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## THE EFFECTS OF A NATURAL INCREASE IN FOOD SUPPLY ON A WILD POPULATION OF HOUSE MICE

**Summary:** Changes in density and breeding of the house mouse (*Mus musculus*) in a New Zealand forest dominated by hard beech (*Nothofagus truncata*) were monitored for 2.5 years. Mice bred during winter and increased dramatically in density only during a beech mast year. Mice readily ate the endosperm and embryo of hard beech seed in the laboratory and chemical analysis showed it to be a very nutritious food source, similar in quality to *Fagus* beech seed in the northern hemisphere. Thus the mouse, introduced to New Zealand, responds to a *Nothofagus* mast year in a similar way to other rodent species in the northern hemisphere during a *Fagus* mast year.

**Keywords:** house mouse; *Mus musculus*; mast year; beech seeds; hard beech; *Nothofagus truncata*; nutrient analysis.

### Introduction

In New Zealand beech forests (*Nothofagus* spp.), huge production of seeds occurs irregularly and infrequently; when this phenomenon occurs it is called a mast year (Wardle, 1984; Poole, 1987; Allen and Platt, 1990). Riney *et al.* (1959) first suggested that house mice (*Mus musculus* L.) and kiore (*Rattus exulans* Peale) may dramatically increase in numbers in response to these mast years. Studying mouse populations in *Nothofagus* forests, Fitzgerald (1978) and King (1982, 1983) both found a positive correlation between the intensity of seeding and abundance of mice. However, until mice are shown to eat *Nothofagus* seeds, and that these seeds are nutritious, this relationship cannot be said to be causal.

Mast years also occur in northern hemisphere beech forests (*Fagus* spp.) (Gysel, 1971; Nielsen, 1977). Most rodent species in these forests belong to the genera *Apodemus* (Muridae) and *Clethrionomys* (Cricetidae). Seeds are an important part of their diet, and both the survival and breeding of these rodents have been shown to be affected by the magnitude of beech seed production (Bergstedt, 1966; Jensen, 1982).

Seeds of the northern hemisphere beech, *F. sylvatica*, are a highly nutritious food source (Jensen, 1982), but the nutritional quality of *Nothofagus* seeds was unknown. Therefore, the aim of this study was (i) to monitor changes in density and breeding of mice in a New Zealand forest dominated by hard beech (*N. truncata*) during a beech mast year; (ii) to determine if mice do eat hard beech seeds; and (iii) to determine the nutritional value of hard beech seeds.

### Methods

#### Study area

The study area was situated in Iwituaroa Reserve (41°16'S, 173°56'E), in the Marlborough Sounds, New Zealand. The reserve is 710.6 ha in area and the flora has been described by Walls (1984). Plant nomenclature follows Allan (1961) and revised names follow Connor and Edgar (1987). Approximately 30% of the study area was covered by pure hard beech canopy, 35% by coastal broadleaf species (e.g., *Meliclytus ramiflorus*, *Pseudopanax arboreus*, *Coprosma robusta* and *C. lucida*), 10% by a mixture of hard beech and coastal broadleaf species, and 25% by a mixture of tawa (*Beilschmiedia tawa*), pukatea (*Laurelia novae-zelandiae*) and kiekie (*Freycinetia baueriana*).

In September 1985, there was a profuse flowering of hard beech trees at Iwituaroa Reserve and it appeared likely that 1986 would be a beech mast year.

#### Seed collection

Nine Beveridge seed trays (Wardle, 1970) were placed in two areas of hard beech in Iwituaroa Reserve. Five trays were placed just below a ridge line and four were placed on a steep face (all trays were 50-100 m from the mouse snap-trap line - see below). Individual tray area was 0.28 m<sup>2</sup> and each tray was suspended between poles about 1 m above the ground. The trays were emptied monthly from February 1986 to January 1987; twigs, leaves and seed capsules were removed and the seeds were then weighed and counted. Viability was assessed

by the ethanol soak method of Ledgard and Cath (1983). This method was checked by opening 100 'viable' and 100 'non-viable' seeds, and examining for the presence of endosperm.

A 1 m<sup>2</sup> plot was also marked on the forest floor near each seedfall tray to determine the timing of beech seed germination (i.e., when seed ceased to be a potential food for rodents) in relation to when the seed fell. All beech seedlings in the plots were removed and counted at monthly intervals.

### Feeding observations

In March 1986, nine mice were live-trapped in the study area and brought to the laboratory. Mice were caged singly in a room with photoperiod of 12 h light, 12 h dark, temperature 20± 1°C and fed Diet 86 pellets (Howie, 1952) for 2-3 weeks. Three trials were undertaken and no mice were used for more than one trial:

- 1) five mice were each provided with 12 hard beech seeds to see if they would eat them;
- 2) two mice were fed a weighed amount of hard beech seed to calculate how much and which part of the seed they ate;
- 3) in a simple food preference test, two mice were not fed for 12 hours and then presented with pellets, wheat and hard beech seeds (approximately 2 g of each).

### Analysis of viable hard beech seeds

Nitrogen content was determined by Kjeldahl analysis (Metson, 1972). Samples of both whole seeds and pericarp only were oven-dried at 40°C for 24 h, ground, and then dried for a further 4 h at 105°C. The ammonium ion concentration was measured using an ammonium electrode connected to an ion analyser.

A Parr 1411 combustion calorimeter (Parr Instrument Company, Moline, Illinois, U.S.A.) was used to measure the caloric content of both whole seeds and pericarp only. Seeds were ground, freeze-dried and samples of approximately 0.2 g were combusted according to the instructions in the manual.

A Philips PW1404 Automatic Sequential X-Ray Spectrometer was used to measure the concentration of 11 minerals in hard beech seeds. A sample of over 200 whole seeds was prepared for the spectrometer by oven-drying (24 h at 40°C), grinding, and pressing into a 5 g pellet.

### Snap-trapping

To provide an index of mouse abundance, and to assess demographic changes, mice were snap-trapped (Ezeset Supreme mouse traps, Australia) using a 1.8 km trap line situated within 20 m of a coastal walking track. The

ninety traps were 20 m apart and baited with a mixture of rolled oats and peanut butter. Traps were checked and re-set each morning for three consecutive days. Traps were left in place permanently and had metal covers to protect them from the weather and to reduce trap disturbance by other animals. Trapping was initially undertaken at monthly intervals from September 1984 to November 1984; then six-weekly intervals from April 1985 until February 1986 and then three monthly intervals until trapping ended in February 1987.

Results are expressed as the number of mice caught per 100 trap nights. A correction for unavailable traps was made by subtracting half a trap night for each trap sprung (Nelson and Clark, 1973). The corrected trap success provides a relative index of mouse abundance and at low capture frequencies (below 20 mice per 100 trap nights) is linearly related to population density (Caughley, 1977).

Total length, body length (British Museum New Method of Jewell and Fullagar, 1966) and weight were measured for each animal. For females the following were recorded: uterus size (thread, string, cord or pregnant), presence or absence of lactation, number of embryos and number of uterine scars. Litter size was determined by the number of viable embryos (Pelikan, 1981). Female mice were considered sexually immature if they had thread uteri (Laurie, 1946) and currently breeding if they were pregnant or lactating. The presence of uterine scars was taken as a sign of past breeding. For males, the visibility of tubules in the cauda epididymis was taken as a sign of sperm production (Laurie, 1946).

Mice were assigned age classes by the degree of wear on the upper molar teeth (Lidicker, 1966). Age estimates given by Lidicker for his toothwear classes were similar to those for mice in the Marlborough Sounds (Murphy, 1989) and were used in this study. Mice were considered adults from age class 3 (2-4 months old), as this was the earliest age class in which breeding was detected (Murphy, 1989).

### Statistics

Means and one standard error are expressed unless otherwise stated. Probability less than 0.05 is considered significant.

## Results

### Beech seedfall

From February 1986 to January 1987, 8652 hard beech seeds, weighing in total 138 g, were collected from nine seedfall trays (equivalent to 3433 seeds m<sup>-2</sup> yr<sup>-1</sup>) of which 68% was viable (Table 1). The first ripe seeds dropped in February (although green seed capsules were

Table 1: The mean ( $\pm 1$  SD) hard beech seedfall collected from nine seedfall trays between February 1986 to January 1987.

Month	Density of seeds (m <sup>-2</sup> )	% Viable seed
February	526 $\pm$ 324	68
March	2232 $\pm$ 652	70
April	358 $\pm$ 255	56
May	115 $\pm$ 63	59
June	127 $\pm$ 74	71
July	47 $\pm$ 33	72
August	14 $\pm$ 7	72
September	6 $\pm$ 6	75
October	3 $\pm$ 2	14
November	0	0
December	0	0
January	6 $\pm$ 7	43

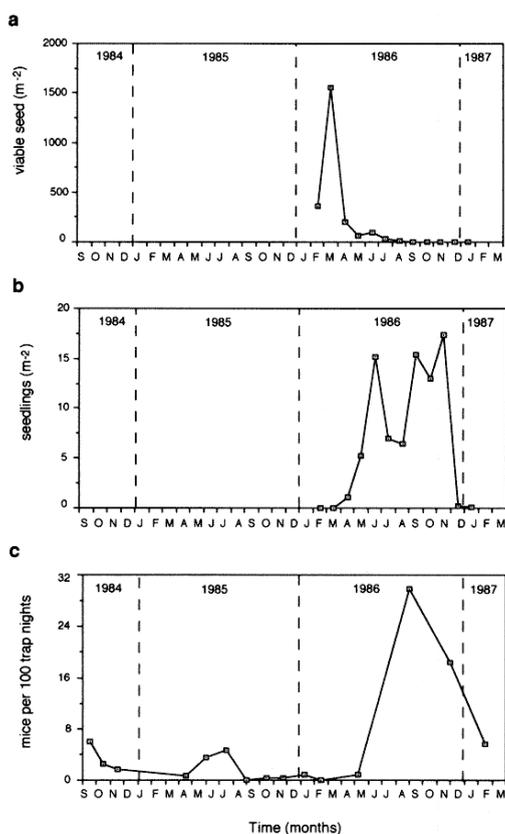


Figure 1: a) The amount of viable hard beech seed collected from the seedfall trays (February 1986 to January 1987). b) The number of beech seedlings collected from the seedling plots (February 1986 to January 1987). c) The number of mice caught per 100 snap-trap nights from September 1984 to February 1987.

found in January after strong winds), with peak fall one month later (Fig. 1a). Seedfall then declined, with very little occurring after June.

Seedlings up to one month old were found from April 1986 to January 1987. Most germination occurred in May and from September to November (Fig. 1b). In the 12 months following the first ripe seed fall, there were 81.1 seedlings m<sup>-2</sup>. Over the same period 2335 viable seeds m<sup>-2</sup> fell, leading to an approximate germination rate of 3.5%. This still left a large potential food source available for mice.

#### Feeding observations

- 1) All five mice ate at least part of the hard beech seeds provided.
- 2) Two mice were fed 0.471 g and 0.457 g of hard beech seed; both ate the endosperm and embryo from the seeds but left the pericarp. The amount of pericarp left was 0.240 g and 0.232 g respectively, indicating that the nutritive (edible) part of the seed makes up about 49% of the total weight.
- 3) The two mice presented with pellets, wheat and beech seeds, ate the nutritive material from the beech seeds before eating the wheat or pellets.

#### Analysis of hard beech seeds

Four samples of whole seeds were tested for nitrogen content. The samples yielded 2.42, 2.29, 2.41 and 2.45% dry weight (dwt) nitrogen (average = 2.39  $\pm$  0.03%). Two samples of pericarp tested for nitrogen content yielded 1.01 and 0.98% dwt nitrogen (average = 1.00%). From these values and assuming that the nutritive material is about 49% of the weight of beech seed, it was calculated that the approximate value of nitrogen in the nutritive material is 3.84% dwt. A crude protein content of 24% for the nutritive material can be calculated on the basis that the average protein contains 16% nitrogen (Knapka, 1983).

Two samples of whole seeds were analysed for caloric content. The values obtained were 24.15 and 23.98 kJg<sup>-1</sup> dwt (average of 24.07 kJg<sup>-1</sup> dwt). Three samples of pericarp were also analysed for caloric content. The values obtained were 19.67, 19.47 and 19.0 kJg<sup>-1</sup> dwt (average of 19.38  $\pm$  0.16 kJg<sup>-1</sup> dwt). From these values it was calculated that the approximate caloric value of the nutritive material (49% of whole seed) is 29.0 kJg<sup>-1</sup> dwt.

The concentrations of 11 minerals in whole hard beech seed were determined. Concentrations of eight of these minerals were compared with those reported for three diets known to produce acceptable growth and reproduction in laboratory mice (Table 2). Levels of all eight minerals were higher in beech seed than in two of the diets; in the third case (the natural diet), four were higher in beech seed and the other four were between

Table 2: The concentrations of 11 minerals present in whole hard beech seeds and in mouse diets known to be adequate for survival and reproduction; a natural ingredient diet (Knapka et al., 1974), a purified diet, AIN-76™ (American Institute of Nutrition, 1977) and recommended concentrations from the National Research Council (NRC), 1978.

Minerals	Beech seeds	Mouse diets		
		Natural	AIN-76™	NRC
Calcium (%)	0.797	1.23	0.52	0.4
Phosphorus (%)	0.492	0.99	0.4	0.4
Potassium (%)	0.459	0.85	0.36	0.2
Magnesium (%)	0.309	0.18	0.05	0.05
Sulphur (%)	0.166	-	-	-
Aluminium (%)	0.004	-	-	-
Chloride (%)	0.003	-	0.16	-
Zinc (mg kg <sup>-1</sup> )	623.0	50.3	30.0	30.0
Manganese (mg kg <sup>-1</sup> )	544.4	104.0	54.0	45.0
Iron (mg kg <sup>-1</sup> )	100.7	255.5	35.0	25.0
Copper (mg kg <sup>-1</sup> )	17.0	16.1	6.0	4.5

40-65% of the reported levels. These results suggest that mineral levels in hard beech seed are adequate for growth and reproduction in mice.

### Mouse abundance

From September 1984 till May 1986, the number of mice caught was less than six mice per 100 trap nights (Fig. 1c). In August 1986, following the peak of beech seedfall in March 1986 (Fig. 1a), there was a dramatic increase in the number of mice (to 30 mice per 100 trap nights) (Fig. 1c). Since snap-trapping was only undertaken every three months, the actual peak in mouse density could have occurred at any time between June and October. The proportion of old mice (> 6 months) in the population did not differ significantly in the seed year (4.4%, n=90) from the preceding year (13.6%, n=22) ( $\chi^2 = 2.5$ , d.f. = 1,  $P > 0.1$ ; Table 3), implying the increase in mouse abundance was due to

Table 3: The percent of mice in each age group caught in snap-traps from autumn 1985 to summer 1986/87. 1986 was a seed year, n = sample size.

	Age (months)				n
	1-2	2-4	4-6	>6	
Autumn 1985	10	40	30	20	10
Winter 1985	0	38	50	13	8
Spring 1985	50	0	50	0	2
Summer 1985/86	0	0	100	0	2
Autumn 1986	0	50	50	0	2
Winter 1986	42	42	14	3	36
Spring 1986	42	34	18	5	38
Summer 1986/87	0	43	50	7	14

recruitment of young mice, rather than immigration of adult mice. No young mice (1-2 months old) were caught in the winter preceding the seedfall but they represented 42% of mice caught in the winter after the seedfall (Table 3).

### Mouse breeding

No breeding was detected in any of the 11 adult females caught in autumn and winter 1985, preceding the mast year. However, in autumn and winter 1986 (after the autumn beech seedfall), 12 out of 14 adult females were either pregnant or lactating. Although mice bred in autumn and winter, breeding was depressed in the following spring and summer. In November, none of seven adult females caught showed any signs of present breeding and only two showed signs of past breeding (i.e., uterine scars). By February 1987, three of nine adult females caught were breeding but the other females showed no signs of present or past breeding.

The delay in sexual maturation normally experienced for females during the colder months was not seen after the seedfall. In 1985, before the mast year, only one of five females 2-4 months old was parous (pregnant or with uterine scars) from April to August, compared to all seven females 2-4 months old caught after the seedfall (Fisher's Exact test,  $P = 0.01$ ).

## Discussion

### Seedfall

The annual seed fall in New Zealand beech forests averages 1000 to 2000 seeds m<sup>-2</sup> but varies considerably, and can range from over 13000 to 1 seed m<sup>-2</sup> (Wardle, 1984). Seasons are usually described as 'full', 'partial' or 'poor' mast years, depending on the quantity of seeds produced. Wardle (1984) suggests a 'full' mast year is one during which more than 4000 seeds m<sup>-2</sup> are produced, 'partial', 500 to 4000 and a 'poor' mast year is one producing less than 500 seeds m<sup>-2</sup>. The quality of the seed is related to the size of the seed crops, a higher proportion of viable seed being recorded from years with maximum production (Allen and Platt, 1990; Poole, 1965; Wardle, 1967; Wardle, 1984). Long-term studies (shortest duration 16 years) of beech seed-fall in black, mountain (*N. solandri* var. *cliffortioides*), silver (*N. menziesii*) and red (*N. fusca*) beech forests show that viable seed ranges from 53.5 to 68.3% in full mast years, from 33.3 to 45.1 % in partial mast years, and from 3.5 to 15.2% in poor mast years (Wardle, 1984). Although in my study, the 3433 seeds m<sup>-2</sup> was slightly less than Wardle's (1984) full mast year definition, the high seed viability (68%) in my study area suggests that 1986 could be considered a full mast year.

Pre-winter germination can occur in all New Zealand beech forests but is mostly limited to the North Island and to altitudes below 600 m (Fitzgerald, 1978; Wardle, 1984). At low altitudes, most seeds germinate within a relatively short time; Wardle (1984) found that 75% of the seed that germinated did so within 32 days at 50 m altitude while at altitudes over 1040 m, it took more than 62 days. In this study, germination peaks were recorded in autumn and in spring and it took over 180 days (April to October) for 75% of the seed that germinated to do so.

The percent of seeds which germinate is dependent on the degree of shade, shelter and soil type; in the field it can vary between 0 - 40% (Wardle, 1984). The germination rate found in my study is a minimum estimate. There was a paucity of undergrowth in the beech forest (because of browsing by deer and pigs), so new seedlings could have become desiccated and died before they were counted. Early seedling survival and establishment is also affected by defoliation or stem girdling by insects (bare stems found in the seedling plots were included in the germination counts), attack by fungi, frosting, smothering by litter movement, rain-wash on bare soils, and uprooting by ground-feeding birds (Kirkland, 1961; June and Ogden, 1975; Wardle, 1984). Mice and rats may also eat cotyledons.

#### Feeding observations and beech seed analysis

The preliminary feeding trials described here showed that wild-caught mice ate the endosperm and embryo but not the pericarp of hard beech seeds. The energy and nitrogen content of the nutritive material, 29.0 kJ g<sup>-1</sup> dwt and 3.8% dwt nitrogen, is comparable to the 29.4 kJ g<sup>-1</sup> dwt and 4.78% dwt nitrogen for *Fagus sylvatica* (Jensen, 1982) and 27.7 kJ g<sup>-1</sup> dwt for *F. grandifolia* (Gysel, 1971). The average caloric value of nutritive material from 27 tree-seeds from the temperate zone of Europe and North America was 25.6±0.8 kJ g<sup>-1</sup> dwt (Grodzinski and Sawicka-Kapusta, 1970). The nutritive material from northern (*F. sylvatica*, *F. grandifolia*) and southern (*N. truncata*) beech seeds thus have a higher energy content than average.

Reviewing a number of studies on mouse nutrition, Knapka (1983) concluded that a concentration of 12 to 14% of "good quality protein" was adequate for growth of mice and that 17 to 19% was adequate for reproduction. The amount of protein estimated to be present in nutritive material of hard beech seeds in this study (24%) should therefore be adequate for reproduction. The required concentration of protein is at least in part dependent on the amino-acid profile of the protein but amino-acid requirements for reproduction in mice have not been reported (Knapka, 1983).

The concentrations of at least eight minerals assayed in beech seeds compared favourably to the

concentrations from three known adequate diets (Table 2). Batzli (1986) provided experimental evidence that mineral deficiencies could cause a decline in rodent reproduction, calcium being particularly important. Calcium levels in hard beech seed were higher than in a purified diet (American Institute of Nutrition, 1977) and those recommended by National Research Council (1978) and were therefore adequate for growth and reproduction. However, quantitative requirements have not been established for most of the minerals that have been shown to be required by mice (Knapka, 1983). Nutrient concentrations of diets that have produced acceptable survival and breeding thus provide the only reliable estimate of the requirements.

#### Mouse abundance

The heavy beech seeding led to increased mouse abundance, as reported by Fitzgerald (1978) and King (1983). This increased abundance was due to winter breeding by both young and old females and by recruitment of their young. The delay in sexual maturation normally experienced by young female mice in autumn was also not observed and this led to a larger breeding population. In contrast, mice were both snap- and live-trapped in adjacent areas without beech forest over the same period, but there mouse abundance remained fairly stable and no breeding mice were ever trapped in winter (Murphy, 1989, and unpublished). These findings are very similar to those of Jensen (1982) for the bank vole, *Clethrionomys glareolus*, following *Fagus sylvatica* mast years in Europe.

Fitzgerald (1978) reported that there was a strong correlation between the amount of *Nothofagus* beech seed produced in autumn and the number of mice present in late spring. In one of the heaviest beech seed falls (over 2000 viable seeds m<sup>-2</sup>), he measured a peak capture rate of about 12 mice per 100 trap nights in November. This was much lower than in my study after a similar seedfall, where 30 mice per 100 trap nights was measured in August. Although trapping regimes were not identical in the two studies, the difference between capture rates is large. One possible explanation is that most of the beech seed in Fitzgerald's study area germinated in the autumn, so the extra food supply was available for a shorter period.

Although King (1983) found an overall significant positive correlation between *Nothofagus* seedfall and the total number of mice per 100 trap nights, there were individual inconsistencies. In the 1976 and 1979 'seedfall years' in the Eglinton valley, the mean seedfall was 22 viable seeds m<sup>-2</sup> and 104 viable seeds m<sup>-2</sup> respectively. However, mouse numbers recorded in spring were higher in 1976 (20.9 mice per 100 trap nights) than in 1979 (12.8 mice per 100 trap nights). Both the 1976 and 1979 seedfalls would have been poor

mast years by Wardle's (1984) classification, yet both resulted in mouse numbers similar to those found after very much higher seedfalls (King, 1983; the present study). This suggests that factors other than amount of beech seedfall are also important in regulating mouse numbers.

In the present study, the peak in mouse abundance was three to seven months after most of the beech seed fell. Such a delay is not unexpected as there would be a lag phase before the mouse population responds to the increased food supply. As most seed did not germinate until the following spring, a potential food source was available throughout winter. Peak mouse numbers following beech mast years in other New Zealand studies were detected from August (as in this study) to the following February (Fitzgerald, 1978; King, 1983). King (1983) suggested that predation may explain the variations in the timing of mouse peaks seen in *Nothofagus* forests. Jensen (1982) also found a delay of between 9 to 12 months in the time of peak abundance of rodents following *Fagus sylvatica* mast years.

#### Mouse breeding

As was found in previous studies (Fitzgerald, 1978; King, 1982), mice bred during the winter after a beech seedfall; however breeding was depressed the following spring and summer. King (1982) also recorded a breeding decline in two very dense mouse populations (77 and 69 mice per 100 trap nights) in the November following a seedfall. This breeding depression may have been due to a decline in the food supply, as this has been shown to affect mouse reproduction (Bomford, 1987; Bomford and Redhead, 1987; Marsteller and Lynch, 1987; Perrigo and Bronson, 1985). However, in my study viable seeds were present until at least November, so there were seeds available to mice in spring.

In previous New Zealand studies in *Nothofagus* forests, few young mice entered the population after spring in a beech mast year, though breeding continued (Fitzgerald, 1978; King, 1982, 1983). Peak populations in these studies consisted mainly of mice older than 6 months, still breeding, but without significant recruitment. This pattern did not occur in my study, where the peak population consisted of mostly young animals. As expected, the distribution of age classes did shift upwards after the population had already started to decline, but the population still consisted mainly of mice younger than 6 months.

#### Conclusion

Masting in trees has been suggested to be an anti-predator adaptation that satiates seed predators with more seeds than they can consume in mast years and limits them in non-mast years by starvation (Janzen,

1971; Silvertown, 1980). There are few records of flowers or seeds of New Zealand beeches being attacked by organisms such as arthropods or fungi, and examination of the seed reveals few if any insect emergence holes (Wardle, 1984). Wardle (1984) suggests that the intermittent nature of flower development and seed production in New Zealand beeches works against the development of a fauna specifically evolved to occupy these niches. However, the introduced house mouse, with its potential to reproduce quickly, appears to have been able to take advantage of this periodic food source.

There is a need to know more about the relationship between beech seedfall and mouse abundance. In spite of the fact that King (1983) found an overall correlation, her data from the Eglinton Valley clearly show a considerable response by mice in some years of low seedfall. There are obvious management implications; Elliott and O'Donnell (1988) found that yellowheads (*Mohoua ochrocephala*) suffered population crashes in response to stoat irruptions after mouse 'plagues'. It is therefore important to know whether a relatively low seedfall threshold exists; mouse (and hence stoat) numbers appear to respond as much to a seedfall of 100 viable seeds m<sup>-2</sup> as to 2000 viable seeds m<sup>-2</sup> (King, 1983). It is also important to determine what other factors can regulate mouse abundance.

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