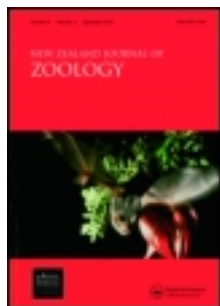


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Predicting the incidence of mohua predation from the seedfall, mouse, and predator fluctuations in beech forests

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Abstract Predator control will be required to save many mohua (*Mohoua ochrocephala*) populations from extinction. However, control may be required only in years when stoat (*Mustela erminea*) densities are high. To manage local stoat populations effectively, a reliable predictor of high risk years is required. We examined whether different levels of beech seedfall and mouse capture rates were related to the levels of mohua predation recorded in the Hawdon Valley, Arthur's Pass National Park, and the Eglinton Valley, Fiordland National Park, between 1989 and 1994. During this period there was only one full beech mast year in each study area during autumn. The full mast seedfall in Hawdon Valley was predominantly of mountain beech (*Nothofagus solandri* var. *cliffortioides*) and red beech (*N. fusca*), and in Eglinton Valley it was predominantly silver beech (*N. menziesii*). During the following summer, mouse and stoat densities, and the predation rate of adult mohua, all increased considerably. There was very little predation on adult mohua in the summers following poor seedfalls when mouse and predator densities remained low. In 1993, a partial mast did not trigger a mouse or stoat irruption.

We conclude that counts of beech seedfall and indices of mouse density are potential predictors of an impending irruption of key predators. Winter mouse density appeared to be the most reliable indicator, because neither stoats nor mice respond to seedfall alone. A combination of these indicators could be used as a basis for management decisions on whether to undertake stoat control to protect mohua populations in the future. However, more information is required on the seedfall thresholds that may trigger sufficient increases in mouse and stoat numbers and, consequently, bird predation.

Keywords mohua; yellowhead; *Mohoua ochrocephala*; beech mast; *Nothofagus*; mouse; *Mus musculus*; predator cycles; stoats; *Mustela erminea*; predation

INTRODUCTION

Studies of beech (*Nothofagus* spp.) seedfall patterns have shown that these trees periodically flower, then seed heavily. However, the amount of seedfall in any year, and the interval between full mast years, are both very variable (Wardle 1984; Allen & Platt 1990; Burrows & Allen 1991). Wardle defined the terms full mast (>4000 seeds/m²), partial mast (500–4000 seed/m²), and poor mast (<500 seeds/m²). Fitzgerald (1978), King (1982, 1983), Murphy (1992), and Fitzgerald et al. (1996) all found that mouse (*Mus musculus*) populations in beech forest increase dramatically following high seedfall. King (1983) quantified a link between increases in mouse, ship rat (*Rattus rattus*), and stoat (*Mustela erminea*) populations as a result of overwinter breeding and increased survival of rodents and high summer productivity of stoats. King suggested that there could be a flow-on effect of increasing the predation rate on birds in beech forest ecosystems.

Population declines of mohua (or yellowhead, *Mohoua ochrocephala*), have resulted from high levels of predation of nesting birds in historic times, and the mohua is now classed as an endangered

species (O'Donnell 1993). Although predator control will be required to save many mohua populations from extinction, it may be necessary only in years when stoat densities are high (O'Donnell 1993). To facilitate effective management, a reliable predictor of high risk years is required. We examined whether beech seedfall and mouse capture rates were good predictors of increased predation on mohua in the Hawdon Valley, Arthurs Pass National Park, and the Eglinton Valley, Fiordland National Park, between 1989 and 1994.

METHODS

Predator trapping and monitoring mohua

The two study areas, and the techniques for trapping predators and monitoring the breeding success of mohua, are described in detail in O'Donnell (1996), O'Donnell et al. (1996), and Dilks et al. (1996). In Eglinton Valley, 56 tunnels, each with two Fenn traps, were laid out in a 100 m grid, covering 50 ha at Deer Flat, and were used to kill-trap stoats and rats. Seventy-six tunnels, laid out in a rectangle and also spaced at 100 m intervals, were used in the Hawdon Valley. Traps were set each summer from October to March, 1990–94, in Eglinton Valley, and from December to January, 1989–94, in Hawdon Valley. Trap spacing differs from that used by King (1983), who caught stoats and rats along a single line of traps 20 km long, with up to 400 m between tunnels. Murphy & Dowding (1994, 1995) undertook live trapping of stoats in forest adjacent to the Eglinton study area.

In Eglinton Valley, mohua breeding in a colour-banded population of up to 20 groups was monitored closely. Nests were checked every 4 days through the October–February 1990–94 breeding seasons, and productivity (number of successful nests and number of fledglings/pair), female mortality, and population change between years recorded (O'Donnell et al. 1996). Breeding in Hawdon Valley was not followed closely, so only population change (number of breeding pairs) between years (1989–94) was recorded.

Beech seedfall

Beech seeds are shed throughout the year, but 70–100% usually fall between March and May, and the peak of seedfall coincides with the period of highest viability of seeds (Wardle 1984). Beech seedfall was sampled using eight seedfall trays placed in a line at c. 50 m intervals in each study area. Trays in

Eglinton Valley had a collection area of 0.279 m², and those in Hawdon Valley 0.5 m². Seedfall was collected at the end of March, April, and May from 1989 to 1993 in Hawdon and from 1990 to 1993 in Eglinton. The seeds were identified to species and counted. The viability of all seeds from Eglinton Valley was checked. In Hawdon Valley, viability of all seeds was checked in samples of up to 200 seeds. However, larger collections were subsampled (200 seeds/species/sample). Seedfall trays in Eglinton Valley were located at Knobs Flat at 360 m a.s.l., at a lower altitude than those used by King (1982, 1983), which were at 480 m a.s.l..

Mouse trapping

Mice were trapped in beech forest to provide an index of their density. Two trap lines were run in the Eglinton Valley (one at Deer Flat and one at Knobs Flat) and one in the Hawdon Valley. The Deer Flat line was 100 m in from, and parallel to, a main road running through the forest interior. The Knobs Flat and Hawdon lines were 50–100 m in from the forest edge. Each line consisted of 25 tunnels with 25 m spacing between tunnels. Within each tunnel were two mouse snap traps, each baited with a mixture of rolled oats and peanut butter. Tunnels were open at both ends and traps set to face either entrance. Netting over the entrances stopped birds from entering the tunnels. Traps were set for three consecutive nights in August, November, February, and May every year from November 1987 to February 1994 in Hawdon Valley and August 1990 to February 1994 in Eglinton Valley. During each period, traps were checked and reset daily, and the number of mice caught and traps sprung was recorded. The capture rate per hundred trap nights (C/100 TN) was calculated using the method outlined by Cunningham & Moors (1993). King (1982, 1983) used one mouse trap and one rat trap per station, and a line of 36 single-entrance boxes with 50 m spacing; thus, our results are not exactly comparable with previous work in Eglinton Valley, since trap spacing and methodology affect capture rate.

RESULTS

Beech seedfall

During the study, one full mast year and three poor mast years were monitored in each study area. One partial mast (1993) was monitored in Hawdon Valley (Table 1). During the full mast of 1990 in Hawdon Valley, seedfall was predominantly from

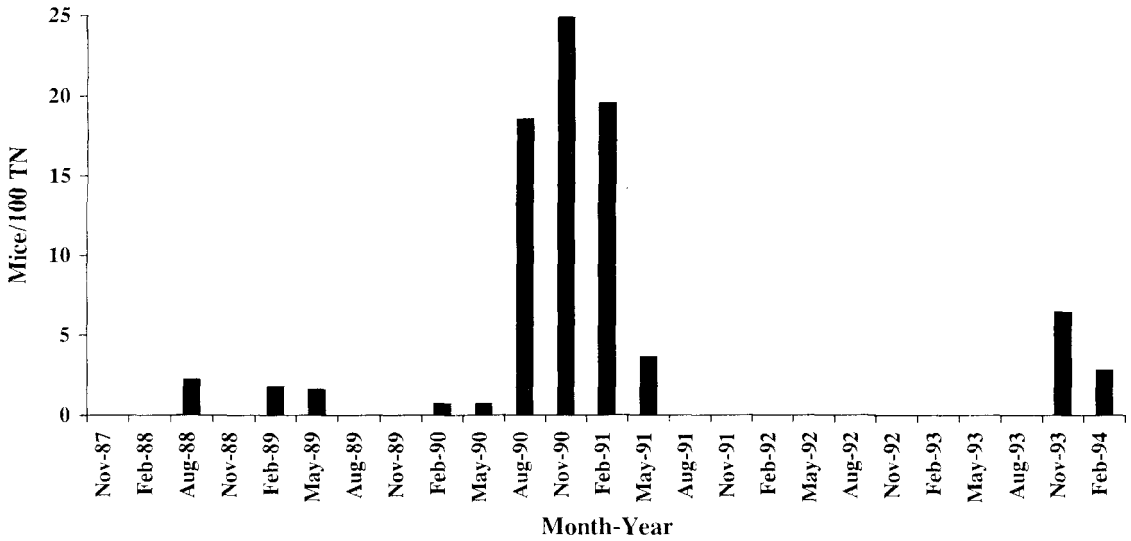


Fig. 1 Number of mice/100 trap nights, Hawdon Valley, 1987–94.

mountain beech (*Nothofagus solandri* var. *cliffortioides*) and red beech (*N. fusca*). In Eglinton Valley, the seed that fell in 1990 was predominantly from silver beech (*N. menziesii*) (Table 1). Little red beech fell despite the relative abundance of this species in the forest.

In both valleys, a high proportion of seeds (60–77%) produced during years of full and partial masts (1990 and 1993) were viable, but during poor mast years few were viable (0–8%, Table 1).

Mouse numbers

Following full mast years, mouse densities rose markedly. In Hawdon Valley, a high mouse capture rate was recorded in the August following full mast (18.5 C/100 TN) and numbers remained high through the summer with 24.8 C/100 TN caught in

November and 19.5 C/100 TN caught in February (Fig. 1). Mouse densities showed little increase in response to the partial mast in 1993 (the number caught, 6.4 C/100 TN, was only a one-quarter of that recorded during the full mast).

The pattern of mouse captures was similar in Eglinton Valley: up to 22.6 mice/100 TN were caught over the summer following full beech mast in 1990 (Fig. 2). However, whereas August mouse captures were high at Deer Flat, the capture rate at Knobs Flat did not reach a high level until November. During poor mast years in Eglinton, few mice were caught (often none) on either trap line.

Response of predators

Ship rats were caught in both study areas only immediately after a full beech mast (Table 2). Follow-

Table 1 Average number of beech seeds/m² in the Hawdon and Eglinton Valleys, March–May 1989–93.

	Hawdon Valley				Eglinton Valley			
	Seeds/m ²	SD	% Viable	% Red/Mountain Beech	Seeds/m ²	SD	% Viable	% Red/Silver/Mountain Beech
1989	183	110.7	?	?	—	—	—	—
1990	7987	2082.2	77.1	48/52	4345	3230.2	59.5	2/90/8
1991	44	15.6	0.9	45/55	2	3.6	0	0/100/0
1992	157	185.2	8.0	0/100	0	—	0	0
1993	1986	976.9	72.7	36/64	260	333.0	0.4	?

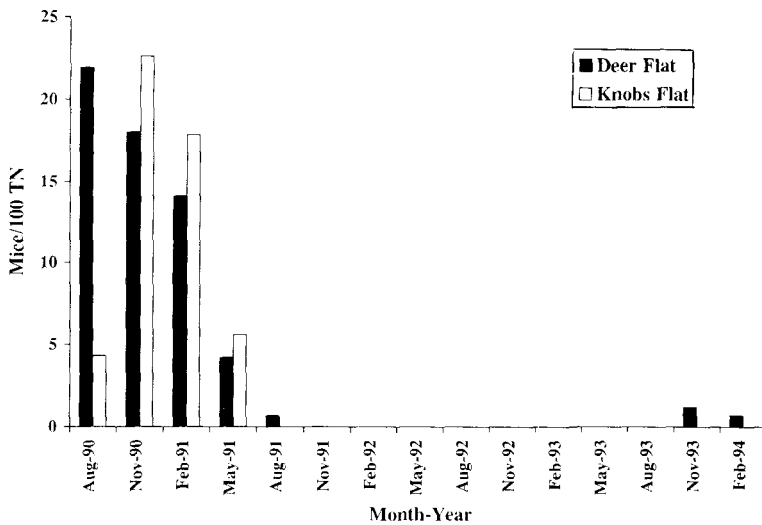


Fig. 2 Number of mice/100 trap nights, Eglinton Valley, 1990–94.

ing full beech mast in Eglinton Valley, nearly five times more stoats were caught during December and January, when the majority of mohua were breeding, than in poor mast years (Table 2). The proportion of juvenile (young of the year) stoats captured varied considerably between years but was highest (97%) during the stoat irruption in 1990/91.

Trapping effort for stoats was more variable in the Hawdon study area (Dilks et al. 1996). However, numbers of stoats caught in December and January (peak mohua breeding) during the irruption were about double that of other years (Table 3) and the overall pattern was similar to that of Eglinton Valley. The partial mast in 1993 in Hawdon Valley did

not trigger a stoat irruption the following summer, and the stoat capture rate was the lowest on record.

Impacts on mohua productivity

Productivity of mohua, and survival of adult females, were both considerably lower during the predator irruptions following a full beech mast. In Eglinton, the number of fledglings produced per pair was halved (Table 2). After the predator irruptions, all breeding pairs vanished from Hawdon Valley and only one-third of the known pairs remained in Eglinton Valley (Tables 2, 3). Direct evidence of predation on chicks and adults was gathered from Eglinton Valley, but not from Hawdon Valley. Only

Table 2 Key indicators of the relationship between beech seedfall, mouse numbers, predator numbers, and mohua productivity in Eglinton Valley, 1990–94 (Sources: 1. this paper; 2. C. O'Donnell, P. Dilks unpubl. data; 3. Dilks et al. 1996; 4. O'Donnell et al. 1996).

	1990/91	1991/92	1992/93	1993/94
Seeds/m ² (Mar–May) ¹	4345	2	0	260
Mice/100 TN (Deer Flat, Aug) ¹	21.9	0.7	0	0
No. rats/100 TN ²	0.03	0	0	0
No. stoats/100 TN (Oct–Mar) ³	0.38	0.18	0.09	0.12
Total stoats caught during peak mohua breeding (Dec–Jan) ³	49	10	4	11
Juvenile stoats (% composition) ³	97	0	50	30
Female mohua mortality (%) ⁴	40	0	0	0
Mohua productivity (fledglings/pr) ⁴	1.1	2.5	1.9	?
Number of breeding pairs (Knobs Flat) 9/3 (beginning/end breeding season) ²		3/3	7/7	6/8

two cases of predation were recorded in years with poor seedfall (one in each area), when predator numbers remained low.

Definition of predictors

The relationships between seedfall, predator levels, and mohua predation are summarised in Tables 2 and 3. Heavy beech seedfall in autumn (March, April, May) appears to be the best and earliest predictor of a subsequent increase in mohua predation. Mouse capture rates in August were also good predictors in all years, with the exception of Knobs Flat in 1990. Although high mouse captures in November also indicated high mohua predation levels, this is too late in the year to provide an early warning of high predation.

The other indicators (Tables 2, 3) either confirm that a predator irruption has happened in the recent past or is now in progress, or else they measure the response of mohua populations to predation. These can only be measured during or after the increases in predation. Although these are useful measures of the performance of predator or mohua populations, they are not useful as early predictors of increased predation on mohua.

DISCUSSION

During the study, a full beech mast triggered mouse and stoat population irruptions, and an increase in rat numbers, in both study areas and led to increased predation of mohua (this paper; Dilks et al. 1996; O'Donnell et al. 1996). These patterns were similar

to those recorded by Elliott & O'Donnell (1988) after previous stoat irruptions, when the number of mohua breeding pairs was reduced by 75% in Hawdon (1986/87) and 50% in Eglinton (1987/88).

Heavy beech seedfall in autumn was a good predictor of an increase in predation levels on mohua during the following summer. Beech trees flower in spring, but flowering itself is not a good predictor because viable seed does not always set. For example, despite obvious flowering of some beech trees, virtually no seed produced in Hawdon Valley in 1991 and 1992, or Eglinton Valley in 1993, was viable.

Although the peak mouse captures were recorded in November, high captures in August gave an earlier warning of an impending stoat irruption. In almost all cases, August mouse captures accurately predicted the subsequent stoat population level (whether it would be high or low), as they did in King's (1982, 1983) studies. The one exception to this pattern was at Knobs Flat in 1990, when a much lower capture rate was recorded than at nearby Deer Flat.

The relationship between the level of seedfall and mouse numbers requires further investigation. Although King (1983) found a good overall correlation between mice and seedfall, her data from Eglinton Valley showed increases in mice during 2 years when seedfall was lower than in the six cases of poor or partial mast for which we recorded no response by mice. King (1978) pointed out the difficulty of using seedfall records alone to predict stoat irruptions. There are three possible reasons for the discrepancy. First, King's seedfall traps were at higher

Table 3 Key indicators of the relationship between beech seedfall, mouse numbers, predator numbers, and mohua productivity in Hawdon Valley, 1989–94 (Sources: 1. this paper; 2. S. Phillipson, C. O'Donnell unpubl. data; 3. Dilks et al. 1996).

	1989/90	1990/91	1991/92	1992/93	1993/94
Seeds/m ² (Mar–May) ¹	183	7987	44	157	1986
Mice/100 TN (Aug) ¹	0	18.5	0	0	0
Rats/100 TN ²	0	0.07	0	0	0
Total stoats caught during peak mohua breeding (Dec–Jan) ^{3*}	19	30	14	11	8
Number of breeding pairs (beginning/end of summer) ²	5/7	7/0	0/1	1/1	1/1

*This index is only broadly indicative of stoat densities because trapping effort in early December varied each year (Dilks et al. 1996).

altitude than those in our study. As seedfall declines with altitude (Wardle 1984), it may take smaller seedfalls to trigger increases in mouse numbers at higher altitudes. Second, the impact of seedfall on mice might also depend on which beech species is seeding heavily in any one year. Red and silver beech are both common in Eglinton Valley. During King's studies, most seedfall was of red beech, but during our study, silver beech was the major component, and little red beech seed fell. As red beech seeds are much larger than those of silver beech, it may take fewer red beech seeds to trigger a mouse irruption. Third, stoats were removed monthly throughout the year in King's study. If mice were thereby released from high predation pressure, their populations may have been free to respond to a lower level of seedfall than in our study (King 1985, C. M. King pers. comm.).

More information is needed to determine if there is a graded or an all-or-nothing response by stoats to the density of mice available each year, and how removal of significant numbers of stoats might influence rodent cycles. In a different situation, predator removal (of cats, *Felis catus*) led to an increase in rat numbers (Fitzgerald 1988).

Predicting the frequency of predation cycles based on mast years may not be possible, as the periodicity of full beech mast appears to vary between beech species, latitudes and altitudes, and in different climatic conditions (Allen & Platt 1990). The extent of this variability is still not fully understood, nor do we have any understanding of the full set of circumstances precipitating elevated levels of predation of forest birds. For example, both study areas contained mixed beech forests, with more than one species seeding at once, although in each area only one species produced a significant proportion of the seed. Because beech seedfall in mixed forests is often dominated by one species in any one year, it is possible that in forests with only one beech species, full mast years are much rarer than in forests containing a mixture of two or three species. In pure silver beech forest in the Takitimu Mountains, there was only one full mast (sensu Wardle 1984) in 18 years, but five heavy partial masts (Burrows & Allen 1991). Therefore, mixed beech forests may have mouse/predator irruptions more often than single species forests. Such a pattern could explain why mohua still remain in relatively high numbers in the pure silver beech forests of the Blue Mountains and the Catlins in Southland. Similarly, if red and silver beech had both seeded heavily in Eglinton during the

last full mast, would the increase in predators and resulting predation have been even greater?

Wardle's (1984) definitions of full mast, partial mast, and poor mast were appropriate categories for predicting a predator irruption in this study, although more information from years with partial masts is required before definite conclusions can be drawn. In addition, if lower levels of red beech seedfall were sufficient to trigger mouse irruptions (cf. the much smaller seeded silver or mountain beech) during King's (1982, 1983) studies, then predictors may need to take into account both seedfall level and beech species represented in that seedfall. The sorting and counting of large numbers of beech seeds is extremely time consuming and not always practical for field managers who have to undertake predator trapping programmes. Weighing seedfall samples could reduce this workload, and this should be investigated in the future.

In conclusion, we found that both the amount of beech seedfall and indices of mouse density were potential predictors of an impending irruption of key predators. Winter mouse density appears to be the most reliable indicator, because neither stoats nor mice respond to seedfall alone. Other factors, such as the history of predator removal (King 1985) and forest insect densities (Fitzgerald et al. 1996), may also have a critical effect on mouse numbers. Stoat control can increase the productivity of mohua and probably other hole-nesting forest birds significantly (O'Donnell et al. 1996); therefore, a combination of these indicators could be used as a basis for management decisions on whether to undertake stoat control to protect mohua populations. However, more information is required on the seedfall thresholds that may trigger sufficient increases in mice and stoat numbers and, consequently, bird predation.

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