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Myths and facts on ratadas: Bamboo blooms, rainfall peaks and rodent outbreaks in South America

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Abstract 'Ratadas' are rodent irruptions or outbreaks that have been recorded in South America since the Spanish conquest in the 16th century. The notion that ratadas are associated with bamboo flowering and subsequent mast seeding at cycles of 30 years has appeared in the literature since the late 1800s. Based on 63 well-documented cases, we show that not only are ratadas associated with bamboo blooming, but also many are associated with rainfall peaks, and that these two outbreak types are geographically interspersed over South America. In addition, we dispel the notion that South American bamboo blooms occur every 30 years, which may only be the case for *Merostachys fistulosa.* For other species the modal cycles occur every 14 (*Merostachys* spp.), 12 (*Chusquea quila* and/or *valdiviensis*) or 14 years (*Chusquea coleou*). We also propose the hypothesis that rainfall-associated ratadas are ultimately caused by the occurrence of El Niño, and discuss the possible population dynamic mechanisms underlying rodent outbreaks in South America. Aiming at setting a standardized framework for spatial and temporal comparisons, we propose a trapping protocol and a threshold density for assigning the 'ratada' label. Several of the mice implicated in ratadas are reservoirs of emerging diseases, thus emphasizing the need for predictive power to forecast disease epidemics that affect human populations. Further, ratadas may be viewed as pulsed resources, thus enabling us to learn more of the ways communities respond to such intermittent inputs.

Key words: Argentina, Bolivia, Brazil, Chile, El Niño, emerging diseases, mast seeding, mouse irruptions, Paraguay, Peru, rainfall, Uruguay.

INTRODUCTION

As early as 1552, chroniclers noted massive rodent irruptions or outbreaks in several parts of South America (de Vivar 1987) and called them 'ratadas' (*rata* = rat) in both Portuguese and Spanish (Pereira 1941; Miller & Rottmann 1976). Although no attempt was made to investigate the natural causes of these outbreaks, naturalists detected that massive flowering and subsequent mast seeding of bamboos in Brazil and Chile preceded several rodent irruptions. Based on the ideas of Derby (1879) and Philippi (1879), it then became customary to associate rodent outbreaks with bamboo blooming (Hershkovitz 1962; Mann 1978; Campos 1986). This happened despite the meagre evidence presented in the much-cited paper by Pereira (1941) on his research in Brazil: 'About 32 years is the period between the "ratadas" which depend upon the vegetative cycle of 'taquara-lixa', *Merostachys fistulosa* Doell. . .'. Scholars who did not read beyond the English abstract of this paper assumed that both bamboo blooming and rodent outbreaks occurred at a 30-year period. But what Pereira (1941) described in his native Portuguese was that bamboo blooming, in the case of 'taquara lisa' *Merostachys* sp., occurred at periods of 11–13 years (based on only three data points: 1914, 1927 and 1938). Later in his paper, Pereira (1941) estimated that blooms of that species occurred at periods of 7–13 years (by adding an earlier series of data points: 1863–1876–1883). For 'taquara lixa' *M. fistulosa*, Pereira (1941) had only two data points, 1909 and 1938–1940 (30-year period), but he assumed that this same species was behind the ratadas of 1843, 1876–1877 and 1909–1910. Indeed, he went on to state that ratadas occurred at intervals of 25–33 years (based on only five data points: 1818, 1843, 1876–1877, 1909–1910 and 1939–1940). Therefore, if the reasoning was correct and the data were accurate, rodents would reach population peaks every third bamboo blooming of 'taquara-lixa' *M. fistulosa.* Why Pereira (1941) disregarded 'taquara lisa' *Merostachys* sp. as a potential trigger of ratadas and what would be the biological mechanisms underlying a 30-year 'cycle' for such short-lived mammals was left unanswered. But there is more to rodent outbreaks than bamboo blooming. Gilmore (1947) was puzzled that he could not detect mast seeding of bamboo prior to or concurrent with a massive and widespread rodent outbreak in early 1944 in southern Peru. In his own words, 'no association [of bamboo blooming] with the rat increase can be affirmed in this case. The local inhabitants do not seem to associate the rat increases with anything except the subsequent agricultural loss. There

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had been no recent noticeable climatic cause that might have been responsible'. It was left to Pearson (1975) to notice that, despite Gilmore's (1947) disclaimer, 'there may, indeed, have been no spectacular weather events but I find that rainfall, as recorded in Lima, was exceptionally heavy in 1941, 1942, and 1943'. Indeed, having studied the 1972–1973 outbreak of *Phyllotis* mice in coastal Peru, Pearson (1975) concluded that, 'as in outbreaks of *Mus* and *Peromyscus* in North America, the outbreak of *Phyllotis* followed two consecutive seasons of unusually favourable weather'. Two years of above-average rainfall may have been necessary in Peru, but a single one has been enough to trigger rodent irruptions in central Chile (Lima *et al.* 1999a, 1999b, 2001; Holmgren *et al.* 2001; Jaksic 2001), and probably also in eastern Argentina. The points we emphasize in this review are that not all ratadas are associated with bamboo blooming, but that many are associated with rainfall peaks, and that these two outbreak types are geographically interspersed over South America. In addition, we dispel the myth of the 30-year bamboo/ratada coupling, we assess the size of rodent outbreaks in different parts of the continent and, using population dynamic theory and an outbreak classification (Berryman 1999), we discuss some possible mechanisms underlying ratadas. With the aim of setting a standardized framework for spatial and temporal comparisons, we propose a trapping protocol and a threshold density for assigning the 'ratada' label. We briefly sketch the intriguing connection between mouse outbreaks and emerging viral diseases in South America, and emphasize that ratadas may be viewed as pulsed resources, thus enabling us to learn more of the ways communities respond to such intermittent inputs.

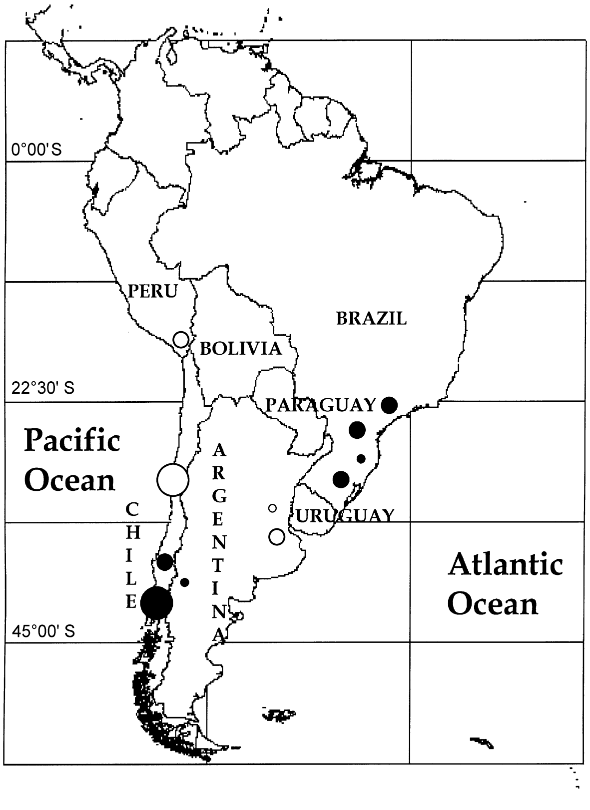

Fig. 1. Sixty-three ratadas that are well-documented in Argentina, Brazil, Chile and Peru (another seven likely ones are not mapped here). Unfilled dots denote rainfall-associated ratadas and black dots correspond to bamboo-associated ones. Small dots denote a single ratada on record, medium-sized dots correspond to areas in which two to 10 ratadas have been recorded and large dots denote areas with >10 ratadas on record. Although there are no written reports of ratadas in Bolivia and Paraguay, they have been noted by trained observers. In Uruguay, ratadas have neither been recorded nor observed.

METHODS

We conducted an exhaustive literature review of references to ratadas in both scientific and historical accounts with specific reference to Argentina, Bolivia, Brazil, Chile, Paraguay, Peru and Uruguay. The most complete data come from Chile because of the extensive reference database available in Jaksic (1997) and the current Chilean databank at http://www.bio.puc.cl/auco/artic04/micromam.htm. In Argentina, Bolivia, Brazil, Paraguay, Peru and Uruguay, the literature is scattered and is comparatively scarce or non-existent; thus, consultation with experts (native or foreign) aided in finding quotable sources.

RESULTS AND DISCUSSION

When, where and how many ratadas?

Sixty-three ratadas are well-documented in the literature reviewed and another seven are likely to have occurred (Appendix I). They span the period from 1552 to 2002 (450 years) and are spread over four of the seven countries examined in South America (Argentina, Brazil, Chile and Peru). Lack of documented irruptions in Bolivia, Paraguay and Uruguay may be the by-product of a cursory search, but O'Connell (1982, 1986) also failed to detect such phenomena in her two exhaustive reviews of rodent population dynamics in South America. In addition, Barlow (1969) indicated that 'no ratadas have been recorded in Uruguay', and Anderson's (1997) most frequent comment under the species accounts of likely irrupting mice (e.g. *Calomys callosus*) was that 'no Bolivian data are available on habitat, habits, behaviour, or food'. Nevertheless, Dr Jorge Salazar-Bravo (pers. comm., 2001) stated: 'I have observed "ratadas" in Bolivia in the high-Andean plateau of Oruro and La

Paz (in 1986 and again in 1990) as well as in the agricultural region of Santa Cruz de la Sierra (1990–1991)'. He indicated that the mice involved belong to *Calomys* and *Oryzomys*. We have chosen not to list these two Bolivian ratadas in Appendix 1 or Fig. 1 because they are not published records, but we have no doubts about the validity of the observations of Dr Salazar-Bravo.

Similarly, Dr James N. Mills (pers. comm., 2001) related to us, 'When I went to the Paraguayan Chaco in December 1995 to investigate an outbreak of hantavirus pulmonary syndrome, there had been some anecdotal reports of high rodent densities'. This viral outbreak occurred after an unusually rainy rainfall season (January – May 1995), but rodent densities measured in December 1995 did not seem to reach irruptive proportions (Williams *et al.* 1997). Perhaps there was a ratada earlier in 1995, before trapping was conducted, but this is just speculation. A follow-up study of the Paraguayan Chaco viral outbreak conducted by Yahnke *et al.* (2001) also failed to detect abnormally high rodent densities from July 1996 to September 1997.

Overall, only 14 rodent outbreaks were recorded from the 16th to the 19th centuries in comparison to 49 during the entire 20th century (Appendix I, considering only written reports). This latter result may be attributed to the thorough observations of professional naturalists as opposed to the more anecdotal or sporadic accounts of chroniclers and travellers of old.

Ratadas of two types: Bamboo-associated and rainfall-associated

Ratadas are not figments of the imagination of early chroniclers, but are sound records made by professional naturalists. They may not be cyclic as presumed by early observers, but rather triggered by exogenous factors such as bamboo blooms and rainfall peaks. There are two types of ratadas: bamboo-associated and rainfall-associated, which have occurred with approximately equal frequency, notwithstanding those of unknown origin (Table 1).

Because of geographical and climatic regional differences, it would appear as if Brazil is affected chiefly by bamboo-associated rodent outbreaks, while Peru, northern Chile and northern Argentina are more affected by rainfall-associated irruptions. No bamboo-associated rodent irruptions have ever been documented in Peru, but they are typical of southern Chile and southern Argentina.

In Brazil, no rainfall-associated outbreaks have ever been recorded. This trend may result from inadequate data because some studies suggest the existence of rainfall-associated rodent outbreaks. For instance,

Table 1. Apparent proximate causes of mouse outbreaks in South America

Apparent proximate cause of outbreak	Argentina (*n*)	Genus	Brazil (*n*)	Genus	Chile (*n*)	Genus	Peru (*n*)	Genus
Associated with bamboo blooming (*n* =28; 44.4%)	1	*Oligoryzomys*	9	*Akodon, Calomys, Delomys, Holochilus,Oligoryzomys, Oxymycterus*	17	*Akodon, Geoxus, Irenomys, Oligoryzomy*	0	
Associated with above-average rainfall (*n* = 27; 42.9%)	4	*Akodon, Calomys, Mus, Oligoryzomys*	0		18	*Akodon, Octodon, Oligoryzomys Phyllotis, Thylamys*†	5	*Oryzomys, Phyllotis*
Unknown (*n* = 8; 12.7%)	6		0		1		1	
Total (*n* = 63; 100%)	11		9		36		6	

†The marsupial mouse *Thylamys* is also included. Sources are given in Appendix I.

Mares and Ernest (1995) found that in a gallery forest of central Brazil, some small mammals displayed a ‘boom-and-bust’ pattern in connection with rainy and dry periods. Cerqueira *et al.* (1993) found that in a coastal scrub of south-eastern Brazil, some mammal species displayed multi-annual patterns of population fluctuation, perhaps associated with rainfall variation. This topic deserves closer scrutiny in Brazil.

In Argentina, rainfall-associated ratadas appear to be more prevalent than bamboo-associated ones (Table 1). But this may be an artefact, because several bamboo-associated ratadas in Argentina have not been properly recorded (Pearson *et al.* 1994). In southern Argentina, the presence of three *Chusquea* bamboo species with well-known blooms (Pearson *et al.* 1994) suggests that ratadas occur there, although Pearson and Pearson (1982) at first failed to detect them. Later, Pearson *et al.* (1994) commented that ‘all accounts of this phenomenon in southern Argentina agree on the great number of mice, but none document what species contributed to the outbreaks. Wherever bamboo grows, one encounters similar accounts of mass blooming followed by outbreaks of rodents’. Sanguinetti and García (2001) reported the most recent bamboo-associated ratada in southern Argentina; that of *Oligoryzomys longicaudatus*, which took place more or less simultaneously in 1997–1998 from La Angostura village (~39°S) to the Llao Llao peninsula in Nahuel Huapi National Park (~41°S), and to Los Alerces National Park (~43°S). The interesting aspect of this ratada is that it occurred concurrently with, not after, the start of the *Chusquea coleou* bloom in Lanín National Park (~40°S).

Chile has reports of both ratada types: rainfall-driven rodent outbreaks in the north and bamboo-bloom-driven rodent irruptions in the south (Table 1).

Table 2. Reported years of bamboo blooming in Chile and Brazil and the estimated period of recurrence in years

Bamboo and locality	Bloom year	Time period (years)
Chusquea spp. (*C. quila* and/or *valdiviensis*)		
Valdivia, Chile	1552	NA
Araucanian district, Chile	1681	129
Valdivia, Chile	1780	99
Osorno, Chile	1797	17
Valdivia, Chile	1869–1870	72
Temuco, Chile	1886–1887	17
Temuco, Chile	1929–1930	43
Southern Chile	1938–1939	11
Bio-Bio River southwards, Chile	1947–1948	9
Southern Chile	1962–1964	15
X Region, Chile	1977–1978	15
Osorno province, Chile	1990–1991	13
Valdivia & Llanquihue provinces, Chile	1991–1992	NA
Northern Chiloé and Palena provinces, Chile	1991–1992	NA
San Martín, Chile	1992–1993	NA
Peulla, Chile	1992–1993	NA
Southern Chiloé province, Chile	1992–1993	NA
Valdivia province, Chile	2001	10
Average recurrence period 1929–2001		12.2
Merostachys spp. (‘taquaras’)		
Sao Paulo State, Brazil (unknown ‘taquara’)	1816	NA
Rio Grande do Sul state, Brazil (unknown ‘taquara’)	1843	27
Rio Grande do Sul state, Brazil (unknown ‘taquara’)	1863	20
Rio Grande do Sul state, Brazil (unknown ‘taquara’)	1876	13
Santa Catarina, Brazil (unknown ‘taquara’)	1876–1877	NA
Paraná State, Brazil (unknown ‘taquara’)	1877	NA
Rio Grande do Sul state, Brazil (unknown ‘taquara’)	1880–1982	4
Paraná State, Brazil (‘taquara lixa’, *M. fistulosa*)	1909	29
Paraná State, Brazil (‘taquara lisa’, *M.* sp.)	1914	5
Sao Paulo State, Brazil (unknown ‘taquara’)	1916	NA
Paraná State, Brazil (unknown ‘taquara’)	1917	NA
Paraná State, Brazil (‘taquara lisa’, *M.* sp.)	1927	10
Paraná State, Brazil (‘taquara lixa’, *M. fistulosa*)	1938–1940	11
Paraná State, Brazil (‘taquara lisa’, *M.* sp.)	1945	7
Average recurrence period 1816–1945		14.0

Sources are given in Appendix I. Blooms that occurred within 3 years of one another are considered to be the same bloom, which is spreading. NA, not applicable.

Interestingly, several of the same rodent genera are associated with either bamboo or rainfall environmental triggers (e.g. *Calomys*, *Akodon* and *Oligoryzomys*). The data are too scant for deciding whether irruptions of *Mus*, *Phyllotis*, *Octodon* or *Thylamys* (a small marsupial) are associated only with rainfall peaks, though it would not be unexpected on account of their distribution in semi-arid and Mediterranean biomes, outside tropical and temperate forests (Redford & Eisenberg 1992). Although not providing evidence, Mann (1978) added another rodent genus (*Irenomys*) to bamboo-associated irrupting rodents in Chile. This information was quoted by Redford and Eisenberg (1992), and does not constitute proof. Because of the long border shared by Chile and Argentina, of the presence of *Chusquea* bamboo throughout (and of similar rodent species on both sides), it seems likely that bamboo-driven ratadas in Argentina have been as frequent as in Chile but have not been reported. This topic requires further examination in Argentina in light of the findings in Chile.

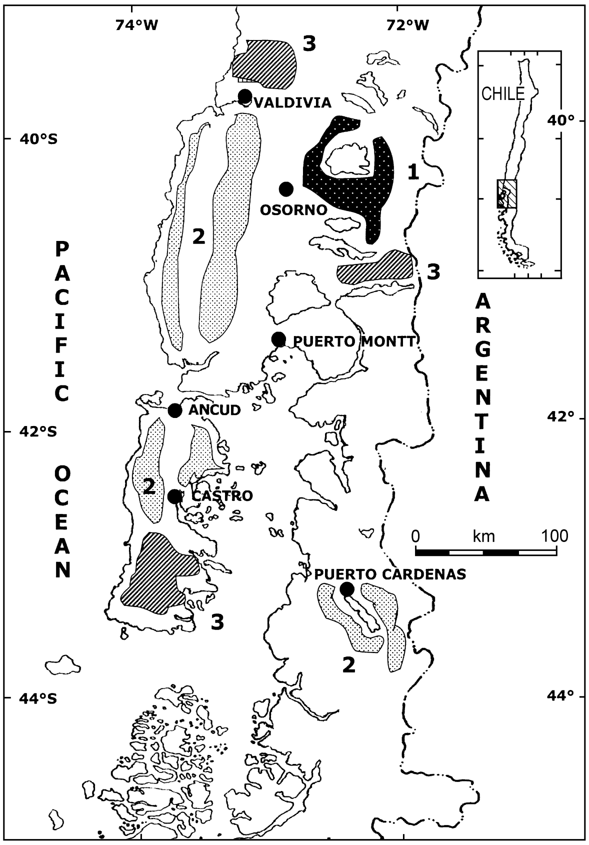

Fig. 2. Spread of *Chusquea* spp. bloom over southern Chile, 1990–1993. 1, summer 1990–1991 bloom; 2, summer 1991–1992 blooms; 3, summer 1992–1993 blooms.

Phenology of bamboo blooms

Bloom years for bamboos differ between Chile and Brazil either because of climatic factors (Chilean forests are temperate, Brazilian forests are chiefly tropical), phylogenetic factors (*Chusquea* spp. *vs* *Merostachys* spp.), or both. Discounting the 16th–19th centuries because of spotty records, it appears that over the 20th century in Chile, *Chusquea* spp. (chiefly *Chusquea quila* and/or *valdiviensis*) have bloomed on average every 12 years ($n = 6$; Table 2). It should be noted that *Chusquea* spp. bloom at slightly different times across southern Chile (González & Donoso 1999). For instance, one of the latest blooms in Chile was first detected in interior Osorno province in the summer of 1990–1991 (Fig. 2). It then spread west and south to Valdivia and Llanquihue provinces during 1991–1992, finally reaching northern Valdivia and the southernmost provinces of Chiloé and Palena in summer 1992–1993 (Table 2; Fig. 2). Note also that the summer 2000–2001 bloom near Lake Panguipulli in Valdivia province apparently expanded from the Argentine side, where *C. coleou* started flowering in 1997, though it did not peak until spring 2000 (Appendix I).

Pearson *et al.* (1994) reported that residents of Nahuel Huapi National Park in Argentina agreed that *C. coleou* bloomed in 1940, 1950–1951, 1968 and 1986 (there was a further bloom in 1997–1998; Appendix I), giving an average recurrence time of around 14 years, which is close to our calculations of 12 years for Chile. Notice that the *C. coleou* blooms in Argentina are ahead of the corresponding blooms in southern Chile by about 2–8 years (1938–1939, 1947–1948, 1962–1964, 1977–1978; Table 2). Sanguinetti and García (2001) report that *C. coleou* in Lanín National Park, Argentina, started blooming as isolated individuals in spring 1997 and summer 1997–1998, increasing in area during 1999 and reaching their peak during spring 2000. Thus, this happened about 6 years after the massive bloom of *C. quila* and/or *valdiviensis* in Chile in 1990–1993 (Table 2). These authors also report that mass blooming started about 2 years earlier in the more northerly Lanín National Park (~40°S) than in the more southerly Nahuel Huapi National Park (~41°S). Sanguinetti and García (2001) stated that even though *C. coleou* blooms on average every 14 years, it takes over 60 years for a bloom to recur at exactly the same site.

Blooms of *Merostachys* spp. in Brazil occur on average every 14 years ($n = 9$). Perhaps this result is epiphenomenic to averaging the assumed 12-year period for 'taquara lisa' *Merostachys* sp. with that of 30 years for 'taquara lixa' *M. fistulosa*. Indeed, Giovannoni *et al.* (1946) called into question the 30-year period for this latter species because in 1946, they witnessed the blooming of *M. fistulosa* in the same area where Pereira (1941) previously reported the bloom of 1939–1940. That is, it took only 6–7 years for the bloom to recur at the same locality. As in Chile, bamboo blooming is not simultaneous. For instance, the bloom of 1876 travelled across three Brazilian states in 3 years, and that of 1938 spread over two states in 3 years (Table 2).

Therefore, we here dispel the notion that South American bamboos bloom every 30 years, because the period depends on the species involved. Brazilian *M. fistulosa* may bloom after such time as described by Pereira (1941), but the data of Giovannoni *et al.* (1946) are hard to ignore. Indeed, *Merostachys* sp. blooms at the much briefer period of 14 years (Pereira 1941). On the other hand, *Chusquea* spp. in Chile and Argentina apparently bloom every 12–14 years, slightly short of the 15–20 years estimated by Gunckel (1948), much shorter than the 30-year period proposed by Schlegel (1993) or the 70-year period put forth by González and Donoso (1999), and at variance with the statement made by Pacheco (1993) that some *Chusquea* spp. flower every 15 or 30 years while others do so at 60-year periods. We agree with Pearson *et al.* (1994) that 'statements concerning intervals of 15–25 years between mass flowering of this species [*C. coleou*] in southern Chile and Argentina are primarily derived from earlier tentative statements . . ., which through repetition have achieved an air of authenticity'. It is still unclear what environmental factors cause bamboos and other plants to flower and mast-seed (Janzen 1976; Silvertown 1980; Lalonde & Roitberg 1992; Kelly 1994; Keeley & Bond 1999; Wright *et al.* 1999; Williamson *et al.* 2000). A suggestion is that El Niño events may be a cue for mast-seeding among trees in south-east Asia (Williamson 2002).

Phenology of ratadas

The association between bamboo blooms, rainfall peaks and rodent outbreaks in South America seems beyond coincidence, but there may be differences in the time lags involved (Appendix I). *Chusquea* bamboos flower during spring of a given year, and mast-seed during the summer of the next year (approximately 18 months later), with rodents irrupting during autumn and winter of that same year (approximately 2 years after the bamboo blooming, or 3–6 months after the seeding). Brazilian *Merostachys* may take less time. In a well-documented case in Paraná State, Giovannoni *et al.* (1946) found that flowering of *Merostachys* sp. started in September and October of 1945 and mast-seeding in March and April of 1946, with rodents irrupting in July 1946, only 3 months later.

With regard to rainfall, most rodent species respond quite soon to rainfall peaks (which in central Chile and coastal Peru come during winter, and in summer in

Table 3. Peak densities of mice during outbreaks in Argentina, Brazil, Chile and Peru, in association with either bamboo blooms or rainfall highs

Proximate cause and locality	Outbreak year	El Niño year	Species	Number ha^{-1}
Associated with bamboo blooms				
Sao Paulo state, Brazil	1989	NA	*Delomys dorsalis*	68
			Akodon nigrita	18
San Martín, Chile	1994	NA	*Oligoryzomys longicaudatus*	116
Peulla, Chile	1995	NA	*Akodon olivaceus*	237
Associated with rainfall highs				
Several Departments, Peru	1944	1940–1941	*Oryzomys xantheolus*	250
Buenos Aires province, Argentina	1969	1968–1969	*Akodon azarae*	115
			Oligoryzomys nigripes	33
Fray Jorge, Chile	1972	1972–1973	*Akodon olivaceus*	97
	1973		*Phyllotis darwini*	46
Guanaqueros, Chile	1973	1972–1973	*Phyllotis darwini*	30
La Serena, Chile	1973	1972–1973	*Oligoryzomys longicaudatus*	154
Aucó, Chile	1988	1987–1988	*Phyllotis darwini*	225
	1988		*Akodon olivaceus*	52
	1988		*Thylamys elegans*	14
Fray Jorge, Chile	1992	1991–1992	*Akodon olivaceus*	157
	1993		*Octodon degus*	91
	1993		*Phyllotis darwini,*	70
	1992		*Oligoryzomys longicaudatus*	46
Aucó, Chile	1998	1997–1998	*Phyllotis darwini*	65
Atiquipa, Peru	1998	1997–1998	*Oryzomys xantheolus*	259

Peruvian 1944 data is based on the estimate of Gilmore (1947); all other data are based on minimum-number-known-alive estimates, except for Aucó 1998, which is based on capture-recapture estimates. Sources are given in Appendix I. NA, not applicable.

central Argentina). Rodent outbreaks occur during spring or summer in Chile and Peru, about 3–6 months after the rains, and during autumn or winter in Argentina, also about 3–6 months after rainfall (Appendix I). Rainfall-associated ratadas may ultimately be caused by intrusions of El Niño (Jaksic 2001). The last six rodent outbreaks in Peru and Chile have occurred 1–2 years after the El Niño events of 1940–1941, 1972–1973, 1987–1988, 1991–1992 and 1997–1998. There appears to be a causal relationship between El Niño and rainfall (Lima *et al.* 1999a), and some rodent species increase after high-rainfall winters with a lag of 0–1 years (Meserve *et al.* 1995; Jaksic *et al.* 1997). Although ratada connections to El Niño are less than perfect, they survive statistical testing and thus are predictable (Lima *et al.* 1999b, 2001). During the past century, El Niño has occurred on average every 8 years, though more frequently during the last two decades (i.e. every 5 years; Jaksic 2001). With every El Niño there has been a corresponding ratada, but the extent or intensity of the irruptions has been different. For instance, the similarly high precipitation levels of 1986–1987 and of 1997–1998 resulted in quite different outbreaks at the same study site in northern Chile (225 ha^{-1} *vs* 70 ha^{-1}, respectively) considering total rodent density (Jaksic 2001).

What is a ratada, numerically speaking?

There is no quantitative definition of what a ratada is. Quantitative reports of rodent outbreaks have judged ratadas from relatively short-term trapping schemes. Outbreak density figures have been identified as high peaks against a background of low-level population fluctuations.

The mice that are said to have reached ratada densities are, in decreasing sequence by peak number (Table 3): *Oryzomys xantheolus* (range = 250–259 individuals ha^{-1}), *Akodon olivaceus* (52–237 ha^{-1}), *Phyllotis darwini* (30–225 ha^{-1}), *Oligoryzomys longicaudatus* (46–154 ha^{-1}), *Akodon azarae* (115 ha^{-1}), *Octodon degus* (91 ha^{-1}), *Delomys dorsalis* (68 ha^{-1}), *Oligoryzomys nigripes* (33 ha^{-1}) and *Akodon nigrita* (18 ha^{-1}). It is noteworthy that a marsupial, *Thylamys elegans*, also reaches comparatively high densities (14 ha^{-1}). Ratadas involve one to four species simultaneously, and therefore the combined densities may be much higher in total (Table 3). On the other hand, not all ratadas of the same species reach the same density, even at the same study site in separate years. For instance, the rodent outbreak of 1972–1973 in Fray Jorge, Chile, was much smaller than that of 1992–1993 at the same site (Table 3). Similarly, there was a massive rodent outbreak in Aucó, Chile, in 1988, but a modest one in 1998 (Table 3). Finally, limited data suggest that rodent density outbreaks associated with bamboo-blooming are similar to those associated with rainfall peaks (Table 3).

Proper detection of ratadas should be based on long-term, regular monitoring of small mammal populations, but we found few such cases in our literature review (Jiménez *et al.* 1992; Meserve *et al.* 1995, 1999; Olmos 1996; González *et al.* 2000; Lima *et al.* 2001). Lacking such monitoring and aiming at setting a standardized framework for spatial and temporal comparisons, we here propose that the 'ratada' label be assigned only to: (i) total small mammal densities exceeding 100 individuals ha^{-1}; or to (ii) single small mammal species densities exceeding 50 individuals ha^{-1}. In addition, we propose that the above criteria be applied to data collected in trapping grids (live trapped or snap trapped), ideally in square layouts of at least seven rows by seven columns, with one or preferably two traps set apart at least 15 m (thus covering about 1 ha) and operated for at least 5 days or nights. Estimates of abundance should be based on capture-mark-recapture (CMR) statistical closed-population models (thus correcting for capture rates). In addition, we advise against the use of trap lines because they are usually set in those places where the trapper expects the maximum yield and render only an estimate of trapping success or efficiency, not of absolute abundance, much less density.

Population dynamics underlying ratadas

Ecologically speaking, ratadas represent explosive increases in population abundance or density of rodents during a relatively short period. Because these irruptions are closely associated with exogenous factors such as unusual rainfall peaks or bamboo-blooms, they appear to be the result of a population closely tracking changes in the environment, with population dynamics being governed by simple regulatory structures dominated by negative feedbacks. However, competitors or predators may induce time lags in the negative feedbacks, thus causing a trend to oscillate around equilibrium points (Royama 1992; Berryman 1999). As a consequence, population cycles may be disrupted under the effects of strong changes in food levels, such as those caused by El Niño-driven productivity (Jaksic 2001) or by bamboo-blooms.

Population dynamic theory and the classification of pest outbreaks by Berryman (1999) enable us to hypothesize the underlying mechanisms causing ratadas. Four main hypotheses may explain population outbreaks of rodents in South America:

1. Population dynamics may be dominated by first-order (instantaneous) negative feedback. Thus, we would expect population peaks proportional to the magnitude of the exogenous factor (rainfall peaks,

bamboo-blooms or mast years). This type of outbreak is called pulse-gradient (Berryman 1999).

2. Population dynamics may be dominated by second-order (delayed) negative feedbacks. We would then expect low frequency or 'cyclic' oscillations, and that fluctuations were not well-coupled with the magnitude of the exogenous factor. This type of outbreak is called cyclical-gradient (Berryman 1999).
3. Population dynamics may be the result of a combination of different feedback structures from time to time in connection with rodent density levels. This type of population dynamics is called meta-stable (Berryman 1999) and two dynamic patterns are possible: bi-stable, when different first-order negative feedbacks dominate at low or high densities, or sustained-irruption, when the feedback structure relaxes at times with a large input of resources (high-rainfall years, bamboo blooms or mast years) and the population reaches high densities.
4. Population dynamics may be a consequence of a change in the order of the feedback structure. A first-order negative feedback may be dominant at low density (low-rainfall years or no-bloom years) and a second-order negative feedback may be dominant at high density (high-rainfall or masting years) because of the arrival of predators or the increased intensity of plant–rodent interactions. This type of outbreak is called pulse-irruption (Berryman 1999).

Because ratadas are so impressive in their magnitude, ecologists have perceived this phenomenon as all-or-none; as irruption versus the normal abundance state (Jiménez *et al.* 1992; Meserve *et al.* 1995). But the population dynamic structure of the species involved may be very different. For instance, results from a well-studied system in northern Chile indicate the existence of complex feedback structures in rodent dynamics. Here, one of the most irruptive rodents (the leaf-eared mouse *P. darwini*), shows negative second-order and direct positive feedback in combination with El Niño disturbances (Lima & Jaksic 1998a, 1998b; Lima *et al.* 1999a, 1999b, 2001). Although we know that leaf-eared mouse ratadas do not show true cyclic dynamics, like those of Northern Hemisphere microtine rodents (Stenseth 1999), we would not be surprised if some of the other rodent species mentioned in this paper exhibit cyclic dynamics in normal or low-density years, as proposed by Murúa and González (1985).

We think that the study of population dynamics and demography of irruptive rodents represents an important challenge for population ecologists. The combination of (i) population dynamic theory; (ii) CMR data and modelling; (iii) long-term monitoring and manipulative experiments; and (iv) population dynamic matrix models, have been useful for understanding ratadas in semi-arid Chile (Meserve *et al.* 1995, 1999; Lima *et al.* 1999b, 2001). We think that a similar four-pronged approach could be applied toward understanding rodent outbreaks in other regions of the continent. The issues discussed here emphasize the importance of determining population feedback structure and exogenous factors for understanding ratadas in South America.

Ecological consequences of ratadas

We have provided a historical and ecological framework for the analysis of ratadas in South America. Perhaps this account will stimulate other researchers to scrutinize local sources for the tracking of ratadas in other countries of the region, and to determine whether they are associated with bamboo blooms, rainfall peaks or other exogenous factors. As the causal factors become better understood, particularly in terms of recurrence, we may develop better predictive abilities to forecast future ratadas. This enhanced predictive ability may also be useful in a different context (Mills & Childs 1998). Several of the mice implicated in ratadas are reservoirs of emerging diseases: *Calomys musculinus* for Junín virus in Argentina (Mills *et al.* 1992), *Calomys callosus* for Machupo virus in Bolivia (Kuns 1965; Johnson 1993), *Oligoryzomys longicaudatus* for Andes virus in both Chile and Argentina, *Akodon azarae* for Andes virus in Argentina (Murúa 1998, 1999; Toro *et al.* 1998; Cantoni *et al.* 2001) and *Calomys laucha* for Laguna Negra virus in Paraguay (Williams *et al.* 1997; Yahnke *et al.* 2001). The coupling of life histories between organisms such as bamboos, mice and viruses with such contrasting longevities poses a challenge to ecologists. But of more relevance to human health, they emphasize the need for the predictive power to forecast disease epidemics that affect human populations (Ostfeld & Keesing 2000).

In addition, ratadas may be viewed more broadly as pulsed resources (Ostfeld & Keesing 2000). That is, as intermittent resources of dramatically higher than normal levels, which then become depleted with time. Such pulsed resources have been described in association with mast-seeding (of bamboos in our case) and with increases of primary production following some environmental cue (such as El Niño-driven rains in our case). The effects of pulsed resources have been tracked for up to three trophic levels in several parts of the world (Ostfeld & Keesing 2000), and rainfall-associated ratadas in northern Chile conform closely to this pattern, from vegetation through herbivores to carnivores (Jaksic *et al.* 1997; Jaksic 2001; Stenseth *et al.* 2002). Nevertheless, no follow up of bamboo-associated ratadas has been documented beyond this direct link (neither to the environment trigger, nor to the predator trophic level). But as soon as ratadas become predictable from bamboo blooming, it should be interesting to study how, or if, they propagate to the top predator level, thus enabling us to learn more of the ways communities respond to these pulsed resources.

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APPENDIX I

Table A1. Mouse outbreaks, rainfall peaks and bamboo blooms in South America (cases are presented in chronological sequence)

Locality of outbreak	Date of outbreak	Rainfall and bamboo blooms	Species involved	Authority
Valdivia, Valdivia province, Chile	1552	Likely associated with *Chusquea* bloom	Rats (unknown species)	de Vivar (1987)
Araucanian district, IX and X regions, Chile	1681	Likely associated with *Chusquea* bloom	Rats (unknown species)	Philippi & Landbeck (1858)
Valdivia, Valdivia province, Chile	1780	Associated with *Chusquea* bloom	Rats (unknown species, larger than *Mus musculus*)	O'Higgins in Gay (1847); Gunckel (1948)
Osorno, Osorno province, Chile	1797	Associated with *Chusquea* bloom	Rats (unknown species)	Gay (1847); Gunckel 1948)
Sao Paulo state, Brazil	1818	*Merostachys* and *Chusquea* bloomed in 1816	Rats (unknown species)	Saint' Hilaire (1851) in Pereira (1941)
Buenos Aires province, Argentina	Autumn 1833	1830 and 1831 were drought years; summer 1833 had high rainfall	Small mice believed to be *Mus musculus*	Sarmiento (1885)
Rio Grande do Sul state, Brazil	1843	*Merostachys* ('taquara') bloomed in 1843	Rats (unknown species)	von Koseritz (1876) in Pereira (1941)
Rio Grande do Sul state, Brazil	Likely in 1864	*Merostachys* likely bloomed in 1863	Unknown species	von Koseritz (1885) in Pereira 1941)
Valdivia, Valdivia province, Chile	1869 or 1870	Associated with mast seeding of *Chusquea*	Rats and mice (unknown species)	Philippi (1879)
Buenos Aires province, Argentina	Summer 1872–1873 to autumn 1873	Summer 1872–1873 was hot and with high rainfall	Mouse (unknown species)	Hudson (1892) in Shinya (1984)
Rio Grande do Sul state, Brazil	1876	*Merostachys* likely bloomed in 1876	*Oxymycterus rufus* *Calomys* sp.	von Ihering (1885) in Pereira (1941)
Santa Catarina state, Brazil	1877	*Merostachys* ('taquara') bloomed in 1876–1877	Rats (unknown species)	von Koseritz (1876) and Mueller (1881) in Pereira (1941)
Paraná state, Brazil	1878	*Merostachys* likely bloomed in 1877	Rats (unknown species)	Derby (1879)
Rio Grande do Sul state, Brazil	Likely in 1882	*Merostachys* likely bloomed in 1880–1882	Unknown species	von Ihering (1885) in Pereira 1941)
Concepción province, Chile	Winter 1877	Associated with floods and likely high rainfall	*Oligoryzomys longicaudatus*	Oliver (1946)
Temuco, Cautín province, Chile	Likely in 1888	*Chusquea* flowered in summer 1886–1887	Unknown species	Gunckel (1948)
Ica, Huncavelica, Ayacucho and Arequipa departments, Peru	1907	Likely associated with above-average rainfall	*Oryzomys xantheolus*	Gilmore (1947)
Paraná state, Brazil	1909–1910	*Merostachys fistulosa* ('taquara lixa') bloomed in 1909	Rats, chiefly *Akodon* sp., secondarily *Oligoryzomys* sp.	Pereira (1941)
Paraná state, Brazil	Likely in 1915	*Merostachys* sp. ('taquara lisa') bloomed in 1914	Unknown species	Pereira (1941)
Sao Paulo state, Brazil	Likely in 1917	*Chusquea* and *Merostachys* bloomed in 1916	Unknown species	Luederwaldt (1918) in Pereira (1941)
Paraná state, Brazil	Likely in 1917	*Chusquea* bloomed in 1917	Unknown species	Lutz *et al.* (1918) in Pereira (1941)

Table A1. (continued)

Locality of outbreak	Date of outbreak	Rainfall and bamboo blooms	Species involved	Authority
Ica, Huncavelica, Ayacucho and Arequipa departments, Peru	1926	1925 had unusually high rainfall	*Oryzomys xantheolus*	Gilmore (1947)
Paraná state, Brazil	Likely in 1928	*Merostachys* sp. ('taquara lisa') bloomed in 1927	Unknown species	Pereira (1941)
Temuco, Cautín province, Chile	Likely in 1931	*Chusquea* flowered in summer 1929–1930	Unknown species	Gunckel (1948)
Southern Chile	Likely in 1940	*Chusquea* flowered in summer 1938–1939	Unknown species	Pacheco (1993); González & Donoso (1999)
Ica, Huncavelica, Ayacucho and Arequipa departments, Peru	1939	Apparently not associated with above-average rainfall	*Oryzomys xantheolus*	Gilmore (1947); Zeballos *et al.* (2000)
Paraná State, Brazil	1939–1941	*Merostachys fistulosa* ('taquara lixa') bloomed in 1938–1940	Rats, *Oligoryzomys* sp. and likely *Akodon* sp.	Pereira (1941)
Sao Paulo state, Brazil	Likely in 1941	*Chusquea* and *Arundinaria* bloomed in 1940–1941	Unknown species	Pereira (1941)
Ica, Huncavelica, Ayacucho and Arequipa departments, Peru	Summer 1943–1944	Rainfall in Lima was heavy in 1941–43; associated with El Niño 1940–1941	*Oryzomys xantheolus* (250 ha^{-1})	Gilmore (1947); Pearson (1975)
Buenos Aires province, Argentina	Summer–winter 1944	Summer 1943–1944 had unusually high rainfall	*Calomys laucha* and*Akodon obscurus*	Crespo (1944)
Vicuña, Elqui province, Chile	1944, 1949, 1952, 1957, 1963, 1965, 1972	1944, 1949, 1952, 1957, 1963, 1965, 1972 were above-average rainfall years	*Phyllotis darwini, Oligoryzomy slongicaudatus and Octodon degus*	Fuentes & Campusano (1985)
Paraná state, Brazil	July 1946	*Merostachys* sp. ('taquara lisa') flowered in September–October 1945 and seeded in March–April 1946	*Holochilus leucogaster, Oligoryzomys eliurus, Calomystener and Akodon nigrita*	Giovannoni *et al.* (1946)
Bio-Bio River southwards, Chile	Likely in 1949	*Chusquea* flowered in summer 1947–1948	Unknown species	Gunckel (1948)
La Serena, Elqui province, Chile	1957, 1961, 1963, 1965, 1972	1957, 1963, 1965, 1972 were above-average rainfall years (but not 1961)	*Phyllotis darwini, Oligoryzomy slongicaudatus and Octodon degus*	Fuentes & Campusano (1985)
Buenos Aires province, Argentina	Winter 1963	Unreported	*Oligoryzomys flavescens, Akodon, azarae and Mus musculus*	Crespo (1966)
Buenos Aires province, Argentina	Autumn and winter 1964	Unreported	*Akodon azarae, Oligoryzomys flavescens and Akodon obscurus*	Crespo (1966)
Southern Chile	Winter 1965	*Chusquea uliginosa* flowered in summer 1962–1963 and summer 1963–1964	*Akodon* sp., *Oligoryzomys* sp., *Geoxus* sp. and *Irenomys* sp.	Pacheco (1993)
Buenos Aires province, Argentina	1967	Unreported	*Calomys laucha* and *Calomysmusculinus*	Carballal *et al.* (1988); Mills *et al.* (1991)

Table A1. (continued)

Locality of outbreak	Date of outbreak	Rainfall and bamboo blooms	Species involved	Authority
Buenos Aires province, Argentina	Summer–winter 1969	Summer 1968–1969 had unusually high rainfall; associated with El Niño 1968–1969	*Akodon azarae* (115 ha^{-1} in March 1969) and *Oligoryzomysnigripes* (33 ha^{-1} in May 1969)	Dalby (1975); O'Connell (1982, 1986); Jaksic (1986)
Tacna and Arequipa departments, Peru	Summer 1972–1973	Heavy rainfall in August 1971 and July–September 1972; associated with El Niño 1972–1973	*Phyllotis darwini* and *Phyllotismagister* (59% trap success overall)	Pearson (1975)
Fray Jorge, Limarí province, Chile	Summer 1972–1973	1972 had unusually high rainfall; associated with El Niño 1972–1973	*Akodon olivaceus* (97 ha^{-1} in November 1972) and *Phyllotisdarwini* (46 ha^{-1} in February 1973)	Fulk (1975); Meserve & Le Boulengé (1987)
Guanaqueros, Elqui province, Chile	Spring 1973	1972 was unusually rainy; associated with El Niño 1972–1973	*Phyllotis darwini* (30 ha^{-1} in November 1973)	Glanz (1977)
La Serena, Elqui province, Chile	Summer 1972–1973	1972 had unusually high rainfall; associated with El Niño 1972–1973	*Oligoryzomys longicaudatus* (154 ha^{-1} in June 1973)	Péfaur *et al.* (1979)
Buenos Aires province, Argentina	1974	Unreported	*Calomys laucha* and*Calomys musculinus*	Carballal *et al.* (1988); Mills *et al.* (1991)
Buenos Aires province, Argentina	1977	Unreported	*Calomys laucha* and*Calomys musculinus*	Carballal *et al.* (1988); Mills *et al.* (1991)
X Region, Chile	Likely in 1979	*Chusquea* flowered in summer 1977–1978	*Oligoryzomys longicaudatus*	Murúa *et al.* (1986); Anonymous (1994); González & Donoso (1999)
Aucó, Choapa province, Chile	Summer (1987–1988) to autumn (1988)	1987 had unusually high rainfall; associated with El Niño 1986–1987	*Phyllotis darwini* (225 ha^{-1} in summer 1987–1988), *Akodonolivaceus* (52 ha^{-1} in autumn 1988) and *Thylamys elegans* (14 ha^{-1} in autumn 1988)	Jiménez *et al.* (1992)
Sao Paulo state, Brazil	1989	*Chusquea meyeriana* flowered in September–November 1988 and seeded in May–August 1989	*Delomys dorsalis* (68 ha^{-1} in April 1989), *Akodon nigrita* (18 ha^{-1} in May 1989), *Oryzomys intermedius* (10 ha^{-1} in August 1989) and*Oryzomys ratticeps* (10 ha^{-1} in October 1989)	Olmos (1991, 1996)
Santa Fe province, Argentina	1989–1990	Summer 1988–1989 was unusually hot and dry; winter 1989 was unusually mild	*Calomys laucha* (62 ha^{-1} in February 1990?) and *Calomysmusculinus* (29 ha^{-1} in February 1990)	Mills *et al.* (1992)
Fray Jorge, Limarí province, Chile	1992–1993	1991 and 1992 had unusually high rainfall associated with El Niño 1991–1992	*Akodon olivaceus* (157 ha^{-1} in December 1992), *Octodon degus*(91 ha^{-1} in May 1993), *Phyllotisdarwini* (70 ha^{-1} in May 1993), and *Oligoryzomys longicaudatus* (46 ha^{-1} in May 1992)	Meserve *et al.* (1995)

Table A1. (continued)

Locality of outbreak	Date of outbreak	Rainfall and bamboo blooms	Species involved	Authority
Puyehue National Park, Osorno province, Chile	Autumn and winter 1993	*Chusquea valdiviensis* flowered in summer 1990–1991 and seeds fell in winter 1992	*Oligoryzomys longicaudatus*	Pacheco (1993); Gallardo & Mercado (1999)
Coastal ranges of Valdivia and Llanquihue provinces, Chile	Autumn 1994	*Chusquea quila* (*valdiviensis*?) flowered in summer 1991–1992 and seeds fell in winter 1993	*Oligoryzomys longicaudatus*	Pacheco (1993); Schlegel (1993); Gallardo & Mercado (1999)
San Martín, Valdivia province, Chile	Autumn 1994	*Chusquea quila* (*valdiviensis*?) flowered in summer 1992–1993 and seeds fell in summer 1993–1994	*Oligoryzomys longicaudatus* (116 ha^{-1} in April 1994)	Murúa *et al.* (1996); González & Donoso (1999); González *et al.* (2000)
Peulla, Llanquihue province, Chile	Autumn and winter 1995	*Chusquea quila* (*valdiviensis*?) flowered in summer 1992–1993 and seeds fell in summer 1993–1994	*Akodon olivaceus* (237 ha^{-1} in July 1995)	Murúa *et al.* (1996); González *et al.* (2000)
Northern half of Chiloé province and Palena province, Chile	Autumn and winter 1994	*Chusquea quila* (*valdiviensis*?) flowered in summer 1991–1992 and seeds fell in winter 1993	*Oligoryzomys longicaudatus*	Gallardo & Mercado (1999)
Southern half of Chiloé province, Chile	Autumn and winter 1995	*Chusquea quila* (*valdiviensis*?) flowered in summer 1992–1993	*Oligoryzomys longicaudatus*and *Akodon olivaceus*	Gallardo & Mercado (1999)
Río Negro and Chubut provinces, Argentina	1997–1998	*Chusquea culeou* started flowering in 1997	*Oligoryzomys longicaudatus*and *Akodon longipilis*	Cantoni *et al.* (2001); Sanguinetti & García (2001)
Aucó, Choapa province, Chile	Summer 1998	1997 had unusually high rainfall; associated with El Niño 1997–1998	*Phyllotis darwini* (65 ha^{-1} in January 1998)	Lima *et al.* (2001)
Arequipa department, Peru	Summer 1998	1997 had unusually high rainfall associated with El Niño 1997–1998	*Oryzomys xantheolus* (186 ha^{-1} and 259 ha^{-1} in two study sites)	Zeballos *et al.* (2000)
Lake Panguipulli, Valdivia province, Chile	Winter 2001	*Chusquea culeou* flowered in Lanín National Park, Río Negro province, Argentina, during Spring 2000	*Oligoryzomys longicaudatus*	Sanguinetti and García (2001); Jaksic & Lima (pers. obs., 2001)