RATADA 2001: A RODENT OUTBREAK FOLLOWING THE FLOWERING OF BAMBOO (*CHUSQUEA CULEOU*) IN SOUTHWESTERN ARGENTINA

RATADA 2001: UNA IRRUPCIÓN DE ROEDORES SIGUIENDO AL FLORECIMIENTO DE BAMBÚ (*CHUSQUEA CULEOU*) EN EL SUROESTE DE LA ARGENTINA

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ABSTRACT

In spring of 2000, *Chusquea culeou* bamboo, the dominant understory plant in Valdivian forest habitat in southwestern Argentina, flowered over a latitudinal range of 100 km and produced a massive amount of seed. Reproductive activity of rodents in the area continued into the subsequent autumn and winter, when rodent numbers reached peak levels and large numbers of drowned rodents appeared on beaches. Owls and foxes reached high numbers, and the mean age in populations of *Oligoryzomys longicaudatus* and *Abrothrix longipilis* declined. In the following (second) spring, reproduction was delayed or suppressed, and by the following (second) autumn populations had declined to unusually low levels. By the third year after the flowering, rodent numbers had returned to levels characteristic of populations in this area.

Oligoryzomys longicaudatus, *Abrothrix longipilis*, *Loxodontomys micropus*, I*renomys tarsalis*, and the introduced *Rattus rattus* increased in numbers following the bamboo bloom; numbers of *Chelemys macronyx* and *Geoxus valdivianus*, species that eat invertebrates, were not affected. These observations strongly imply that the abundance of bamboo seed caused this outbreak, and suggest that food availability is the main factor limiting numbers of rodents in these forests.

Key words. Argentina, bamboo, mast seeding, rodents, population regulation, outbreaks, reproduction, emigration, mortality, obesity, *Chusquea culeou*, *Oligoryzomys*, *Abrothrix*, *Loxodontomys*, *Rattus*, *Irenomys*, *Chelemys*, *Geoxus*.

RESUMEN

Durante la primavera de 2000, la caña *Chusquea culeou*, la planta dominante del sotobosque de los bosques Valdivianos del sudoeste de Argentina, floreció a lo largo

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[1] Deceased, 4 March 2003

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de un rango latitudinal de 100 km produciendo una gran cantidad de semillas. En el área, la actividad reproductiva de los roedores continuó durante el otoño e invierno siguientes, cuando el número de roedores alcanzó el nivel máximo y una gran cantidad de individuos aparecieron ahogados en las costas de los lagos. El número de zorros y lechuzas aumentó considerablemente, y la edad promedio en poblaciones de *Oligoryzomys longicaudatus* y *Abrothrix longipilis* disminuyó. En la siguiente (segunda) primavera, la reproducción estuvo retrasada o suprimida, y durante el siguiente (segundo) otoño las poblaciones disminuyeron a niveles inusualmente bajos. Para el tercer año luego de la floración, el número de roedores retomó sus valores característicos para las poblaciones de esta área.

Oligoryzomys longicaudatus, *Abrothrix longipilis*, *Loxodontomys micropus*, *Irenomys tarsalis*, y la introducida *Rattus rattus* aumentaron sus números poblacionales luego de la floración masiva de la caña; mientras que para *Chelemys macronyx* y *Geoxus valdivianus*, especies que comen invertebrados, no hubo cambios. Estas observaciones fuertemente implican que la abundancia de semillas de caña fue la causa de la ratada, y sugieren que la disponibilidad de alimento es el factor principal que limita el número de roedores en estos bosques.

Palabras claves. Argentina, caña, semillazón masiva, roedores, regulación poblacional, ratada, reproducción, emigración, mortalidad, obesidad, *Chusquea culeou*, *Oligoryzomys*, *Abrothrix*, *Loxodontomys*, *Rattus*, *Irenomys*, *Chelemys*, *Geoxus*.

INTRODUCTION

Valdivian temperate rainforest dominated by *Nothofagus* trees is a major habitat in southwestern South America (Dimitri, 1959; Veblen et al., 1983, 1996; Wilcox, 1996). Primary understory plants in these forests are bamboos of the genus *Chusquea*, and in Argentine forests the predominant bamboo species is *Chusquea culeou* (E. Desvaux in Gay, 1853). After a long period of vegetative growth, *C. culeou* flowers once, sets seed, and dies. Nearly all bamboo plants in an area flower synchronously, resulting in production of a massive amount of seed and a population explosion among local granivorous rodents. Such outbreaks of mice have been reported from Chile, from other parts of South America, and from Asia, following the gregarious flowering of different species of bamboos (Gunkel, 1948; Seal et al., 1951; Tanaka, 1956, 1957; Janzen, 1976; Murúa et al., 1996; Gallardo and Mercado, 1999). A recent review emphasized our poor understanding of these events (Jaksic and Lima, 2003).

In spring of 2000 a population of *C. culeou* flowered and set seed over a north-south distance of 100 km and east-west distance of 80 km in adjacent parts of Argentina and Chile (Anonymous, 2001a, 2001b; Sanguinetti and García, 2001). The main goal of this paper is to describe the changes in numbers, reproductive behavior, age structure, movements, and mortality of rodent species during this outbreak. In addition, we compare these results with the behavior of these same species from forests where the bamboo remained in the vegetative (green) phase of the life cycle, and suggest what information will be needed for a more predictive understanding of bamboo-induced outbreaks in these forests. Two reports on the responses of rodents to a synchronous flowering of bamboo in Chilean forests (Murúa et al., 1996; Gallardo and Mercado,

1999) involved a different species of *Chusquea*. This is the first analysis of an outbreak in which *C. culeou* is the flowering bamboo species.

MATERIALS AND METHODS

Study Sites and Terminology

Our study area is within Valdivian rainforests along the western border of Argentina, between 39° 52′ S and 40° 35′ S latitude and within the boundaries of Parque Nacional Lanín. The largest town in the area is San Martín de Los Andes (Fig. 1). We collected

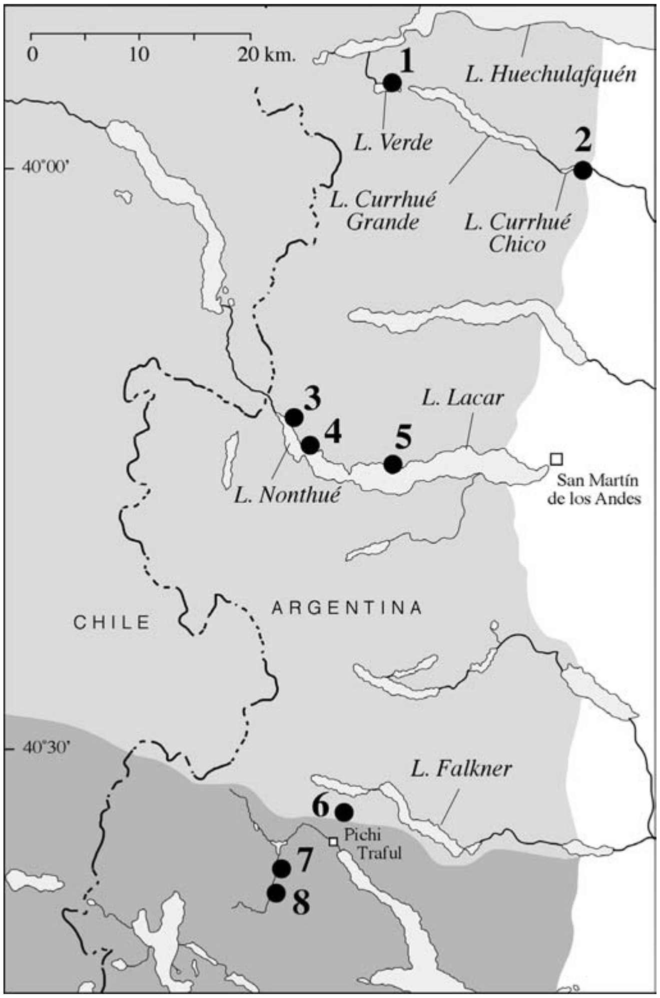

Figure 1. Map showing the area where *Chusquea culeou* bloomed (light stipple) and where it did not (dark stipple) in the western area of Neuquén Province, Argentina, and adjacent parts of Chile. Numbers indicate collection localities.

mice at 8 places and in 2 types of bamboo habitat (Table 1). Six localities (localities 1 – 6) were in the area where a high percentage of bamboo plants flowered (Sanguinetti and García, 2001), and these sites are considered as the flowered-bamboo habitat. The bamboo remained in the vegetative stage at the other 2 localities (localities 7, 8), and these are treated as the green-bamboo habitat. Thus we use 6 replicates for flowered-bamboo and 2 replicates for green-bamboo habitat scores to test for differences between habitat types. While vegetation conditions at the green-bamboo localities contrasted with those where the bamboo flowered, they resembled conditions of baseline rodent populations described by Pearson (2002).

We number the seasons and years of study sequentially, starting from the time the bamboo flowered; thus, Spring-1 corresponds to September through November, 2000, the first year of our study. Seasons in this part of Argentina are: September to November (spring), December to February (summer), March to May (autumn), and June to August (winter).

Trapping Methods, Collections, and Autopsies

We made 5 collections over 3 years; these included Spring-1 (17-22 November 2000), Autumn-1 (29 April – 6 May 2001), Spring-2 (12–24 October 2001), Autumn-2 (3-14 May, 2002), and late Autumn-3 (19 May – 4 June 2003). No samples were taken during Spring-3. We sampled Currhué Chico and Hua Hum during all 5 periods, and Yuco, Traful North, Traful South-1, and Traful South-2 during 3 periods; additionally, we have single collections from Laguna Verde (based on traps) and Lago Nonthué (drowned mice picked up by JS on one day in Spring-2, along a 100-m stretch of beach).

Traplines were set for up to 3 consecutive nights in an area, with 5 to 59 traps per line (Appendix Table 1). Traps were set in late afternoon, picked up the following morning, and reset in a different place that afternoon. Traplines were set in nearly the same places in successive collecting periods. Trap success was calculated as the number of mice caught divided by the number of traps on a trapline, without correcting for traps that were closed and without a mouse. Because traps were moved daily, we treat each nightly trapline as an independent replicate for estimating density by means of trap success for a particular locality, between the 2 habitat types, and among collecting periods. Our measures of trap success were based only on results from live traps (7.5 x 9 x 22.5 cm, Model LFA, H. B. Sherman Traps, Inc.), because only live traps were used during the Autumn-2 collecting period. In other trapping periods we alternately set folding aluminum live traps and Museum Special kill traps (Woodstream Corporation). Traps were baited with a mixture of oat and corn meal and set 5 m apart. A small number of animals were caught in wire mesh live traps (41 x 13 x 13 cm, Model TLT201, Tomahawk Live Trap Co.) and number 0 jump traps (Oneida Victor Co.). During the last 4 trapping periods we also set Sherman traps in standing bamboo, 1– 2.5 m aboveground. These arboreal traps were taped onto thick single canes or groups of smaller canes that were at an approximately horizontal angle, and baited like those on the ground. They were left in place for up to 3 days. Arboreal trap success was calculated separately from the terrestrial trap success described above, and differed somewhat as an index measure because many of the trap nights involved the same trap set in the same place for 2 or 3 nights.

Mice were killed by cervical dislocation, with carbon dioxide, or with an overdose of sodium pentobarbital. All trapped mice were weighed, measured for body length

Table 1. Collecting localities in Neuquén Province, Argentina. General locality names are used throughout the text.

Loc. No.	General Name	Location	Habitat Description	Bamboo Condition
1	Laguna Verde	West of Lago Currhué Grande [71°31′00″W; 39°50′20″S], 1000 m el.	Bamboo in *Nothofagus dombeyi*/*N. obliqua* forest	Flowered
2	Currhué Chico	Around eastern end of Lago Currhué Chico[71°20′00″W; 39°54′20″S], 1050 m el.	Bamboo in *N. antarctica* woodland, and an adjacent grassland	" "
3	Hua Hum	3 km ESE of Seccional Hua Hum [71°38′30″W; 40°8′30″S], 650 m el.	Bamboo in *N. dombeyi*/*N. obliqua* forest	" "
4	Lago Nonthué	Along shoreline of Lago Nonthué, [71°37′30″W; 40°9′10″S], 650 m el.	Dead on beach	" "
5	Yuco	Seccional Yuco [71°31′30″W; 40°10′15″S], 650 m el.	Bamboo in *N. dombeyi*/ *N. obliqua* forest	" "
6	Traful North	3.3 km N, 0.8 km E of jct. Ruta 234 with Río Pichi Traful [71°35′20″W; 40°28′40″S], 950 m el.	Bamboo in *N. dombeyi* forest	Limited flowering
7	Traful South-1	4.6 km S, 5.5 km W of jct. Ruta 234 with Río Pichi Traful [71°39′50″W; 40°31′45″S], 900 m el.	" "	Green (did not flower)
8	Traful South-2	10.8 km S, 5.7 km W of jct. Ruta 234 with Río Pichi Traful [71°39′50″W; 40°34′50″S], 900 m el.	" "	" "

(head and trunk), and examined for tail scars or torn ears. We recorded the presence/absence of scars on the tails and ears of many of the animals. Tail scarring was recorded from nearly all trapped animals, but could not be scored on the drowned mice from Lago Nonthué because the condition of the tail skin on many of the specimens was not good enough to see scars. Tears and holes in the ears remained visible in most of the drowned mice, and we scored ear damage in these and other mice trapped in Spring-2. Upon dissection, the length of a testis was measured, the widths and/or presence of scars in the uteri, and the numbers and lengths (crown-rump length, CRL) of embryos were recorded. Females with enlarged nipples with milk were considered as reproductively active. The amount of intra-abdominal fat was scored with a qualitative index: 0 = small amounts of fat that was restricted to the gonads; 1 = enlarged gonadal fat pads; 2 = enlarged gonadal and mesenteric fat pads; 3 = enlarged pads as well as fat covering the heart and kidneys. In addition to saving the skulls, carcasses from the final 3 collections were preserved in 10% neutral-buffered formalin. Dried tissue was cleaned from the skulls using dermestid beetles. One specimen was donated to the Universidad Nacional del Comahue, S. C. de Bariloche, and the remains of 20 other specimens were lost in the field. All other specimens have been deposited in the Museum of Vertebrate Zoology, University of California, Berkeley, California, USA. The MVZ catalogue numbers for these specimens are: 196312 – 196352, 196841 – 197031, 198850 – 199133, 199656 – 199735, 201039 – 201073, 201079 – 201091, 201109 – 201191, 201193 – 201198, 201201 – 201202.

Age of *Oligoryzomys longicaudatus* and *Abrothrix longipilis* specimens was determined from cusp measurements on molar teeth, as described by Pearson (1975, 1992). Using a video microscope (USB Microscope M2™, Scalar Corp., Tokyo), cusp heights were measured from images on the video screen, corrected for magnification, and grouped into 5 age-class intervals. The intervals (0.10 mm/interval in *Oligoryzomys* and 0.16 mm/interval in *A. longipilis*) were then used to define the 5 age-classes, numbered in order of declining cusp height. Thus age class-1 are young animals with tall cusps and age class-5 are old animals with short cusps.

Rodent Fauna

We collected specimens of 8 species identified as members of the native rodent community in these forests (Pearson, 1983): these included (in descending order of abundance) *Oligoryzomys longicaudatus*, *Abrothrix longipilis*, *A. olivaceus*, *Loxodontomys micropus*, *Irenomys tarsalis*, *Geoxus valdivianus*, *Chelemys macronyx*, and *Aconaemys porteri*. In addition we caught specimens of *Octodon bridgesii*, *Phyllotis xanthopygus*, *Reithrodon auritus*, and the non-native *Rattus rattus*. Many aspects of the life histories of the native species in forests with a mature but non-flowering bamboo understory are known (Pearson and Pearson, 1982; Pearson, 1983, 2002; Murúa and González, 1986; Murúa et al., 1986, 1987, 1996; Patterson et al., 1989, 1990; Kelt, 1994, 2000).

Analyses

Analyses were conducted with SPSS 11.0® (SPSS Inc., Chicago, IL), and included single- and 2-factor analysis of variance (ANOVA), analysis of covariance (ANCOVA), and Spearman rank correlation; results were considered significant at $p \leq 0.05$. Throughout the text we present mean values followed by standard errors. Analysis of variance and covariance were used to assess effects of independent variables. Darlington and Smulders (2001) discussed the statistical advantages of ANCOVA for studies of the 'condition' of animals. Cusp height (as a proxy variable for age) was treated as a covariate when testing for the effects of time or habitat on the response variables of interest. One output in the SPSS General Linear Model analysis is the least-squares means of the dependent variable adjusted for the covariance structure of the main effects and interactions. These adjusted means are presented throughout the text. When no mice were caught in a trapline (0% success) a 'dummy value' of 0.01 mice was entered.

RESULTS

General Patterns of Bamboo Flowering, Amounts of Seed, and Rodent Numbers

The length of the vegetative stage of the life cycle of *C. culeou* is not well established. The last major flowering in the area of our study was in 1938 (Sanguinetti and García, 2001), indicating a life span of 62 years for this population of *C. culeou*. When *C. culeou* flowered in Argentina in 2000, it also flowered in adjacent areas of Chile, as reported in the newspaper El Diario Austral de Valdivia (Anonymous, 2001a, 2001b). In Spring-1 an estimated 98% of bamboo plants in the study area were in bloom, with much pollen in evidence (Plate 1A). By late in Summer-1 (February, 2001) seeds had formed and were beginning to drop to the forest floor. In Autumn-1 seed fall was heavy and bamboo leaves were dead on the canes (Plate 1B). In Spring-2 there were still some seeds on the surface of the ground and many bamboo leaves had fallen. Seedlings were abundant. By Autumn-2 no seeds remained on the surface, the dead bamboo canes were leafless, and seedlings up to 20 cm tall were abundant. Seedlings remained abundant to the end of our study and the dead canes became increasingly brittle and sagged towards the ground.

To estimate the amount of bamboo seed available to rodents, we counted and weighed fertile seeds (caryopses) on 6 representative bamboo culms collected in Autumn-1. The 6 culms held an average of 6,799±3,143 [range 1,112 – 21,454] well-formed seeds, and the mean dry weight of an individual seed was 7.3±0.58 mg [5.4 - 9.3 mg]. Since there may be up to 120,000 live culms/ha in similarly dense bamboo habitat (Pearson et al., 1994), we estimate that as many as 81,000 fertile seeds/m^2, weighing up to 0.59 kg may have been available to animals in bamboo thickets at this time.

By Summer-1, rodents were noticeably abundant. Forest residents reported that their cats and dogs started bringing mice into their homes. During our visit in Autumn-1 we saw rodents in the afternoon while setting traps, caught them within minutes of setting the traps, and watched many active animals in the bamboo thickets at night. Later in Autumn-1, rodents began to enter houses and outbuildings. A family living near Hua Hum abandoned their home in Winter-1 because the number of mice indoors became intolerable (Monica Sosa, pers. comm.). Rodents were still abundant in Spring-2, and carcasses washed up on the shores of lakes in the region by the thousands. But, at this time they were not as active in the forest as in Autumn-1. Unlike Autumn-1, no mice were observed while setting traps during the Autumn-2 and Autumn-3 collecting periods.

Species Abundances

A total of 757 animals were collected. *Oligoryzomys* was the most abundant species collected, forming 41% of the total collection, followed by *A. longipilis* (29%), *A. olivaceus* (13%), *Loxodontomys* (9%), *Rattus* (3%), *Irenomys* (1.5%), *Geoxus* (1.2%), and *Chelemys* (0.9%). *Oligoryzomys* and *A. longipilis* were the only species collected at all sites. Ten specimens (5 *Aconaemys porteri*, 3 *Octodon bridgesii*, 1 *Phyllotis xanthopygus*, and 1 *Reithrodon auritus*) will not be considered further because of limited captures and/or their atypical occurrence in the forest habitat (*Octodon*, *Phyllotis*, and *Reithrodon*). Numbers of all other species collected at each locality and in each period are listed in Appendix Table 2.

Plate 1. The bamboo understory on a hillside at the Hua Hum locality (A) in Spring 1 when the plants were alive and flowering and (B) after they had died in Autumn 1. Oliver P. Pearson in (A) and Anita K. Pearson in (B) for scale.

The relative abundances of the rodent species changed over time and habitat (Table 2). In the flowered bamboo habitat *Oligoryzomys* was 2-3 times more common than *A. longipilis* in 3 of the 5 collecting periods. Only during Autumn-1 and Autumn-3 did *A. longipilis* become as abundant as *Oligoryzomys*. In the green bamboo habitat *A. longipilis* was twice as abundant as *Oligoryzomys* in Autumn-2 and Autumn-3, but *Oligoryzomys* was the more common species in Spring-2. *Rattus* increased to its greatest relative abundance in the flowered bamboo during Autumn-2, when they composed one-quarter of all animals collected. At the same time *A. longipilis* declined in relative abundance while *Oligoryzomys* remained common. *Rattus* was not collected in Autumn-3. *Abrothrix olivaceus* was relatively uncommon (about 10% of the collection) in the flowered bamboo, but in Autumn-3 became equally as common (31%) as *Oligoryzomys* and *A. longipilis*; at the same time its abundance in the green bamboo habitat remained low (11%). The semifossorial taxa, *Geoxus* and *Chelemys*, remained uncommon in our traps in all periods and localities (Appendix Table 2).

Trap Success and Abundance

Overall trap success on the ground was 29% (546 animals during 1888 trap nights; Appendix Table 1). An ANOVA showed significant main effects of trap type ($F = 29$, $d.f. = 1, 78$, $p < 0.001$), collecting period ($F = 15$, $d.f. = 4, 78$, $p < 0.001$), and bamboo habitat

Table 2. Relative abundances of four rodent species, measured as the proportion of the total sample of mice trapped during each collecting period in flowered and green bamboo habitats, Neuquén Province, Argentina. Drowned mice from Lago Nonthué are not included in the calculations for the flowered bamboo habitat in Spring-2. Trapping in green bamboo habitats did not begin until Spring-2.

Collecting period	Sample size: Flowered/Green	*Oligoryzomys longicaudatus*		*Abrothrix longipilis*		*Abrothrix olivaceus*		*Rattus rattus*	
		Flowered	Green	Flowered	Green	Flowered	Green	Flowered	Green
Spring-1	41/--	0.71	--	0.22	--	0.02	--	0	--
Autumn-1	188/--	0.37	--	0.43	--	0.15	--	0.005	--
Spring-2	263/40	0.47	0.52	0.16	0.32	0.08	0.10	0.05	0
Autumn-2	43/35	0.49	0.26	0.16	0.49	0.07	0.14	0.26	0
Autumn-3	110/27	0.31	0.22	0.32	0.48	0.31	0.11	0	0

($F = 6.9$, *d.f.* = 1, 78, $p = 0.01$) on trap success. In the same analysis two interaction effects were significant (both $p < 0.001$): trap x period ($F = 14$, *d.f.* = 3, 78) and period x bamboo ($F = 8.7$, *d.f.* = 2, 78). Mean trap success was lower with live than kill traps (0.26 ± 0.021 and 0.51 ± 0.025, respectively). Analysis using only results with live traps showed a highly significant main effect ($p < 0.001$) of collecting period ($F = 7.8$, *d.f.* = 4, 46) and of the period x bamboo interaction ($F = 10$, *d.f.* = 2, 46), but a non-significant effect ($p = 0.25$) for bamboo habitat alone ($F = 1.4$, *d.f.* = 1, 46).

In the flowered bamboo habitat trap success increased from spring to autumn in the first year (10% to 51%) but decreased over the same seasons in the second year (44% to 12%) (Table 3). The actual increase in density from Spring-1 to Autumn-1 was probably greater than 5-fold, since a deficiency of open traps probably limited the number of captures at each station. By Autumn-3, trap success had increased to 24%, which is close to autumn trap success in baseline populations (29.3%; Pearson, 2002). Trap success differed between green and flowered habitats. Whereas trap success in flowered bamboo habitats dropped from Spring-2 to Autumn-2, it increased from 23% to 34% during this period in the green bamboo woods. In Autumn-3, trap success was higher in the flowered (24%) than in the green (8%) bamboo habitat.

Drowning Rodents

A conspicuous feature of the outbreak was the large number of drowned rodents on lake shores. Residents and park rangers first noticed this during Winter-1. We observed drowned animals at Lago Nonthué (150 mice in 100 m of beach) and at Lago Currhué Grande (325 carcasses in 100 m) in Spring-2 (Plate 2A, B, and C). In mid-October, 2001, a man reported being within sight of drowned mice for most of the day as he sailed on 50 km-long Lago Lacar (pers. comm. to JS). At campsites and towns near lakes the drowned rodents caused considerable concern among both campers and civic leaders because of fears of infection with a hantavirus (Andes virus) that has caused fatalities in these areas (Baro et al., 1999; Calderon et al., 1999; Lazaro et al., 2000).

The drowned mice retrieved from the beach at Lago Nonthué differed in species composition from the rodents trapped in nearby woods (Table 4). *Oligoryzomys* was abundant in both collections. While *A. longipilis* was the second most abundant rodent

Table 3. Mean frequency of live-trap success in 54 trap lines over time and bamboo habitat. The values reported with means are standard errors, and the numbers of trap lines per collecting period/habitat are shown within parentheses. Trapping in green bamboo habitats did not begin until Spring-2.

Collecting period	Flowered bamboo	Green bamboo
Spring-1	0.10±0.061 (5)	--
Autumn-1	0.51±0.068 (4)	--
Spring-2	0.44±0.043 (10)	0.23±0.051 (7)
Autumn-2	0.12±0.043 (10)	0.34±0.068 (4)
Autmn-3	0.24±0.043 (10)	0.08±0.068 (4)

Plate 2. (A, B, C). Drowned rodents (mostly *O. longicaudatus*) along the western shore of Lago Currhué Grande in Neuquén Province, 16 October 2001. (D) Picking up drowned rodents from the beach at San Martín de Los Andes. The workers are wearing filter masks because of concern about possible infection with a hantavirus that occurs in one species of the drowned mice (*O. longicaudatus*).

Table 4. The percent species composition and numbers (in parentheses) of drowned mice picked up on the beach at Lago Nonthué compared to those trapped in the nearby woods at Hua Hum in the same (Spring-2) collecting period.

Species	Lago Nonthué	Hua Hum
Oligoryzomys longicaudatus	37 (43)	55 (40)
Abrothrix longipilis	1 (1)	38 (28)
Abrothrix olivaceus	3 (4)	1 (1)
Loxodontomys micropus	43 (50)	4 (3)
Rattus rattus	10 (12)	0
Irenomys tarsalis	6 (7)	0
Geoxus valdivianus	0	1 (1)
Totals	(117)	(73)

in the forest sample (39%), it was rare (1%) among the drowned mice. Conversely, *L. micropus* was abundant in the lake collection (42%) and rare in forest (4%) samples. Substantial numbers of *I. tarsalis* were present among the drowned animals (7%) but were not collected at all in the forest during the same time; similarly, *R. rattus* was present in the lake sample (10%) but absent in the nearby Hua Hum collection. However, mutilation of some snap-trapped rodents in Spring-2 at Hua Hum suggested that black rats were present at this trapping site.

Public health concerns about the drowned rodents prompted the municipal government of San Martín de Los Andes to remove the carcasses from their 400-m public beach every morning (Plate 2D). Between October, 2001 and February, 2002 the municipal workers picked up 11,245 mice, an average of 110 per day. Over this 4-month period there were noticeable declines in the number of animals retrieved in weeks 3, 7, and 12 (Fig. 2). Each of these declines were associated with full moon phases (in the middle of weeks 3 and 7, and the last night of week 11, thereby immediately preceding week 12). We conducted a stepwise multiple regression analysis on the relationship between the numbers of mice picked up each week (dependent variable) and two independent variables: (1) week number and (2) a proxy variable for the relative amount of moonlight during that week (0 for the new moon, 0.5 for first and last quarter moons, and 1 for the full moon phase). The best-fit regression [(number of mice picked up = 2227 – 129 (week) – 849 (moon phase)] was highly significant ($F = 22$, $d.f. = 2, 13$, $p < 0.001$). The time variable (week) explained most of the variation in numbers ($r^2 = 0.64$), but inclusion of lunar phase into the regression model significantly increased ($p = 0.02$) its explanatory power by 14% ($r^2 = 0.78$). Thus, fewer mice washed up on the beach in weeks when the nights were brightest. This could reflect reduced activity on bright nights; rodents in other systems are known to reduce their activity during the full moon (Price et al., 1984; Abramsky et al., 1990; Yunger et al., 2002; Kelt et al., 2004).

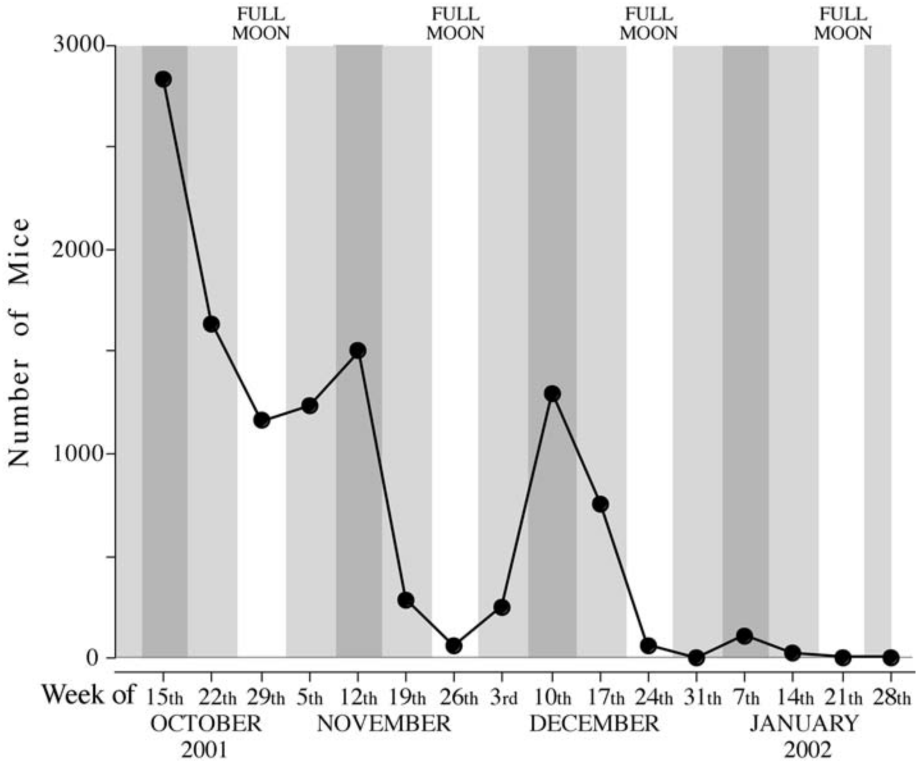

Figure 2. Weekly numbers of drowned rodents picked up by municipal workers on the shore of Lago Lacar at San Martin de Los Andes. The clear columns mark the weeks of the full moons.

Tooth Wear and Age Structure

Mean cusp height of the *Oligoryzomys* sample was 0.46 ± 0.005 mm (range: 0.17 - 0.67 mm). Comparable values for *A. longipilis* were 0.78 ± 0.012 mm (range: 0.22 – 1.04 mm). No difference was detected across gender (*Oligoryzomys* $F = 1.4$, *d.f.* = 1, 304, $p = 0.20$; *A. longipilis* $F = 3.3$, *d.f.* = 1, 211, $p = 0.07$). However, relationships between tooth wear and measurements of body size differed between the 2 species. In *Oligoryzomys* the correlation of cusp height with body length ($r_s = 0.06$, $p = 0.3$) and with body weight ($r_s = -0.02$, $p = 0.8$) was not significant. In *A. longipilis*, cusp height was significantly correlated with body length ($r_s = -0.23$, $p = 0.001$) and body weight ($r_s = -0.22$, $p = 0.001$).

Tooth-wear age categories differed over collecting period and bamboo habitat, and between the 2 species (Table 5). Mean age declined by 43% in *Oligoryzomys* (age class 3.5 to 2.0) and by 52% in *A. longipilis* (age class 3.1 to 1.5) from Spring-1 to Autumn-1 in the flowered bamboo habitat, reflecting continued breeding and recruitment of young animals during this interval. Mean age increased 20% over the first winter in *Oligoryzomys* populations (2.0 to 2.5) but remained stable and young among *A. longipilis* in Autumn-1 and Spring-2 (1.5 vs. 1.6, Table 5). In Spring-2, the youngest *A. longipilis* (age class-1) predominated in the collections (Table 5). Unlike the first year, mean ages of animals of both species increased rather than decreased from Spring-2

Table 5. Mean age class and frequency (based on tooth wear) in *Oligoryzomys longicaudatus* and *Abrothrix longipilis* samples over time and in flowered and green bamboo habitats, Neuquén Province, Argentina.

Collecting period	Bamboo habitat	Mean±SE (*N*)	Age class 1	2	3	4	5
Oligoryzomys longicaudatus							
Spring-1	flowered	3.5±0.18 (29)	0.07	0.07	0.21	0.59	0.07
Autumn-1	flowered	2.0±0.08 (69)	0.20	0.68	0.07	0.04	
Spring-2	flowered	2.5±0.06 (118)	0.02	0.51	0.42	0.05	0.01
“	green	2.7±0.13 (21)		0.38	0.57	0.05	
Autumn-2	flowered	3.3±0.12 (21)		0.05	0.62	0.33	
“	green	3.1±0.20 (9)		0.11	0.67	0.22	
Autumn-3	flowered	2.9±0.11 (33)		0.24	0.61	0.15	
“	green	2.8±0.17 (6)		0.17	0.83		
Abrothrix longipilis							
Spring-1	flowered	3.1±0.20 (9)		0.11	0.67	0.22	
Autumn-1	flowered	1.5±0.10 (80)	0.64	0.29	0.01	0.05	0.01
Spring-2	flowered	1.6±0.10 (40)	0.52	0.40	0.08		
“	green	3.8±0.26 (13)		0.08	0.31	0.38	0.23
Autumn-2	flowered	3.1±0.34 (7)		0.14	0.71		0.14
“	green	2.6±0.27 (17)	0.06	0.53	0.23	0.06	0.12
Autumn-3	flowered	2.2±0.10 (34)	0.03	0.82	0.09	0.06	
“	green	2.5±0.31 (13)		0.77	0.08		0.15

to Autumn-2 (24% in *Oligoryzomys* and 48% in *A. longipilis*, Table 5). These Autumn-2 animals were the oldest of the 3 autumn populations. In Autumn-3 individuals of both species were still, on average, older than those of Autumn-1. During the second and third years the mean ages of the species varied in different ways in the two habitats. Mean age of *Oligoryzomys* populations exhibited parallel trajectories in both habitats, ageing through Summer-2 and being relatively old in Autumn-3 (Table 5). In contrast, the mean age of *A. longipilis* populations in the green bamboo habitat declined over Summer-2 while neighboring populations in the flowered bamboo habitat increased in age (Table 5). For *Oligoryzomys* there was a significant effect of collecting period ($F = 35$, *d.f.* = 4, 298, $p < 0.001$), and non-significant effects of bamboo habitat ($F = 0.06$, *d.f.* = 1, 298, $p = 0.8$) and the interaction of period x bamboo ($F = 0.6$, *d.f.* = 2, 298, $p = 0.6$). For *A. longipilis* there were highly significant effects of collecting period ($F = 13$, *d.f.* = 4, 205, $p < 0.001$), bamboo habitat ($F = 16$, *d.f.* = 1, 205, $p < 0.001$), and their interaction ($F = 22$, *d.f.* = 2, 205, $p < 0.001$).

Age structure of *Oligoryzomys* in the sample of drowned mice from Lago Nonthué was not different from that of the contemporary population in the nearby Hua Hum forest (1-way ANOVA; $F = 2.9$, *d.f.* = 1, 75, $p = 0.10$).

Reproduction

Females. In Spring-1 the majority of captured animals were reproductively active (Table 6). Nine of 15 female *Oligoryzomys* were pregnant with fetuses up to 24 mm CRL, and 2 were lactating. Four of 5 female *A. longipilis* collected at this time showed signs of active reproduction: 2 females had small fetuses (5 and 10 mm CRL), another had 3 small uterine bumps, and a fourth was lactating. The single female *L. micropus* in the Spring-1 collection had corpora lutea and uterine swellings, indicating an early pregnancy.

In Autumn-1 many mice were reproductively active. Most (86%) female *Oligoryzomys* were pregnant, including 7 of 10 mice in the youngest age class. Average litter sizes were larger than in the previous spring (6.9 versus 5.4; Table 7). Two females were carrying 11 embryos, which equals the maximum reported for this species (Pearson, 1983), and a third mouse had 10 embryos. One pregnant female (in age

Table 6. Percentages of reproductively active female mice (i.e., with fetuses or lactating) of four species from the flowered and green bamboo habitats, Neuquén Province, Argentina. The number of females in each sample is shown within parentheses.

Collecting Period	*Oligoryzomys longicaudatus*		*Abrothrix longipilis*		*Abrothrix olivaceus*		*Loxodontomys micropus*	
	Flowered	Green	Flowered	Green	Flowered	Green	Flowered	Green
Spring-1	60 (15)		100 (5)		—		100 (1)	
Autumn-1	8 (29)		15 (48)		15 (13)		80 (5)	
Spring-2	0 (55)	0 (7)	10 (21)	100 (4)	0 (10)	0 (2)	5 (19)	0 (1)
Autumn-2	0 (11)	0 (3)	—	0 (10)	0 (5)	0 (3)	—	—
Autumn-3	9 (11)	0 (1)	0 (11)	0 (4)	0 (15)	0 (1)	—	0 (2)

class-1) had the highest cusp height that we measured in the entire sample of female *O. longicaudatus*, demonstrating that precocial, young-of-the-year breeding occurs in this species when conditions are favorable. Only 14% of the 48 female *A. longipilis* were pregnant in Autumn-1. But as was the case with *Oligoryzomys*, mean litter size was larger in Autumn-1 than in Spring-1 (3.9 vs. 3.3, Table 7) in *A. longipilis*. Twelve non-pregnant mice had prominent nipples, indicating recent pregnancies. Two of these 12 were old (class-4) and the other 10 were young (age class-1 and -2). Among the pregnant mice 3 were in age class-1 and 3 were in age class-2. The youngest of the pregnant females had a cusp height of 0.96 mm, the sixth tallest teeth among 85 females measured. As with *Oligoryzomys*, this dental information shows that precocial reproduction was taking place in this late-autumn population of *A. longipilis*. In a study of the reproductive biology of this species Pearson (1992) found no evidence of late season breeding by young-of-the-year females. Four of the 5 *L. micropus* were pregnant in Autumn-1, with a mean litter size of 6.2±0.63 and a range of 5 - 8. The 8 embryos increases the maximum litter size reported for this species by 1 (Pearson, 1983). The fifth animal had enlarged uteri and prominent nipples, suggesting that she had recently bred. Two of 13 female *A. olivaceus* were pregnant (with 5 and 6 embryos), and 4 non-pregnant mice with enlarged uteri and prominent nipples had recently finished breeding. The remaining 7 *A. olivaceus* were nulliparous, with threadlike uteri.

In summary, *A. longipilis* exhibited a lower level of reproductive activity (14%) than in *O. longicaudatus* (86%) in Autumn-1 samples, suggesting that *A. longipilis* was ending the autumnal breeding, while this was continuing in *O. longicaudatus*. The high percentage (80%) of pregnant *Loxodontomys* indicates that, like *Oligoryzomys*, it continued its autumnal breeding season. *Abrothrix olivaceus*, with a low percentage of pregnancies, was behaving like the congeneric *A. longipilis* and ending its breeding season.

In Spring-2, despite dissecting more than 6 times as many mice as in Spring-1, we found no signs of reproduction (Table 6). All female *Oligoryzomys* had threadlike, translucent uteri, indicating that this species had not begun to breed in either bamboo habitat. The reproductive behavior of *A. longipilis* differed from that of *Oligoryzomys* in Spring-2. While only 2 of 21 females from the flowered bamboo habitat were pregnant, all 4 from the green bamboo were reproductively active (3 were pregnant, and one had an enlarged uterus with scars). The 2 pregnant animals from the flowered area were older (class-2 and –3) individuals, while 14 of the reproductively inactive animals

Table 7. Litter sizes in *Oligoryzomys longicaudatus* and *Abrothrix longipilis* over time in the flowered bamboo habitat, Neuquén Province, Argentina. Mean litter size and standard error are followed by the range [ ] and sample size ( ).

Collecting period	*Oligoryzomys longicaudatus*	*Abrothrix longipilis*
Spring-1	5.4±0.50 [2 – 7] (9)	3.3±0.67 [2 – 4] (3)
Autumn-1	6.9±0.42 [4 – 11] (24)	3.9±0.34 [3 – 5] (7)
Spring-2	No data	4.5 [4, 5] (2)
Autumn-3	7 (1)	No data

were class-1 individuals. The 4 reproductively active animals from green bamboo localities also were older animals (age classes 3 to 5). Thus, in Spring-2 only the oldest *A. longipilis* females showed signs of early breeding in both habitats. Zero of 10 female *A. olivaceus* were pregnant in the Spring-2 collection, and threadlike uteri were recorded for most specimens. There were also no signs of embryos or corpora lutea in 20 *L. micropus*. The uterine horns of 7 *R. rattus* were 1 – 2 mm wide, but no corpora lutea were seen; uterine scars present in 2 *R. rattus* suggested earlier pregnancies. Five *Irenomys* showed no signs of reproductive activity. In summary, there was much less reproductive activity recorded in Spring-2 than in Spring-1, and where observed (in *A. longipilis*) it was restricted to older animals.

In Autumn-2 no animals showed signs of reproductive activity. In Autumn-3 one of 12 female *Oligoryzomys* was pregnant, indicating that some breeding extended into this autumn. Intense autumnal breeding was only observed in Autumn-1.

Testis Size. Mean testis length in *Oligoryzomys* declined over the study period in the flowered bamboo habitat (Table 8). Length was greatest in Spring-1, when 60% of females were breeding (Table 6) and mean age was greatest (Table 5). The mean length in Autumn-1 was smaller than in Spring-1, although the percentage (88%) of females that were breeding then was the highest found during our study (Table 6). The distribution of testis length in this Autumn-1 sample of 41 males was bimodal (kurtosis = -1.3), with modes at 4 and 7 mm. Testis length among the 7 oldest mice (in age classes-3 to -5) ranged from 6 to 8 mm. Testis length among the 21 youngest mice (in age class-1) ranged from 3 to 9 mm. Six of these animals had testis lengths between 7 and 9 mm, suggesting that sexual maturity can be reached at a very young age when conditions are favorable. In Spring-2 mean testis length further declined from that in the previous autumn (Table 8), even though the animals were now older (Table 5). Mean length in Spring-2 was significantly lower than in Spring-1 ($p = 0.005$ in a Tamhane T2 test for post hoc multiple comparisons among testis lengths from all 5 periods). Testis size was smallest in Autumn-2 and only slightly larger in Autumn-3 (Table 8). Means of these 2 autumn samples were both significantly smaller than that observed in Autumn-1 ($p < 0.001$ for Autumn-1 vs. -2 and $p < 0.001$ for Autumn-1 vs. -3 in the same multiple comparison tests described above). These small testes in the

Table 8. Mean testis length (mm) and standard error for *Oligoryzomys longicaudatus* and *Abrothrix longipilis* over time and in flowered and green bamboo habitats, Neuquén Province, Argentina. Means are adjusted to a standard body length of 103 mm for *O. longicaudatus* and 107 mm for *A. longipilis*. Sample sizes are within parentheses.

Collecting period	*Oligoryzomys longicaudatus*		*Abrothrix longipilis*	
	Flowered	Green	Flowered	Green
Spring-1	6.4±0.31 (14)	--	13.0±0.97 (4)	--
Autumn-1	5.3±0.18 (41)	--	7.1±0.34 (33)	--
Spring-2	4.9±0.14 (69)	5.7±0.30 (15)	3.6±0.43 (21)	9.4±0.69 (9)
Autumn-2	3.3±0.36 (10)	3.6±0.47 (6)	3.8±0.73 (7)	4.3±0.73 (7)
Autumn-3	3.6±0.25 (23)	4.3±0.52 (5)	4.2±0.42 (24)	4.1±0.65 (9)

Autumn-2 and -3 males occurred when females were also not reproductively active (Table 6). The length pattern in the green bamboo habitat during the second and third years paralleled that in the flowered habitat: they were largest in Spring-2, smallest in Autumn-2, and intermediate sized in Autumn-3 (Table 8). No significant difference existed between mean size in these 2 habitats when only the males from the last 3 collecting periods were compared ($F = 2.3$, *d.f.* = 1, 122, $p = 0.13$).

Changes in testis size in *A. longipilis* in the flowered bamboo habitat were similar to that in *Oligoryzomys*: largest in Spring-1 and declining through Autumn-3 (Table 8). Lengths in the Autumn-1 sample were bimodally distributed, as was also the case with the *Oligoryzomys* at this time. The modes for the *A. longipilis* were at 4 and 12 mm. The 3 oldest males (age classes 4 and 5) had testes 12 mm long. Five of the 22 youngest (age class-1) animals had testes between 10 and 12 mm long, suggesting that they too had reached sexual maturity. Mean length declined to its smallest value in Spring-2 (Table 8), when all but 1 *A. longipilis* had testes between 3 and 6 mm in length. Mean length remained small in Autumn-2 and -3. A notable difference in testis size was observed in Spring-2 between animals from the flowered and green bamboo habitats. At this time the 9 males from the green bamboo had testes ranging in length from 10 to 12 mm, while only 1 of 21 *A. longipilis* from the flowered bamboo had a testis in that length range. However, the animals with large testes in the green bamboo were much older than the animals in the flowered habitat (Table 5), and their greater ages may be the reason for their larger testes. Testis size in animals from green bamboo habitat declined to the same small size as Autumn-2 and -3 males in the flowered habitat.

Body Conditions

Fatness. The amount of fat varied among individuals as a function of species, time, and habitat. A striking feature of some mice was their great amount of intra-abdominal fat. In the fattest animals (class-3), the fat completely covered the heart, kidneys, testes/uteri, and lower intestines. We only recorded 20 such animals (19 *Oligoryzomys* and 1 *L. micropus*), and all were collected in Spring-2 in the flowered bamboo habitat. None of 214 *A. longipilis* was in a fat class higher than 1. The average 'fatness' of *Oligoryzomys* and *A. longipilis* was reversed in Spring-2 in the 2 habitats: in flowered bamboo, 0-class individuals were less frequent (47%) in *Oligoryzomys* and more so (93%) *A. longipilis*, whereas the respective percentages were 67 and 46 (Table 9) in the green bamboo. On average the *Oligoryzomys* were fatter than *A. longipilis* in the flowered habitat (1.1 vs. 0.07) and leaner (0.3 vs. 0.5) in the green bamboo habitat (Table 9); suggesting more efficient use of bamboo seeds by *Oligoryzomys* than *Abrothrix*.

Standardized Weight Changes. We compared weights of mice across time and habitats to test for possible beneficial effects of the bamboo seed on body condition, assuming that a heavier animal was in better condition than a lighter one of the same size and age. The standardized weights across time and habitat in *Oligoryzomys* and *A. longipilis* were examined with ANCOVA using body length as a covariate of body size and cusp height as a covariate of age. Sex was not a significant variable in either species. Age (molar cusp height) was not a significant covariate in *Oligoryzomys* but was statistically important ($p < 0.01$) in *A. longipilis*. Body weight was significantly associated ($p < 0.001$) with body length for both species. Finally, collecting period was a significant factor ($p < 0.001$) for both species but bamboo habitat was not.

Table 9. Frequencies of intra-abdominal fat scores in *Oligoryzomys longicaudatus and Abrothrix longipilis* trapped in different habitats in Spring-2, Neuquén Province, Argentina. Class values range from small amounts of fat restricted to gonads (0) to enlarged pads plus fat covering kidneys and heart (3). Mean and standard error are reported, with sample size (*N*) in parentheses.

Species	Bamboo Habitat	Frequency of fat-class scores				Mean
		0	1	2	3	
Oligoryzomys	Flowered	0.47	0.14	0.2	0.19	1.1±0.14 (79)
" "	Green	0.67	0.33	0	0	0.3±0.10 (21)
Abrothrix	Flowered	0.93	0.07	0	0	0.07±0.041 (41)
" "	Green	0.46	0.54	0	0	0.5±0.14 (13)

In the flowered habitat the heaviest *Oligoryzomys* (estimated weight 39 g at the standardized body length of 99 mm) were collected in Spring-1 (Table 10). Despite their weight all of these animals had virtually no fat (class-0). The estimated mean body weight in Autumn-1 was 32 g, representing an 18% decline from Spring-1. From Autumn-1 to Spring-2 body weights did not change in the flowered bamboo habitat, even though obese animals (class-3) were present in the latter period (Table 9). By Autumn-2, however, the standardized weight of these flowered-bamboo animals had declined another 6 g, to 29 g, and reaching their lightest standardized weight recorded during the study (Table 10). This was also the period when overall abundance of rodents was at its lowest level (Tables 2 and 3). In the next year (Autumn-3) standardized weight had increased to 28 g, but it was still 12% lower than the 32-g weight of the

Table 10. Estimated mean body weight (g) at different times and in different bamboo habitats for *Oligoryzomys longicaudatus* and *Abrothrix longipilis*, Neuquén Province, Argentina. Estimated weights are at adjusted mean body length of 99 mm in *Oligoryzomys* and 107 mm in *A. longipilis*. Mean and standard error are reported, with sample size (*N*) in parentheses.

Collecting Period	Bamboo Habitat	*Oligoryzomys longicaudatus*	*Abrothrix longipilis*
Spring-1	flowered	39±0.9 (29)	39±1.5 (9)
Autumn-1	" "	32±0.6 (69)	36±0.5 (80)
Spring-2	" "	32±0.6 (78)	32±0.7 (39)
" "	green	29±1.1 (21)	31±1.4 (13)
Autumn-2	flowered	26±1.1 (21)	29±1.7 (7)
" "	green	28±1.6 (9)	32±1.1 (17)
Autumn-3	flowered	28±0.9 (34)	30±0.8 (34)
" "	green	28±2.0 (6)	31±1.2 (13)

Autumn-1 animals. The animals in the green bamboo habitat in Spring-2, Autumn-2, and Autumn-3 were always lighter in weight than those in the flowered bamboo during the time (Autumn-1 and Spring-2) when there was much seed available (Table 10). But these green bamboo animals were heavier than those in the flowered bamboo in Autumn-2, the time when the rodents had declined to their lowest abundances during the study (Tables 2 and 3).

Abrothrix longipilis exhibited similar temporal patterns in standardized weight. The heaviest animals were collected in Spring-1, after which weights declined (Table 10). There was a 3 g decline (9%) in mean body weight from Spring-1 to Autumn-1. Body weights declined another 10% over the winter, to 32 g in Spring-2. From Spring-2 to Autumn-2, the standardized weight of *A. longipilis* continued to decline by another 3 g (9%). Similar to *Oligoryzomys*, we documented a difference in the amount of weight loss in *A. longipilis* during the second growing season between the flowered and green bamboo habitats (Table 10). Spring-2 animals in flowered areas averaged slightly (albeit not significantly) heavier (1 g) than those in the green bamboo habitat, but in Autumn-2 the green bamboo mice weighed 3 g more (also not significant). Although the patterns of reversals in weight were similar in *Oligoryzomys* and *A. longipilis*, the differences approached statistical significance only in the former species. Our data suggest there was an overall decline of about 30% in estimated body weight over the course of the study in both species and this was not closely linked to the abundance of bamboo seed.

Tail Scars and Torn Ears. We examined the patterns of scars on the tails and torn ears on the assumption that these wounds were the results of fights between mice and/or signs of escape from predators. Males had a higher frequency than females of at least 1 tail scar in both *Oligoryzomys* (0.42 ($N = 159$) vs. 0.34 ($N = 110$)) and *A. longipilis* (0.56 ($N = 113$) vs. 0.29 ($N = 102$)). The difference between sexes was highly significant in *A. longipilis* ($F = 16$, *d.f.* = 1, 214, $p < 0.001$) but not in *Oligoryzomys* ($F = 1.6$, *d.f.* = 1, 268, $p = 0.2$). In *A. longipilis* there was a highly significant effect of age class on the presence/absence of a tail scar ($F = 5.6$, *d.f.* = 4, 209, $p = > 0.001$), with the frequency increasing nearly monotonically from 0.25 in age class-1 to 0.78 in age class-5 animals. There was a near significant age effect in *Oligoryzomys* ($F = 2.1$, *d.f.* = 4, 268, $p = 0.08$), but the intermediate age classes of -2, -3, and -4 had the highest frequencies of tail scarring (0.48, 0.36, and 0.46, respectively) while the youngest and oldest animals had lower frequencies. The frequency of scarring changed across time and habitats (Table 11). We examined the effects of species, sex, age class based on tooth wear, bamboo condition, and collecting period on scarring patterns with ANCOVA, using age class as a covariate. The significant main effects were collecting period ($F = 22$, *d.f.* = 4, 4.9, $p = 0.003$), bamboo condition ($F = 6.5$, *d.f.* = 1, 2.7, $p = 0.092$), and age ($F = 6.7$, *d.f.* = 1, 447, $p = 0.010$) and the only significant interaction term was between collecting period and species ($F = 7.9$, *d.f.* = 4, 5.8, $p = 0.016$). In the flowered bamboo habitat scarring frequencies in both species were low in Spring-1, when animals were relatively old (Table 5) and population densities were low (Tables 2 and 3). Levels of scarring in *Oligoryzomys* were low in all 3 autumn collections (Table 11), even though densities and ages of autumn animals differed among years. In Autumn-1 the densities were high and the animals were young, while in Autumn-2 and Autumn-3 the densities were comparatively lower (Tables 2 and 3) and the animals were older (Table 5). The highest incidence of tail scars occurred among Spring-2 animals, when densities were

Table 11. Mean frequency of mice with at least one scar on tail among trapped *Oligoryzomys longicaudatus* and *Abrothrix longipilis* across collecting periods and bamboo conditions, Neuquén Province, Argentina. Mean and standard error are reported, with sample size (*N*) in parentheses.

Collecting Period	Bamboo Condition	*Oligoryzomys longicaudatus*	*Abrothrix longipilis*
Spring-1	flowered	0.08±0.078 (29)	0.33±0.137 (9)
Autumn-1	" "	0.19±0.050 (69)	0.11±0.046 (81)
Spring-2	" "	0.64±0.046 (78)	0.73±0.064 (41)
" "	green	0.78±0.089 (21)	1.00±0.114 (13)
Autumn-2	flowered	0.34±0.091 (21)	0.86±0.155 (7)
" "	green	0.52±0.137 (9)	0.53±0.100 (17)
Autumn-3	flowered	0.19±0.072 (34)	0.49±0.069 (35)
" "	green	0.29±0.168 (6)	0.50±0.119 (12)

still high but beginning to decline. At this time large numbers of *Oligoryzomys* were drowning in the nearby lakes. These scarred Spring-2 mice were older than those of the preceding autumn (Table 5) and were not reproductively active (Table 6, 8).

Abrothrix longipilis differed in a number of ways from *Oligoryzomys* with respect to scarring. Frequency of scars in the former species was lower in Autumn-1 than Spring-1 (Table 11), even though densities were higher. Many of these autumn *A. longipilis* were very young and perhaps they had not yet reached the age where fighting starts in this species. By Spring-2 the incidence of tail scars was 3 times higher than in Autumn-1, and the animals were somewhat older (Table 5) and densities were still high. Some feature of the social or predatory environment may have changed in the interval between Autumn-1 and Spring-2, leading to this increased amount of wounding. But unlike in *Oligoryzomys*, the high frequency of tail scars in *A. longipilis* was not associated with drownings during Spring-2. In Autumn-2 the frequency of tail scars reached the highest level that we recorded in the flowered bamboo (Table 11); at this time the abundance of *A. longipilis* had dropped to its lowest level, and these animals were as old as those from Spring-1 (Table 5). By Autumn-3 scarring had declined to a moderate level, among mice that now were younger but more abundant than in the preceding year.

In green bamboo the patterns of tail scarring were similar in both species, declining continuously from Spring-2 to Autumn-3 (Table 11). But in Spring-2 the scarred *Oligoryzomys* were of middle-age, while more than half of the *A. longipilis* individuals were in the oldest 2 age classes and the sample had the highest mean age among our collections (Table 5). By Autumn-2 the frequency of scarring in both species had declined although density had increased from the preceding spring. The Autumn-2 *Oligoryzomys* were older, and *A. longipilis* younger, than in Spring-2. In Autumn-3 the incidence of tail scarring was lower in *Oligoryzomys* and about the same in *A. longipilis* as it was in the preceding autumn. The ages of these Autumn-3 animals were similar to those in Autumn-2 (Table 5).

In summary, the frequency of tail scarring showed a complicated relationship with age, species, and population density. One consistent trend in these 2 species was the 3- to 6-fold increase in scarring during Winter-1, which was the time when the populations reached their peak densities and rodents began leaving the forest habitat in large numbers.

Mice were both abundant and drowning in Spring-2, and we compared whether fighting (torn ears) was at the same level in the mice that drowned and the nearby flowered habitat. For 3 species the frequency of torn ears was higher among the drowned than the trapped animals: *Oligoryzomys*, 25% of 36 animals (drowned in L. Nonthue) vs. 10% of 59 animals (collected in flowered bamboo habitat); *A. longipilis*, 50% of 2 vs. 18% of 34; *Loxodontomys*, 41% of 46 vs. 0% of 4. Drowned mice had significantly higher frequencies of torn ears than live-trapped mice (ANOVA, $F = 5.0$, *d.f.* = 1, 175, $p = 0.03$), suggesting that near the time when mouse densities were declining from their peak levels, the mice entering the water had suffered more wounding than those remaining in the forest.

Arboreal Activity

We observed rodents climbing on seed-laden bamboo canes in Autumn-1 using night-vision binoculars. This prompted us to set arboreal lines of live traps to determine which species were foraging in bamboo. With 294 trap-nights over 28 arboreal trap lines, the weighted mean trap success per trap line was 0.12 ± 0.023 (range: 0 - 0.46). Trap success ranged from 0 to 30% (Table 12) and was not significantly influenced by collecting period, bamboo habitat, or the interaction of these 2 factors (ANOVA, all $p > 0.05$). The highest success was in one line of traps in flowered bamboo in Autumn-1, which also was the time of greatest trap success on the ground (Table 3). Arboreal trap success declined to 12% and 15% in the flowered bamboo in Autumn-2 and -3, when there was no more seed on the dead canes. Trap success in Spring-2 was notably lower in the green bamboo (0%) than in the flowered bamboo (15%), when some bamboo seed still remained on the flowered stalks (Table 12).

We caught 40 mice in arboreal traps and identified 39 of them (one escaped): 25 *O. longicaudatus* in the flowered bamboo habitat and 1 in the green bamboo; 4 *A. longipilis* in the flowered and 5 in the green bamboo habitats; 1 *A. olivaceus* in each habitat, and

Table 12. Trap-success frequency in 28 arboreal trap lines over time and bamboo habitat, Neuquén Province, Argentina. Means and standard errors are reported, with numbers of trap lines shown in parentheses.

Collecting Period	Flowered Bamboo	Green Bamboo
Autumn-1	0.30 (1)	--
Spring-2	0.15±0.042 (7)	0 (4)
Autumn-2	0.12±0.057 (5)	0.12±0.073 (3)
Autumn-3	0.15±0.057 (5)	0.10±0.073 (3)

2 *R. rattus* in the flowered bamboo. The predominance of *Oligoryzomys* (67%) was not surprising as it was the most abundant species present and is known to be somewhat arboreal (Contreras, 1972; Pearson, 1983). Likewise, to catch *R. rattus* up in the canes was not unexpected, as two of its common names (roof rat and climbing rat) refer to its arboreal behavior. The 2 *Abrothrix* species are primarily terrestrial, yet both were also caught up in the canes. *Oligoryzomys* was the most common rodent caught in arboreal traps in the flowered bamboo (78%), whereas *A. longipilis* was the most common in the green bamboo habitat (71%). The difference in abundance of these 2 species between the 2 habitats was highly significant (Mann-Whitney U-test, $z = -3.5$, $p < 0.001$).

Predator Abundances

During Autumn-1 barn owls (*Tyto alba*) were abundant, and were heard calling every night near our campsites. Park Ranger Monica Sosa reported that during Winter-1 owls commonly flew in front of her headlights at night near Yuco (Locality 5), and that dead barn owls were found in Summer-2. In Spring-2 a few barn owls were heard by one of us (RDS) while camped at Hua Hum and Currhué Chico, whereas in Autumn-2 only 1 barn owl was heard calling during 7 nights at the same sites, and in Autumn-3 a barn owl was heard only once during 4 nights of camping at Hua Hum and Currhué Chico. Based on these qualitative observations and accounts, the abundance of this generalist nocturnal predator appears to have closely paralleled that of the rodents. In a separate study one of us (JS) has been monitoring a series of scent stations near Lago Currhué Grande, and observed a 30% increase in the number of Andean red fox, or culpeo (*Pseudalopex culpaeus*) visiting scent-stations in Summer-2 compared with visits in the (pre-flowering) summer of 1998.

DISCUSSION

Ratada-2001*: Its Cause and Structure*. Both large and small fluctuations in numbers of rodents in Valdivian rainforest have been reported and their varying causes are becoming better understood (see below). We have described a large fluctuation in the vicinity of San Martín de Los Andes over a 3-year period from 2000 to 2003. The most notable features of this cycle to the general public were the invasion of human dwellings by the rodents and their drownings in lakes in 2001; thus, we name this the *Ratada-2001*. The cycle, however, was initiated in the spring (October) of 2000 almost certainly by the flowering and production of a massive amount of seed. That the ratada was ultimately caused by the production of bamboo seed rather than some other factor is supported by the close correspondence between the areas where the bamboo flowered and where mice invaded buildings or drowned in high numbers (Plate 2A, B, and C).

When *C. culeou* began to flower in Spring-1 rodent populations were in the low phase of the annual cycle (Fig. 3), and densities were similar to those of baseline populations (Pearson, 2002). Numbers increased during the breeding season of Spring-1 and Summer-1. Bamboo seed matured in late Summer-1 and began falling to the ground. Seed was abundant on the ground in Autumn-1, and probably became an *ad libitum* food resource for mice until Spring-2. Derting (1989) found that with *ad libitum* food supplies, young *Sigmodon hispidus* grew more rapidly and reached first estrus at an earlier date than did individuals with a more limited food supply. The abundance of very young (age class-1) and pregnant *Oligoryzomys* and *A. longipilis* in our Autumn-1 sample suggests that a similar acceleration to reproductive age occurred in late Summer-1. Such precocial reproduction provides a fitness advantage to the individual female and contributes importantly to the size of the population at the end of the breeding season (Lambin and Yoccoz, 2001). Because of the abundance of bamboo seed, reproduction in 4 of the native rodents continued at a high intensity through Autumn-1, and the breeding season was 3 months longer than typical. Extension of the breeding season due to a superabundance of food was reported for *Oligoryzomys* in Chile (Murúa et al., 1986; Gonzáles et al., 1989). A similar extension of breeding occurs in some Northern Hemisphere species reaching high densities (e.g. Jensen, 1982; Pucek et al., 1993). If generation times of these Argentine species are similar to rodents like *Microtus agrestis* (6 weeks), *Mus domesticus* (7 weeks), and *Rattus norwegicus* (8 weeks) (Cockrum, 1962), then 1 to 2 more cycles could have occurred in the season when the bamboo flowered. Our data show that litter sizes in *Oligoryzomys* were larger than normal during this final part of the breeding season. Because of the likely shortened generation time plus larger litter sizes, the population growth rate (R) during these 'extra' rounds of breeding was higher than normal and led to the final population growth of the rodents to outbreak (plague) numbers.

In early Winter-1 reproduction ended, populations reached their highest densities, and the decline phase began (Fig. 3). Three lines of evidence suggest an immediate start to this decline. In late Winter-1 park rangers reported seeing high numbers of owls, permanent residents within Parque Nacional Lanín reported rodent invasions of their buildings, and rodents began to drown in large numbers. All 3 of these factors (predation, emigration, and drowning) should have contributed to declining rodent numbers. We infer that the decline phase lasted from Winter-1 into Summer-2 based on the beach records at Lago Lacar (Fig. 2), and was due to continued mortality from drowning, predation, and low recruitment during the second season. Evidence for low recruitment was the virtual absence of breeding female *Oligoryzomys* or *A. longipilis* in Spring-2 (Table 6), the scarcity of young animals (Table 5), and low numbers of *A. longipilis* in the Autumn-2 collections (Table 2, Appendix Table 2). Absence of young animals suggests that little reproduction occurred during the last half of Summer-2, and low autumnal numbers indicates little recruitment during the second breeding season. Delayed maturation plus a late start and short duration of the breeding season is commonly observed in rodent cycles after peak densities are reached (Krebs and Myers, 1974: Hansson and Henttonen, 1985; Fitzgerald et al., 2004).

One possible reason for delayed, or reduced, reproduction in the flowered bamboo habitat in Spring-2 was that over-wintered animals were comparatively younger than the Spring-1 population of the previous year when there was probably no autumn (and winter) breeding. Evidence consistent with this hypothesis comes from comparing *A. longipilis* from the flowered and green bamboo habitats in Spring-2. Four of 4 females from the green habitats, but only 2 of 20 from the flowered habitats, were reproductively active, and mice from green bamboo habitat were older than those from the flowered bamboo habitat (Table 5). Autumn breeding is uncommon (Pearson, 1992, 2002), so Spring-2 females in the green bamboo likely had been born during Summer-1, and were >6 months old. In the flowered bamboo habitat we know that breeding continued into early Winter-1, so the Spring-2 population included disproportionately more females that were about 4 months old. However, the observation that precocial (young-of-the-

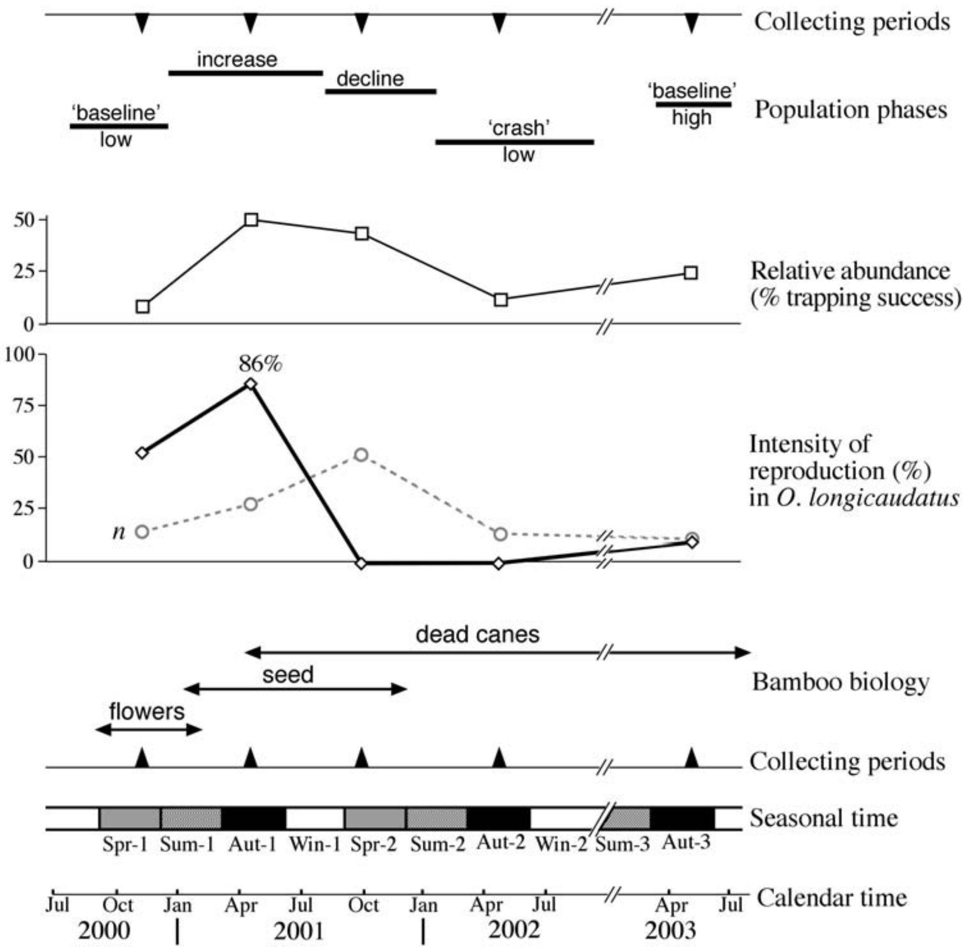

Figure 3. Chronology of Ratada-2001. The chart shows major events in the phenology of the flowering bamboo and rodent populations with respect to the 5 collecting periods, the passage of the annual seasons, and the calendar dates. The graph of the intensity of reproduction in *O. longicaudatus* shows the percentage of females that were reproductively active in a sampling period, with *N* indicating the number of animals autopsied.

year) female *A. longipilis* were breeding in Autumn-1 contradicts the hypothesis that females in the flowered bamboo habitat were 'too young' (at about 4 months of age) to breed in Spring-2.

Why *Oligoryzomys* females in both habitats were not in breeding condition in Spring-2 is unknown. The explanation in flowered bamboo habitats could be the same as for *A. longipilis*, that they were mostly winter-born and 'too young' when we sampled in Spring-2. This could also be the reason for lack of reproduction in the females from the green bamboo habitat, as the animals in this habitat also consisted of young animals (Table 5). But this argument is also contradicted by the extremely young (age class-1) and pregnant *Oligoryzomys* in Autumn-1.

Two other, more general speculations about the apparent reduction (or failure) of reproduction in *Oligoryzomys* and *A. longipilis* in the second year in the flowered bamboo habitat are suggested from the body conditions of the Spring-2 animals. Many of the *Oligoryzomys* at this time were obese (Table 9), and tail scars (Table 11) and torn ears (see Results) were frequent in both species. Fertility is frequently reduced in obese laboratory rodents (Coleman and Hummel, 1967; Good et al., 1997; Hellman, 1967). Such a side-effect of obesity might explain why these forest rodents did not have high reproductive success during the second breeding season after the bamboo flowered in their habitat. The high level of wounds in Spring-2 probably resulted from fighting during this time of high densities. If this is true, then the animals that had lived through the high density conditions existing from Autumn-1 to Spring-2 had been experiencing chronic stress for more than 1 generation due to fighting. Prenatal stress of the mother negatively affects the fertility of her offspring in various mammalian taxa, including rodents (Ward, 1972; Herrenkohl, 1979; Pollard and Dyer, 1985; Marchlewska-Koj et al., 2003), canids (Osadchuk et al., 2003), and humans (de Zegher and Ibáñez, 2004); and similar effects may have developed in the *Oligoryzomys*, *A. longipilis*, and other rodents living under the stress of high densities during the peak phase of this outbreak. Experimentally induced prenatal stress in laboratory rats (Pollard, 1986; Holemans et al., 1998; Francis et al., 1999) and nutritional deprivation of pregnant humans (Duncan and Scott, 2004) resulted in detrimental effects in offspring lasting at least 2 generations after the application of the stress. Such intergenerational transmission could amplify these negative, prenatal effects on reproductive ability of the forest rodents and have demographic consequences. Reproductive failure likely played a major role in the crash at the end of *Ratada-2001*, and determining its cause should be a major goal of future studies of rodent outbreaks when *C. culeou* flowers in other areas.

The outbreak ended and populations returned to 'control' conditions in terms of population size and structure sometime during the third season after the bamboo flowered (Fig. 3). By Autumn-3 rodent populations in flowered bamboo habitat were twice as abundant as during the Autumn-2 low (Table 3). The age-structure of both *Oligoryzomys* and *A. longipilis* populations had shifted toward younger age (Table 5), which suggests that reproduction had been successful in the third breeding season. Additional evidence for this return to normal conditions was the increase in relative numbers of *A. longipilis* trapped in Autumn-3 (32% of the period total) compared to their low abundance (16% of the period total) in Autumn-2 (Table 2).

The Rattus rattus *Outbreak – A Different Story*. In 20 years of trapping 2 of the authors (OPP and AKP) had never collected *R. rattus* in the native forests, and so our collection of many specimens of this species in this habitat was completely unexpected. Not only was the outbreak of this species surprising, but its timing appears to have differed from that of the native species. Our earliest indication of the presence of rats in the native habitat came in Autumn-1, when we found that a number of our snap-trapped mice at Hua Hum had been badly chewed. *Rattus* are known to do this to trapped specimens and it constituted indirect evidence of their presence at this time. These damaged animals were only found in traps placed in a small marshy area at the study site. One *Rattus* was trapped at Currhué Chico in Autumn-1, but at that time we presumed that this was only a stray from a population in buildings of a government outpost about 5 km away. In Spring-2 however, rats comprised 10% of the drowned mice picked up on the beach (Table 4). We continued to find badly chewed mice in the same small area at Hua Hum where this had happened in Autumn-1, but we did not trap any rats. Only in Autumn-2 did we catch many *Rattus*. At this time rats were captured well away from the marshy area at Hua Hum, including high up on the hillside and in arboreal traps. And during this period, when autumn trapping success reached its lowest level (Table 3), we captured this species at Currhué Chico, Hua Hum, and Yuco, where they comprised one-third of the 33 animals that we collected from these 3 localities (Appendix Table 2).

Our success in trapping this species from many areas within the flowered bamboo habitat suggests that, of our 5 collecting periods, they were most abundant in Autumn-2. One of us (JS) trapped *Rattus* during Summer-2 in the forests near Lago Currhué Grande (near Locality 1) and at Lago Huechulafquén (approximately 20 km NW of Locality 2); animals were captured in native forests and far from human dwellings. During Summer-2 tourists at campsites and landholders within Parque Nacional Lanín reported sightings of rats to park rangers. This is further evidence of the extensive occupation of the native forests by this rodent, and that numbers were highest in the second year after the bamboo flowered.

These trapping records and observations indicate that the dynamics of the *Rattus* population was different from that of the native species. Peak numbers of the rats was reached in Summer-2 or Autumn-2, 6 to 9 months after the native mice reached their highest abundance. Given that the rats established dense populations only in the areas of Parque Nacional Lanín where the bamboo had flowered, it appears that their ability to expand their local distribution away from urbanized areas was in some way directly linked to the flowering of the bamboo. *Rattus rattus* was the most abundant native rodent species during bamboo-associated outbreaks in the forests of Assam, India (Seal et al., 1951) and Japan (Tanaka, 1957), so a similar response to a bamboo seeding in its introduced range in South America is not surprising. However, the factors causing the time of peak rat abundance to differ from that of the native species are unknown. If our interpretation is correct that the rats reached their highest densities in the second summer or autumn, then their presence among the drowned animals in Spring-2 disagrees with a hypothesis that rodents were drowning because of their efforts to disperse to less crowded habitats. If the dispersal hypothesis was correct for the *Rattus*, then one would predict that they would have continued drowning through Spring-2, Summer-2, and into Autumn-2, which was not observed nor reported to the park rangers. The rise and fall of black rats in the Valdivian forests of Argentina remains largely mysterious.

Comparisons of the Ratada-2001 *and Baseline Populations*. Based on 20 years of field data on *Oligoryzomys* and *A. longipilis* in this general region, Pearson (2002) described the normal population structure of these species and emphasized their general long-term stability. Similar studies of *Oligoryzomys* and *A. longipilis* in Chile have shown that numbers of these species regularly fluctuate, albeit with low amplitudes, linked to fluctuations in oceanic weather systems (Murúa et al., 2003a, 2003b). During years of high seed production by forest trees, however, Chilean populations of *Oligoryzomys* regularly undergo large and rapid increases in number (Gonzáles et al., 1989). A comparison of biological features in the Baseline and *Ratada-2001* populations may clarify which factors become important in shifting these populations to outbreak levels rather than staying within their normal system of low-amplitude, weather-linked fluctuations (Table 13).

Baseline populations increase in numbers from a springtime low to an autumn high in the normal annual cycle. The increase from 16 to 30% in overall trap success of the Baseline population reflects a normal doubling of the population size, and contrasts with the ca. 5-fold or greater increase (10 to 51%) between Spring-1 and Autumn-1 in the ratada population (Table 13). This difference could result from an increased breeding effort per female in the form of larger litter sizes, and/or a continual buildup in the percentages of breeding females during the reproductive season. In comparison to the Baseline average, mean litter size in the *Ratada-2001* population of *Oligoryzomys* was one-half embryo higher in Spring-1, and during the extended reproductive season in Autumn-1 the mean increased to 2 embryos above Baseline (Table 13).

In contrast, there was no significant difference in reproductive output between female *A. longipilis* in *Ratada-2001* and Baseline populations. The Autumn-1, ratada females increased their average litter sizes by only one-half embryo over the Spring-1 females, and by only one-tenth of an embryo over the long-term average of the Baseline females (Table 13). Also the range in numbers of embryos/litter of this species did not change in the ratada population during this increase phase of the population, whereas it did increase in *Oligoryzomys* (Table 13). This stability in reproductive values in *A. longipilis* may reflect an inability of this species to respond reproductively to changes in food availability. The unusual ovulatory cycle of *A. longipilis* (Pearson, 1992) may be related to this apparent inability to vary litter size in this species. Both *Oligoryzomys* and *A. longipilis* increased in numbers during the outbreak, but evidently by different means; *Oligoryzomys* increased individual reproductive effort whereas *A. longipilis* employed some other means, perhaps by precocial breeding of summer-born females who would not normally have bred until the following spring.

Age structure of the *Ratada-2001* and the Baseline populations differed most notably in their spring populations. Both types of populations were similar in having relatively few old animals (4 and 7%, respectively) in autumn. In spring, however, 40% of Baseline populations of *Oligoryzomys* and *A. longipilis* were older animals (Table 13); comparable percentages in the Spring-2 *Ratada-2001* populations were 6% and 0%, respectively. This downwards shift in age reflected continued recruitment from the extended Autumn-1 breeding season during the outbreak.

The *Ratada-2001* and the Baseline populations also differed in density changes over the winter period. Nearly half of Baseline populations fail to survive from Autumn to Spring (Table 13). During Ratada-2001 however, trap success only dropped 7% from Autumn-1 to Spring-2, leading to an estimated 87% over-winter survival. The ratada populations continued breeding and increased in size after our Autumn-1 sampling, which likely is the reason we did not record declines in Spring-2. In contrast, Baseline populations finish breeding before the autumn sampling period, at which time they are close to peak densities and may already be starting their normal, intra-annual decline.

In summary, Baseline and Ratada-2001 populations differed in the timing of breeding; Baseline populations experienced a short season, whereas Ratada-2001 populations had an extended season during the increase phase but little or no breeding during the decline phase. As a result of these different breeding regimes the spring and autumn age structures differed between these 2 populations: Baseline populations were characterized by a predominance of old animals in spring and young animals in autumn, whereas during Ratada-2001 we observed a predominance of young animals

Table 13. Comparisons of biological features in Baseline and *Ratada-2001* Populations. Information in the table is from Pearson (2002) and this report, respectively.

Feature	Baseline Populations	*Ratada-2001* Populations
Abundance in spring vs. autumn, based on percent trap success*	Spring = 16	Spring-1 = 10 Spring-2 = 44
	Autumn = 30	Autumn-1 = 51 Autumn-2 = 12 Autumn-3 = 24
Reproduction (litter size)**	*O. l.* = 4.9±0.23 (2 – 11)	*O. l.* (Spring-1) = 5.4±0.5 (2 – 7) *O. l.* (Autumn-1) = 6.9±0.42 (4 – 11)
	A. l. = 3.8±0.11 (2 – 5)	*A. l.* (Spring-1) = 3.3±0.67 (2 – 4) *A. l.* (Autumn-1) = 3.9±0.34 (3 – 5)
Spring age structure (percent in older segment of population)***	*O. l.* = 40	*O. l.* = 6
	A. l. = 41	*A. l.* = 0
Autumn age structure (percent in older segment of population)***	*O. l.* = 7	*O. l.* = 4
	A. l. = 28	*A. l.* = 6
Overwinter mortality (percent) ****	47	14

* Percentages for the overall Baseline population are from Pearson (2002:197), and for the *Ratada-2001* populations they are from Table 3.

** Information for the Baseline Populations comes from Table 1 in Pearson (2002), and for the *Ratada-2001* Population from Table 7.

*** This percentage was estimated for the Baseline populations of *Oligoryzomys* from Fig. 2A in Pearson (2002) using the oldest 2 of the 5 age categories, and for *A. longipilis* using the oldest 4 of the 11 categories. For the *Ratada-2001* populations the values were compiled from Table 6 using age classes IV and V.

**** In this table the percent overwintering mortality was calculated as 1 – (spring/autumn trapping abundance). The comparison done for the *Ratada-2001* Populations is of the Spring-2/Autumn-1 abundance in the flowered bamboo habitats.

during both the autumn and spring of the increase and peak phases and the high numbers of old animals in the autumn of the crash phase.

Comparison of the Ratada-2001 *with Another Local Outbreak.* An outbreak occurred in 1997 in forests south of the present study area, and was not caused by the flowering of bamboo (Pearson, 2002; Table 14). Neither unusual climatic conditions nor an unusually large seed production by a forest tree species was thought to explain this outbreak (Pearson, 2002). While the latitudinal extent of the 1997 ratada was 3 times greater than that of the bamboo-induced *Ratada-2001*, the high numbers of mice were distributed spottily compared to the uniformly high numbers throughout the flowered bamboo region during *Ratada-2001*. This could imply that the stimulus for *Ratada-1997* was patchily distributed compared to the uniformly high production of bamboo seeds in forests from Lago Huechulafquén to Lago Falkner (Sanguinetti and García, 2001).

Both outbreaks shared the feature of an extended breeding season before peak densities were reached (Table 14). Trap successes were equally high in the spring following the winter peak, suggesting that peak densities were similar in both outbreaks. Body condition of peak-stage animals, as measured by fat scores, was also similar (Table 14), including the same difference in amount of fat between *Oligoryzomys* (high) and *A. longipilis* (low scores). Large numbers of mice drowned during the decline phase in both of these outbreaks, and the drownings occurred in approximately the same period of time, i.e. late winter and into spring (Table 14). The high fat levels observed in drowned *Oligoryzomys* suggest that they had not left the forest habitat because of starvation. Not only were the Spring-2 ratada animals fat, but at the same time that they were drowning there was still bamboo seed on the forest floor and on stalks of the dead plants. A high fat index has not been clearly related to a high nutritional condition in other rodents (Batzli and Esseks, 1992; Krebs and Singleton, 1993), and perhaps the drowning of fat mice in these 2 outbreaks indicates that they too were not in a good nutritional state. Species composition of the drowned rodents in the 2 outbreaks was also similar (Table 14): *Oligoryzomys* was the predominant species, followed by *L. micropus*, and few *A. longipilis*. In both outbreaks the relative abundance of drowned rodents and those trapped in nearby woods differed (Table 14); *A. longipilis* was common in the forest and rare in the drowned sample while the reverse was the case for *L. micropus*. The abundance of drowned *L. micropus* during both outbreaks is puzzling in light of their apparent rarity inside the forests. Trap shyness probably is not the explanation for the low catch of forest *L. micropus*, as we have caught many of them in more open habitats to the east of the forest. Other possible explanations for the different frequencies of drowned versus trapped *L micropus* and *A. longipilis* might be that (1) *A. longipilis* are better swimmers than *L. micropus* and drown less frequently, or (2) that when overall rodent densities rise individual *L. micropus* leave the forests before *A. longipilis*. Under this second hypothesis even uncommon species might try to leave the forest when overall rodent densities are high. This hypothesis also may explain why *I. tarsalis*, a decidedly uncommon species in traps, also appeared among the drowned animals (Table 4).

Another feature common to the ratadas of 1997 and 2001 was the reduced level of reproduction in the season following the peak. Judging by the inactive and/or immature condition of the ovaries of Spring-2 animals in *Ratada-2001*, reproduction in that season was delayed and possibly reduced. The 1997 outbreak collections were made in late spring and early summer, when reproductive activity usually is obvious, but at that time gonads were inactive (Pearson, 2002). To some ecologists the lack of reproduction by microtine rodents during the decline phase of demographic cycles is considered the central problem to understanding rodent population cycles (Christian, 1950; Boonstra, 1994).

A notable difference between the 2 outbreaks was the absence of *R. rattus* during the 1997 outbreak, whereas they became a dominant species in the forest fauna during *Ratada-2001*. This apparently was a real difference, as *R. rattus* also were present

Table 14. Similarities and differences in features of two rodent outbreaks (in 1997 and 2001) in southwestern Argentina. The information in the table is from Pearson (2002) and this report, respectively.

Features of Outbreak	Ratada-1997	Ratada-2001
Initiated by bamboo flowering	No	Yes
Latitudinal extent of outbreak	300 km	100 km
Extended breeding season in previous year	Yes (implied from ages of drowned animals)	Yes (observed in Autumn-1)
Percent trap-success in spring of peak density	*43, 62, & 63	**Live traps: 47 (range: 30-75; *N* = 7) Snap traps: 60 (range: 36-67; *N* = 7)
Body condition of animals	*O. longicaudatus*: most were fat *A. longipilis*: few were fat	*O. longicaudatus*: most were fat *A. longipilis*: fewer were fat
Rattus rattus	None observed	Became abundant
Drownings	Spring	Late winter to mid-summer
Relative species abundance among drowned animals	*O.l. > L. m. >> A. l.*	*O. l. > L. m. >> A. l.= A. o.*
Relative species abundance of trapped animals	****O. l. > A. l. >> A. o. > L. m.*	*O. l. > A. l. >> L. m.= A. o.*
Female breeding condition in season following peak density	Non-reproductive in late spring (1997)	Non-reproductive in early Spring-2 (2001)

* Pearson (2002) presented the combined success of equal numbers of live and snap traps. We present values from his Table 1 for November trappings at Lago Espejo Chico and Parque Nacional Los Alerces.

** Success values are means for Spring-2 collections from flowered bamboo habitats, computed from information in Appendix Table 2.

*** Abundances of rodent species trapped at Lago Espejo Chico on 5 and 24 November, 1997 were calculated from the records in the field catalogue of OPP.

among the drowned Lago Nonthué animals in 2001 but absent from the drowned (beach) collection in 1997. Furthermore, black rats were caught in the woods during the second outbreak but not in the earlier one, even though the same traps and the same trapping methods were used on both occasions.

In summary, these 2 outbreaks show many similarities in the responses of the main species: an extended breeding season in the autumn preceding the peak density; large stores of fat; periods of mass drownings; and lack of breeding during the reproductive season in which the decline phase occurred. The major difference between the 2 outbreaks was that one did not involve the flowering and masting of a bamboo species, whereas the other was caused by this botanical event.

Comparison of the Ratada-2001 *with Chilean Bamboo Ratadas*. Two bamboo-induced ratadas in the Valdivian forest ecosystem in Chile were described by Murúa et al. (1996) and Gallardo and Mercado (1999). A notable difference between the ratadas in the 2 countries was the time lag between the onset of bamboo flowering and the peak in rodent densities (Table 15). In our study this happened about 10 months after the *C. culeou* bamboo flowered. However, in Chile this peak occurred 18 to 21 months (i.e., in "Autumn-2", using the terminology describing the seasons of the Ratada-2001 outbreak) after the quila bamboo (*C. quila*) flowered. This evidently occurred because the ripe seed of quila is not available to the rodents until the second season after flowering (i.e., in "Summer-2"); in the study area of Murúa et al. (1996) the peak in rodent density occurred a few months after most of the year-old seed had fallen to the ground. The intensive reproduction by the rodents needed to reach this high Autumn-2 density must have occurred late in the second growing season, because in Autumn-1, when seeds were still on the plants (González and Donoso, 1999), populations of both *O. longicaudatus* and *A. olivaceus* were at typical densities (Murúa et al., 1996). We suggest 2 possible reasons for this delay in intensive reproduction in these Chilean rodents. First, rodents may not climb up quila canes as readily as they do colihue canes because the former grow high into the forest canopy whereas the latter remain in the understory. Thus, the seeds on the canes may be unavailable in sufficient amounts in Autumn-1 to allow breeding by the mice; in Chile these seeds apparently do not become an *ad libitum* food supply to the mice until they fall to the ground in Summer-2 (González and Donoso, 1999). A second possibility might be that the seeds are unpalatable while they are still on the plant. Studies of the levels of arboreal activity of the Chilean rodents and the palatability of the retained seeds are needed to learn why the rodents do not begin breeding in the season that the quila bamboo flowers. Another possible difference between the *C. culeou* and *C. quila* ratadas is the season(s) when the peak densities and declines take place. In our study area, peak rodent densities occurred in winter and the decline took place over the subsequent spring and early summer. From the limited information on Chilean ratadas, it appears that the peak density is reached in autumn and the decline occurs during the winter. Murúa et al. (1996) observed an abrupt decline, from an estimated 244 animals / ha to 0 animals / ha over a 3-month period of 'Winter-2' (using our notation for seasons during an outbreak) at their study site in Peulla. Only after more of these bamboo-caused outbreaks are described will we be able to assess how the peaks and declines in rodent populations differ depending on the species of bamboo causing the outbreak.

One similarity in Chilean and Argentine ratadas appears to be which rodent species increased in numbers during the outbreaks in the 2 countries. The most common species in all but one of the Chilean outbreaks was *Oligoryzomys* (Table 15). The apparent exception was at Peulla in July, 1995, where 93% of the animals were *A. olivaceus* according to Murúa et al. (1996). However, there seems to be a contradiction about the most common species at Peulla, because Ruiz and Simeone (2001) reported that more than 90% of 140 prey items that they identified from the feces of Kelp Gulls

Table 15. Behaviors of rodents in bamboo-caused ratadas in Argentina (this study) and in Chile. Information on the Chilean outbreaks at San Martín and Peulla are from Murúa et al. (1996), and at Puyehue, Queilen, and Yaldad are from Gallardo and Mercado (1999). Mauro E. Gonzales (pers. comm.) said that bamboo flowered at Yaldad in the spring of 1993, not the spring of 1992 as stated in Gallardo and Mercado (1999). We use the name *C. quila* for the bamboo that flowered in Chile, as suggested by M. E. Gonzales (pers. comm.).

	Outbreaks			
	This study	San Martín	Peulla	Puyehue (P), Queilen(Q), Yaldad (Y)
Species flowering	*C. culeou*	*C. quila*	*C. quila*	*C. quila*
Season of peak density (time from initial spring flowering to ratada	Winter-1 (approx. 10 months post-flowering)	Autumn-2 (approx. 18 months post-flowering)	Winter-2 (approx. 21 months post-flowering)	P: Winter (18-21 mos. post-flowering) Q & Y: Autumn-2 (approx. 18 mos. post-flowering)
Autumn breeding	Yes	--	Yes	--
Time of steepest decline	Winter-1 through Spring-2	Winter-2 (after Autumn-2	Winter-2	Not studied
Relative species diversity at peak density	*O.l.* > *A. l.* >> *A. o.* = *L. m.*	*O. l.* >> *A. o.*	*A. o.* >> *O. l.*	P: primarily *O. l.* Q: *O. l.* >>> *A. o.* Y: *O. l.* > *A. o.*
Condition of gonads at peak and in decline	Inactive in both sexes	--	--	Q: Inactive in both sexes Y: Inactive in both sexes
Autumn breeding before peak	Yes	--	Yes	--

(*Larus dominicanus*) collected in May, 1995 in the same area were *Oligoryzomys* and only 2% were *A. olivaceus*. The predominance of *Oligoryzomys* reported in most of the bamboo-induced ratadas may be because this species is the most granivorous of the Valdivian forest rodents (Pearson, 1983; Meserve et al., 1988), pre-adapting it to be the most efficient species in digesting and metabolizing bamboo seed.

Another difference following the flowering of *C. culeou* and *C. quila* may be the rarity of mass drownings during quila-ratadas. Neither Murúa et al. (1996) nor Gallardo and Mercado (1999) mentioned mass drownings in the outbreaks that they studied. But a report of aggregations of gulls feeding on dead mice along the banks of the Rio Peulla (Ruiz and Simeone, 2001) suggests that this phenomenon did occur in some areas. The absence or reduction of drownings during quila ratadas might be related to the water temperatures when the populations peak and start to decline; water temperatures at the time of the autumn peak of *quila*-ratadas would not be as cold as when *culeou*-ratadas reach their peak later in the winter and so most of the Chilean mice might not be overcome by hypothermia and survive their swim after entering the water.

Neither Murúa et al. (1996) nor Gallardo and Mercado (1999) mentioned the presence of *R. rattus* in the Chilean outbreaks, although the species has been reported from natural habitats in central Chile (Simonetti, 1983). The absence of this species would be another difference between *quila*- and *culeou*-ratadas. Gunckel (1948) quoted a report on a 1780 ratada in Valdivia, Chile, in which Ambrosio Higgins referred to drowned animals as "pericotes," which in Argentina is a vernacular name for *R. rattus*. Unfortunately there is no verification that he was using this vernacular name in the same way, rather than in reference to rodents of another species. Higgins also wrote of the flowering of "colihue" bamboo, and this raises the possibility that the "pericote" drownings he mentioned really involved *R. rattus* following the flowering of *C. culeou* rather than *C. quila*.

Predicting Ratadas in the Valdivian Forests. A recent review of rodent outbreaks in South America (Jaksic and Lima, 2003) presents a confusing picture of the frequency and distribution of bamboo ratadas in the Valdivian forest ecosystem. There are 2 reasons for this confusion. The first is that there is a poor understanding of the flowering biology of species of *Chusquea*, in spite of its distribution and importance (Judziewicz et al., 1999). Second, there have been only 2 studies of flowerings and subsequent ratadas with sufficient information about the species of bamboo and the time and place of flowering to be helpful (Murúa et al., 1996; Gallardo and Mercado, 1999). The paucity of information on the reproductive biology of *Chusquea* species is understandable in light of the decadal-long vegetative phase of the life cycle of these bamboos. Many reports of flowerings and of subsequent ratadas have been anecdotal remarks by visiting chroniclers, or a local event sufficiently noteworthy to be reported in a newspaper. Bamboos of different species have different generation times, and even within recognized species, local populations may flower in different years (Janzen, 1976). From the phenology of the flowering and seeding patterns of the Chilean and Argentine *Chusquea* we know that there are differences among species in seed dehiscence, and this has important consequences on the timing of subsequent rodent outbreaks. Recognition of this difference in seeding strategy between these 2 bamboo species clarifies why the lag between flowering and ratadas ranges from 1 to 2 years. Since the seed-holding strategies are still only known for 2 of the 12 species of *Chusquea* in the Valdivian forest (Judziewicz et al., 1999), we lack critical pieces of knowledge needed to predict the time when a ratada will occur after a particular species flowers.

Another aspect of the life histories of the Valdivian chusqueas that complicates the development of a predictive model of ratadas is lack of synchrony in flowering within the same nominal "species." Cohorts of *C. quila* flowered in different places in Chile over a 3-year period in the 1990s (Gallardo and Mercado, 1999; Jaksic and Lima, 2003). Each of these year cohorts occupied a relatively large geographical area, and a ratada developed 2 years after each cohort flowered. A similar pattern of spatially asynchronous flowering over large ranges apparently exists within *C. culeou*, as the cohort that flowered in 2000 covered about one-fifth of the 550 km long, total distribution of this species in Argentina. Even within the same area there can be cohorts that flower on different cycles. Within our study area there are 2 morphotypes of *C. culeou*. The tall (approximately 4 m high) plants flowered in 2000, while the partially sympatric shorter (2-3 m height) plants have remained green. Presumably these year- and morphological-cohorts will flower at different times and produce ratadas in different areas, but as yet we are ignorant about these temporal and geographic sequences. In Chile there may be more than one species of bamboo growing at the same locality, each on a different flowering regime. This sympatry further complicates the timing of local rodent outbreaks. The significance of this taxonomic, temporal, and geographical variability among bamboos has not been appreciated for its importance to the timing and location of ratadas. A consequence of this variability in the life cycles of the many species and populations of bamboos is that flowering and the associated rodent outbreaks may appear to be haphazard across the full range of *Chusquea*, even though this is not the case. Much more careful study of the reproductive biology of the Chilean and Argentinean chusqueas is needed before we can have a predictive science of bamboo-associated outbreaks throughout the Valdivian forest ecosystem. The current lack of predictability has important consequences for a wide range of human activities, including public health campaigns (i.e. planning for possible outbreaks of rodent-associated diseases), negative effects on tourism, and opportunities by biologists to plan studies of these uncommon events.

SUMMARY AND CONCLUSIONS

Beyond their impacts on public health and the tourism industry, how do bamboo ratadas fit into our understanding of what regulates population size in rodents? Two environmental factors (food and predation) had major impacts in *Ratada-2001*, but at different times during the outbreak. The superabundance of seed in Summer-1 and Autumn-1 certainly was the most important environmental factor promoting the increase phase that led to the high densities achieved by *Oligoryzomys*, *A. longipilis*, and *R. rattus*. The extended individual reproductive performances and/or precocial breeding of females directly caused the population densities to reach high levels. Superabundant food may also have caused a marked increase in the numbers of *L. micropus* and *I. tarsalis*, if their presence among the drowned mice in Spring-2 indicates high density and not a pathological behavior. Because there were still bamboo seeds on the ground and mice were still fat in Spring-2 while mice were dying in the lakes, we doubt that a shortage of food was an important factor causing the decline phase. Predation probably was unimportant in limiting or stopping the increase phase in

Summer-1 and Autumn-1, but may have played a major role during the decline and crash phases from Winter-1 to Autumn-2. The increased numbers of predatory birds and mammals from Winter-1 into Summer-2 probably lowered the survival chances of each individual mouse. We don't know how important this factor is, however, compared to the mortality that resulted from individuals drowning in the lakes, and we lack an explanation for the drownings. If the drownings are an incidental consequence of a dispersal 'drive', then this individual performance factor may have played a major direct role in causing population densities to decline in Spring-2 and Summer-2. We do know from the observations made by the park rangers that mice were crossing the roads and entering houses at the time that they began drowning in the lakes, but it remains to be shown that the mice that drowned were dispersing and not in the water because of a pathological condition that might be associated with their obesity and/or repressed reproductive condition. In this ratada the environmental factors of weather and habitat probably had much smaller impacts than food and predation on determining the maximal and minimal sizes of the populations.

Although another bamboo-induced ratada caused by the flowering of *C. culeou* is unlikely to happen in this particular part of the Valdivian woods during the next 60 years, we think it would be a mistake to dismiss these outbreaks as merely idiosyncratic and without instructive value. The kind of outbreak described here is infrequent within our temporal reference frame, but they are of regular occurrence. Since the Holocene began, 12,000 years ago, it is highly likely that there may have been as many as 200 or more such flowerings and associated ratadas in our study area; we know that a bamboo-induced ratada happens about every 12 to 14 years somewhere within the Valdivian forest ecosystem (Jaksic and Lima, 2003). If other cohorts of *C. culeou* each occupy similar percentages (one-fifth) of the total range of this species in Argentina as the one that flowered in 2000, then there may be as many as 4 more flowerings of the tall morphotype in the near future. Such flowerings represent what Diamond (1986) called 'natural perturbation experiments,' where an *ad libitum* amount of food is added to the environment over a large area. From this perspective, each of the future bamboo flowerings offer ecologists a natural experimental system in which to test ideas concerning (1) What limits populations?; (2) What prevents further population growth?; and (3) What limits density in habitats of different quality? These are the questions that Krebs (2002) considers most important for understanding the general process of population regulation and limitation.

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APPENDIX TABLE 1

Weighted mean success (percent) with live (L) or snap (S) traps on the ground, Neuquén Province, Argentina. Number of mice captured and the number of traps set in a trapline during each night of a collecting period are shown within parentheses. No traps were set at some localities during different collecting periods. We did not correct our results for traps that were closed or sprung and empty.

	Flowered bamboo habitats					Green bamboo habitats	
Collecting period	Laguna Verde	Currhué Chico	Hua Hum	Yuco	Traful North	Traful South-1	Traful South-2
Spring-1	L = 5% (2/40) S = 2% (1/40)	L = 28% (11/40) S= 25% (10/40)	L = 6% (4/50, 2/50) S = 3% (3/50, 0/50)	L = 7% (3/45) S = 7% (3/45)	--	--	--
Autumn-1	--	L = 62% (27/45, 4/5) S = 74% (36/45, 1/5)	L = 18% (9/50) S = 56% (28/50)	L = 45% (18/40) S = 49% (19/39)	--	--	--
Spring-2	--	L=43% (9/16, 4/9, 5/14, 3/10) S = 54% (10/16, 4/11, 5/8)	L = 54% (15/20, 7/20, 5/10) S = 64% (13/21, 14/21, 14/21, 6/10)	--	L = 36% (5/14, 4/7, 3/12) S = 73% (7/8, 4/7, 5/7)	L = 18% (2/14, 2/12, 1/12, 4/12) S = 36% (2/8, 4/6, 2/7, 2/7)	L = 29% (6/14, 4/14, 2/14) S = 42% (4/8, 4/8, 2/8)

Appendix Table 1 (continued)							
Autumn-2	--	L = 10% (3/40, 3/40, 6/41)	L = 7% (2/14, 1/36, 5/59)	L = 10% (6/40, 0/20)	L = 19% (7/21, 5/41)	L = 27% (6/20, 6/25)	L = 41% (9/20, 10/26)
Autumn-3	--	L = 33% (7/29, 9/20) S = 50% (3/6)	L = 8% (2/12, 1/20, 0/7) S = 82% (6/6, 5/6, 3/5)	L = 29% (9/20, 4/15) S=100% (6/6, 6/6)	L = 29% (6/19, 5/20, 3/12) S = 78% (5/6, 9/12)	L = 3% (1/13, 0/20) S = 64% (3/5, 4/6)	L = 12% (2/20, 3/20) S = 58% (5/9, 6/10)

APPENDIX TABLE 2

Total number of individuals and numbers and sex of 8 species of rodents collected during 5 periods in Neuquén Province, Argentina. The general name of each site is as given in Table 1. The sample size in each collecting period is shown inside parentheses and separated from one another with a slash (/) mark, i.e. (Spring-1/Autumn-1/Spring-2/Autumn-2/ Autumn-3). A dash (-) for the Spring-2 period at Yuco indicates that no trapping was done then. Collections were made only once at Laguna Verde (Spring-1) and Lago Nonthué (Spring-2). At Traful North, Traful South-1, and Traful South-2 collections were made in Spring-2, Autumn-2, and Autumn-3, and the information shown is for these 3 periods.

Species	Sex	Laguna Verde	Currhué Chico	Hua Hum	Lago Nonthué	Yuco	Traful North	Traful South-1	Traful South-2
Oligoryzomys longicaudatus (313)	f	0	49 (11/15/14/7/2)	34 (2/12/16/2/2)	20	8 (2/1/-/1/4)	9 (5/1/3)	4 (3/0/1)	6 (3/3/0)
	m	1	65 (8/31/16/5/5)	50 (4/9/24/3/10)	23	9 (1/1/-/1/6)	9 (6/1/2)	13 (8/2/3)	13 (7/4/2)
Abrothrix longipilis (217)	f	2	24 (1/13/3/0/7)	36 (1/19/15/0/1)	1	17 (1/16/-/0/0)	5 (2/0/3)	12 (3/7/2)	6 (1/3/2)
	m	0	18 (0/8/2/2/6)	27 (1/10/13/0/3)	0	18 (3/15/-/0/0)	26 (6/5/15)	9 (4/1/4)	16 (5/6/5)
Abrothrix olivaceus (101)	f	0	22 (0/12/5/0/5)	5 (0/1/0/0/4)	1	4 (0/0/-/0/4)	8 (4/2/2)	4 (1/3/0)	2 (1/0/1)
	m	0	13 (0/8/4/0/1)	13 (1/8/1/0/3)	3	11 (0/0/-/0/11)	9 (4/1/4)	1 (1/0/0)	5 (1/2/2)

Appendix Table 2 (continued).

Loxodontomys micropus (67)	f	0	5 (1/4/0/0/0)	2 (0/1/1/0/0)	18	0	0	1 (1/0/0)	3 (1/0/2)
	m	0	1 (0/0/1/0/0)	2 (0/0/2/0/0)	32	0	1 (1/0/0)	1 (0/1/0)	1 (0/1/0)
Rattus rattus (24)	f	0	1 (0/0/0/1/0)	2 (0/0/0/2/0)	7	2 (0/0/-/2/0)	0	0	0
	m	0	1 (0/1/0/0/0)	4 (0/0/0/4/0)	5	2 (0/0/-/2/0)	0	0	0
Irenomys tarsalis (12)	f	0	0	0	5	0	1 (0/0/1)	1 (0/0/1)	0
	m	0	1 (0/0/0/0/1)	2 (1/1/0/0)	2	0	0	0	0
Geoxus valdivianus (9)	f	0	1 (0/1/0/0/0)	1 (0/0/0/0/1)	0	1 (0/1/-/0/0)	2 (0/0/2)	0	0
	m		1 (0/0/0/0/1)	2 (0/0/1/0/1)	0	0	0	1 (0/1/0)	0
Chelemys macronyx (7)	m	0	0	1 (0/0/0/1/0)	0	0	1 (0/0/1)	2 (0/2/0)	3 (1/0/2)
Locality totals:		3	202	181	117	72	71	49	55

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