Population dynamics of five sigmodontine rodents of northwestern Patagonia

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Population dynamics of five rodent species were studied, from March 1991 to August 1994, in an area located in the ecotonal steppe of northwestern Patagonia, Argentina (at about 40°S). Seasonal and annual fluctuations in population numbers were found in all sigmodontine species. The reproductive period, sex ratio and longevity of the five species were also studied. *Abrothrix xanthorhinus* (Waterhouse, 1837), a habitat generalist, was the most abundant species. *Eligmodontia morgani* (Allen, 1901), *Abrothrix longipilis* (Waterhouse, 1837), *Reithrodon auritus* (Fischer, 1814) and *Oligoryzomys longicaudatus* (Bennett, 1832) were subdominant. The present study is a first description of the population dynamics in this rodent community, whose ecological characteristics gather importance considering that some of these species are Hantavirus reservoirs.

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Introduction

Communities are dynamic entities; consequently, an understanding of community structure is possible only within the appropriate framework of temporal and spatial variation (Wiens 1986, Morris 1990). Among rodent species, population fluctuations may vary on the order of seasons or years (Lidicker 1988, Anderson *et al*. 1992, Krebs 1992). Therefore, long term studies are important to understand rodent community structure and species coexistence (M'Closkey 1972, Kaufman *et al*. 1995).

In this study we examined a rodent community over a period of 42 months in northwestern Patagonia. The study area is located in a transition zone, of a few kilometres wide, between the western Andean forest and the eastern semiarid Patagonian steppe. Each biome, on either side of this ecotonal strip, contains characteristic small mammal faunas which have been studied by many authors (eg Murúa and González 1981, 1982, 1986, González *et al*. 1982, 1989, Meserve *et al*. 1982, 1988, 1991, Glanz 1984, Meserve and Le Boulengé 1987, Murúa *et al*.

1987, Pearson *et al.* 1987, Pearson 1988, 1992, Patterson *et al.* 1989). The ecotonal fauna has no endemic species, rather it consists of assemblages of forest and steppe rodents (eg Pearson and Pearson 1982, Johnson *et al.* 1990, Kelt 1994, 1996). The steppe species found in this study were *Abrothrix xanthorhinus* (Waterhouse, 1837), *Eligmodontia morgani* (Allen, 1901) and *Reithrodon auritus* (Fischer, 1814). The first is an omnivorous small mouse (82 mm of head-body length and 52 mm of tail length, 17 g) that inhabits the semiarid steppe and bunchgrass in north-western Patagonia (Pearson 1995). The second is a granivorous small mouse (82 and 82 mm, 20 g) of sandy soils and open vegetation, and the third is an herbivorous large mouse (130 and 85 mm, 80 g) of open grassy areas (Pearson 1988, 1995, Pearson *et al.* 1987). The forest species were *Abrothrix longipilis* (Waterhouse, 1837) a medium sized, omnivorous mouse (105 and 80 mm, 38 g) widely dispersed from dense forests to marshes and bushy steppe, and *Oligoryzomys longicaudatus* (Bennett, 1832) a granivorous mouse (95 and 120 mm, 37 g) abundant in brush areas and forest edges (Meserve *et al.* 1982, Pearson 1995, Patterson *et al.* 1989).

Previous studies performed in this transition habitat focused on the distribution of small mammals and community characteristics such as species richness and diversity, demography, reproduction, trophic structure, and the relative size of populations (Pearson and Pearson 1982, Pearson 1995, Johnson *et al.* 1990, Kelt 1994, 1996). However, long term studies of these rodent communities have not been previously undertaken. In addition, information about ecological aspects of the studied species has become relevant since the detection, in this region, of Hantavirus Pulmonary Syndrome transmitted by sigmodontine rodents.

This work examines the population dynamics of the five most representative species of a rodent community in a Patagonian transition zone. Changes in relative abundance of rodent populations over time, seasonality of reproduction, sex ratio and longevity are analysed.

Material and methods

The study site was an ecotonal steppe located in a flat area, 8 km east of Bariloche Argentina (41°S, 71°W). Its vegetation consists of patches of low grass (*Stipa speciosa*), xerophylous cushion plants (*Acaena splendens*) and bushes characteristically either of the steppe (*Senecio bracteolatus, Baccharis linearis, Discaria articulata*) or of the Andean forest (*Schinus patagonicus, Berberis* spp.). The European rose bush, *Rosa rubiginosa* is also abundant. The region receives strong westerly winds and has a mean annual temperature of 8°C, a mean maximum temperature of 14.1°C, a mean minimum temperature of 2.4°C. The mean annual precipitation is 800 mm and it is concentrated in autumn and winter (March to September) (Bariloche Airport Meteorological Service). The combined increase in temperature and decrease in rainfall during spring and summer (October to February) cause a moderate hydric stress (Barros and Mattio 1977).

Rodents were sampled monthly from March 1991 to November 1994 on a 10 × 10 Sherman trap grid with a 10 m inter-station distance. In each trapping session, traps were set on 4 consecutive days and were baited with rolled oats. The caught animals were toe-clipped for identification. Species were determined following Monjeau *et al.* (1994), and data such as sex, reproductive condition and body

measurements (weight, total length and tail length) were recorded. The reproductive condition was assessed by taking into account the scrotal position of testes in males, and in females by detecting perforated vaginas, pregnancy by palpation, increased nipple size, and milk production.

The abundance of each species was estimated by the direct enumeration method using a calendar of captures, and was expressed as the minimum number known alive (MNKA) (Krebs 1966). Individuals that had not been captured for more than 3 months were considered absent from the grid in that period. Abundance fluctuations were compared between years for each species and for the community by means of a Kolmogorov-Smirnov two sample test (Conover 1980). The period considered for this test ran from March to August of each year, in order to compare the four years.

Abundance coefficients of variation (CV) of each species and of the total community were estimated for the 42 month sampling period. The differences between each species' CV and the total community CV were tested following Zar (1984). Non-parametric correlations between species abundances were calculated by means of the Spearman coefficient. As populations fluctuate seasonally, only the period of February through June was considered, which is when abundance peaks occurred for all species.

Sex ratio, expressed as number of females over the total number of individuals, was estimated for the total sampling period. Deviations from 0.50 were tested using a χ^2-test. Individuals of lower body weight than the lowest weight of reproductive individuals found in all the study period were considered juveniles. The monthly proportion of reproductive animals for each sex was calculated as a ratio of reproductive individuals referred to the number of adults. Adult individuals captured only in a single trapping session were considered transients. A monthly residence indicator was expressed as the proportion of individuals that were recaptured one or more months later. The mean length of residence on the grid was also estimated, excluding transients.

Individuals were classified into cohorts according to their birth periods. As the capture-recapture method does not allow estimates of individual relative age by measuring tooth wear, other sources of evidence were used to determine age (Meserve and Le Boulengé 1987). Body weight over time of individuals captured as juveniles was used to estimate the age of other adult individuals. In addition, data on reproductive condition, individual residence period, and season when caught supported the cohort estimation based on body weight. Transients were excluded from this estimation. The longevity of each species was inferred by means of the longest residence duration and the estimated age from the cohort study.

Results

The total number of captures was 3545 in a trapping effort of 16 800 trap-nights. Individuals of five species of murid rodents were captured: 360 *Abrothrix xanthorhinus*, 130 *A. longipilis*, 196 *Eligmodontia morgani*, 65 *Reithrodon auritus*, 106 *Oligoryzomys longicaudatus*.

Abundance fluctuations

Seasonal fluctuations occurred in all species. Total community abundance peaks occurred from February through May (summer–autumn). These maximum values varied from 70 to 95 MNKA (Fig. 1). On the other hand, the minimum community abundance values occurred from July through December (winter–spring). The total abundance fluctuation did not differ significantly from year to year.

The definite moment at which each population peaked annually differed between species. Population peaks of *A. xanthorhinus* and *A. longipilis* occurred at the end of summer–beginning of fall (February–March), but *A. longipilis* tended to peak earlier (usually in February). *R. auritus* and *E. morgani* were most

abundant at the end of fall (April–May). *E. morgani* population maxima were
generally later than those of *R. auritus*. Abundance peaks in *O. longicaudatus*
occurred both in spring (October) and in autumn (April–May) (Fig. 1).

A. xanthorhinus was the most abundant species during the study. Abundance
peaks consisted of 60 MNKA in 1991 and 1993, and approximately 35 MNKA in
1992 and 1994. Abundance minima occurred in spring (September–December) with
about 20 MNKA in 1992 and 1993, and less than 10 MNKA in 1991. The 1993
abundance curve differed significantly from that of 1992 and 1994 ($p < 0.05$).

E. morgani presented abundance peaks similar to *A. xanthorhinus* in the two
first years. However, their numbers decreased about 50% per year, from 60 MNKA
in 1991 to less than 10 MNKA in 1994 (Fig. 1). The 1991 abundance fluctuation
curve differed significantly from the 1993 and 1994 curves. Moreover, the 1992
abundance curve differed significantly from the 1994 one ($p < 0.05$). Population
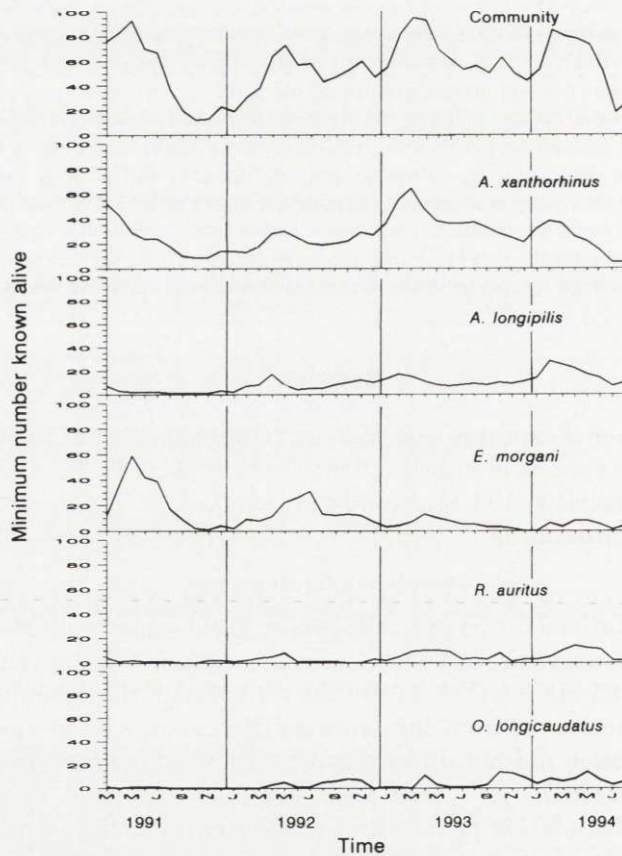minima of *E. morgani* were always much lower than those of *A. xanthorhinus*.

Fig. 1. Abundance fluctuations, expressed as minimum number known alive, of the total community
and of each of the five species. March 1991 through August 1994.

A. longipilis, *R. auritus* and *O. longicaudatus* population numbers were scarce at the beginning of the study but increased during the years. *A. longipilis* was the most abundant of them (30 MNKA in 1994) (Fig. 1). Its 1991 abundance curve differed significantly from the following years ($p < 0.05$). *R. auritus* and *O. longicaudatus* reached abundance peaks of about 10 MNKA in 1993 and 15 MNKA in 1994. Abundance curves of *R. auritus* differed significantly between 1991 and 1993, while *O. longicaudatus* showed significant differences between 1991 and 1994, and between 1992 and 1994 ($p < 0.05$). The populations of *R. auritus* and *O. longicaudatus* presented very low minimum abundances.

The abundance coefficients of variation of *A. xanthorhinus* (49%) and of the total community (40%) were both significantly lower than those of *A. longipilis* (70%), *E. morgani* (110%), *R. auritus* (94%) and *O. longicaudatus* (112%) ($p < 0.05$). Spearman rank correlation coefficients among population abundances of *A. longipilis*, *R. auritus* and *O. longicaudatus* were significant and positive ($r_S = 0.70$ between *A. longipilis* and *R. auritus*, $r_S = 0.60$ between *A. longipilis* and *O. longicaudatus*, and $r_S = 0.71$ between *R. auritus* and *O. longicaudatus*, $p < 0.01$). The correlations between *E. morgani* and the above mentioned species were negative ($r_S = -0.79$ with *A. longipilis*, $p < 0.001$; $r_S = -0.59$ with *R. auritus*, $p < 0.01$; and the negative correlation with *O. longicaudatus* was not significant). Insignificant correlations were found between *A. xanthorhinus* and the other species.

Abrothrix xanthorhinus

Two cohorts were discriminated in *A. xanthorhinus* population: (a) individuals born from October to January which reproduce in the same reproductive season, (b) individuals born from February on, which reproduce in the following reproductive season (Fig. 2). From April or May until winter neither cohort differed in body weight. Adults captured in spring (September to December) were overwintering individuals born during the previous summer. These individuals seldom survived until their second summer. The mean body weight tended to decrease during winter and increase at the beginning of spring (Fig. 2).

A. xanthorhinus population did not present significant differences in sex ratios (proportion of males = 0.54, $n = 350$). The reproductive period was relatively long (August to April) (Fig. 2). Juveniles (individuals lighter than 12 g) began to be captured as of October–November, two months after the detection of the first adults in reproductive condition (Fig. 2). The highest percentage of reproductive individuals was recorded during spring (higher than 60%) and the highest percentage of juveniles was observed in summer.

The mean residence time of individuals was 4.6 months. The proportion of transients captured during the complete study was 47%. The monthly residence was quite high (70%). The longest individual follow-ups were 12 month. These individuals were captured for the first time when they were one or two months old, suggesting a longevity of about 14 months.

Abrothrix longipilis

The breeding period was relatively short (September to March) and no individuals were found to reproduce during their birth year. Therefore, only one annual cohort was recognised (Fig. 2). Individuals could survive for up to two reproductive seasons later, and therefore individuals of three different annual cohorts were found to coexist. Juveniles (less than 19 g) were captured during three months only, mostly during February (Fig. 2). The mean body weight tended to decrease during winter and increase during spring, as described in *A. xanthorhinus* (Fig. 2).

Sex ratio of this species was generally biased towards males (proportion of males = 0.70, $n = 130$, $p < 0.05$). The mean residence time of individuals was of 5.45 months, and was the highest compared with the other four species. The monthly residence rates were generally high (70%) but decreased during spring and the beginning of summer when overwintering individuals tended to disappear and the proportion of transients tended to increase. The proportion of transient
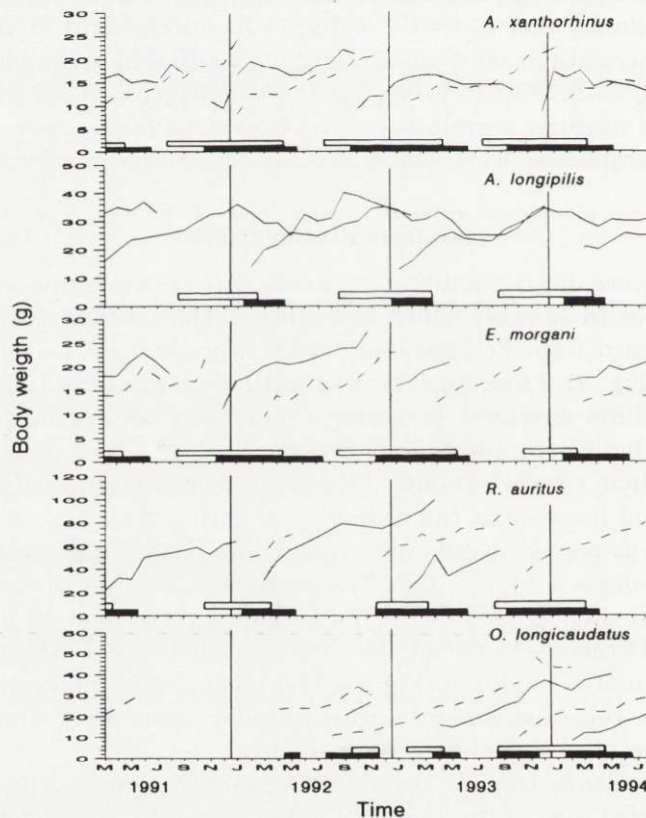

Fig. 2. Cohorts. Fluctuations of body weight means of the distinct cohorts of each species from March 1991 through August 1994. The solid lines represent the spring cohorts and the dashed lines correspond to the summer cohorts. The white bars at the foot of each graph indicate breeding activity, and the black bars indicate the period when juveniles were captured.

individuals during the complete study was 47%, similar to that of *A. xanthorhinus*. Some overwintering adults were recaptured for 14 months. These data together with the cohort study (Fig. 2) suggest a longevity of two years.

Eligmodontia morgani

Two cohorts were defined, as in *A. xanthorhinus* (Fig. 2). The mean body weight of the summer cohort tended to decrease during winter and increase at the beginning of spring (Fig. 2). The breeding period was long (September to May) and the highest number of reproductive individuals was recorded during fall (March to May) (Figs 1 and 2). Juveniles (less than 17 g) were captured from December to July, but they were scarce during summer. The sex ratio was male biased (proportion of males = 0.64, $n = 180$, $p < 0.05$).

The mean residence was 4.11 months. The monthly residence rates were lower than those of *A. xanthorhinus* and *A. longipilis*. A marked population discontinuity was observed in the spring–summer period. This corresponds with a high proportion of individuals captured for the last time during spring, and a predominance of transients at the end of spring and the beginning of summer. The proportion of transients over the whole study was 52%. The longest residence time (11 months) and the study of cohorts suggest a longevity of 1 year.

Reithrodon auritus

Reproductive individuals were captured from September to March (Fig. 2). Juveniles (less than 50 g) were recorded in spring (October to December) and in higher number and proportion during summer–fall (December to April) (Fig. 2). Two cohorts were distinguished: (a) individuals captured as juveniles in summer that could be recaptured until the following autumn, (b) individuals captured as juveniles in spring that could survive until the following spring (Fig. 2).

The sex ratio did not differ from 0.50 (proportion of males = 0.56). The mean permanence of individuals was 3.7 months. The monthly residence rate was particularly low during spring. The proportion of transients captured during the whole study was 48%. The longest follow-ups of individuals were 8 months, but the study of cohorts suggests a longevity of 15 months (Fig. 2).

Oligoryzomys longicaudatus

Reproductive individuals were captured from September to April (Fig. 2). Two cohorts were differentiated: (a) juveniles (less than 17 g) captured in early spring that could be recaptured until the following summer, (b) juveniles recruited in late summer and fall that could be recaptured until the following autumn (Fig. 2). There were no significant biases in sex ratio (proportion of males = 0.50).

Residence rates were low and the monthly transient proportions were high. The proportion of transients captured throughout the whole study was very high (80%), and the mean residence low (3.3 months). The longest individual follow-ups were 9 months. However, the study of cohorts suggests a longevity of 18 months (Fig. 2).

Discussion

Most sigmodontine populations of the studied rodent community showed interannual changes in abundance. The relatively high variation coefficients found throughout the total survey period were related to a marked decrease in the population of *E. morgani* and to the gradual increases in abundance of *A. longipilis*, *O. longicaudatus* and *R. auritus*. *A. xanthorhinus* presented the highest abundance, with minor variation, over the years. In spite of the noticeable interannual variations in abundance of most of the species, the total population number of the whole community did not differ significantly between years. The complementarity of certain population changes (negative Spearman rank correlations) contributed to the stabilisation of the sigmodontine assemblage fluctuations.

Moreover, all five populations studied presented seasonal fluctuations although each species' peak occurred at a different time and with a dissimilar magnitude. *A. xanthorhinus* and *A. longipilis* showed moderate seasonal fluctuations, high survival and low emigration rates (suggested by the high monthly residence). *A. xanthorhinus* had a long and continuous reproductive period while *A. longipilis* longevity was relatively high. Previous studies highlight the relative population stability of the latter species (Meserve *et al.* 1982, Pearson 1983, Meserve and Le Boulengé 1987). On the other hand, *R. auritus*, *E. morgani* and *O. longicaudatus* presented abrupt seasonal decreases in abundance as described in other studies for the latter two species (Meserve 1981, Meserve and Le Boulengé 1987, Pearson *et al.* 1987). For *O. longicaudatus*, the high frequency of transients and first-time captures of adults of this relatively long-lived species, suggest an important role of migration in its population dynamics. The observed spring population turnover of *E. morgani* agrees with the short life span of this species.

The cohort study shows a body weight decrease during winter (June through August) and an increase in spring (October through December) as has been observed in other small mammals of temperate environments (eg Iverson and Turner 1974, Wirminghaus and Perrin 1993). Body weight decrease could be related to the usual harsh winter conditions. Some authors have found a correlation between body weight increase in spring and reproduction, body fat accumulation and diet quality (eg Evans 1973, Wirminghaus and Perrin 1993). The sexual maturation delay in summer cohorts as was observed during this study, has also been described for other rodent species (eg González and Murúa 1985, Zuleta *et al.* 1988). *A. longipilis* individuals became sexually mature a year after they were born as described by Pearson (1992).

Due to the fact that Hantavirus Pulmonary Syndrome (HPS) is seriously affecting this region and that sigmodontine species are its vector, studies on rodent population dynamics may contribute to the clarification of the relationship between the ecological characteristics of the reservoirs and the occurrence of the disease. For instance, it was recently found that *O. longicaudatus* is one of the Hantavirus reservoirs, and the higher frequency of HPS cases is concordant with the increase

in abundance of this particular rodent (ie spring and autumn) (N. Guthmann, pers. obs., Argentine National Public Health).

The current study is a first approach towards a long term analysis of ecological characteristics of five sigmodontine rodents in the northwest Patagonian steppe. It describes different population dynamics that could reflect distinct life strategies of five coexisting species in the transition zone. This population pattern approach might enable future studies which develop and test hypotheses about the processes driving these fluctuations.

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