

A house mouse (*Mus musculus*) population eruption in response to rimu (*Dacrydium cupressinum*) seedfall in southern New Zealand

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Abstract: We document an increase in house mouse (*Mus musculus*) abundance in a year (2002) when there was light beech (*Nothofagus* species) seedfall but very heavy rimu (*Dacrydium cupressinum*) seedfall in Waitutu Forest, southern New Zealand. On our nine study grids, mouse numbers in November were highly correlated with rimu seedfall. Feeding trials with wild-caught captive mice showed that mice typically opened the rimu nut and ate the seed (endosperm and embryo) leaving the husk. Chemical analysis showed that the nutritional content and calorific value of rimu seed was more than sufficient to sustain growth and reproduction in house mice. We conclude that the heavy rimu seedfall drove the house mouse population eruption in Waitutu Forest. Although large increases in house mouse populations in beech forest systems are well documented, this is the first description of a mouse population increase as a result of a podocarp seeding event in New Zealand. We highlight the potential risk these dynamics pose to threatened native birds living in mixed forest systems.

Keywords: *Dacrydium cupressinum*; house mouse; *Mus musculus*; rimu; seedfall.

Introduction

Mouse population eruptions in New Zealand beech (*Nothofagus* species) forests were first reported by Wodzicki (1950) and Riney *et al.* (1959). Since then many beech forest studies have documented house mouse (*Mus musculus*) population increases associated with high levels of beech seedfall (see King, 1983; Murphy, 1992; Fitzgerald *et al.*, 1996; Choquenot and Ruscoe, 2000; and Ruscoe, 2001 for review). In recent years, these studies led to the development of predictive models of mouse population increases using beech seedfall as a predictor variable (O'Donnell and Phillipson, 1996; Choquenot and Ruscoe, 2000; Ruscoe *et al.*, 2003). House mice have been indirectly implicated in the decline of many native birds (kaka, *Nestor meridionalis*; kakariki, *Cyanoramphus auriceps*; and mohua, *Mohoua ochrocephala*), as large mouse populations are causally linked to an increase in predator numbers (predominantly stoats, *Mustela erminea*) (King, 1983; O'Donnell *et al.*, 1996; Wilson *et al.*, 1998). Understanding the effect seedfall has on mouse population dynamics is the first step in predicting the subsequent effects of stoat predation on native biota.

For mammalian herbivores, nitrogen availability limits protein synthesis. Evidence comes from Bomford (1987) who suggested that protein was a limiting nutrient in wild populations of mice in Australian

grain-growing areas. Knapka (1983) and later White (2002) discuss the *quality* of protein required to sustain reproduction. Murphy (1992) showed that hard beech (*N. truncata*) seed is high in nitrogen (estimated 24% protein), other major minerals and in energy value and hence it is likely that the sudden availability of beech seed during a high seedfall year is directly responsible for the population increase. Following heavy beech-seedfall events, house mice are in better physiological condition (Ruscoe *et al.*, 2003), and the observed population increase is due to young animals entering the population (King, 1982; Ruscoe *et al.*, 2003), indicating a reproductive response to the increased food supply. We expect that such house mouse population eruptions are possible whenever there is a sudden increase in the supply of a critical resource (e.g. protein). To date, seedfall, and the parallel increase in invertebrates (Fitzgerald *et al.*, 1996; Alley *et al.*, 2001) in beech forest, have been the only resources where such a response has been quantitatively demonstrated in New Zealand forests.

In this paper we document an increase in house mouse numbers in a year of light beech but very heavy rimu (*Dacrydium cupressinum*) seedfall in Waitutu Forest, southern New Zealand. We are unaware of any previous link of house mouse population eruptions to heavy rimu seedfall. We also demonstrate that mice do eat rimu seed and that the rimu seedfall in Waitutu

Forest was of sufficient quantity and quality to induce a house mouse population eruption. Finally we consider the implications of these findings for within- and among-year mouse population dynamics in mixed forests.

Methods

Study sites and field methods

As part of a detailed forest ecosystem study, nine rodent-trapping grids were established between the Waitutu River (46°14.4'S, 167°3.9'E) and the Crombie Stream (46°15.7'S, 167°12.9'E) catchments on the south coast of New Zealand's South Island. The grids sampled three forest communities along a marine terrace sequence varying in age and soil fertility (Mark *et al.*, 1988). Three grids were on infertile soils (*c.* 300 m a.s.l.) dominated by the podocarps *Halocarpus bidwillii*, *H. biformis* and *Lepidothamnus intermedius*, and the angiosperms mountain beech (*N. solandri* var. *cliffortioides*), *Leptospermum scoparium* and *Dracophyllum longifolium*. Three grids were on intermediate-fertility sites (*c.* 100 m a.s.l.) dominated by the podocarps rimu, miro (*Prumnopitys ferruginea*) and Hall's totara (*Podocarpus hallii*), and the angiosperms silver beech (*N. menziesii*), mountain beech, kamahi (*Weinmannia racemosa*), southern rata (*Metrosideros umbellata*) in the canopy and subcanopy, and in places a dense turf of *Blechnum procerum*. Three grids were on fertile alluvial valley terraces (< 40 m a.s.l.) of the Waitutu River and Crombie Stream. The dominant canopy tree species were silver beech and kamahi, with scattered emergents of rimu and kahikatea (*Dacrycarpus dacrydioides*). Subcanopy trees included mahoe (*Meliclytus ramiflorus*), pate (*Schefflera digitata*) and tree ferns (*Dicksonia squarrosa* and *Cyathea smithii*). The understorey in most places was a dense cover of crown fern (*Blechnum discolor*).

Trapping began in May 2001 and all grids were trapped at six-monthly intervals while only a few rodents were being caught and there was very little beech seeding, *i.e.* trapping in November 2001 and May 2002. Two of the intermediate-fertility grids that were reasonably close together were also trapped in August 2002 to determine whether the rodent population was responding to the heavy rimu seedfall measured in winter 2002. Following a large increase in mouse abundance in November 2002 (confirmed by the November 2002 trapping results), all grids were trapped again in February 2003.

Each trapping grid comprised 64 Elliott live-traps set at 20-m intervals in an 8×8 array. Traps were set for 5 nights on each occasion (except August 2002 when they were set for 4 nights) and baited with a peanut butter and rolled oats mixture. Traps contained hay for

bedding and were placed inside permanently located plastic tunnels that kept rain out. Each trapped animal was individually marked with an ear tag (No. 1 Fingerling tag), and its weight, head-body length, sex and location were recorded before it was released. We used the minimum number of animals known to be alive (*MNA*; Krebs, 1966) as an index of population size. The minimum density of mice on each grid was calculated as the *MNA* / trapping grid area with a 10-m boundary (Ruscoe *et al.*, 2001), giving an area of 2.56 ha for each grid.

Potential seed food for mice was ascertained from seedfall traps. On each grid, nine seedfall traps (0.28 m²) were established in February 2001. This number was increased to 15 on the intermediate- and high-fertility sites in winter 2001. Seedfall traps consisted of a circular metal frame attached 1 m above the ground to three free-standing posts with a collection net suspended from the frame. Seedfall was collected during each trapping trip and nuts were sorted and counted by species. Seedfall for each species on each grid was converted to number of nuts m⁻² and log-transformed as in previous studies (King, 1983; Choquenot and Ruscoe, 2000; Ruscoe *et al.*, 2003).

Feeding trial

Collected nuts of rimu, miro and *Lepidothamnus intermedius* were most common in seedfall traps and therefore used in feeding trials. The nuts were brought back to the Landcare Research Animal Facility in Lincoln and fed to wild-caught house mice from Kowai Bush, Canterbury, which were being acclimatised for another feeding experiment. For one night, nuts and associated fruit of each of the three species were fed to two mice, in addition to the normal laboratory food and water they had available.

Nutritional analysis of seeds

We noted that mice opened the nut and ate only the seed, leaving the husk. As we wished to determine the nutritional value of seeds to mice, we extracted the seeds from nuts of rimu and miro collected in Waitutu Forest. Landcare Research Environmental Chemistry Laboratory analysed the chemical content of seed samples. Nitrogen, phosphorus, potassium, calcium and magnesium concentrations of the seed were assessed using a modified Kjeldahl method (Method 204) (Hill, 2000). The SGS Ngakawau Mineral Laboratory in Westport carried out a calorific assessment. As mouse population eruptions have previously only been linked to beech seedfall, we also collected mountain beech nuts from Craigieburn Forest, Canterbury, in April 2002 as there was insufficient beech seed available from Waitutu in 2002. These were analysed for comparison with rimu and miro.

Results

Field results

Only two mice were caught in the first two trapping sessions, May 2001 and November 2001, on the nine trapping grids in Waitutu Forest (Fig. 1). No animals were trapped in May and August 2002. In November 2002 mice numbers dramatically increased, along with kiore (*Rattus exulans*), ship rats (*R. rattus*) and stoats (Ruscoe, 2004). Mouse numbers were still high in February 2003.

This increase was due to breeding and recruitment of juveniles into the Waitutu population in November and February. Trapped animals ranged from very small (48 mm head-body length) to large adults (92 mm head-body length) in both months. In November, 23 females were visibly pregnant. This equated to 41% of the female population over 72 mm head-body length (the smallest recorded length of a pregnant female). Of a sample of 210 animals in November, 25 (12%) were small recruits (≤ 65 mm head-body length). The demographics had changed by February ($n = 360$), with only 5.6% females over 72 mm head body-length visibly pregnant. Small recruits made up 32% of the population. Pregnancy rates were likely to be higher as early pregnancy stages were not detected.

In 2001 there was a very light seedfall of both beech (0–9 nuts m^{-2}) and rimu (0–12 nuts m^{-2} , though one site recorded 127 nuts m^{-2}). During 2002, rimu trees in Waitutu produced a heavy seedfall (up to 2100 nuts m^{-2}). In contrast, beech did not seed heavily in Waitutu [between 8 and 360 nuts m^{-2} , equivalent to a “poor” mast year; Wardle (1984)]. The timing of seedfall also varied between the species. Ninety-eight

percent of the beech nuts had fallen by the time seedfall traps were collected on 10 May 2002, whereas an average of only 44% of rimu nuts per grid had fallen by this date. Therefore, almost 60% of the total number of rimu nuts to fall were still in the trees after virtually all beech nuts had fallen. This would indicate a difference of 2–3 months in the timing of peak seedfall between the two species. Miro nuts were also detected in seedfall traps in small quantities. We included *Lepidothamnus intermedius* nuts (collected from the low-fertility sites only) in the “rimu” totals as we found it difficult to distinguish them (*L. intermedius* was formerly included in the genus *Dacrydium*). Feeding trials showed that mice ate the seed out of *L. intermedius* nuts as they did with rimu.

The relationship between the $\ln(\text{number})$ of rimu nuts falling in 2002 and the number of mice trapped on each grid in February 2003 is shown in Fig. 2. Mouse numbers were also natural log transformed prior to calculating correlation coefficients due to increasing variation with increasing mouse number. The $\ln(MNA)$ in February was significantly correlated to $\ln(\text{rimu nut})$ ($r_7 = 0.74, P = 0.02$) and $\ln(\text{total nut})$ production (rimu + beech: $r_7 = 0.74, P = 0.02$), but not $\ln(\text{beech nut})$ production ($r_7 = 0.43, P = 0.25$).

Multiple regression using both $\ln(\text{number of rimu nuts})$ and $\ln(\text{number of beech nuts})$ as independent predictors of $\ln(MNA)$ in February 2003 showed rimu seedfall was a significant predictor of mouse abundance ($t_6 = 2.64, P = 0.03$), but beech seedfall was not ($t_6 = 1.128, P = 0.30$). Rimu and beech nut numbers explained 54% of the variation in $\ln(MNA)$ ($F_{2,6} = 4.96, P = 0.05$), but rimu nut numbers alone also explained 54% of the variation in $\ln(MNA)$ ($F_{1,7} =$

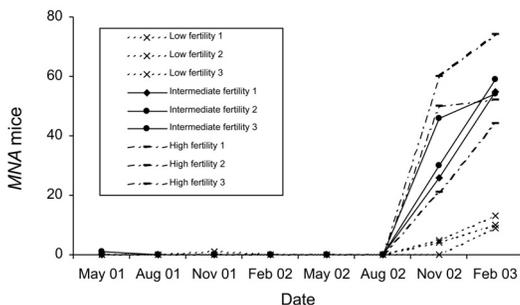


Figure 1. Minimum number of mice known to be alive (MNA) on each of the trapping grids in Waitutu Forest between May 2001 and February 2003.

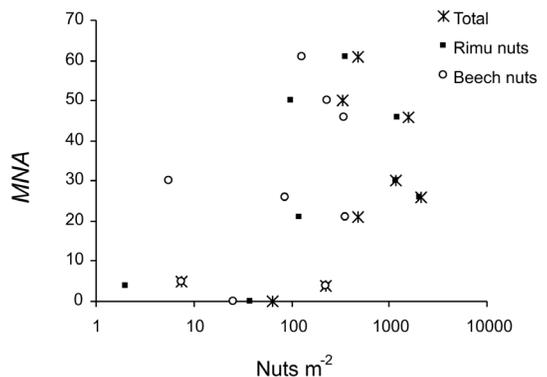


Figure 2. Relationship between nut fall (nuts m^{-2}) of rimu (including *Lepidothamnus intermedius*), beech only, and total (beech + rimu) in 2002 and the numbers of individual mice (MNA) trapped on each of the nine grids in Waitutu Forest in November 2002.

8.32, $P = 0.023$). Rimu nut numbers were a better predictor of mouse numbers in November 2002 ($r^2 = 74\%$), but this is not surprising as density-dependent mechanisms become more influential as mouse numbers increase (November to February period).

Feeding trial

In all instances, mice opened all the rimu and *L. intermedius* nuts and ate out the seed (endosperm and embryo). Miro nuts and fruit were not touched.

Seed nutrients

Rimu was average in its energy and mineral content compared with the other species sampled, except for a much higher calcium content (Table 1). Rimu was similar in protein content to hard beech (Murphy, 1992), but intermediate between miro (also collected from Waitutu) and the high protein mountain beech seeds collected from Craigieburn.

Discussion

Although it has long been known that seeding drives mouse eruptions in beech forests, this is the first time that heavy rimu seeding has been implicated as the precursor of a house mouse population eruption in forest containing a mixture of beech and podocarps. Minimum densities of mice in a red beech (*N. fusca*) forest (Eglington Valley, Fiordland) in November 1999 following a very heavy seedfall (approximately 4000 seeds m^{-2}) in March to May, were between 12 and 30 mice ha^{-1} [based on data in Ruscoe *et al.* (2001), using *MNA* per 3.24 ha to estimate density]. Densities

calculated from the present study in Waitutu were comparable (8–28 mice ha^{-1}). Previous studies have related mouse abundance to beech seedfall, but levels of beech seedfall in both 2001 and 2002 in Waitutu do not explain the observed mouse population eruption. However, we were able to relate November 2002 densities of mice to rimu seedfall over the previous six months, and observed a high breeding and juvenile recruitment rate in the population.

Implications of forests containing multiple seeding trees on among-year variation in mouse abundance

This link between podocarp seedfall and house mouse eruption has important consequences for mouse population dynamics, their predators and native birds in mixed forests. House mouse populations increased from very low numbers (virtually undetectable by our trapping) in 2001 and autumn and winter 2002 to substantial numbers in spring 2002. Similar increases in New Zealand have often been reported following heavy beech seedfall (e.g. King, 1983; Choquenot and Ruscoe, 2000; Ruscoe *et al.*, 2003), but only once in a non-beech system (King *et al.*, 1996) when mouse numbers increased in summer along road edges in a pine plantation.

Weather, specifically temperature, is believed to be the external driving force that determines the timing of heavy seedfall events (masting) in many New Zealand native species (Allen and Platt, 1990; Schaubert *et al.*, 2002). Rimu masts two years after a cool summer (the time of floral initiation) and in the year of a warm summer (Schaubert *et al.*, 2002). Beech, in contrast, masts in the year after a warm summer (requiring warm temperatures during floral initiation) (Allen and Platt, 1990). Due to the different temperature prompts, rimu

Table 1. Nutritional quality of seed collected from Waitutu Forest in May 2002 and Craigieburn Forest in April 2002. Data are mean values of three samples (\pm SD).

	Podocarps		Southern beeches	
	Rimu	Miro	Mountain beech	Hard beech ¹
Source	Waitutu	Waitutu	Craigieburn	Marlborough
No. of seeds	425	45	520	
Dry wt seed ¹ (g)	0.0031	0.0217	0.0041	
Nitrogen (%)	3.64 (0.083)	2.10 (0.161)	5.26 (0.296)	3.8
Protein ² (%)	22.75	13.12	32.87	24
Phosphorus (%)	0.47 (0.006)	0.38 (0.019)	0.81 (0.050)	0.492
Potassium (%)	0.63 (0.007)	0.61 (0.073)	0.97 (0.036)	0.459
Calcium (%)	1.16 (0.039)	0.37 (0.041)	0.38 (0.032)	0.797
Magnesium (%)	0.33 (0.006)	0.29 (0.038)	0.46 (0.022)	0.309
Energy (MJ Kg^{-1})	30.36 (0.150)	34.67 (0.168)	30.23 (0.028)	29.0

¹Hard beech data from Murphy (1992) for comparison [mineral content was for whole nuts (seed and husk), but calorific content was calculated for the seed only].

²A crude measure of protein calculated on the basis that the average protein contains 16% nitrogen (Knapka, 1983).

and beech mast asynchronously. In mixed forests, if certain summer temperature sequences occur, it is possible that heavy rimu seedfall one year will be followed by heavy beech seedfall the next. Rodent populations are then likely to be high two years in a row.

The numbers of juvenile stoats produced after a single seedfall (and mouse population eruption) is likely to be high if there is no food (rodent) shortage while (1) female stoats are implanting and maximum litter size is set during August to December (King, 2002) and, (2) they are being weaned during January to March (Powell and King, 1997). In Waitutu, rodent numbers only increased after August 2002, which may have resulted in low stoat implantation rates; but the high numbers of mice in February 2003 probably increased post-weaning survival and led to a high density of stoats during 2003. The high rodent population in February becomes the base population for a further eruption should another tree species (e.g. beech) seed heavily in the following autumn (February to May), starting the cycle over.

Within-year variation in seedfall and its implication for mouse abundance

The onset of the mouse population increase occurred later in the year in Waitutu than has been observed in beech forest. Previous studies (King, 1983; Choquenot and Ruscoe, 2000; Ruscoe *et al.*, 2001; 2003) reported rapid population increases between autumn and winter (May to August) following heavy beech seedfall. In this study, no mice were recorded in May and none on the two sites trapped in August. Wardle (1984) found that the first beech nuts fall in February or March, with peak production a month or two later (April). Beech in Waitutu Forest had dropped 98% of the total seedfall by 10 May, supporting Wardle's comment. Rimu, however, dropped mature nuts much later, with 66% of nuts still to fall after mid-May. This suggests that the peak in rimu nut production could be 2–3 months later than that of beech in this area. Ruscoe *et al.* (2003) recorded increasing mouse numbers over two successive years of heavy beech seedfall. In both years the majority of sound seed fell between February and May, and mouse numbers increased during this time to peaks in August or November, about 6–9 months after seedfall began, declining over summer. This pattern was consistent with findings of previous studies in beech forest (King, 1983; Fitzgerald *et al.*, 1996). If a similar time lag occurred with rimu seedfall and mice in Waitutu, we would not expect to detect large numbers of mice for at least 6 months from the beginning of rimu seedfall, especially as mouse numbers were increasing from undetectable levels. This may explain why mice were not caught in August. The apparent shift in the timing of peak mouse numbers may have a

large impact on predator populations. For example, with high numbers of mice during summer, there is a plentiful supply of food available for juvenile stoats that are being weaned, which would increase juvenile survival.

Seedfall as a driver of mouse population eruptions

The most obvious precursor of a mouse eruption is a sudden increase in supply of a resource that allows animals to attain reproductive condition, and for females to sustain pregnancy and lactation, which are very energy demanding (Grodzinski, 1985). Rimu seed was a plentiful nitrogenous food source that became available prior to the mouse population eruption at Waitutu. Knapka (1983) reviewed a number of studies on mouse nutrition and concluded that 12–14% of "good quality protein" was adequate for mouse growth and 17–19% was adequate for reproduction. Protein in mountain beech (33% of the seed) from Craigieburn, rimu (23%) from Waitutu and hard beech (24%; Murphy, 1992) all exceeded this level, though we have no idea of the "quality" or accessibility and digestibility of the nitrogen (protein) in any of these seeds.

All the seeds we analysed had higher calorific value than seeds of *Fagus* spp. and many other species of trees from temperate North America and Europe that are susceptible to rodent predation (see Murphy, 1992). Miller (1999) estimated that an average mouse needs 91 kJ d⁻¹ for survival. Based on our measure of 30 kJ g⁻¹ of rimu seed, a mouse needs to eat approximately 3 g (dry weight) of rimu seed per day. This equates to eating 969 rimu seeds per day if they are not eating anything else. We believe that mice can eat 969 rimu seeds daily, since they ate up to 1100 beech seeds over 24 hours in small field enclosures and over 250 beech seeds in one hour in laboratory trials (Ruscoe, *pers. obs.*). Seedfall as high as 12 000 beech nuts m⁻² have been recorded in Craigieburn forest, but the highest reported rimu seedfall has been 1600 nuts m⁻² (Norton and Kelly, 1988) and this study (2100 nuts m⁻²).

Murphy (1992) compared the concentrations of minerals of whole hard beech nuts (including the husk) with a purified mouse diet [AIN-76TM; American Institute of Nutrition (1977)] and mineral concentrations recommended by the National Research Council (1978), U.S.A. She concluded that the hard beech nuts were sufficiently nutritious for mouse growth and reproduction. The concentration of all minerals, except phosphorus, found in rimu seeds from Waitutu exceeded that of hard beech nuts. This result is not surprising as Murphy (1992) incorporated the seed and husk in analysis rather than just the nutritious seed eaten by mice. Therefore a diet high in rimu seed would provide the energy and nutritional requirements for reproduction in house mice. Miro trees produced some seed in both years, but feeding trials suggested

that the seed is not available to mice, probably because the husk is too hard for mice to bite through. It is the larger ship rats and kiore that are known predators of miro seeds (Daniel, 1973; Wilmshurst and Higham, 2004, *in press*).

Other food sources that we did not measure may have been available. For example, fungi are often found in the stomachs of mice, but our seed traps would not indicate their availability. Invertebrates are also common in the diet of mice, most commonly in the warm summer months (December–February; Fitzgerald *et al.*, 1996; Miller, 1999). It is possible that invertebrates, other nuts and fruits contributed to the measured increase in mouse numbers. However, rimu nuts and the bright red aril (fruit) attached were very plentiful on the ground in winter, much more so than any other seed-producing species.

Conclusions

We have shown that a house mouse population eruption in Waitutu Forest occurred in 2002 and was coincident with a sudden increase in the availability of a critical resource, a nitrogenous food, supplied by a heavy rimu seedfall. Rimu seed was shown to be eaten by mice and provided the major nutrients and energy required to support reproduction. The timing of seedfall was consistent with the relatively late eruption in mouse numbers relative to the timing of eruptions in pure beech forest. We conclude that the relationship between rimu seedfall in winter 2002 and the subsequent increase in house mouse numbers in Waitutu forest was causative.

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