home range size was mean = 2071.4 ± 986.0 , $n = 25$ and in the outbreak year, 1994, was mean = 1458.3 ± 1152.4 , $n = 18$, but no statistical differences between years was observed ($t = 1.83$, $P > 0.05$, $n = 41$). *O. longicaudatus* is a more mobile species, so it was not surprising that its home range was twice that of *A. olivaceus* for either of the years considered. However, little difference in home range size was observed between years with high versus low numbers in *O. longicaudatus* unlike *A. olivaceus*.

DISCUSSION

The dramatic numerical response of rodents to seed crops of *Chusquea* described for two different areas of southern Chile provided the opportunity to clearly discriminate between years with high and low numbers of animals. It was also a unique occasion to study the habitat selection and the effects of rodent population density.

In Chile, habitat has been analyzed with PCA to investigate utilization pattern of sympatric species of small mammals (Patterson et al. 1990). A similar approach has been used for different small mammal communities in different landscapes (Schoener 1974, Cody 1985). Studies in central and southern Chile have analyzed the habitat of small mammals at two different scales; first at an extensive (geographic) or macrohabitat scale (e.g., plant cover or seral stage of an animal's habitat) (Greer 1968, Fulk 1975, Glanz 1977, Meserve & Glanz 1978), and second, at an intensive or microhabitat scale that focuses on specific vegetation characteristic (e.g., Murua & Gonzalez 1979, 1982, Kelt et al. 1994, Murua et al. 1996). Both approaches have shown that rodents and marsupials select patches of habitat although these studies differ in temporal and spatial scale. These studies show that local patterns of habitat use for common small mammals and marsupials species are often concordant and related to vegetational variables associated with herbaceous and shrub strata and trees in forested environments.

Here, the most common species, *Oligoryzomys longicaudatus* and *Abrothrix olivaceus*, exhibited segregation in habitat with defined microhabitat selection in coastal temperate rain forests (Murua & Gonzalez 1982), in spite of the vagility of *O.*

TABLE 1

Logistic regression between vegetational variables and *O. longicaudatus* or *A. olivaceus*

Regresión logística entre variables vegetacionales y *O. longicaudatus* o *A. olivaceus*

	<i>O. longicaudatus</i> San Martín			<i>A. olivaceus</i> Peulla		
	Chi square (χ^2)	df	P	Chi square (χ^2)	df	P
Years of low numbers (1993 in San Martín and 1996 in Peulla)	24.660	11	0.053	20.332	13	0.003
Years of high numbers (1994 in San Martín and 1995 in Peulla)	17.020	11	0.198	15.096	13	0.211

longicaudatus. These species also maintain strong habitat selectivity in the Andean temperate rain forest (Kelt et al. 1994). In contrast, Patterson et al. (1990) noted weak habitat selectivity in the same species studied by Kelt et al. (1994). However, this difference could be a consequence of the methodological approach, related to the spatial and temporal scales or to the invasive techniques used, such as removal trapping procedures (Kelt et al. 1994). Thus, the spatial scale of observation may greatly affect the perception of the pattern of animal habitat association.

A critical point in the assessment of microhabitat selection at high densities is the possibility for traps saturation effect that causes animals to utilize traps at stations that would be ordinary empty. However, our analysis showed that the proportion of traps used was always low.

Is important taking into account that could occur another traps effects? Should the response variable be the numbers of occasions in which the traps is occupied regardless the identity of the animals? or should the response be the number of different individuals that occupy the traps?. This approach would introduce into the analysis the behavioural interactions of animals. Further work about this effect is needed.

In this paper a logistic regression was used to associate microsites with trap occupancy status, which assume that comparison sites come from different populations in order to minimize statistical artefacts related to the use of multivariate methods. The latter is due to the violation in the assumptions of the multivariate normality and equal covariance structure (North & Reynolds 1996). The binary logistic regression does not require the above assumptions and the use of maximum likelihood techniques.

The logistic regression model only showed associations between traps occupied by rodents and vegetational variables in low population density years whereas no associations was found in high population density years

The results obtained with the binary logistic regression were not discordant with those of multivariate methods used here (Murua & Gonzalez 1982), which revealed similar associations with habitat variables.

Thus, habitat preference is strongly influenced by population density and field conditions. Furthermore, all other things being equal, individuals select habitat types depending on the quality and population density of the habitat (Wiens 1976). According to the Fretwell-Lucas model at low density only the optimal patch types would be occupied and as density increases, other habitat types would become equally suitable. At this

point habitat occupancy by a species is modified, including additional habitats given the assumption of perfect ability to evaluate habitat quality (Wiens 1976). This could be the situation in years of high numbers when rodent selectivity decreases and all habitats, optimal and suboptimal, are colonized, such that habitat selection is reduced by population density. The model explains the distribution of density among habitats by the so called ideal habitat distribution in which organisms equalize their fitness by distributing individuals among habitats, in proportion to resources available in those habitats (Rosenzweig 1991). At least two of the major assumptions proposed in the mechanism of density-dependent habitat selection were observed in the present results. The rapid population extinction observed in both areas soon after the outbreaks can only be explained by a high rate of mortality and dispersal. This fact could be a consequence of changes in the fitness due to the influence of population densities and the habitat chosen. The circumstantial evidence observed here with respect to the abundance of resources (seeds) and consumers (rodents) responses supports one of the subvertive assumption for the existence of an ideal free distribution in the Fretwell-Lucas model (Rosenzweig 1991).

Both species seems to adjust their home range to short term fluctuations in food resources. Large home ranges allow enough resources to be harvested in years with minimal productivity, but, if a sudden localized increase in resources occurs in one part of the habitat, the animal decrease its total area of activity and concentrate its effort in harvesting the resources. This strategy is supported by the positive relation of animal abundance and the amount of seeds found in *O. longicaudatus* (Gonzalez et al. 1989). A similar situation has been also described in other granivorous species such *Tamias striatus* (Mares et al. 1982).

Previous studies on spatial distribution estimated by the nearest neighbour test (Clark & Evans 1954) found an aggregate distribution in *A. olivaceus* and random one in *Oligoryzomys longicaudatus* at San Martin Preserve (Murua & Gonzalez 1979). This finding may be associated with demographic features, such residency exhibited by *A. olivaceus* in the temperate rain forest (Murua et al. 1987) and the high vagility described as one of the most conspicuous demographic trait in *O. longicaudatus* (Murua et al. 1986, Kelt et al. 1994).

Habitat occupancy patterns are also reflected by home ranges of both species in the years of the high or low populations. *A. olivaceus* substantially reduced home range sizes when population density increased during the outbreaks in Peulla

but, *O. longicaudatus* did not show significant differences in sizes of home range between years of high and low numbers. The fact is that *A. olivaceus* selects habitat patches in environments with different quality of patches, and *O. longicaudatus* did not select. From the present results it can be inferred that *O. longicaudatus* behaved as a fine-grain strategist while *A. olivaceus* might be considered as a coarse grain one (sensu Wiens 1976). This situation was observed at low and regular densities. But, during the outbreaks the distribution of individuals appears more fine-grained because additional lower quality habitats are used.

The results presented here broaden out the list of taxa showing density dependent habitat selection that confirms the ideal free distribution as a paradigm in current behavioural ecology.

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