

MAST SEEDING OF BAMBOO SHRUBS AND MOUSE OUTBREAKS IN SOUTHERN CHILE

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ABSTRACT. Mast seeding is a massive reproductive output and subsequent death of long-lived plants. This multiannual phenomenon, affecting the bamboo shrub *Chusquea valdiviensis* started in the spring 1990 and covered 1,200,000 hectares in Southern Chile. Due to seed surplus and ideal nesting sites, mast seeding of bamboo has been associated historically with mouse outbreaks followed by invasion of homes and subsequent calamities of different sort. Here, we report the most recent explosive population growth of the granivorous rice rat, *Oligoryzomys longicaudatus* following a mast seeding episode. The food resource hypothesis predicting an increase in body weight of outbreak mouse is partially supported by the data. The explosive population growth experienced by the natural hantavirus reservoir and invasion of human settlements drastically increased the chances for rodent-to-rodent infection, and probably its bearing on the subsequent emergence of the hantaviral disease in humans.

RESUMEN. Fructificación masiva del bambú y ratadas en el sur de Chile. La semillación masiva corresponde al potencial reproductivo y muerte ulterior de plantas de larga vida. Este fenómeno multianual que afectó a la bambusácea *Chusquea valdiviensis*, comenzó en la primavera de 1990 y cubrió 1.200.000 hectáreas del sur de Chile. Debido a la sobreproducción de semillas y sitios de anidamiento, la semillación masiva se ha asociado históricamente con "ratadas", seguidas de invasión a las viviendas y calamidades posteriores de distinto tipo. Aquí reportamos el crecimiento poblacional explosivo más reciente que afectó a *Oligoryzomys longicaudatus* luego de un evento de semillación masiva. La hipótesis de recursos alimentarios que predice un aumento del peso corporal es parcialmente apoyada por los datos. Este crecimiento poblacional explosivo experimentado por el reservorio natural del hantavirus y su invasión a los asentamientos humanos aumentó drásticamente la posibilidad de infección entre roedores, y probablemente, la incidencia en la emergencia posterior de la enfermedad hantaviral en humanos.

Key words: mast seeding, mouse outbreak, *Oligoryzomys longicaudatus*, *Chusquea valdiviensis*.

Palabras clave: fructificación masiva, ratadas, *Oligoryzomys longicaudatus*, *Chusquea valdiviensis*.

INTRODUCTION

Mast seeding is a supra-annual flowering phenomenon referring to the synchronized and intermittent production of large seed crops by long-lived plants (Kelly, 1994). Several bamboo species genus *Chusquea* occurring in the temperate rainforests of Southern Chile undergo fruiting episodes that extend from 15 to

40 years (Pereira, 1941; Parodi, 1945; Gunckel, 1948; Seifriz, 1950; Muñoz, 1980). Although different adaptive interpretations have been advanced, the causal explanation for those cycles and the factors governing the length of the intermast period are unknown (Janzen, 1976; Waller, 1993; Pearson et al., 1994).

The most recent massive blooming of *Chusquea valdiviensis* started in pre-Andean

areas of the Osorno Province, in 1990 (Pacheco, 1993; Schlegel, 1993). Two years later, 1.2 million hectares of dried bamboo were estimated to have bloomed massively in five provinces having 7.3 million hectares of total surface (Acción Ganadera, 1994). Semelpary of *Chusquea* shrubs is associated with the regeneration of the southern beech forests (*Nothofagus spp.*, Veblen et al., 1979; Veblen et al., 1983) since the thickets of bamboo plants interfere with seedling establishment and germination of beech trees due to a shading effect (Veblen, 1982).

The enormous nutritional input of *Ch. valdiviensis* seeds is reflected by an estimate of 51 million seeds per hectare (Murúa et al., 1996). Extra food has an immediate effect on population densities of native rodents (Gilbert and Krebs, 1981; Wolf, 1996), and poses a causal relationship between the cycles of bamboo blooming and mouse outbreaks ("ratadas" sensu Hershkovitz, 1962). After the population peak, exposure, hunger, and intraspecific competition produce a precipitous drop in the rodent populations (Hershkovitz, 1962).

Massive invasion into homes by rice rats (*Oligoryzomys longicaudatus*) has been recognized since 1552 as reported by the Spanish conquerors (De Vivar, 1987) and it is usually associated with famine, calamities, diseases, and bad luck (Philippi, 1879; Pereira, 1941; Gunckel, 1948;). The apparent causal relationship between mast seeding and diseases is the logical derivation of the fact that whenever densities of native rodents increase abnormally, increased risks of human infection are expected due to a larger natural reservoir (Schrag and Wiener, 1995). Due to the lack of direct observations relating an outbreak of mice to an episode of mast seeding, preliminary field observations affecting rice rats *O. longicaudatus* (= colilargo) and *Abrothrix olivaceus* are presented. Since a causal relation between the seed surplus and changes in rodent population density has long been suggested, the hypothesis that body weight of rice rats increases with seed surplus is also tested.

MATERIALS AND METHODS

Estimates of the natural populations being sampled is based on the trapping success of 80 oat-baited, medium sized Sherman traps, and includes data from the following locations (**Fig. 1**): Valdivia Province (San Martín Reserve: 39°31'S, 72°58'W), Osorno Province (Puyehue National Park: 40°42'S, 72°18'W), Chiloé Province, (Queilen: 42°54'S, 73°30'W, Yaldad: 43°07'S, 73°43'W) and Palena Province (Puerto Cárdenas: 43°11'S, 72°26'W; Puerto Ramírez: 43°25'S, 72°13'W). The reproductive condition of outbreak mouse was used to estimate the ecological age of 141 animals trapped in Queilen, Yaldad and P. Cárdenas (adult males: scrotal testis over eight mm long; adult females: vascularized uterus, perforated vagina, or lactogenic nipples).

To test the food resource hypothesis, a single regression of the total body length versus the weight (with and without pooling by sex), was performed for each locality. To minimize deviations in body weight, tested and control animals were selected from the same season and local area. The homogeneity of regressions per sample was tested by a one-tailed ANCOVA. This test allows to compare the variation between the regression coefficient of the sample and each individual observation. Consequently, different F- values were obtained according to the variable sample size of each comparison. Statistical analyses were done by use of SPSS/pc+ 5.0 (Norusis, 1992).

Estimates of age distribution in the outbreak samples (Queilen, P. Cárdenas) were obtained in 1994. The Yaldad control data is based on previous, same-season records as of the outbreak sample. In order to avoid the interference of prevailing seed surplus over the predictive value of body weight, total body length was used to estimate age distribution.

RESULTS

Field observations and personal records indicate that the latest massive and latitudinally widespread flowering cycle of *Ch. valdiviensis* started in the austral spring-summer (1990-1991), in the Puyehue and Vicente Pérez Rosales National Parks, Osorno province (Pacheco, 1993; Schlegel, 1993). Massive flowering was observed in the coastal range from Valdivia to Llanquihue provinces in the spring-summer of 1991-1992. The same effect was observed in Palena Province, and in the northern half of the Chiloé island (up to the Compu stream,

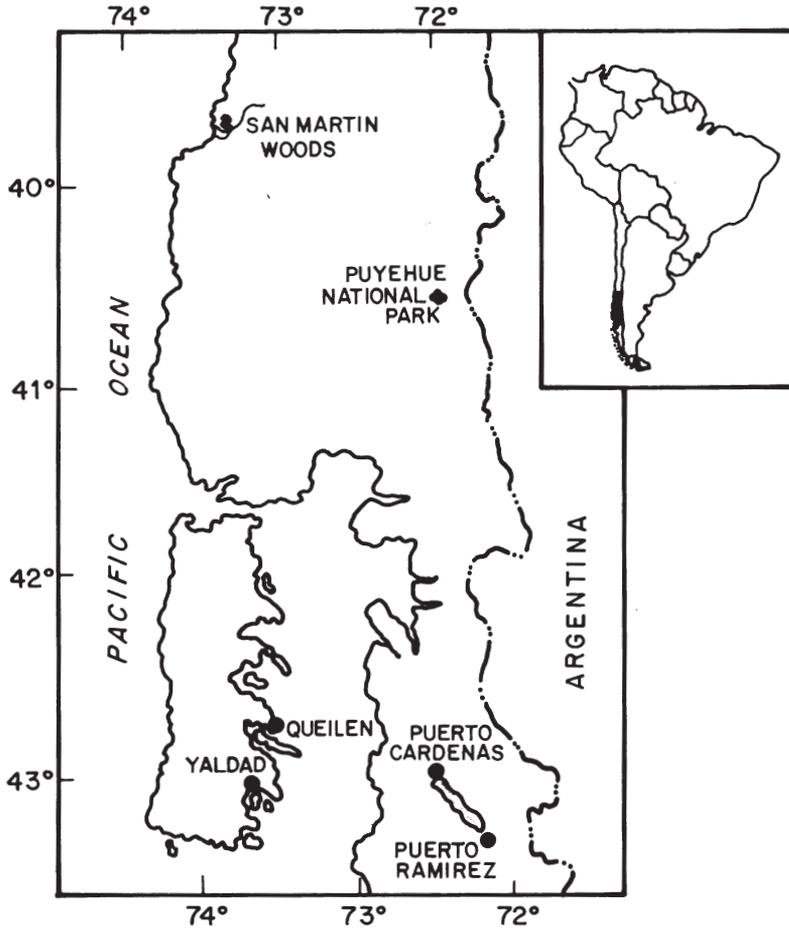


Fig. 1. Localities affected by mouse outbreaks occurred in Southern Chile after mast seeding of bamboo plants (genus *Chusquea*). See text for details.

approximately). Massive flowering of bamboos from the southern part of Chiloé Island took place in the spring-summer of 1992-1993.

One year after the mast seeding in Puyehue National Park, a four-day field-trip (November, 1992) was conducted to estimate rodents density. Only one *Abrothrix olivaceus* (1.3% trap success) and one *A. longipilis* (1.3%) were trapped around a thick clump of dried bamboo, during the first night. No animals were collected in the second night, and only three *A. olivaceus* (3.6%) were collected in the third night. No *O. longicaudatus* were collected in the area.

Two years after the massive flowering of

Ch. valdiviensis in Puyehue, an outbreak of mice was reported as occurring in the Puyehue National Park (May-July, 1993). The number of rice rats had increased steadily during the summer, and later on irrupted into the visitor's center and park houses. Another outbreak consisting mainly of *O. longicaudatus* was reported from Anticura, at the southeastern side of the Puyehue National Park, during 1994 (N. Pacheco, personal communication).

Two mouse outbreaks were also reported from the southern half of Chiloé island, during May-June, 1995. One month after the outburst consisting mainly of rice rats, an 80% trap success was obtained in Queilen (25 males,

39 females). All female rice rats had filiform uteri and all males had abdominal testes of 2x1 mm. Cannibalism was common since animals trapped with Museum Special traps were almost totally eaten by the next morning.

A similar situation was observed in Yaldad, where trapping success was 86% four weeks after the outburst. Forty-five *O. longicaudatus* (25 males, 20 females) and 23 *A. olivaceus* (13 males, 10 females) were collected in one night (**Table 1**). All females had filiform uterus and males had abdominal testes of 2.7x1.7 mm. Most mice trapped with snap traps were eaten by the next morning. Cannibalism also resulted if two *A. olivaceus* were caged together. Since the mouse outbreak in Puyehue and San Martín took place during 1993, the trap success observed during 1994 corresponds to a post outbreak effect (**Table 1**).

The effect of seed surplus on the weight of *O. longicaudatus* was corroborated by the significant differences ($P < 0.05$) of the covariance of the slopes (**Table 2**). Thus, average weights of the Yaldad and P. Cárdenas samples differed significantly from the Yaldad control when both sexes were pooled together. Nevertheless, no difference in body weight was detected when the outbreak and the control samples were segregated by sex (**Table 2**).

Body length variation in outbreak mice exhibited a typical normal distribution that made possible the recognition of three different size groups in Queilen and P. Cárdenas (**Fig. 2**). Considering the small-sized testes on males, and the filiform uterus in females, these categories corresponded approximately to juveniles, medium- and large-sized young adults.

DISCUSSION

O. longicaudatus is an ecologically and geographically widely distributed granivorous species occupying habitats as diverse as mesic grasslands, streams, rainforests and Patagonian steppes (Gallardo and Palma, 1990). Since unusual climatic events generally predict abundance of nutrients, extrinsic factors have been responsible for mouse outbreaks of *Phyllotis darwini* (Pearson, 1975), *Abrothrix olivaceus*, *Thylamys elegans* (Jimenez et al., 1992) and

O. longicaudatus (Péfaur et al., 1979) in Northcentral Chile. Since populational fluctuations of *O. longicaudatus* are related to seed availability (Murúa et al., 1986; 1996), mast seeding of *Chusquea* in Valdivia provided abundant food resources for the rice rats to respond to.

Our estimates based on trap success of 80 Sherman traps averaged across this species during winters prior to the outbreak have been 9% in Southern Chile (unpublished data). These figures rose to 80% in Queilen, 86% in Yaldad, and 125% in P. Cárdenas after the outbreak (**Table 1**). Similarly, the average 8.7% trap success for *O. longicaudatus* in previous years rose to 80% in Queilen, 56.4% in Yaldad, and 96.3% in P. Cárdenas during the outbreaks (**Table 1**).

A. olivaceus is one of the most ubiquitous rodents in southern Chile, although not the most abundant one as estimated by its average trap success during fall-winter (5.7%). The species' absence in the outbreak sample from Queilen, its 14% trap success from P. Cárdenas, and its 29% trap success from the Yaldad sample suggest the species' high variance in response to food supply. Since *A. olivaceus* shares low demographic values with *O. longicaudatus* during summer, its lack of response to seed surplus in Queilen may be attributed to its lesser granivorous preference, although the effect of intrinsic population parameters cannot be ruled out. It is noteworthy that other sympatric, herbivorous rodents found in the temperate forests (i.e., *Abrothrix longipilis*, *A. sanborni*, and *Loxodontomys micropus*) were not trapped in localities undergoing outbreaks of mice, thus suggesting a more genetically constrained than environmentally-induced reproductive biology.

A large variance between two successive masting episodes, spanning from 15 to 40 years is reported in the literature (Gunckel, 1948). This imprecision stems partially from the fact that "quila" is the common name given by non-native laymen to all *Chusquea* species, whereas "quila", "taihuén", "tihuén", and "colihue" are common names given by native countrymen to mainly sympatric *Ch. valdiviensis*, *Ch. uliginosa*, *Ch. montana*, and

Ch. culeou, respectively. Thus, the preceding mast seeding episode that occurred in Puyehue during 1962 did not affect *Ch. valdiviensis* (“quila”) but *Ch. uliginosa* (“taihuén”), whereas the 1990 phenomenon did (Pacheco, 1993).

Several studies have found a direct and complex response of small mammals to food resources (Wolf, 1996; Selás, 1997). This pleio-

tropic response affects population density parameters, reproduction rate and length, migration patterns, and behavior. Thus, the addition of extra food has resulted in a two- to three-fold increase in the population density of rodents (Gilbert and Krebs, 1981; Taitt, 1981; Taitt and Krebs, 1981). Supplemental feeding has been demonstrated to significantly increase

Table 1. Estimates of trap success (in percent) before and during the mouse outbreak in Yaldad. Pre and post outbreak data from Puyehue and San Martín are given as a reference.

	YALDAD			PUYEHUE			SAN MARTÍN		
	1984	1994	1995	1984	1994	1995	1984	1994	1995
<i>O. longicaudatus</i>	6.3	6.2	56.4	10.0	16.3	10.0	7.5	13.8	10.0
<i>A. olivaceus</i>	7.5	12.4	29.1	3.7	6.3	1.3	8.8	6.3	1.3
TOTAL	13.8	18.6	85.5	13.7	22.6	11.3	16.3	20.1	11.3

Table 2. Output of the regressed values of body weight and total length of control *Oligoryzomys longicaudatus* (Yaldad) and outbreak mice from Yaldad and P. Cárdenas.

		r	b	d.f.	F
YALDAD	♂ ♀	0.8696	0.3982	1 38	9.38*
	♀	0.8677	0.2936	1 17	4.47
	♂	0.8726	0.4781	1 17	2.51
PUERTO CÁRDENAS	♂ ♀	0.6897	0.2867	1 84	12.28*
	♀	0.7046	0.2114	1 42	2.27
	♂	0.7246	0.3415	1 38	0.16

*P<0.05; r = regression coefficient; b = slope; d.f. = degree of freedom

CONTROL YALDAD

$$\text{♂ ♀ } y = -19.0724 + (0.1901 \times X)$$

$$\text{♀ } y = -1.0980 + (0.1118 \times X)$$

$$\text{♂ } y = -43.1402 + (0.3020 \times X)$$

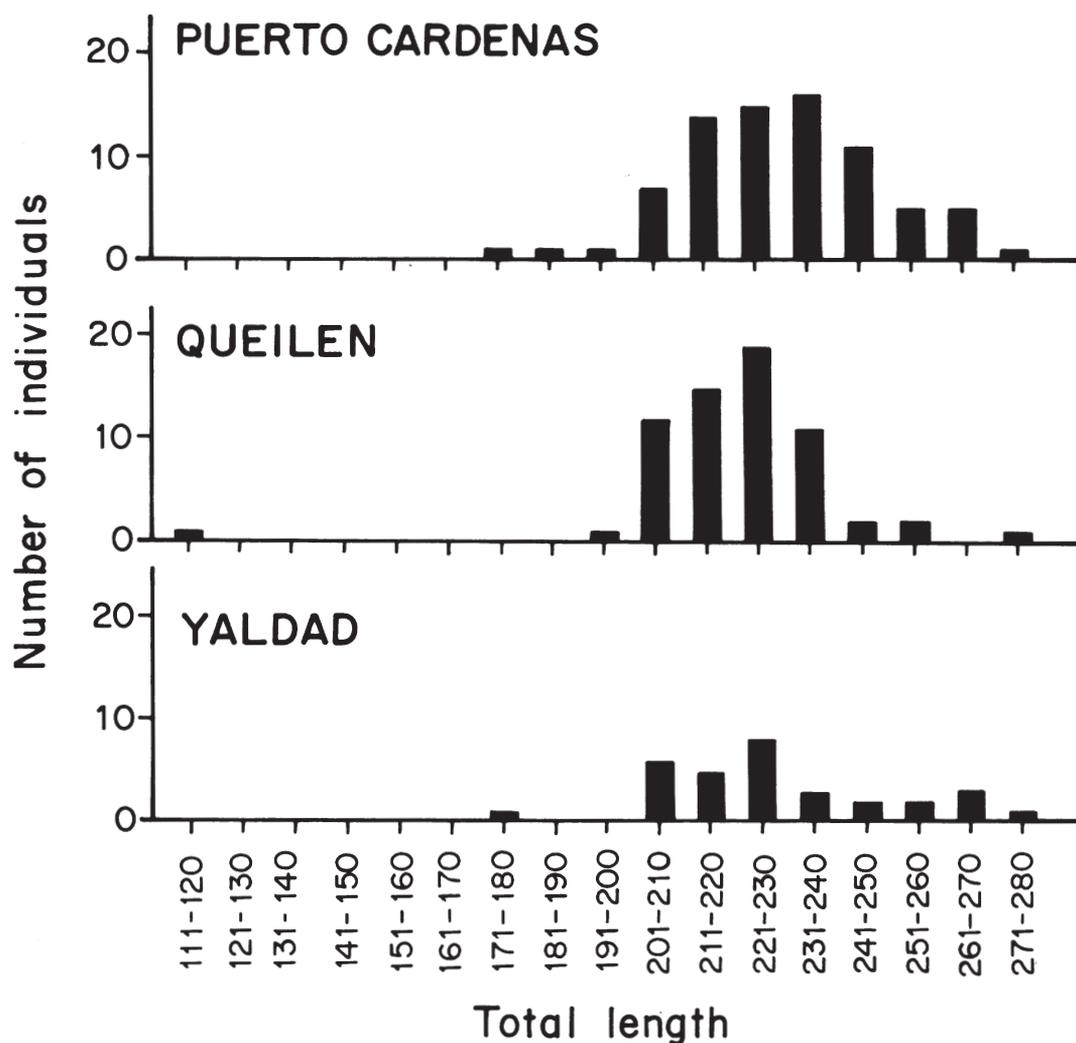


Fig. 2. Normal distribution of total length and number of *Oligoryzomys longicaudatus* collected during the outbreak of mice occurred in P. Cárdenas, Yaldad and Queilen.

both population size due to early juvenile survival, and migration patterns to areas with extra food (Gilbert and Krebs, 1981). Similarly, long term studies have also demonstrated that during years of high production of mast, several mice species bred all winter, which results in high densities the following summer (Wolf, 1996). Nevertheless, survival of adult rodents as well as body weight may not be affected by feeding (Gilbert and Krebs, 1981). Apparently, the annual or supraannual fluctuation in numbers of rodents are a consequence of seasonal

reproductive behavior, which, limited by food availability, constitutes a major factor producing a local increase in population density (Taitt, 1981).

Although seed surplus produced concomitant demographic effects in *O. longicaudatus*, a two-year delay in mouse response to the flowering episode has been reported also from the coastal Valdivian rainforest (Murúa et al., 1996). Apparently this delay is due to the permanence of bamboo seeds within the spikelets, and their release to the ground one year

after ripening (personal observations). This course of events probably explains the lack of response obtained in Puyehue, one year after flowering, whereas it confirms the two-year delay of outbreak mice in Queilen and Yaldad.

As predicted by the food resource hypothesis, significantly heavier body weights were confirmed in the outbreak samples of Yaldad and P. Cárdenas (**Table 2**). Reduced sample size in sexually dimorphic rice rats (Gallardo and Palma, 1990) probably accounts for some of the non-significant difference observed (data not shown).

Three different size groups composed the outbreak sample of P. Cárdenas (**Fig. 2**). Remarkably enough, no evidence of pregnancy and no reproductively active males were collected in any sample. Since no fully adult animals were present according to their reproductive condition, no overwinter survivors but only medium- and large-sized juveniles apparently formed the outbreak samples.

The effects of an impressive mouse outbreak were observed by the senior author in Puerto Cárdenas (15-18 June, 1994). This catastrophic phenomenon was reported by the local newspaper as simultaneously taking place in P. Ramírez, across Yelcho Lake (**Fig. 1**). The outbreak in P. Cárdenas consisted mainly of *O. longicaudatus*, although *A. olivaceus* was also trapped. Thousands of wandering rice rats coming from the woods suddenly irrupted into the police station and concentrated in an outbuilding used for animal food storage. The local residents were forced to leave the area.

Repeated nesting of rice rats on the back of resting sheep as well as biting and chewing of the sheep's dorsal wool and fat was also reported to the police as occurring in El Correntoso farm, across the lake. While leaving the area, 15 barn owls (*Tyto alba*) were counted along the road in the first 3 km NE of P. Ramírez. Not a single raptor was observed in the next 70 km to our field station.

A trap design orally passed through generations, was the most efficient device for intensive trapping in P. Cárdenas. It consisted of a 200 lt open metal barrel filled with 30 cm of water, and accessed by 2-3 boards connected to the barrel top. A pivotal, round stick having

a grease-baited tin lid nailed mid-way to the edges, crossed the open top of the barrel. Animals accessing the barrel managed to walk to the baited lid and stepped on it. The device flipped over and the rodents fell into the barrel. The lid-bearing stick returned to its resting position, and could be triggered again. According to their records, police officers collected 2,000-2,500 mice per night in four barrel-traps set around the police station. They estimate to have trapped 9,500-12,000 rice rats during the first week after the irruption.

Two weeks after the irruption of mice in P. Cardenas, 100 animals (125%) were trapped in one night, using 80 Sherman traps. The sample consisted of 94 *O. longicaudatus* (46 males, 48 females), 4 *A. olivaceus* (2 males, 2 females), and 2 male *A. longipilis*. All female rice rats had filiform uteri whereas males had small, non-scrotal testes averaging 3x2 mm. Male *A. olivaceus* had testes averaging 3x2 mm, and females had filiform uteri. No intergeneric cannibalism was noticed by the next morning although cannibalism occurred in all traps containing two *O. longicaudatus*. Most mice collected with Museum Special traps were partially eaten by the next morning.

In the past 15 years, a number of seemingly emerging diseases have posed serious threats to human health. By triggering explosive population growth, changes in weather conditions or in hosts have contributed to the emergence of rodent-borne diseases (Hjelle et al., 1995; Schrag and Wiener, 1995; Song et al., 1996; Wells et al., 1997). For example, the recognition of a previously unknown hantaviral disease as the cause of the pulmonary syndrome (Andes virus-HPS) is an example of virus emergence in Patagonian Argentina and Southern Chile (Levis et al., 1997; Schmaljohn and Hjelle, 1997). The principal rodent reservoir for the Andes hantaviral outbreaks of 1994 and 1996 is *O. longicaudatus* although other oryzomine rodents (i.e., *O. microtis*, *O. palustris*) harbor specific hantavirus (Bharadwaj et al., 1997; Torres-Martínez et al., 1998). Hantavirus infection is apparently not deleterious to its rodent reservoir host, but produces a lifetime infection (Schmaljohn and Hjelle, 1997). Al-

though the aerosol route of infection is the most common means of transmission among rodents and to humans, age-dependent horizontal transmission among mice results from cannibalism, bites, or direct contact among cage-mates (Mills et al., 1996; Schmaljohn and Hjelle, 1997).

The recent mast seeding episode and subsequent seed surplus triggered an explosive population growth of granivorous *O. longicaudatus* in Southern Chile. Thus, by favoring of the natural hantavirus reservoir, the chances for rodent-to-rodent infection increased drastically with a larger reservoir (Schmaljohn and Hjelle, 1997). Undoubtedly, vicious competition, cannibalism and crowding after invasion of homes have contributed also to the spreading of the disease. Although person-to-person transmission for developing hantavirus diseases has been reported (Wells et al., 1997), exposure to aerosols of rodent fecal pellets is considered to be the most important risk factor and seems an unavoidable aspect of the pastoral way of life in rural areas of Southern Chile and Argentina (Clement et al., 1997).

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