Studies on Neotropical Fauna and Environment
2002, Vol. 37, No. 3, pp. 187–200

0165-0521/02/3703-187$16.00

A Perplexing Outbreak of Mice in Patagonia, Argentina

Oliver P. Pearson

Museum of Vertebrate Zoology, University of California, Berkeley, U.S.A.

Abstract

Early in spring, 1997, remarkably large numbers of mice appeared in the dense forests near the western end of Lago Nahuel Huapi, Argentina. Dead mice that washed up on nearby beaches at this time were fat, had full stomachs and were young or young-adults born unusually late in the preceding autumn and winter. These mice represented an aperiodic outbreak that extended over 300 km along the Andes. By analysis of trapped samples, the demographics of the two main species in this outbreak (*Oligoryzomys longicaudatus* and *Abrothrix longipilis*) were compared with demographics of the same species during the preceding 21 years. In spring of 1997, trap success for *O. longicaudatus* in areas of the outbreak was as high as 46%; for *A. longipilis* it was 22%. Neither males nor females of either species entered breeding condition in 1997 during the usual season of reproduction in spring, nor in the following summer, leading to the collapse of the populations. Numbers of *Oligoryzomys* decreased steadily to 15% in autumn and a normal 2% in the following spring, at which time reproduction resumed. The 1997 springtime populations in adjacent ecotone and steppe habitats to the east had not increased, contained no young individuals, and overwinter individuals reproduced normally. During the breeding season, *O. longicaudatus* in these populations increased more rapidly than did *A. longipilis*, and during the winter, they decreased faster.

The unusual winter reproduction preceding the outbreak may have resulted from an increase in some deep-forest food source that in turn was responding to two successive, unusually warm winters. Predation played a negligible role in the population collapse. The mouse outbreak was not accompanied by an increase in human cases of hanta pulmonary syndrome, a disease for which *O. longicaudatus* is a reservoir.

Keywords: Population dynamics, *Oligoryzomys longicaudatus*, *Abrothrix longipilis*, mouse outbreak, breeding season, Patagonia, Argentina.

Introduction

While there is something of a consensus developing on the syndrome of characteristics involved in rodent population cycles (Oli & Dobson, 2001; Turchin & Hanski, 2001), only now are we beginning to recognize that aperiodic outbreaks occur in many rodent species. Less studied than the classic periodic type, these other outbreaks can be equally dramatic. It is not yet clear, however, whether a common set of factors and biological characteristics drive these aperiodic outbreaks. Whereas periodic (cyclic) outbreaks occur in structurally simple habitats where mice are vulnerable to predation (Pearson, 1985), the aperiodic outbreak described here occurred in a complex, forested habitat with few predators. The purpose of this paper is to call attention to this class of outbreak, and to describe the demographic characteristics of one example.

Outbreaks of mice are known to occur in South America, such as following the massive blooming and seeding of certain species of bamboo (Gallardo & Mercado, 1999; Murua et al., 1996). These bamboo seedings are cyclic with a period of several decades, and the ensuing increase in mouse populations is triggered by this single, longterm periodic event. In the winter of 1997, a dramatic increase of mice occurred in southern Argentina in the absence of such an event. Here we compare the abundance, reproductive performance and age structure of the two species that dominated this outbreak (*Oligoryzomys longicaudatus* and *Abrothrix longipilis*) with similar information from non-outbreak populations living nearby, and with data accumulated in the *same* areas over the preceding 20 years.

The appearance of a dangerous strain of hantavirus in the study area in 1995 lends urgency to the study of the population dynamics of local mice, because *Oligoryzomys* is a reservoir of the hantavirus pulmonary syndrome (Calderon et al., 1999).

Received: 10 October 2000
Accepted: 22 June 2002

Correspondence: O. P. Pearson, Museum of Vertebrate Zoology, Valley Life Sciences Building 3101, University of California, Berkeley, CA 94720, U.S.A. Fax: +1 643-8238; E-mail: opearson@vdn.com

Materials and methods

Study area

The study area is approximately 30 km wide, and extends from latitude 40°00′S–42°48′S in Argentina along longitude 71°W (Fig. 1). Much of this mountainous area is in National Parks or Reserves and is somewhat protected from human impact. Precipitation comes primarily from the west. Rainfall is abundant in the mountains that separate Chile from Argentina, and decreases to the east. At the latitude of Lago Nahuel Huapi (41°S), annual precipitation decreases from 3000 mm in forests on the Chilean border, to 500 mm at the town of Bariloche 50 km to the east, and to 350 mm at Pilcaniyeu 50 km farther east. The vegetation responds conspicuously to this cline: southern beech forests (*Nothofagus*) and bamboo (*Chusquea culeou*) in the mountains, and semi-arid bush and grassland steppe in the precordillera to the east. The forest is still relatively undisturbed, with light browsing by cattles and horses. The steppe was grazed by guanacos in past centuries and by sheep throughout the 20th century.

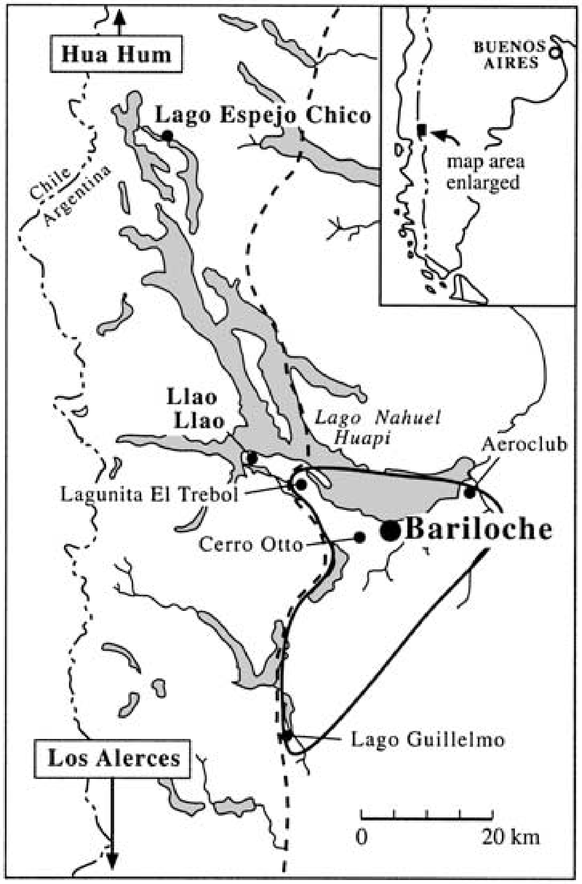

Fig. 1. Localities of samples of mice trapped in 1997 and 1998. The triangular area defined by Aeroclub, Lagunita El Trebol and Lago Guillelmo encloses all of the localities designated as Bariloche Ecotone in the text. The boundary between ecotonal vegetation and beech (*Nothofagus dombeyi*)/bamboo forest is suggested by a broken line; forest to the west. Placement of this line is based on my observations and on the vegetation map of Mermoz and Martin (1987).

The small mammal faunas of forest and steppe are rather distinct, but where the two habitats meet, the vegetation is patchy and the two faunas mix. More than a dozen species of mammals smaller than 200 g occur in such mixed habitat near the town of Bariloche on the southeastern shore of Lago Nahuel Huapi (Pearson, 1983, 1995; Christie, 1984). The forests, although comprised of only a few species of trees, support a similar high diversity and density of small mammals (Pearson & Pearson, 1982).

Collection sites

In the Southern Hemisphere spring of 1997 (October) residents near Lago Nahuel Huapi in northern Patagonia reported seeing large numbers of mice crossing the roads, and rafts of dead mice floating in the lake and washing up on the beaches. At one beach Rangers at Parque Nacional Nahuel Huapi reported that each night about 150 mice fell into a 400-litre container installed in the sand. Described below are sites in affected areas and in nearby control areas where I began trapping in early November 1997. Local residents agreed that the abundance of mice had decreased by then, and only a few carcasses were still appearing on the beaches.

a) Lago Espejo Chico (40°37′S; 71°40′W, elevation 760 m). This is a forested region within Parque Nacional Nahuel Huapi (Fig. 1). Homesteads were cleared almost a century ago and some cattle still graze the roadsides and the occasional meadows, or browse on bamboo and shrubs in the forest. Four species of southern beech (*Nothofagus*) account for an estimated 95% of the forest canopy, much of it *N. dombeyi*. In October 1997, park rangers gathered 50 mouse carcasses from beaches on Lago Espejo, Lago Espejo Chico, and Lago Correntoso, and froze them for my dissection. We found 14 additional carcasses on these beaches in early November. We trapped at Lago Espejo Chico in November and December, 1997, and in April and November of 1998. The habitat sampled most intensively was ñire forest (*N. antarctica*) draped with lichen (*Usnea* sp.), a cattle-browsed understory of bamboo (*Chusquea culeou*), *Gaultheria* sp., *Pernettya* sp., three species of *Berberis*, *Ribes*, and a few green, grazed meadows. Noteworthy was an almost complete absence of the introduced wild rose (*Rosa rubiginosa*) and scotch broom (*Cytisus scoparius*), two invasive plant species that dominate many disturbed areas and provide food for some species of mice such as *Oligoryzomys*.

b) Llao Llao Peninsula (41°03′S; 71°32′W, elevation 760 m) is located on the southern margin of Lago Nahuel Huapi, across the lake and 35 km from Lago Espejo Chico (Fig. 1). It is densely forested and has not been grazed for 60 years. The forest is composed mainly of *N. dombeyi* and *Austroce-*

drus chilensis with bamboo understory. Wild rose and scotch broom are abundant on roadsides and disturbed areas. We trapped on the Llao Llao Peninsula in November and December of 1997, and in April, October and November of 1998. We also have trapping records for this site during many earlier years.

c) Parque Nacional Los Alerces (42°50′S; 71°50′W). In spring of 1997 mice were unusually abundant at this site 200 km south of Lago Nahuel Huapi; one resident documented that in October and November 1997 an average of 73 mice per day fell into pit traps near his home on the southern edge of Lago Futalaufquen (J. Oszlost, pers. com.). In November–December 1997 we trapped a few hundred m inland from the lake in a forest of *N. dombeyi*, *Austrocedrus chilensis*, *Lomatia hirsuta*, and occasional clumps of bamboo. Wild rose was present in the clearings. We also trapped at Rio Arrayanes (between Lago Verde and Lago Futalaufquen), in a large meadow being invaded by wild rose, and in the surrounding forest of *N. dombeyi* trees and bamboo.

d) Hua Hum (40°07′S; 71°40′W; elevation 780 m). This site at the west end of Lago Lacar (Parque Nacional Lanín, Neuquen Province), was trapped to increase the geographical area sampled. It is 60 km north of Lago Espejo Chico. Habitats trapped included open meadow bordered by blackberry and wild rose, and bamboo, second growth forest, and primary forest. We trapped there in April–May, 1998.

e) Bariloche Ecotone (41°09′S; 71°18′W; elevation 760 m). This includes four localities where we trapped in November 1997, each in a different direction from the town of Bariloche (Fig. 1).

Lagunita El Trebol is 5 km SE of the Llao Llao Peninsula and 15 km WNW of Bariloche. The vegetation is dense scrub composed of *N. antarctica*, *Berberis*, *Lomatia hirsuta*, and *Colletia spinosissima*. There was no wild rose, no bamboo, and very little grass. Patches of *N. dombeyi* forest and bamboo could be found nearby. The site may have burned repeatedly in past decades. In May 1998, we trapped at a site 1 km to the west, where the habitat was a rose-choked meadow surrounded by second-growth *N. dombeyi* and *A. chilensis*.

Lago Guillelmo is 40 km SSW of Bariloche with a mosaic of meadows and *N. antarcticus* forest with a bamboo understory.

Cerro Otto is 10 km east of Bariloche, at an elevation of 1145 m. The habitat is a *N. pumilio* forest with a bamboo understory and no wild rose or scotch broom.

Aeroclub is 12 km NE of Bariloche and includes four trapping sites within a few km of each other. The habitats consist of roadside tangles of wild rose, *Mulinum spinosum*, *Acaena splendens*, *Eryngium*, *Berberis*, scotch broom, *Diostea juncea*, and grasses. The sites were on the edge of heavily grazed steppe east of the *Nothofagus* forest. We trapped here in November December 1997, and April and November 1998.

The Baseline Population

Twenty years of data (1976–1996) from eight additional nearby localities containing *O. longicaudatus* and *A. longipilis* have been used to enlarge the database for ‘normal’ years and thus to represent non-outbreak ‘Baseline Populations’. These localities all fall within the triangle connecting Lagunita El Trebol, Lago Guillelmo, and Aeroclub (Fig. 1), and include: Cerro Leones, Las Victorias, Hipodromo, Pampa de Hueñuleo, Lago Gutierrez, Rio Casa de Piedras, Lago Perito Moreno, Bariloche, Paloma Blanca, Melipal, and Pampa Quemada (near Centro Atomico). The same rodent species found in the outbreaks at Llao Llao and Lago Espejo Chico occur in these areas, as well as a few steppe species that do not live in dense forest.

Method of capture and analysis

The same trapping procedure was used throughout the 20 years covered in this report, and the same two people carried out almost all of the trapping. Consequently, trapping results should be comparable. Traps were set in lines, 5 to 10 m between traps. Folding, aluminum Sherman box traps (7.5 × 9 × 22.5 cm) were set alternately with Museum Special kill traps (14 × 7 cm), or else a pair of these traps (one Sherman and one Museum Special) was set within a few m of each other about every 10 m. Rolled oats, corn meal, or a mixture of the two was used for bait.

Trap success (the percent of traps capturing animals during the first night of trapping on each trap line) was used as a measure of the abundance of each species of mouse.

Examination of mice

Mice captured alive were killed by cervical dislocation or with carbon monoxide. Autopsies carried out under low magnification included measurements of total length, length of tail, length of hind foot, ears, and tail, body weight, and reproductive condition. In males, length of a testis and of a seminal vesicle were recorded. Either of these measurements indicated whether the animal was in breeding condition. In doubtful cases, the visibility of the tubule of the cauda epididymis was noted, or a smear of the cauda epididymis was examined for the presence of spermatozoa. In females, record was kept of open or closed vagina, size of nipples, presence or absence of uterine scars, of fetuses, of mammary tissue and of milk in the nipples. In all 1997 and 1998 specimens, notes were also made on the number of scars on the tail, amount of subcutaneous and abdominal fat [scored from none (0) to great (2)], and the condition of the liver and lungs.

The weight of specimens washed up on the beaches was corrected for the extra weight of their wet fur. A correction factor was calculated by weighing a number of dry, trapped specimens of comparable size, soaking their fur, mopping excess water with paper towels, and then re-weighing them.

Skulls of all specimens in 1997 and most specimens in earlier years were dried and later cleaned by larvae of dermestid beetles. Wear on two molar teeth was then measured as described in Pearson (1975), and these measurements (cusp height) were used to estimate the age of each individual *O. longicaudatus* (Pearson, 1983) and *A. longipilis* (Pearson, 1992). The smaller the toothwear number, the older the individual. To construct age pyramids, toothwear cohorts were chosen appropriate to the range of measurements encountered in each species.

Results

Beached samples

The 50 mouse carcasses collected by Park personnel on 3–5 October 1997 included: 34 *Oligoryzomys longicaudatus*, 11 *Loxodontomys micropus*, one *Abrothrix longipilis*, one *Irenomys tarsalis*, and one *Geoxus valdivianus*. Two partly-eaten carcasses were not identifiable. The 14 carcasses found on the beach on November 6 comprised: 12 *O. longicaudatus*, one *L. micropus*, and one *Abrothrix olivaceus*.

Neither males nor females of any species in the beached samples were breeding. Almost the entire *Oligoryzomys* sample consisted of individuals with an average age of 4.5 months (Fig. 3B below, Row 1, left pyramid), implying that many of these mice had been born in the winter months of May, June and July. Very few tails were scarred, suggesting that they had not been fighting among themselves. Livers appeared to be normal. Lungs of all except the *Geoxus*, the *Loxodontomys*, and one *Oligoryzomys* were recorded as having grossly visible hemorrhagic spots. In two specimens of *Oligoryzomys* examined by Dr. Donna Kusewitt at the University of New Mexico, immunohistochemical staining of the lungs gave a positive reponse for hantavirus.

Trapped samples of *Oligoryzomys longicaudatus*

Abundance: Springtime abundances of the Baseline Population of *Oligoryzomys* during the 20 years preceding the 1997 outbreak were consistently below 10%, and averaged 3.4% (Fig. 2). In contrast, trap success for *Oligoryzomys* at Lago Espejo Chico, Llao Llao Peninsula and Los Alerces in November 1997 (Table 1, Fig. 2) was four to more than ten times higher and declined in December. Trapping at the first two sites in the following April showed that populations had not increased appreciably during the summer, and by the following spring (November 1998) trap success had diminished to its usual low value (Table 1).

Trapping on November 22 and December 9, 1997, on the Llao Llao Peninsula achieved trap successes for *Oligoryzomys* of 25% and 14%, respectively. These percentages are above the 20-year record of the Baseline Population (Fig. 2), and well above the 2.3% achieved during 1025 additional trap nights on the Llao Llao Peninsula in the springtime of various years between 1981 and 1991.

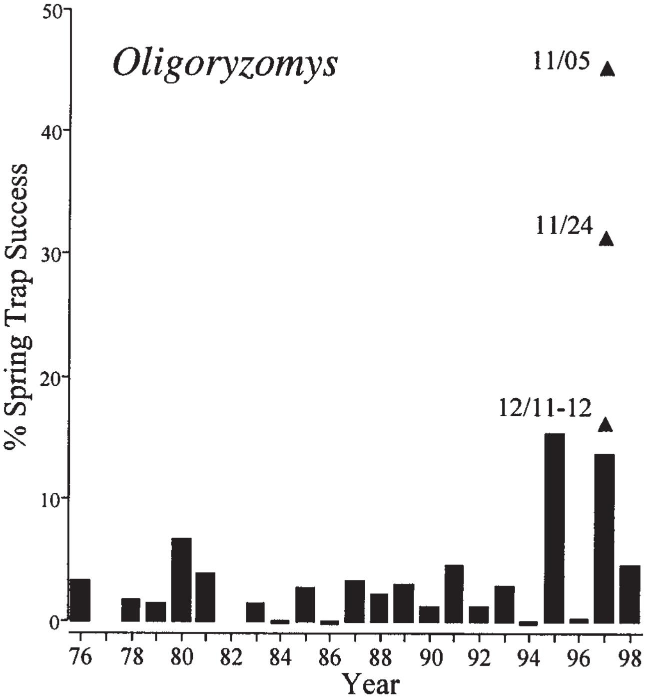

Fig. 2. Springtime trap success for the Baseline Population of *Oligoryzomys* from 1976 to 1996. Data come from an area centered on Lago Nahuel Huapi, and includes localities known to support *Oligoryzomys* but not shown in Fig. 1. Triangles near the right margin show trap success for three collections at Lago Espejo Chico in the spring of 1997. The 1994 and 1995 points are each based on only 14 trap nights; the points for 1993, 1996, 1997 and 1998 are each based on more than 600 trap nights and therefore are more reliable.

At the four localities included in the Bariloche Ecotone (Fig. 1), trap success between November 9 and December 6, 1997, averaged a normal 2.9% (Table 1), almost the same as that registered for this area in the springtime of earlier years (3.06% on 3567 trap nights between 1981 and 1996). Trap success at the end of summer was similar to all other sites but dropped down overwinter (Table 1).

Sex ratio: Spring samples tended to be biased toward males, even those from non-outbreak Bariloche populations. Autumn samples were closer to the expected 1 : 1 ratio.

Fat index: *Oligoryzomys* trapped at Lago Espejo Chico had high fat scores while mice trapped at Llao Llao in the same spring were only moderately fat. After spring of 1997, however, no mice trapped at any of our sites were fat (Table 1).

Tail scars: The average number of scars ranged from 0 to 0.28 per tail (Table 1) and did not seem to be correlated with either high trap success or fat scores. In 56 museum specimens of *O. longicaudatus* there was an average of 0.14 scars per tail.

Lungs: All samples from outbreak sites as well as from sites with more usual population densities, contained many individuals with hemorrhagic spots on the lungs.

Table 1. Data on *Oligoryzomys* populations sampled in 1997–1998. Standard errors are given for the means of Head and Body Length, Mass, and Cusp Height of the molars.

Locality	Date	Traps	Trap success			Length*	Mass	Cusp Height	♂♂	Hemo. lungs**	Tail scars	Fat score	Breeding
		n	All spp. %	*O. longi-caudatus* %	*n*	$\bar{x}$ ± SE (mm)	$\bar{x}$ ± SE (g)	$\bar{x}$ ± SE (µm)	%	%	$\bar{x}$	$\bar{x}$	%
Lago Espejo Chico et al.													
Beaches	10/3/97				34	99.9 ± 1.16	37.4 ± 1.57	403 ± 9.3	68	97	0.24	1.12	0
Beaches	11/06/97				12	96.8	27.8 ± 2.07	383 ± 7.1	75	100	0.08	0.08	0
Lago Espejo Chico													
Traps	11/05/97	83	63	46	36	89.3 ± 1.56	25.5 ± 1.44	378 ± 7	72	22	0.08	0.53	0
Traps	11/24/97	100	43	30	29	91.4 ± 1.69	24.7 ± 1.14	369 ± 12	62	17	0.28	0.38	0
Traps	12/11/97	188	30	13	16	87.2 ± 1.79	24.3 ± 1.66	350 ± 13.9	75	37	0.25	0.44	0
Traps	4/23, 24, 29/98	281	31	15	43	82.7 ± 1.34	18.7 ± 0.8	392 ± 13.1	49	68	0.25	0.1	0
Traps	11/12–14/98	326	13	1	4	96.8	33.6	162	25	50	0.25	0	100
Llao Llao Peninsula													
Traps	11/22/97	101	57	25	27	89.4 ± 1.16	26.6 ± 0.99	315 ± 10	67	33	0	0.44	0
Traps	12/09/97	93	38	14	13	84.8 ± 1.99	22.8 ± 1.37	286 ± 10.6	54	31	0.08	0.23	8
Traps	4/18/98	139	40	17	24	95.9 ± 1.9	24.0 ± 1.42	258 ± 12.6	48	70	0.22	0.13	0
Traps	10/28–11/26/98	278	15	2	7	90.6 ± 5.9	31.1 ± 4.6	187 ± 39.9	71	14	0.14	0	86
Bariloche ecotone													
Traps	11/9–12/6/97	450	22	3	14	92.2 ± 1.68	31.9 ± 2.03	306 ± 13.4	86	50	0	0.07	92
Traps	4/20, 5/5/98	207	38	19	40	86.4 ± 1.51	23.2 ± 1.2	390 ± 10.6	52	45	0.15	0	45
Traps	11/3–19/98	294	20	7	21	93.9 ± 1.88	28 ± 1.69	268 ± 14.6	43	30	0	0	62
Parque Nacional Los Alerces													
Traps	11/29/97	184	62	21	39	93.8 ± 1.58	28.3 ± 1.43	295 ± 9.8	56	28	0.18	0.05	44
Hua Hum													
Traps	4/30, 5/1/98	170	26	17	30	91.4 ± 1.59	23.6 ± 1.38	356 ± 14.7	55	31	0.03	0.03	3

* Head and body.

** Hemorrhagic lungs.

Histological sections of formalin-fixed lungs showed lung congestion, intra-alveolar hemorrhage, peribronchial cuffing with lymphocytes admixed with eosinophils, and even infection by lung mites. Even after populations had returned to normal levels in the spring of 1998, as many as half the individuals had hemorrhagic lungs (Table 1).

Age: As measured by the height of the molar cusps, all samples except the spring of 1998 were composed of young, but not juvenile individuals (Fig. 3B). (Juveniles were mice whose third upper molars had not fully emerged.) The sample comprised of the youngest individuals was the first one (i.e., beached corpses, October 3, 1997). Three subsequent spring samples from Lago Espejo Chico showed a slowly increasing mean age (Table 1, Fig. 3B, Row 1). Only one fully adult specimen appeared in these four samples. The age pyramids for these springtime populations of *Oligoryzomys* resemble the autumn pyramid of the Baseline Population rather than that of the spring (Fig. 3A).

The two spring samples from the Llao Llao Peninsula in 1997 (Fig. 3B, Row 2) are slightly older than the Lago Espejo Chico samples, but adult and old animals are almost absent. By autumn 1998 the population has aged somewhat, a few young adults have appeared, but the profile of the pyramid is still more vernal than autumnal. By spring 1998, however, the profile has a normal spring profile showing adults and a few young. The sample from Los Alerces (Fig. 3B, Row 4) averages older but still lacks the older animals expected in a spring sample. The Bariloche spring sample for 1997 (Fig.

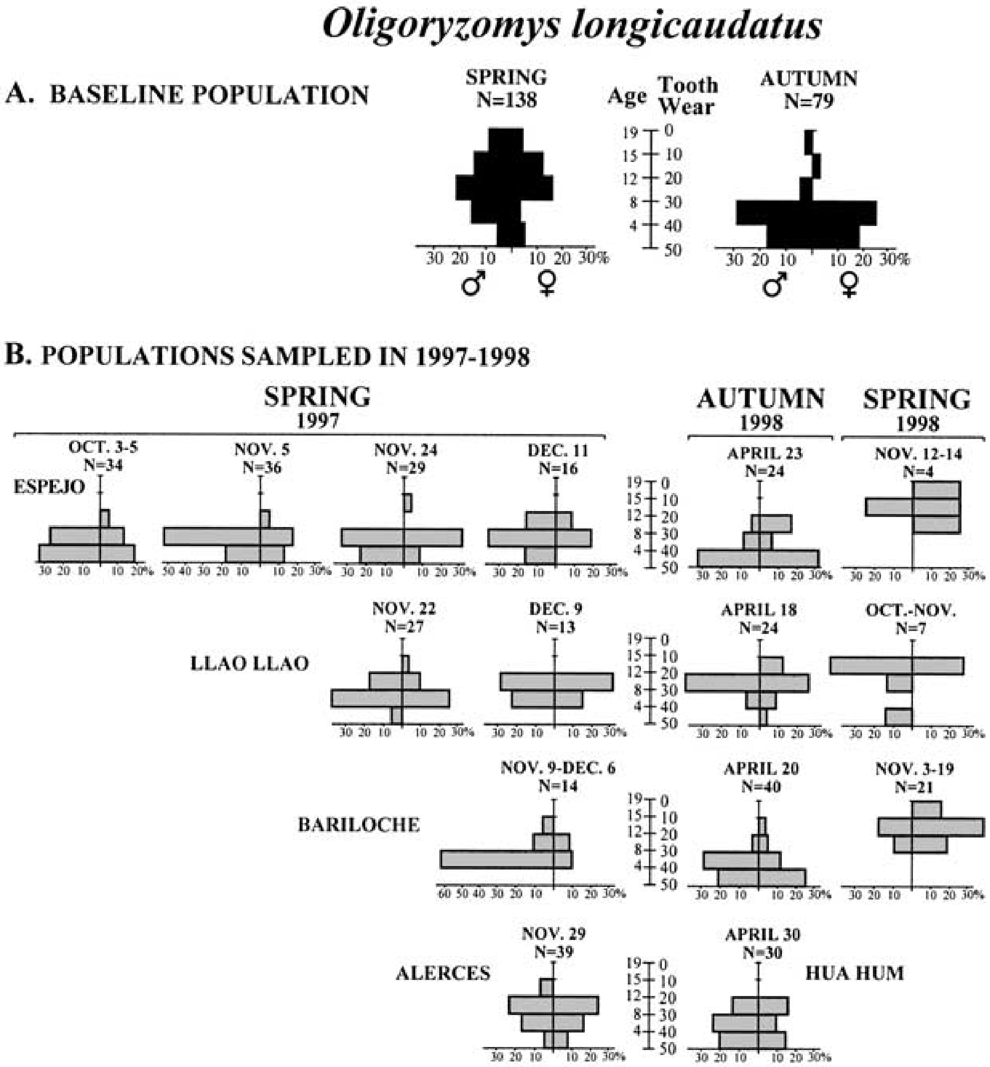

Fig. 3. Age pyramids of population samples of *Oligoryzomys*. The vertical axes represent cusp height of molar teeth (mm × 100) and estimated age in months; old cohorts at the top, young cohorts at the bottom. The horizontal axes represent percent frequency of males (left) and females in each cohort. (A) Age pyramids for the pre-outbreak, Baseline Population centered around Lago Nahuel Huapi. (B) Age pyramids of other populations. The sample from Lago Espejo Chico (row 1, extreme left) was picked up on the beach; all other samples were trapped.

3B, Row 3) also is more similar to an autumnal pyramid than to a vernal pyramid, but by April of 1998 has reverted to the 'expected' autumn configuration, and in the following spring (1998) has returned to a normal adult profile. The April sample from Hua Hum (Fig. 3B, Row 4) resembles a normal autumnal age pyramid.

Reproduction: None of the beached or trapped mice at Lago Espejo Chico in spring of 1997 and autumn of 1998 were in breeding condition (Table 1), although three of the oldest females were parous. On the Llao Llao Peninsula, only one of 40 springtime specimens of *Oligoryzomys* was in breeding condition (a male on December 9); females were neither pregnant nor parous. At Los Alerces 77% of the males were in breeding condition, but no females were pregnant; three of the older females were parous. In contrast, most specimens in the Bariloche Ecotone were breeding in the spring of 1997, and many were breeding in the following autumn as well. By spring of 1998, however, outbreak populations in the forested habitats (Lago Espejo Chico and Llao Llao) were reproducing as expected (Table 1 and Fig. 3).

Trapped samples of *Abrothrix longipilis*

Abundance: Trap success for *A. longipilis* in three springtime trappings at Lago Espejo Chico in 1997 was similar (Table 2) and only slightly higher than the average spring trap success at nearby sites between 1978 and 1989 (8.1% in 432 trap nights).

At Llao Llao Peninsula trap success in spring of 1997 was higher than the average spring trap success at the same site between l981 and l991 (13% on l025 trap nights) and also higher than spring values from Lago Espejo Chico (Table 2).

Trap success at Los Alerces in 1997 was 16% (Table 2).

The trap success of 14% in the Bariloche Ecotone in spring 1997 was somewhat greater than in previous years (8.1% in 3567 trap nights), but was within the range of values from other sampling areas (Table 2).

Sex ratio: Sex ratios varied greatly between sites (Table 2).

Fat index: The only specimen recorded as being fat was the single male found dead on a beach on October 3. It was larger, heavier, and younger than most trapped individuals.

Tail scars: The average number of tail scars in different samples varied from 0.08 to 1.81. Number of scars was not correlated with abundance of mice, and the greatest incidence of scarring was in the Lago Espejo Chico and Llao Llao populations in the spring of 1998. At that time the individuals in these populations were older than those caught during the outbreak (Table 2). The number of scars in our samples was considerably higher than the average in 175 museum skins, which was 0.05. Tail scars in the outbreak populations were not fresh, and they were not accompanied by body scarring.

Lungs: In every sample from the outbreak populations, 40% or more of the individuals had hemorrhagic patches on the lungs. In the spring of 1998, a year after the outbreak, lung hemorrhages had decreased considerably in the forested habitats where the outbreak populations lived, but remained high in the non-outbreak Bariloche populations (Table 2).

Age: Mice in the spring samples of 1997 were approximately 4.5 to 6.5 months old, born unusually late in the preceding autumn and winter. Age pyramids of samples trapped at Lago Espejo Chico and Llao Llao at this time reflect a young population (Fig. 4B, Rows 1 and 2). They resemble pyramids from an autumn population rather than from a spring population. Old individuals are lacking. The average age of the Los Alerces population (Fig. 4B, Row 4) was older than that of the outbreak populations at Lago Espejo Chico and Llao Llao. This is accounted for by the survival of a cohort of year-old animals almost lacking in the other outbreak samples.

The Bariloche Ecotone sample in spring of 1997 (Fig. 4B, Row 3) shows a distribution of ages similar to that of *A. longipilis* in non-outbreak years (Fig. 4A, left). In the following autumn (1998), the Bariloche sample displays a young pyramid, as expected, but without any old individuals (Fig. 4B, Row 3), and by the following spring (1998) the age pyramid has the same mature profile as the Baseline Population of *A. longipilis* (Fig. 4A, left).

Reproduction: No breeding males or females were encountered in the spring and autumn samples 1997–1998 at Lago Espejo Chico and Llao Llao Peninsula. At Los Alerces none of the females was pregnant in spring 1997, but two of the year-old cohort were parous. A few males were in breeding condition, including two of the year-old cohort. In the Bariloche Ecotone, most springtime (1997) mice were in breeding conditon (Table 2). Ninety-four percent of the males were sexually competent, two juvenile males had small testes, and 28% of the females were visibly pregnant. Many other females had recent corpora lutea. By springtime, 1998, outbreak populations at Espejo Chico and Llao Llao had returned to the normal, full-breeding schedule, and the Bariloche Ecotone populations continued their usual spring reproduction.

Baseline Populations

In nine years for which I have data from autumn and from the following spring, trap success for all species of mice combined dropped from an autumn average of 29.3% to 16.5% in the spring (Fig. 5A). This suggests a surviving population only 0.56 times as large in the spring as in the preceding autumn. In the same Baseline Population at the same time, trap success for *Oligoryzomys* (Fig. 5A) dropped from 5.3% to 2.4% (survival of 0.45). In the outbreak areas at Lago Espejo Chico amd Llao Llao Peninsula, post-peak survival rates of overwintering *Oligoryzomys* were much lower: 0.08 and 0.14 (Fig. 5B). In the Bariloche Ecotone

Table 2. Data on *Abrothrix longipilis* populations sampled in 1997–1998. Standard errors are given for the means of Head and Body Length, Mass, and Cusp Height of the molars.

Locality	Date	Traps *n*	Trap success All spp. %	Trap success *A. longipilis* %	Trap success *A. longipilis* *n*	Length* $\bar{x} \pm$ SE (mm)	Mass $\bar{x} \pm$ SE (g)	Cusp height $\bar{x} \pm$ SE (µm)	♂♂ %	Hemo. lungs** %	Tail scars $\bar{x}$	Fat score $\bar{x}$	Breeding %
Lago Espejo Chico et al.													
Beaches	10/3/97				1	111	38.8	777	100	100	2	1	0
Beaches	11/06/97				0								
Lago Espejo Chico													
Traps	11/05/97	83	63	11	9	94.4 ± 1.13	28.2 ± 1.01	692 ± 23.6	44	55	0.67	0	0
Traps	11/29/97	100	43	11	11	102 ± 1.43	29.3 ± 0.98	656 ± 42.5	18	100	0.45	0	0
Traps	12/11/97	188	30	10	18	95.3 ± 2.5	29.2 ± 0.87	664 ± 14.1	67	72	0.28	0	0
Traps	4/23, 24, 29/98	281	31	10	27	105 ± 0.93	32.7 ± 0.63	566 ± 12.5	58	62	0.84	0	0
Traps	11/12–14/98	326	13	10	32	110.2 ± 2.44	39.4 ± 4.7	333 ± 15.2	66	16	1.25	0	97
Llao Llao Peninsula													
Traps	11/22/97	101	57	22	20	99.4 ± 1.49	32.2 ± 0.69	656 ± 14.4	45	55	0.6	0	0
Traps	12/09/97	93	38	16	15	96.5 ± 1.54	32.8 ± 0.84	653 ± 14.2	80	60	0.08	0	0
Traps	4/18/98	139	40	12	17	97.6 ± 1.59	30.3 ± 0.91	607 ± 20.9	27	40	0.67	0.07	0
Traps	10/28–11/26/98	278	15	10	27	104.6 ± 1.49	39.6 ± 1.07	440 ± 20.7	52	30	1.81	0	81
Bariloche ecotone													
Traps	11/9–12/6/97	450	22	14	63	96.6 ± 0.93	36.4 ± 0.89	401 ± 20.3	59	80	0.72	0	68
Traps	4/20, 5/5/98	207	38	13	27	94.7 ± 1.36	28.1 ± 0.64	591 ± 18.3	52	70	0.37	0	0
Traps	11/3–11/19/98	294	20	9	26	102.5 ± 2.60	32.8 ± 1.07	389 ± 22.1	62	81	0.5	0	88
Parque Nacional Alerces													
Traps	11/29/97	184	62	16	29	98.3 ± 1.75	31.9 ± 1.52	598 ± 32	56	55	0.1	0	14
Hua Hum													
Traps	4/30, 5/1/98	170	26	5	4	103	33.3		75	25	0.75	0	0

* Head and body.

** Hemorrhagic lungs.

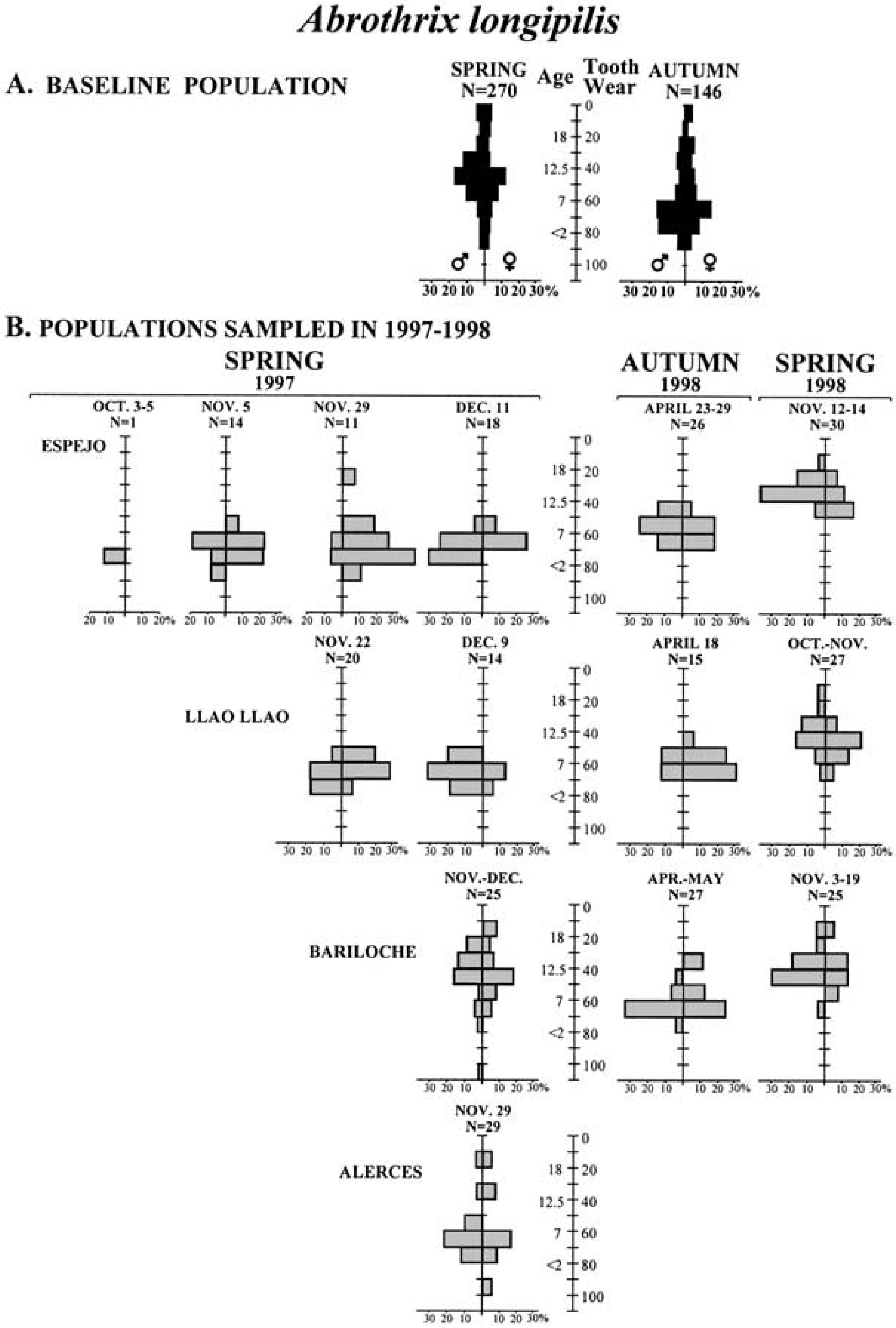

Fig. 4. Age pyramids of populations of *Abrothrix longipilis*. Axes as in Fig. 3. (A) Age pyramids for the Baseline Population. (B) Other populations sampled from spring of 1997 through spring of 1998. All but the October Espejo sample (left) were trapped.

population, which did not experience an outbreak, the overwinter survival value for all species was 0.53 and for Oligoryzomys 0.37 (Fig. 5C) – values much closer to those of the non-erupting Baseline Population (Fig. 5A).

Comparisons of trap success for spring and the following autumn in the Baseline Population measures reproductive success for an average breeding season (Fig. 5A). Trap success for all species rises from 15.8% to 32.3% from spring to autumn. This reflects a 2.04-fold net increase (reproduction plus immigration minus mortality and emigration). Considering only captures of *Oligoryzomys*, the summer increase was greater (2.95) and the winter attrition more severe (0.45)

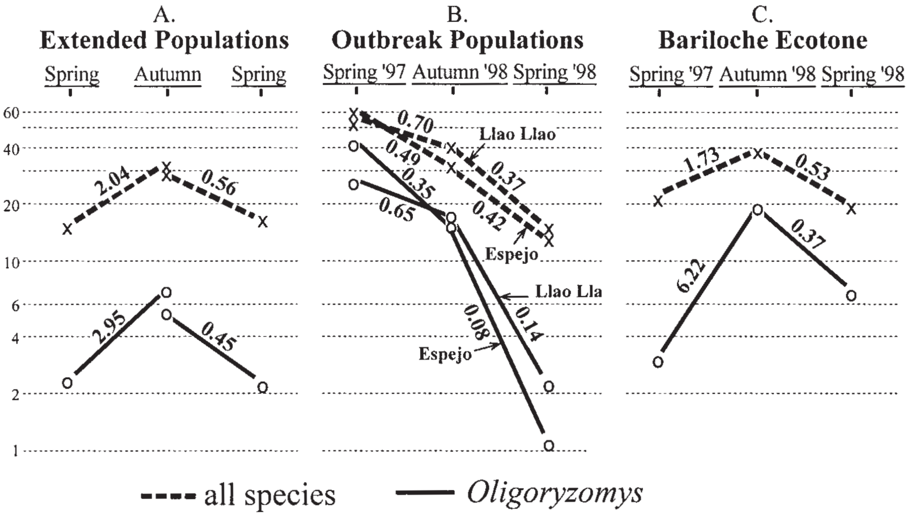

Fig. 5. Changes in trap success and survival rates (terminal trap success divided by initial trap success) from autumn to spring (over-winter decline) and spring to autumn (breeding season increase) of three populations of *Oligoryzomys* and of all species of mice. Survival rates are placed along the lines connecting trap successes. Vertical axis is logarithmic. (A) The Baseline Population during nine different seasons: for comparison with B and C. (B) Populations at Lago Espejo Chico and Llao Llao Peninsula during collapse of the outbreak populations there. (C) Populations in the Bariloche ecotonal area during collapse of the Espejo and Llao Llao populations.

than for all species combined (Fig. 5A), probably reflecting greater fecundity and mortality in *Oligoryzomys*.

Instead of the normal 2.04 increase between spring and autumn (Fig. 5A), trap success for these outbreak populations decreased (Fig. 5B). The decrease of *Oligoryzomys* itself at the same time and place was at a rate of 0.35 and 0.65. The negative slope of the lines representing trap success in the spring and summer of 1997–1998 reflects failure of reproduction during that breeding season.

Discussion

Reproduction in outbreak populations

The outbreak documented here, presumably aperiodic, occurred only in forested areas, and resulted from a breeding season that continued unusually late into the autumn and winter of 1997. The abundant mice present in the following spring were fat, many had food in their stomachs, many were old enough to breed, but none were breeding. In cyclic lemming populations such as *Lemmus trimucronatus* in Alaska, ovulation rates and embryo counts remain high in years with peak populations (Mullen, 1968). Population increase of lemmings depends upon attenuation of the breeding season by a favourable temperature regime. Clearly, reproduction plays a different role in the cyclic lemming populations than it does in Patagonian mice we have documented.

In the Baseline Population, *Oligoryzomys* was reproductively active between one and two months of age in the spring (Pearson, 1983), and *A. longipilis* at 4.5 months (Pearson, 1992). In the spring outbreak populations in our study, females as old as 7 months were not breeding. It is clear that mice in this burgeoning population were not breeding at a younger age than usual, a reproductive stratagem found in microtines that contributes powerfully to rapid growth of populations (Cole, 1954). The delay in reproduction of our outbreak population accompanied a decline in numbers, and by spring of 1998, mice were present at their usual densities.

Unusual mortality or natality?

For populations of mice to reach the abundance encountered in spring 1997, mortality or natality, or both, must have been drastically modified. The species involved in the outbreak are essentially annuals; very few individuals survive more than one breeding season (Pearson, 1983, 1995; Murua et al., 1986; Kelt, 1994; Guthmann, 1998). Mortality seems to have played a minor role in the dynamics of the outbreak. Even after the mass drownings early in October 1997, populations remained high at Lago Espejo Chico.

In the forests of Lago Espejo Chico, Llao Llao Peninsula, and Los Alerces, where mouse populations were demonstrably high, we could not detect an increase in the number of owls, hawks, and carnivores. Carnivores such as foxes catch very few *Oligoryzomys* (Martinez et al., 1993), and residents of the area remarked that there seemed to be fewer than usual chimangos (*Milvago chimango*), the ubiquitous scavenger/predator. After October 1997, the relatively modest rates of decrease in trap success presumably reflect attrition and emigration of the mice. This decrease is much less severe than in, for example, non-breeding populations of microtine rodents under heavy predation pressure, which lose as much as 33% of the population per month (Pearson, 1971). Therefore, predation on the Argentine outbreak populations was not severe. Indeed, the rafts of dead mice on the lakes and beaches demonstrate the ineffectiveness of predation in controlling this kind of outbreak. The outbreak was too brief to attract predators from elsewhere or to support increased reproduction among the predators themselves.

Pathology of mice and relations to HPS virus

The role of lung pathology in the dynamics of the outbreak and decline of the populations is not clear. Since multiple small foci of hemorrhage can be associated with death from numerous kinds of trauma, it cannot be assumed that disease was killing these mice. Death of the beached samples was presumably caused by drowning and trapped specimens were killed in other ways, yet all samples contained specimens showing lung pathology. Lung pathologies noted in outbreaks of mice in other regions have been associated with infections by protozoa, bacteria, mycoplasms, and viruses (Findlay & Middleton, 1936; Jensen & Duncan, 1980; Descoteaux & Mihok, 1986; Smith et al., 1993).

In Argentina, exceptional interest focuses on lung pathologies and on viruses because in the autumn of 1995 hantavirus pulmonary syndrome (HPS), caused by the previously unknown Andes strain of hantavirus, appeared in the study area. After an alarming number of human fatalities from HPS in the spring of 1996, the outbreak of HPS receded just before the outbreak of mice documented in this report. The related Sin Nombre virus responsible for HPS in the United States is carried by deer mice (*Peromyscus maniculatus*) and causes not only HPS in humans but pathologies of the lungs of host mice (Netski et al., 1999). *O. longicaudatus* is a species with appearance and habits very similar to those of *P. maniculatus* and has been shown to be a reservoir of the Andes strain of hantavirus (Calderon et al., 1999). The present study has not established a direct connection between mice and human cases of HPS. The relationship is probably complex, since the number of human cases reached a peak a year before the *Oligoryzomys* outbreak.

The small number of mice with tail scars indicates a low level of aggression among the outbreak mice in our study. Individual *Oligoryzomys* and *Abrothrix abrothrix* trapped alive behaved like normal mice of their species, unlike peaking lemmings in Finnish Lapland (Henttonen & Kaikusalo, 1993).

Except for tapeworm hydatids in the liver of numerous *Oligoryzomys* from the Bariloche Ecotone, examination of the livers and hearts revealed no pathologies. In conclusion, unusual pathologies do not seem to be important factors in explaining the rise and fall of these mouse populations.

Despite the lack of breeding in spring samples of 1997 in the forest population of Lago Espejo Chico, *Oligoryzomys* reproduced during the following summer, as evidenced by the many young in the fall population of 1998 (Fig. 3B, Row 1). The broad base of this *Oligoryzomys* pyramid, however, did not result in an abundance of this mouse. Trap success remained at 15%, with no old individuals. In the Bariloche ecotone in 1997, spring and summer reproduction was normal: trap success for *Oligoryzomys* rose from 3% in the spring to 19% in the autumn (Table 1). By spring, 1998, males and females were breeding normally both in the forest populations and in the Bariloche Ecotone. *Abrothrix* populations followed the same pattern.

Comparison with other outbreaks

Large numbers of mice appeared at various places in southern Argentina and Chile in the years 1995 to 1998. One outbreak at Ushuaia in Tierra del Fuego, 1600 km south of Bariloche, occurred in August and September of 1996 while snow was still on the ground. Natalie Goodall (pers. com.) counted 460 mice along 45 km of road, most of them on a 10 km section. Many of them were eating carcasses of previously squashed mice. In another situation, Nadia Guthmann (pers. com.) had more than 50% trap success for mice in December of 1996 at Lago Puelo, 120 km south of Bariloche, but only low success nearby at El Bolson. The vegetation in these two areas is quite distinct, and neither outbreak appeared to be related to a vegetative event, so presumably they were aperiodic outbreaks.

Trap success of *Mus* in seasons following the cyclic mast seeding of *Nothofagus* in New Zealand increased to levels similar to those we encountered with *Oligoryzomys* in the Patagonian outbreak. Reproduction in New Zealand, as in Patagonia, continued into the winter in seed years and ceased earlier in the spring. However, peak New Zealand populations, in contrast to Patagonian, consisted mainly of older mice, still breeding, but without significant recruitment (King, 1982, 1983).

A spectacular outbreak of the periodic category occurred in Chile, 150 km west of Bariloche, in 1994 and 1995 in response to an infrequent but cyclic flowering and seeding of the quila bamboo (*Chusquea valdiviensis*). *Oligoryzomys* became so abundant that in one region trap success reached 125% in four hours of trapping, and more than 2000 individuals were trapped in four 200-liter barrels in one night (Gallardo & Mercado, 1999). Murua et al. (1996) studied similar events at two localities in Chile. At one of their sites they had monitored the mouse populations for 15 years and were able to document that the number of *Oligoryzomys* increased to a level 14 times greater than in previous seasons, probably in response to the production of as many as five million bamboo seeds per week per hectare on that study area.

The aperiodic outbreak of mice in 1997 at Lago Espejo Chico and on the Llao Llao Peninsula did not extend into populations near Bariloche (Fig. 1). It must be concluded that outbreaks of mice can be patchily distributed, are not necessarily synchronous, and can have more than one cause, since they occur in vegetationally diverse regions.

Possible causes of the perplexing outbreak

Outbreaks of mice in other parts of the world have been associated with unusually favorable weather or food conditions which can support two extended breeding seasons, the second one compounding the population increase resulting from the first. Examples are: feral house mice (*Mus domesticus*) following mild winters in California (Pearson, 1963); lemmings (*Lemmus lemmus*) following mild winters in Finnish Lapland (Henttonen & Kaikusalo, 1993); mice following unusually abundant rainfall in the coastal desert of Peru and northern Chile for one season (Lima et al., 1999), or for two seasons (Pearson, 1975; Jaksic et al., 1997).

The winter of 1996 was unusually dry, 1997 was wet, and 1998 was unusually dry (Fig. 6B). Thus, the warm dry winter of 1996 might be considered to have been favorable to reproduction, but it was followed by a normal June, a wet July, a normal August, and then a very dry winter in 1998 (Fig. 6B). Apparently, precipitation does not correlate with the unusual winter breeding shown by *Oligoryzomys* and *A. longipilis*.

The weather extremes accompanying the El Niño event of 1997–1998 on the Pacific coast of Chile and Peru were detectable but subdued in the region of this study. Temperature records for 18 years at Bariloche disclose that every month except four between July 1996, and November 1998, was distinctly warmer than usual; the four colder months were insignificantly colder than normal (Fig. 6A). The age pyramids of *Oligoryzomys* and *Abrothrix* from the outbreak regions in the spring of 1997 show that almost the entire population had been born late in the previous autumn and in midwinter, a time of year when breeding had not been noted before. Therefore, it might be inferred that warm weather in two consecutive winters had permitted winter breeding, and resulted in a build-up of mouse populations. However, the observation that mouse populations in the nearby Bariloche Ecotone maintained a normal breeding regime (Fig. 5C) in spite of a similar temperature regime, suggests that the warm winters influenced breeding in some indirect manner.

It is possible that the weather regime increased the production of some forest food item that in turn stimulated winter reproduction, early sexual maturity, or both. Winter breeding following abundant food production has been demonstrated in other rodents (Wolff, 1996). Murua et al. (1980) noted that captive *Oligoryzomys* ate seeds of *Nothofagus dombeyi*, but Meserve et al. (1988) failed to find *dombeyi* seeds in stomachs of wild-caught mice. We found no evidence of unusually great seed production by any of the *Nothofagus* species in the area of our study. However, there were windrows of the racemes and terminal leaves of tineo trees (*Weinmannia trichosperma*, Cunoniaceae) on beaches where drowned mice had been found. *W. trichosperma* is a small tree, not common in the region, but fragments of this plant may have blown in from Chile where it is more abundant. *Oligoryzomys* showed a strong preference for *W. trichosperma* seeds in dietary tests (Murua et al., 1980), and its seeds were common in stomachs of wild-caught *Oligoryzomys* and other species in Chile (Meserve et al., 1988). It is possible that these seeds were responsible for the outbreak we observed.

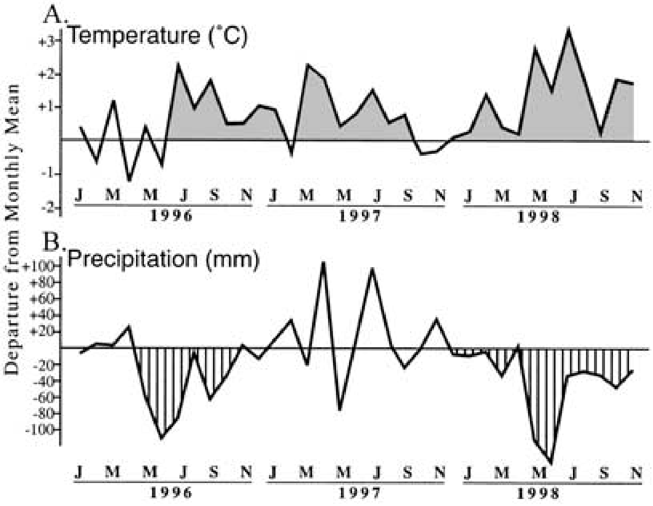

Fig. 6. Departures of mean monthly weather data for each month during the study from the long-term mean monthly data at Bariloche from 1981–1995. The shaded areas emphasize significant departures from the long-term mean. (A) Temperature. (B) Precipitation.

The events that produced this acyclic outbreak that extended almost 300 km along the Andes have not been identified with certainty. It will be interesting to see whether the more recent outbreak driven by the cyclic widespread flowering and seeding of the bamboo in this area produces a similar or different suite of demographic events.

Acknowledgements

For assistance in collecting and processing mice in the field I am grateful to Anita Pearson, Richard Sage, and Adrian Monjeau. For providing valuable information and support from Park Guards I am indebted to Claudio Chehebar, Eduardo Ramilo, and Gustavo Iglesias of the Delegacion Regional Patagonia of the Administracion de Parques Nacionales in Bariloche. Carlos Bustos of INTA kindly supplied weather data. Finally, I am indebted to the following people for their eager searches for pathologies in lung and heart tissues: Maureen Davidson (University of Florida), Linda Lowenstine (University of California, Davis), Brian Hjelle, Wendy Green, Rich Feddersen, and especially Donna Kusewitt (University of New Mexico), and James Mills and Shieh Wun-Ju (Center for Disease Control and Prevention, Department of Health and Human Services, Atlanta).

References

Calderon G, Pini N, Bolpe J, Levis S, Mills J, Segura E, Guthmann N, Cantoni G, Becker J, Fonollat A, Ripoll C, Bortman M, Benedetti R, Sabattini M, Enria D (1999): Hantavirus reservoir hosts associated with peridomestic habitats in Argentina. *Emerg Infect Dis 5*: 792–797.

Christie MI [1984] not dated: *Informe preliminar del relevamiento de fauna de Parques Nacionales Lanin y Nahuel Huapi*, Vol. 3. Mamíferos. Trabajo realizado en colaboracion APN/INVAP S.E. bajo contrato ‘Plan Inventario’, Bariloche, Argentina, 71 pp.

Cole LC (1954): The population consequences of life history phenomena. *Q Rev Biol 29*: 103–137.

Descoteaux J-P, Mihok S (1986): Serological study on the prevalence of murine viruses in a population of wild meadow voles (*Microtus pennsylvanicus*). *J Wildlife Dis 22*: 314–319.

Findlay GM, Middleton AD (1934): Epidemic disease among voles (*Microtus*) with special reference to *Toxoplasma*. *J Anim Ecol 3*: 150–160.

Gallardo M, Mercado C (1999): Mast seeding of bamboo shrubs and mouse outbreaks in southern Chile. *Mastozool Neotrop 6*: 103–111.

Guthmann N (1998): Colilargo (*Oligoryzomys longicaudatus*). In: *Patagonia Silvestre*. Sociedad Naturalista Andino Patagonica, Serie Tecnica, Bariloche, Argentina, Fauna Andinopatagonica No. 2: 20–23.

Henttonen H, Kaikusalo A (1993): Lemming movements. In: Stenseth NC, Ims RA, eds., *The Biology of Lemmings*. Linnean Society Symposium Series No. 15. Academic Press, San Diego, CA, pp. 157–186.

Jaksic FM, Silva SI, Meserve PL, Gutierrez JR (1997): A long-term study of vertebrate predator responses to an El Niño (ENSO) disturbance in western South America. *Oikos 78*: 341–354.

Jensen WI, Duncan RM (1980): *Bordatella bronchiseptica* associated with pulmonary disease in mountain voles (Microtus montanus). *J Wildlife Dis 16*: 11–13.

Kelt DA (1994): The natural history of small mammals from Aisen region, southern Chile. *Rev Chil Hist Nat 67*: 183–207.

King CM (1982): Age structure and reproduction in feral New Zealand populations of the house mouse (*Mus musculus*), in relation to seedfall in southern beech. *New Zeal J Zool 9*: 467–480.

King CM (1983): The relationships between beech (*Nothofagus* sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats *Mustela erminea*, in three New Zealand forests. *J Anim Ecol 52*: 141–166.

Lima M, Marquet PA, Jaksic FM (1999): El Niño events, precipitation patterns, and rodent outbreaks are statistically associated in semiarid Chile. *Ecography 22*: 213–218.

Martinez DR, Rau JR, Murua RE, Tilleria MS (1993): Depredacion selectiva de roedores por zorros chillas (*Pseudalopex griseus*) en la pluviselva valdiviana, Chile. *Rev Chil Hist Nat 66*: 419–426.

Mermoz M, Martin C (1987): *Mapa de Vegetacion del Parque y La Reserva Nacional Nahuel Huapi*. Secretaria de Ciencia y Tecnica de la Nacion, Administracion de Parques Nacionales, Delegacion Regional Patagonia, Bariloche, Argentina, 22 pp. and map.

Meserve PL, Lang BK, Patterson BD (1988): Trophic relationships of small mammals in a Chilean temperate rainforest. *J Mammal 69*: 721–730.

Mullen D (1968): Reproduction in brown lemmings (*Lemmus trimucronatus*) and its relevance to the cycle of abundance. *U Calif Publ Zool 85*: 1–25.

Murua R, Gonzalez LA, Gonzalez M, Jofr YC (1996): Efectos del florecimiento del arbusto *Chusquea quila* (Poaceae) sobre la demografia de poblaciones de roedores de los bosques templados frios del sur chileno. *Bol Soc Biol Concepcíon 67*: 37–42.

Murua R, Gonzalez LA, Jofr C (1980): Experimental food preferences of two southern Chilean rodents. *J Mammal 61*: 138–140.

Murua R, Gonzalez LA, Meserve PL (1986): Population ecology of *Oryzomys longicaudatus philippii* (Rodentia: Cricetidae) in southern Chile. *J Anim Ecol 55*: 281–293.

Netski D, Thran BH, St.Jeor SC (1999): Sin Nombre virus pathogenesis in *Peromyscus maniculatus*. *J Virol 1999*: 585–591.

Oli MK, Dobson FS (2001) Population cycles in small mammals: the alpha hypothesis. *J Mammal 82*: 573–581.

Pearson OP (1963): History of two local outbreaks of feral house mice. *Ecology 44*: 540–549.

Pearson OP (1971): Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). *J Mammal 52*: 41–49.

Pearson OP (1975): An outbreak of mice in the coastal desert of Peru. *Mammalia 39*: 375–386.

Pearson OP (1983): Characteristics of a mammalian fauna from forests in Patagonia, southern Argentina. *J Mammal 64*: 476–492.

Pearson OP (1985): Predation. In: Tamarin RH, ed., *Biology of New World Microtus*. Am Soc Mammal, Sp Publ 8, pp. 535–566.

Pearson OP (1992): Reproduction in a South American mouse, *Abrothrix longipilis*. *Anat Rec 234*: 73–88.

Pearson OP (1995): Annotated keys for identifying small mammals living in or near Nahuel Huapi National Park or Lanin National Park, southern Argentina. *Mastozool Neotrop 2*: 99–148.

Pearson OP, Pearson AK (1982): Ecology and biogeography of the southern rainforests of Argentina. In: Mares MA, Genoways HH, eds., *Mammalian Biology in South America*. Pymatuning Lab Ecol, Univ Pittsburgh Sp Publ Series 6, Linesville, PA, pp. 129–142.

Smith AL, Singleton GR, Hansen GM, Shellam G (1993): A serologic survey for viruses and *Mycoplasma pulmonis* among wild house mice (*Mus domesticus*) in southeastern Australia. *J Wildlife Dis 29*: 219–229.

Turchin P, Hanski I (2001): Contrasting alternative hypotheses about rodent cycles by translating them into parameterized models. *Ecol Lett 4*: 267–276.

Wolff JO (1996): Population fluctuations of mast-eating rodent are correlated with production of acorns. *J Mammal 77*: 850–856.