

## Heavy rimu (*Dacrydium cupressinum*) mast seeding and rat (*Rattus* spp.) population eruptions on Stewart Island/Rakiura

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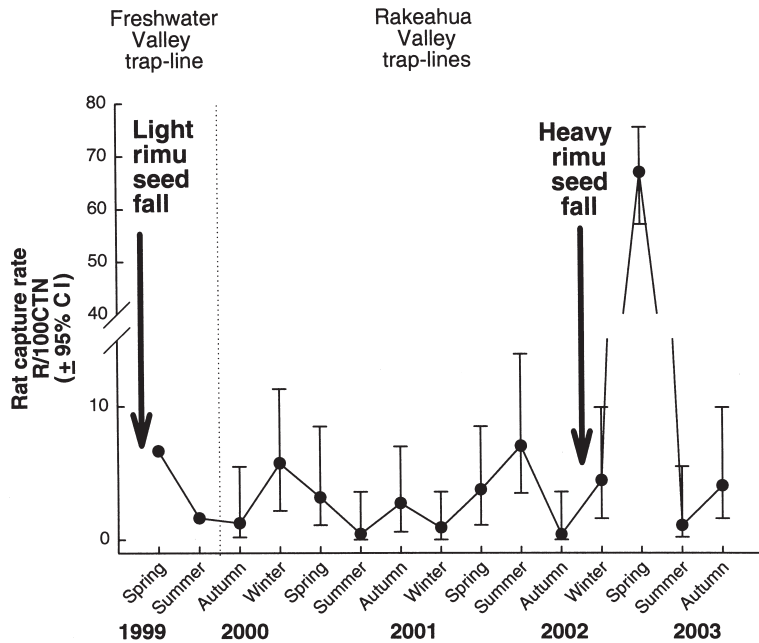
**Abstract** This study aimed to quantify changes in rat abundance and population structure before, during, and after a rimu (*Dacrydium cupressinum*) mast seed event in lowland forest on Stewart Island, New Zealand. Rats, primarily ship rats (*Rattus rattus*), were trapped in low numbers throughout the study period (March 2000–March 2003), except when they erupted to very high abundance in spring 2002, shortly after heavy rimu seed fall. In the immediate post-peak phase, scavenging of trapped rats increased substantially; rats were seen and trapped in daylight; and weights of adult female rats were low in relation to their size, which suggests that food shortage was the cause of the subsequent steep decline in abundance. Rat eruptions have been observed on Stewart Island after heavy rimu seed fall several times over the past 40 years. Eruptions of rats caused by heavy rimu seed-fall may have triggered the invasion of nearby islands by rats, and caused the extinction of several native species on Stewart Island.

**Keywords** *Rattus rattus*; ship rat; *Rattus norvegicus*; Norway rat; seeding; *Dacrydium cupressinum*; rimu; Stewart Island

## INTRODUCTION

Introduced rats and mice become more abundant following moderate to heavy mast seeding by southern beech (*Nothofagus* spp.) in New Zealand (Fitzgerald 1978; King 1983; King & Moller 1997; Fitzgerald et al. 2004). Mast seed events by *Nothofagus* are of concern to wildlife managers due to the deleterious effects of large numbers of ship rats (*Rattus rattus*) and other predators, like stoats (*Mustela erminea*), on native birds (King 1983; O'Donnell & Philipson 1996; Murphy et al. 1998; Dilks et al. 2003). Rimu (*Dacrydium cupressinum*), in lowland podocarp-broadleaf forest also mast seed every 2–5 years, with little seed produced in intervening years (Norton & Kelly 1988). Some research has been conducted on rat population dynamics in podocarp-broadleaf forest where rimu is present (Daniel 1972; Best 1973; Innes et al. 2001), but little on the response of a rat population to rimu mast seeding. Beveridge (1964) suggested that “an increase in [rat] numbers could occur after a good seed fall [from podocarp species]”. Daniel (1978), after an 8-year study in the Orongorongo Valley, concluded that larger autumn seed crops from non-podocarp trees increase the length of breeding seasons for rats, and improve overwinter survival in lowland broadleaf forest. These results suggest that the breeding success and numbers of rats could increase in heavy rimu mast-seed years, when seed-fall may exceed over 1000 seeds per m<sup>2</sup> (Norton & Kelly 1988).

The aim of this study was to compare the demographics of rats in podocarp-broadleaf forest in “normal” years with those in a mast-seed year, to improve our understanding and management of eruptive rat events in lowland forest. Stewart Island/Rakiura was selected as a study site because it has a simple predator-prey system and relatively high and stable rat numbers compared with southern beech forest (King & Moller 1997). Ship rats are the most common rat species in rimu-dominated podocarp-broadleaf forest on Stewart Island/Rakiura. *Nothofagus* species are absent from the island (Wilson 1987). Two other rodent species, Pacific rats (*R. exulans*)



**Fig. 1** Abundance indices of rats in podocarp-broadleaf forest, Freshwater and Rakeahua Valleys, Stewart Island, spring 1999–autumn 2003.

and Norway rats (*R. norvegicus*), are present, but are more common in other vegetation types (Taylor 1975; Sturmer 1988; Harper 2002). Feral cats (*Felis catus*) are the sole mammalian predator, as stoats (*Mustela erminea*) and other mustelids are absent.

## METHODS

### Rat trapping

Two rat-trapping lines were set up in the Rakeahua Valley (47°S, 167°50'E), Stewart Island, from March 2000 to March 2003, in lowland forest dominated by rimu, kamahi (*Weinmannia racemosa*), and southern rata (*Metrosideros umbellata*). Trapping methods followed Cunningham & Moors (1996). A single line of 25 paired traps was also set in spring and summer 1999 in podocarp-broadleaf forest on the north-east side of the Freshwater Valley, where there had been a light rimu mast in the previous autumn. Paired "Ezeset" rat traps, baited with a mixture of peanut butter and rolled oats, were set under 25 mm mesh covers to exclude non-target species. The traps and mesh covers were secured with wire stakes. All traps were checked daily; any rats were removed and processed later. Traps that were sprung or had bait taken were noted and then re-baited and/or set.

The traps were dried and stored between trapping sessions. One trap line was set on the south side of the valley on the Table Hill track, the other on the north side of the valley on the track leading up to Mt Rakeahua.

The trap lines were run every season (March = autumn, June = winter, September = spring, December = summer) from March 2000 to March 2003. From March 2000 to March 2002 seven pairs of traps were set for 9 days on each trap line (126 trap nights), and from June 2002, 25 pairs of traps were set for 3 days on each trap line (150 trap nights). The latter set-up was used in the Freshwater Valley for one line in 1999.

Rats were processed on the day of capture, following Cunningham & Moors (1996). Weight (g), head-body length (HBL), and tail length (TL) (mm), species, sex, and approximate age: adult or juvenile (perforate or imperforate vagina for females and presence or absence of visible tubules within the cauda epididymis for males), and in adult females, the number of embryos or uterine scars, were recorded. Any scavenged rats were identified to species, sex or age as best as possible, depending on the state of the remains. The rate of rat capture was defined as the number of rats (R) caught per 100 trap nights (TN) corrected (C) for sprung traps (Nelson & Clarke 1973) and notated as R/100CTN (Cunningham &

Moors 1996). The capture rates on the two lines were averaged to obtain a mean capture rate, and the confidence intervals derived from these.

### Rimu mast

To confirm a rimu mast seed event, observations of rimu seed abundance on Whenua Hou/Codfish Island, 2 km north-west of Stewart Island, were used to interpret seasonal observations of ripe seed on rimu in the Rakeahua Valley. The percentage of tips of branches with seeds on female rimu has been recorded seasonally on Whenua Hou since 1997 (G. Elliott pers. comm.). When the percentage of tips with seeds exceeded 5% in March of the seed fall season, when fruit matured, it was regarded as a rimu mast year. Up to 12% could be regarded as a light mast, between about 12 and 20% a medium mast, and above 20%, a heavy seed mast.

### Historical rat eruptions

To confirm a relationship between high rat numbers and rimu mast events, recorded rimu mast-seed years (Beveridge 1973), defined by Norton & Kelly (1988) as years with a total seed fall of greater than 150 per  $m^{-2}$ , were compared with historical observations of abundant rats in references relating to Stewart Island and in reports held at Southland Conservancy, DOC, and at National Archives, Dunedin. Unfortunately, there is no numerical correspondence between observations of seeds on branch tips and seed fall counts.

### Statistical analysis

A paired *t*-test was used to compare the seasonal abundance of rats between the north and south trap lines. Non-parametric Mann-Whitney U tests (Sokal & Rolf 1995) were used to compare the morpho-

metrics of adult female rats between years. Too few male rats were trapped in 2001 to make statistical comparisons.

## RESULTS

### Rimu mast in 2002

There was a rimu mast seed event in the Rakeahua Valley in autumn 2002. The seeds fell in late autumn, and by June 2002 areas of fallen seed, obvious due to the distinctive red arils, were noted under many rimu. The rimu mast on Whenua Hou in 2002 was the heaviest recorded since 1997, with a high rate of seed fertility (G. Elliott pers. comm.).

### Temporal and spatial differences in rat abundance

In the 2 years preceding 2002 the mean relative abundance of rats was 3.14 R/100CTN (95% CI = 0–14). In the spring following the heavy rimu seed-fall in autumn 2002, relative abundance increased to a mean of 66.7 R/100CTN (95% CI = 57–75). Three months later the relative abundance had declined to 1.1 R/100CTN (95% CI = 0.2–6) (Fig. 1).

Although more rats were trapped on the north-facing than the south-facing Rakeahua trap line (mean north:  $11.03 \pm 7.5$  SE R/100CTN, versus mean south:  $4.62 \pm 2.4$  SE R/100CTN) there was no significant difference in capture rates between the two lines ( $t_{12} = 1.23$ ,  $P = 0.24$ ).

### Scavenging

Thirty-eight of 99 trapped rats (38.4%) were scavenged in spring 2002 (Table 1). Before this, scavenging had been recorded in four out of eight seasons at

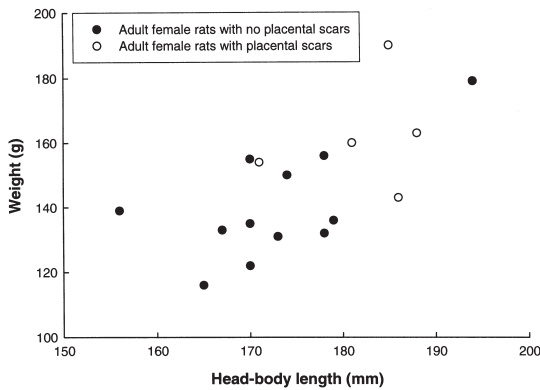
**Table 1** Morphometrics of adult female ship rats; the percentage of juvenile ship rats; the percentage of Norway rats; and the percentage of scavenged rats trapped in spring 2000, 2001, and 2002.  $N$  = Number of adult ship rats measured;  $N_1$  = number of ship rats identified to age (i.e., not scavenged);  $N_2$  = total number of ship rats and Norway rats trapped.

Year	Adult female ship rats				Juvenile ship rats (%)	$N_1$	Norway rats (%)	$N_2$	Scavenged rats (%)	
	Mean weight (g)	Mean HBL (mm)	Mean TL (g)	$N$					$N_2$	$N_2$
2000	–	–	–	0	50	6	5	7	3	39
2001	128.0	153.6	198.6	5	50	10	0	10	0	10
2002*	149.7	176.2‡	216.2†	21	41	59	6	99	38	99

\*Rimu mast-seed year.

†Significantly different from 2001 at 5% level (Mann-Whitney U test).

‡Significantly different from 2001 at 1% level (Mann-Whitney U test).



**Fig. 2** Reproductive condition, weight, and body length of adult female ship rats, Rakeahua Valley, Stewart Island, spring 2002.

a mean rate of 4.6% of trapped rats scavenged per season recorded.

### Age structure and breeding

Approximately half of all ship rats trapped in spring of all years were juveniles (Table 1). In winter 2002 one of eight (12.5%) of trapped ship rats were juveniles (95% CI = 0–2). By spring 2002, 24 of the 59 (40.7%) non-scavenged trapped ship rats were juveniles (95% CI = 17–32, Table 1) which declined to 0% ( $n = 3$ , 95% CI = 0–2) by summer 2002, then increased to one out of 10 (10%) (95% CI = 0.03–5) by autumn 2003.

In the winter of 2002 only eight rats were trapped, three of which were adult females (38%,

95% CI = 1–8). Two of these females had 12 and 18 uterine scars each, suggesting they had already produced two and three litters, respectively (Innes et al. 2001). The remaining female had not been pregnant. No pregnant ship rats were trapped in spring in any year, but in spring 2002 five of the 17 (29.4%) adult female ship rats caught had placental scars. These females were significantly heavier (172.8 versus 140.3 g, Mann-Whitney  $U = 9.0$ ,  $P = 0.03$ ), with significantly longer bodies (182.0 versus 162 mm,  $U = 10.0$ ,  $P = 0.034$ ) than females without scars (Fig. 2). The adult females caught in spring 2002 were not significantly heavier ( $U = 31.5$ ,  $P = 0.18$ ), but had longer bodies ( $U = 5.5$ ,  $P < 0.01$ ), and tails ( $U = 14.5$ ,  $P = 0.01$ ) than the females caught in spring 2001 (Table 1).

### Norway rats

Norway rats were trapped in small numbers in podocarp-broadleaf forest throughout the study period, at a mean rate of 5.3% of total numbers of rats caught per year. More Norway rats were caught in spring 2002 than in previous spring trapping periods, but the percentage of Norway rats in relation to the total number of rats caught was similar to previous years (Table 1).

### Abundant rats and heavy rimu mast seed events

Abundant rats have been reported in 4 years since 1962 (Table 2). These observations tallied with rimu mast-seed years (Beveridge 1973; Norton & Kelly 1988). There was a light rimu mast on Whenua Hou in 1999, when 8% of rimu branch tips had ripe seed in March. Abundant rats were not noted in spring

**Table 2** Rimu mast-seed years recorded on the North Island and West Coast before 1986, and Whenua Hou/Codfish Island from 1997, compared with years when abundant rats were observed or trapped on Stewart Island. ✓✓ = Double mast years; \* = heavy mast year  $\geq 1000$  seed  $m^2$  or 20% rimu seed on branch tips. R/100CTN = number of rats (R) caught per 100 trap nights (TN) corrected (C).

Year	Abundant rats reported	Rimu seed fall $\geq 150 m^2$	% rimu on tips	Abundance of rats trapped in spring (R/100CTN)
1962	✓ <sup>1</sup>	✓(*?) <sup>6,7</sup>	–	–
1974–75	✓ <sup>2</sup>	✓✓* <sup>7</sup>	–	–
1978–79	✓ <sup>3</sup>	✓ <sup>7</sup>	–	–
1985	✓ <sup>4</sup>	✓* <sup>7</sup>	–	–
1999	✕ <sup>5</sup>	–	8 <sup>8</sup>	6.7
2002	✓ <sup>5</sup>	–	27* <sup>8</sup>	66.7

<sup>1</sup>Macarthur (1962); <sup>2</sup>Buckingham (1981), Traill (1981); <sup>3</sup>Wilson (1987); <sup>4</sup>Powlesland et al. (1995); <sup>5</sup>pers. obs.; <sup>6</sup>Beveridge (1973); <sup>7</sup>Norton & Kelly (1988); <sup>8</sup>G. Elliott (pers. comm.).

1999 and the relative abundance of rats trapped in the Freshwater Valley was only 6.7/100CTN (95% CI = 3–13). After the very heavy seed fall in spring 2002, ship rats were seen several times each day, and many were trapped during daylight, which was highly unusual. Also unusual was the large number of rats that swam to most of the 20–30 boats moored 100–200 m offshore in Halfmoon Bay and Golden Bay, north-east Stewart Island, in the late winter and spring of 2002 (B. Beaven pers. comm.). Some damage was done to fittings, and in four cases wiring had to be replaced (G. Lewis pers. comm.) The species of rats were generally not identified, but the two rats killed on the Department of Conservation boat *Jester* were both *R. norvegicus* (B. Beaven pers. comm.).

## DISCUSSION

### Ship rat populations and rimu mast seed events

Ship rats in the Rakeahua Valley responded to a heavy rimu mast in early 2002 with a massive increase in abundance over the late winter and spring immediately following seed fall. The small numbers of mainly adult ship rats trapped in winter 2002 is difficult to reconcile with the numbers caught in spring, and suggests that many juveniles were not trapped in winter. Possibly, dominant rats excluded juveniles from the traps over the 3-day trapping period. The increase in abundance was due to breeding and recruitment of juveniles into the spring population, and was followed by a sharp decline in abundance by early summer.

Previous studies have shown that ship rats respond to moderate to heavy autumn beech seed falls in *Nothofagus* forest with increases in abundance due to a breeding pulse over the following winter and spring (King & Moller 1997). Ship rat abundance in the Eglinton Valley in the 1970s increased from 0.2 rats/100CTN (95% CI = 0.17–0.35) in non-seed years to 1.5 rats/100CTN (95% CI = 0.74–1.70) in seed years. Similarly, following a heavy rimu mast in mixed beech-podocarp forest of southern Fiordland in the winter and spring 2002, two ship rats were trapped for the first time after 13 440 trap nights over 21 months (Ruscoe 2004). In podocarp-broadleaf forest, ship rats became significantly more abundant after seed falls than they do than in beech forest (c. 20× versus c. 7×), probably because rats are more abundant in podocarp-broadleaf forest initially. If exponential growth curves of rat abundance were

identical in beech forest and podocarp-broadleaf forest over the same time period, the result would be substantially more animals in those forests with greater initial abundances. The absence of stoats is unlikely to affect a rat eruption on Stewart Island; even on the mainland, stoat breeding biology restricts stoats' ability to control eruptions (King & Moller 1997; Blackwell et al. 2003; Dilks et al. 2003).

Judging by the swift increase in rat abundance on Stewart Island after seed fall in May/June, ship rats were consuming rimu seed directly. Ship rats prefer rimu seed, which has a relatively large seed and fleshy aril, to other podocarp seed (Beveridge 1964).

Although food supply is the driver for rodent eruptions in New Zealand (Blackwell et al. 2003), the lack of increase in numbers of ship rats following the lighter rimu mast in spring 1999 suggests that a substantial energy input is required for rats to attain the sustained reproductive output leading to an eruption. For future predictions of eruptions a measure of the energy threshold required to initiate an eruption of rats would be useful (defined as either the minimum count of seeds falling per m<sup>2</sup>, or the percentage of seed on branch tips).

### Reasons for the decline in rat abundance

The rat population sampled in spring 2002 appeared to be entering a post-peak phase. No females were pregnant at the time of trapping; only larger, heavier adult female rats had recently been pregnant; and there was a cohort of young, non-breeding adult females entering the population (Fig. 2). The adult female rats trapped in a mast-seed year had significantly longer bodies and tails than females trapped in a non-mast year, as noted by Innes et al. (2001) for rats in a post-peak period. The adult females collected in the mast-seed year were, however, not significantly heavier than females collected in a non-mast seed year, which suggests they were beginning to lose condition. Deteriorating physical condition or density-dependent effects on reproductive behaviour may explain the lack of pregnant females in spring 2002, and either or both effects may have hastened the decline over the next 3 months. The high rate of scavenging of trapped rats, which was substantially higher than in other years on Stewart Island and has been reported elsewhere in New Zealand (Moller & Tilley 1986), suggests that the rats were under food stress, implying that a food shortage was the principal cause of the population crash. On seabird islands, where ship rats can also reach high densities,

scavenging of conspecifics is rare, probably because food is readily available (e.g., dead seabirds, insects) (G. A. Harper unpubl. data). It is also possible that other factors associated with high densities could contribute to decline in numbers, with or without a food shortage (Lidicker 1966). Social stress, leading to increased dispersal, reduced immuno-competency or an increase in disease may have hastened the decline. It is less likely that predation helped. Cats were at very low densities at the time (Harper 2002), and cannot rapidly increase in numbers when prey numbers increase.

Ship rats are susceptible to cold and wet stress (Daniel 1972; Macdonald & Barrett 1995), which will certainly hasten a decline (Blackwell et al. 2001). The spring of 2002 was cooler and much wetter than normal. At Halfmoon Bay, some 22 km away, the mean temperature over the 3 months of spring (September–November) 2002 was 0.43°C cooler than the average of 10.23°C. The weather was also substantially wetter, with 677.7 mm of rainfall recorded for the 3 spring months, almost 40% above the average of 488.8 mm (NIWA).

The diurnal activity of ship rats noted in spring 2002 would be risky behaviour, especially if efficient rodent predators such as feral cats were present. This disregard of predation risk at high density and low food availability has also been reported for mice in Australia, and has been termed the “Stalingrad effect”, invoking the behaviour of starving German soldiers during the siege of the city in the winter of 1942 (Brown et al. 1997; Ylönen et al. 2002). It may have been related to an increase in the prevalence of *Toxoplasma gondii* in the rat population. *Toxoplasma* is found in cats in New Zealand, and often cycles in a cat-rat system (McKenna 2001). Rats infected with *Toxoplasma* are significantly less neophobic, and more prone to cat predation (Webster et al. 1994).

### Rimu seeding and rat predation on native species

The observations of rats on boats after a heavy rimu seed fall strengthens the possibility that the ship rat invasion and subsequent eruption on 900 ha Taukihepa/Big South Cape Island, Pukeweka and Rerewhakaupoko/Solomon Islands (1.5 km south-west Stewart Island) in 1963, and the ensuing loss of three endemic species (Bell 1978), was indirectly due to the rimu mast of autumn 1962 (Norton & Kelly 1988). High densities of rats were reported on the east coast of Stewart Island the year before the eruption, which may have favoured dispersal of ship rats to fishing boats moored in the vicinity of Stewart

Island in the spring of 1962. All the fishing boats that moored in northern Port Pegasus were apparently infested with ship rats at this time (M. J. Daniel in Bell 1978). Rats on Stewart Island also became very abundant in several other years. For example, Norway rats were reported in large numbers in one year in the 1880s (Thompson 1922). Noticeably, abundant ship rats have been recorded in the springs and/or summers of several of the past 40 years, coinciding with rimu mast years recorded on the West Coast of the South Island (Norton & Kelly 1988) and a rimu mast year in 1962 in the North Island (Beveridge 1973) (Table 2). As mast seeding by *D. cupressinum* is synchronised across New Zealand (Schauber et al. 2002), these patterns suggest that the rats were responding to rimu seed fall on Stewart Island in these years.

Eruptions of ship rats in beech forest over winter and spring probably increase predation on native birds, and in some cases lead to local extinction (King & Moller 1997). Rats can reach higher abundances in podocarp-broadleaf forest than in beech forest, increasing the risk of associated high levels of predation on the nests of native birds by ship rats in mixed forest (Innes 1990; Innes et al. 2001). Ship rats have been implicated in the declines of several bird species on Stewart Island, and in the local extinction of mohua (*Mohoua ochrocephala*), rifleman (*Acanthisitta chloris*) and yellow-crowned parakeets (*Cyanoramphus auriceps*) (Harper 2002). The periodic eruptions of ship rats on Stewart Island after heavy rimu masts and the subsequent desperate foraging by rats as food becomes scarce in the spring suggests that heavier mast years will result in periods of particularly severe predation pressure on native birds in podocarp-broadleaf forest, particularly during nesting in spring (Cockrem 1995). Historical declines and extinctions of native birds in lowland forests of New Zealand could be re-interpreted to consider the role of past podocarp mast-induced rat irruptions. In addition, managers of lowland forest ecosystems should monitor rats and initiate rat controls, such as large-scale poisoning programmes to knock initial abundance down, in response to likely increases in rat numbers following periodic large podocarp mast-seed events.

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