

Predation of beech seed by mice: effects of numerical and functional responses

WENDY A. RUSCOE*, JOSEPH S. ELKINTON†, DAVID CHOQUENOT‡ and ROBERT B. ALLEN*

*Landcare Research, PO Box 69, Lincoln 8152, New Zealand; †Department of Entomology, and Graduate Program in Ecology and Evolutionary Biology, University of Massachusetts, Amherst, Massachusetts 01003, USA; and ‡Landcare Research, Private Bag 92170, Auckland, New Zealand

Summary

1. The functional response of post-dispersal seed predators (house mouse, *Mus musculus*) to absolute densities of southern beech seed (*Nothofagus solandri* var. *cliffortioides*) was studied in laboratory and field trials. House mice showed a Type II (hyperbolic) functional response to seed availability and this was not modified by the presence of an alternative food source.
2. Maximum daily intake rate of beech seeds during field trials averaged 1042 seeds mouse⁻¹. This is sufficient to provide house mice with both the energy and protein required for growth and reproduction.
3. We explicitly incorporated the functional response into the numerical response of house mice to beech seed, measured for field populations monitored in a New Zealand beech forest. House mice showed a strong numerical response to beech seed intake rate that was modified by some density-dependent mechanism(s).
4. We developed a model that simulated seedfall, house mouse population growth and seed reserve depletion over one year. We found that the previously reported decline in house-mouse populations in beech forests during spring and summer is likely to be related to spring beech seed germination that renders seed no longer available as a food source for house mice.
5. From our simulation model it does not appear that house-mouse populations can completely eat-out beech seed reserves prior to germination in a year of large seedfall. ‘Masting’ behaviour in New Zealand native beech trees is therefore sufficient to satiate an eruptive population of an exotic mammalian omnivore, despite the lack of a long co-evolutionary interaction.

Key-words: *Mus musculus*, *Nothofagus solandri* var. *cliffortioides*, predator satiation, simulation model.

Journal of Animal Ecology (2005) **74**, 1005–1019
doi: 10.1111/j.1365-2656.2005.00998.x

Introduction

Predation of seeds, once they have been shed by the parent tree (post-dispersal predation), is thought to play an important but largely unknown role in colonization ability, seedling establishment and ultimately the spatial distribution of trees (Price & Jenkins 1986; Hulme 1993, 1996, 1998). The capacity of a rodent population to affect seed reserves at the scale of a forest will depend

on whether, and if so how frequently, the overall rate of seed consumption exceeds the rate of seed production. The intermittent mass production of seeds (so-called ‘masting’ events) is often invoked as a strategy evolved by some plant taxa to overwhelm the capacity of seed predators to consume all seed (predator satiation) (Janzen 1971; Silvertown 1980; Kelly & Sork 2002). The success of such a strategy will depend partly on the length of period over which seeds are vulnerable to predators, relative to the speed with which the predators can adjust their overall seed-consumption rate. The prevailing rate of seed consumption by rodents will be the product of (1) the per capita rate at which they

Correspondence: Dr Wendy Ruscoe, Landcare Research, PO Box 69, Lincoln 8152, New Zealand. Tel: +64 33256700; Fax: +64 33252418; E-mail: RuscoeW@LandcareResearch.co.nz

consume seed and (2) their current abundance. Solomon (1949) described variation in per capita rates of prey consumption, and variation in predator abundance, in relation to prey abundance, as the *functional* and *numerical* responses of the predator, respectively. Hence, the overall impact of a rodent population on forest dynamics through seed predation will depend on its functional and numerical response to changes in seed availability.

FUNCTIONAL RESPONSE

Holling (1959a) described three general forms of predator functional response, with the specific form reflecting aspects of predatory behaviour in relation to variation in prey abundance (Taylor 1982). All three forms impose an upper limit on prey consumption, or intake, representing the capacity of a predator to capture and consume a prey item once it has been located. While Type I responses describe a proportional (linear) increase in consumption from 0 to a maximum with increasing prey availability, Type II (or hyperbolic) responses describe a decelerating increase. That is, the proportion of prey consumed is highest at low levels of prey availability and a possible 100% consumption at the lowest prey density implies that predators have the potential to eliminate a resource entirely. In contrast, Type III responses describe an accelerating (sigmoidal) increase from low levels of prey availability, such that the proportion of prey consumed is highest at some intermediate level of resource availability and that this proportion declines as availability approaches zero. The rate of prey consumption could vary in this way where prey at low densities have access to some spatially limited refuge from predators (Holling 1959a), or where predators switch their attention to an alternative prey type when their principal prey become scarce (Holling 1959a; Tinbergen 1960). In either case, the potential for predators to deplete a resource entirely is reduced considerably where predators display a Type III functional response (Hassell 1978). Most empirical studies of the functional response of vertebrate predators have focused on differentiating Type II from Type III responses because of their different consequence for prey-population stability (Sinclair 1989).

NUMERICAL RESPONSE

Since Solomon's (1949) original definition, two types of numerical response have been defined and used to elaborate the interactive dynamics of consumer and resource populations (Bayliss & Choquenot 2002); a *demographic* numerical response that links rate of change in population abundance to food availability (Caughley & Lawton 1981) and an *isocline* numerical response that links consumer and resource abundance (Holling 1965, 1966).

The product of an isocline numerical response and an equivalent functional response describes variation

in total prey offtake with prey abundance, often termed the predator population's *total* response. By contrasting the total response of a predator population with the density-dependent productivity of a prey population, the stability properties of a predator–prey (or plant–herbivore) system can be explored (Holling 1959a; Boutin 1992; Caughley & Sinclair 1994). However, because the isocline numerical response subsumes many of the interactions that link predators and prey, comparisons between the productivity and offtake of a prey population and the consequences of density-independent perturbations in predator or prey abundance can only be considered implicitly (Choquenot & Parkes 2001). In contrast, the combination of the functional response of predators to changes in prey abundance and their demographic numerical response describe explicitly the feedback loop that links predator and prey abundance dynamically (Caughley 1976). This allows the effect that density-independent perturbation of the system has on its stability properties to be considered directly (Caughley 1987).

HOUSE MICE AS SEED PREDATORS IN NEW ZEALAND BEECH FORESTS

Seed predation by rodents introduced to New Zealand beech (*Nothofagus* spp.) forests provides a model system to investigate consumer–resource interactions. Forests dominated by beech are distributed widely throughout New Zealand, but also occur in eastern Australia, New Guinea, New Caledonia and South America (Wardle 1984). Currently 72% of New Zealand's indigenous forest is either beech-dominated or mixed forest containing beech (Hall *et al.* 2001) and these forests are generally associated with montane regions with higher rainfall (> 750 mm/year). There is large annual seedfall variation in beech forest. For example, over 35 years at Craigieburn Forest, mountain beech (*Nothofagus solandri* var. *cliffortioides* (Hook.f) Poole: Fagaceae) seedfall ranged from 0 to 12 000 seeds m⁻² year⁻¹ (Allen & Platt 1990; Richardson *et al.* 2005). Although prehistorically New Zealand had abundant avian and invertebrate beech seed predators, seed-eating rodents have only recently been introduced. Kiore (Pacific rat, *Rattus exulans* Peale) were introduced to New Zealand by Polynesians and have been present for at least 800 years (Atkinson & Towns 2001; Wilmshurst & Higham 2004). They became widespread in New Zealand forests, which were previously devoid of rodents and, in fact, all terrestrial mammals apart from bats. House mice (*Mus musculus* Linnaean), ship rats (*R. rattus* Linnaean) and Norway rats (*R. norvegicus* Berkenhout) were introduced by Europeans during the period 1792–1860. The house mouse has been a particularly successful invader of beech-dominated forests and is the most abundant rodent in these systems (King 1983). While the house-mouse diet in beech forests consists of plant and animal matter (Murphy 1992; Fitzgerald *et al.* 1996), large population eruptions in native forest are

associated strongly with beech masting (King 1983; Choquenot & Ruscoe 2000).

Even if masting has evolved in New Zealand beech species as a way of limiting the impact of seed predators, the characteristics of masting events may not yet be adapted to the levels of seed offtake imposed by exotic mammalian omnivores. This may be particularly true of house mice, which are able to generate very high rates of population increase (Ruscoe & Murphy *in press*). If house mice have the capacity to limit significantly the amount of beech seed available for germination, they may have a long-term influence on recruitment processes in beech-dominated forests.

In this study, we estimated the functional and numerical response of house mice to beech seed, and used these responses to simulate seed consumption by a house-mouse population. In estimating the functional response, we were specifically interested in whether (1) it was of Type II or III form, and (2) whether the form of the functional response was influenced by the availability of an alternative food source. If the functional response took Type III form naturally, or because the presence of an alternative food source led to switching at low levels of seed availability, it would be unlikely that house mice would deplete seed reserves entirely. In estimating the numerical response, we tested a general model of how the influence of food availability on rate of change in rodent abundance was modified by density-dependent mechanisms. Combining these two responses into a simple accounting model (Korpimäki & Krebs 1996), we explored the conditions under which seed predation by house mice could entirely deplete beech-seed reserves.

Methods

FUNCTIONAL RESPONSE OF HOUSE MICE TO BEECH SEEDS

We undertook two types of trials to investigate and parameterize the functional response of house mice to the availability of beech seeds. Laboratory trials assessed the capacity of house mice to locate and consume beech seeds across a range of availabilities, and also investigated the influence that an alternative food source (lepidopteran larvae) had on that capacity. Field trials parameterized the functional response under more natural conditions.

LABORATORY TRIALS

Forty wild-caught house mice were kept separately in 0.04-m² cages and were allocated randomly one of eight quantities of seed availability (five mice availability⁻¹). House mice used in trials were non-breeding adults, trapped at two beech-forest locations in Canterbury, New Zealand. House mice were transported to the laboratory and maintained on rodent chow and water for a maximum of 7 days before being used in trials.

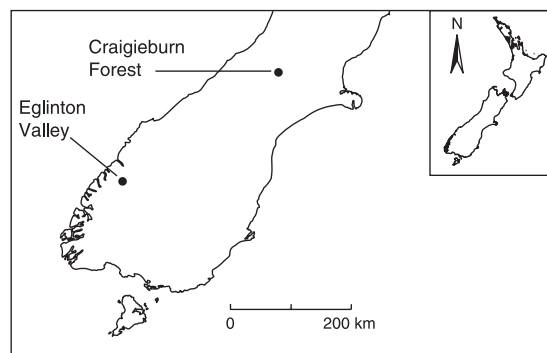


Fig. 1. New Zealand map showing the location of Craigieburn Forest, Canterbury, where the functional response field trials were carried out, and the Eglinton Valley, Fiordland National Park, where house-mouse population estimates and beech-seedfall quantities were obtained for the numerical response parameterization.

Mountain beech seeds were collected from Craigieburn Forest (43°13' S, 171°69' E, 950 m a.s.l.) (Fig. 1) over a 3-week period as they approached maturity. The average weight of beech seeds collected at this time was 4.1 mg (Ruscoe *et al.* 2004). The range of seed availabilities used in the trials covered the possible range of seed intake by house mice, ascertained from a preliminary trial.

Prior to each trial, laboratory food was withheld from house mice for 6 h. Seeds (nuts containing an edible endosperm or kernel) and mountain beech leaf litter were added to the cages for the duration of the trials. Animals had to forage through the litter to find the seeds. At the end of the trial, all litter, remaining intact seeds and husks (where seeds had been eaten out) were recovered and counted. Trials were of either 1-h (18:00–19:00 h, which was the first hour of darkness in the animal facility) or 12-h duration (19:00–07:00 h). We used the 12-h trial as a surrogate for 1 day (24 h), given that mice are generally nocturnal in the wild and are therefore expected to forage over approximately 12 h. These are referred to as 'seed-only' trials.

Additionally, in a replicated series of the 1-h laboratory trials, mice were allocated beech seed randomly (the same quantities as in the seed-only trial) plus lepidopteran larvae (*Tingena armigerella* Walker: Oecophoridae). Larvae, a known food of wild house mice (Fitzgerald *et al.* 1996), were obtained from leaf litter collected at Craigieburn Forest and processed through a Berlese-Tullgren funnel (Southwood & Henderson 2000). Larvae were divided into larger and smaller individuals, and either five larger or 10 smaller larvae were used in each replicate trial to deliver approximately equal biomass. At the end of the trial, seeds, husks and larvae that remained were recovered and counted.

FIELD TRIALS

Enclosures measuring 1 × 1 × 1 m were erected in Craigieburn Forest (Fig. 1). Enclosures had lids and the

sides were dug into the soil leaving a natural ground surface. Surface seed was cleared from within each enclosure, leaving the leaf-litter substrate. Single wild-caught house mice from Craigieburn Forest were acclimatized to enclosures for 24 h, over which time they were fed commercial rodent seed mix and fruit, and provided with a nest box. Food was then removed from the enclosure and the house mice allocated randomly one of eight quantities of seed availability (five mice availability⁻¹) that were spread over the enclosure floor and left undisturbed for a 24-h period. At the end of each feeding trial, the remaining seeds and husks were recovered from the enclosure and counted. To evaluate the efficiency with which we recovered uneaten seeds from the field enclosures we undertook a number of test-counts, in which known numbers of seeds were placed in enclosures that did not contain house mice. Seeds were recovered and counted 24 h later.

In field trials, 'natural' alternative food items in the form of fungi and soil and/or litter-dwelling invertebrates were available to the house mice. Also, predators and other wild house mice could be seen and smelt through the mesh enclosure, possibly influencing the foraging behaviour of the enclosed house mouse. As such, these trials simulated a more 'natural' setting but did not entirely account for the effect that intra- and interspecific interactions might have had on individual house-mouse foraging behaviour.

STATISTICAL ANALYSIS

To evaluate the form of the relationship between seed availability and seed consumption in all laboratory and field trials, we followed the two-step process recommended by Juliano (1993). First we fitted a polynomial GLM model of seed availability (numbers per plot) to the logit-transformed proportion of seeds consumed over the test period (Trexler, McCulloch & Travis 1988). We began with a cubic model and eliminated any non-significant highest-order terms (SYSTAT 7, SPSS Inc. 1997). We then plotted the resulting best-fitting model against seed availability and examined it for regions of positive or negative density dependence. Positive density dependence (an increase in the proportion of seeds consumed as seed density increased from 0) would indicate a sigmoidal relationship between seed intake and seed availability consistent with a Type III functional response. Negative density dependence (a decline in the proportion of seeds consumed as seed availability increased from 0) would indicate a monotonically decelerating relationship between seed intake and seed availability consistent with a Type II functional response.

MODEL FITTING

Having determined the shape of the functional response, we fitted data collected from field trials to models of the relationship between seed intake (IR) and seed availability (S). For a Type II functional response we fitted:

(i) Holling's disc equation (Holling 1959b):

$$IR = \frac{aTS}{1 + aT_h S} \quad \text{eqn 1}$$

where S is the initial number of seeds presented, T is the total time available (we assigned $T = 1$ day for field trials, $T = 12$ for the 12-h laboratory trial, and $T = 1$ for the 1-h laboratory trials), T_h is the handling time per seed (hours), and a is the instantaneous attack rate.

(ii) Roger's random predator equation (Rogers 1972), where a is the proportional area searched (or re-searched), and S , T and T_h are as above:

$$IR = S(1 - \exp^{-a(T_h IR - T)}) \quad \text{eqn 2}$$

This model is rarely used because it is cumbersome, in that IR appears on both sides of the equation. However, it is theoretically more appropriate than the Holling disc equation for nearly all functional responses derived experimentally where food resources are not replenished as they are consumed (see Juliano 1993).

(iii) Ivlev's inverted exponential equation (Ivlev 1961; Noy-Meir 1975, 1978):

$$IR = m(1 - \exp^{-S/k}) \quad \text{eqn 3}$$

Where m is the maximum seed intake rate and k is a measure of foraging efficiency, summarizing how rapidly seed intake approaches its maximum rate with increasing seed availability (Short 1985, 1987).

All functional response models were primarily fitted using maximum likelihood estimation assuming a binomial probability distribution (PopTools, Hood 2004) and Solver (Microsoft Excel 2000). A large range of starting values were used and parameters a , T_h and m were constrained to be ≥ 0.0 . We compared the fit of all three functional response models to the field trial data using Aikake's information criterion (AIC_c) corrected for small sample sizes (Akaike 1973; Burnham & Anderson 1998).

To examine the effect that provision of lepidopteran larvae had on maximum beech-seed intake by mice, we fitted Ivlev's inverted exponential equation to data from 1-h seed only, and seed plus larvae laboratory trials, and compared estimates of maximum seed intake.

NUMERICAL RESPONSE OF HOUSE MICE TO BEECH SEED

Field trial

In order to estimate the relationship between the instantaneous change in house-mouse abundance (r) and seed availability, we monitored both in beech-dominated forest located in the Eglinton Valley, New Zealand (44°2' S, 168°5' E, 450 m a.s.l., Fig. 1). Between 1999 and 2001, mice were live-trapped in quarterly sessions over 33 months on two 3.24-ha trapping grids, each consisting of 81 Elliot traps (Elliot Scientific,

Australia) (9×9 traps separated by 20 m) baited with rolled oats and peanut butter (22 abundance estimates in total). Each trapping session ran for 5 consecutive nights, with all mice caught during a session individually marked. These data were used to calculate (1) the minimum number of mice known to be alive on each grid during each trapping session (Krebs 1966) and (2) mark–recapture estimates of population abundance using the M_h (jackknife) method (Burnham & Overton 1978) in program CAPTURE. Because estimates of minimum number of animals known to be alive provide a precise index of mouse abundance with fewer assumptions than mark–recapture estimates, they were used to estimate r (Ruscoe, Goldsmith & Choquenot 2001; Davis *et al.* 2003). However, mark–recapture estimates were used to calibrate simulation models that required estimates of absolute house-mouse population size (see below). Beech availability (seed m^{-2}) was estimated from four seed traps positioned on each trapping grid. As with the functional response trials, only nuts that contained an edible kernel were counted as ‘seeds’.

Model fitting

For each trapping grid, we estimated r on a quarterly basis from sequential estimates of the minimum number of mice known to be alive (N):

$$r = \ln \left(\frac{N_{t+1}}{N_t} \right) \quad \text{eqn 4}$$

We fitted four alternative models to the relationship between r and beech seed availability (S).

(i) An inverted exponential model formulated by Caughley & Lawton (1981):

$$r = -b + c(1 - \exp^{-dS}) \quad \text{eqn 5}$$

where b is the maximum rate of population decline when seed is entirely depleted, c is the rate at which b is progressively ameliorated by increasing seed availability and d is a measure of the population’s demographic efficiency, quantifying its capacity to maintain a positive rate of increase as seed availability declines.

(ii) A variation on the first model that incorporates linear density dependence, formulated by Caughley & Krebs (1983) and Pech *et al.* (1999):

$$r = b + c \cdot \exp^{-dS} + g \cdot N \quad \text{eqn 6}$$

where g is a measure of the strength of density dependence.

(iii) A model that links variation in predator abundance to a hyperbolic (Type II) seed intake (IR) rather than seed availability *per se* and was developed by Rosenzweig & MacArthur (1963). Bazykin (1974, cited in Turchin 2003: 98) added a ‘self-limitation’ term to the Rosenzweig–MacArthur model that assumed linear density dependence. Choquenot & Ruscoe (2003) modified this model by using the inverted exponential equation of Ivlev (1961) to describe intake rate:

$$r = b + d \cdot IR + g \cdot N \quad \text{eqn 7}$$

where d is a measure of the population’s demographic efficiency and g is a measure of the strength of density dependence. Equation 7 assumes that per capita intake rate of seeds and mouse population density have independent effects on rate of population increase.

(iv) Finally, a ratio-dependent food-consumption model (Skalski & Gilliam 2001) using a modified Michaelis–Menten function for intake rate (IR) was applied to the data. In this model, the effect of multiple predators (house mice, N) is incorporated as part of the seed intake rate (IR), using *per capita* seed availability (S/N). In this model both seed and house-mouse density affect rate of increase, but they are not independent:

$$r = b + d \cdot IR, \text{ where } IR = \left[\frac{x \left(\frac{S}{N} \right)}{1 + y \left(\frac{S}{N} \right)} \right] \quad \text{eqn 8}$$

All four numerical response models were fitted with maximum likelihood estimation methods using PopTools (Hood 2004) and Solver (Microsoft Excel 2000), and were compared using (AIC_c) (Akaike 1973; Burnham & Anderson 1998).

SIMULATING BEECH-SEED CONSUMPTION BY HOUSE MICE

We developed a simple accounting model to investigate the level to which house mice could deplete seed reserves in New Zealand beech forests. The model simulated a time-series in the abundance of house mice and the availability of seeds. In the model, we assumed that all seeds fell over a 12-week period in late summer–autumn, corresponding to the months February–May. Seed accumulated on the forest floor at a constant weekly rate and was available to house mice. In reality, while most beech seed falls within this period (70–100%), seedfall in some years can continue beyond autumn, and is not distributed evenly through time (Wardle 1984). Seed available to house mice was accounted weekly by subtracting seed-offtake by mice from the cumulative seedfall. Offtake by house mice was the product of prevailing house-mouse population size and their per capita seed consumption, estimated from their functional response. Prevailing house-mouse population size varied from week to week, according to their numbers at the start of the week, and rate of change in their abundance predicted from their numerical response.

Seed germination in spring reduces the availability of beech seeds to house mice. Germination starts in late September and October, and at low altitudes 75% of germination occurred within 32 days (Wardle 1984). At higher altitudes (treeline) the period over which most germination occurs increases to 73 days. To account for this variation in time to germination, the modelled availability of seeds was reduced by 35% from the last

Table 1. Type II functional response parameter values (\pm SE) for attack rate (a) and handling time (T_h) for Holling's disc equation (Holling 1959b) and the random predator equation (Rogers 1972), and maximum intake rate per experimental time unit (m) and foraging efficiency (k) for the inverted exponential equation (Ivlev 1961) estimated for house mice feeding on beech seeds in laboratory and field experiments. For Holling's disc equation and the random predator equation, maximum intake is T_h^{-1} multiplied by the number of hours the experiment ran

Trials	Holling disc equation		Random predator equation		Ivlev inverted exponential equation	
	a	T_h	a	T_h	m	k
Laboratory 12 h	0.042 \pm 0.00581	0.00651 \pm 0.00362	0.0101 \pm 0.0255	0.0098 \pm 0.0049	2118 \pm 1071	0.00047 \pm 0.00029
Laboratory 1 h	0.879 \pm 0.391	0.0041 \pm 0.00109	0.701 \pm 0.414	0.00274 \pm 0.0021	179.92 \pm 31.9	0.00425 \pm 0.00173
Laboratory 1 h with larvae	1.542 \pm 0.639	0.00597 \pm 0.00106	2.90 \pm 0.015	0.0065 \pm 0.00048	136.86 \pm 15.21	0.00877 \pm 0.00313
Field 24 h	0.067 \pm 0.0115	0.0163 \pm 0.0024	0.182 \pm 0.0842	0.0213 \pm 0.0024	1042.1 \pm 99.92	0.00139 \pm 0.00029

Table 2. Type II functional response models that describe variation in the per capita beech seed intake of mice (IR) per 24 h as a function of seed availability (seeds m^{-2} , S) from field trials. Akaike's information criterion (AIC_C) values are measures of parsimony between the fitted models and data, lower scores indicating greater parsimony

Model source	Fitted model	AIC_C	Eqn
Holling's (1959b) disc equation (eqn 1)	$IR = (0.067 * 24 * S) / (1 + 0.067 * 0.00068 * S)$	319.33	9
Roger's (1972) random predator equation (eqn 2)	$IR = S(1 - e^{[0.182(0.00089*IR-24)])}$	349.36	10
Ivlev's (1961) inverted exponential equation (eqn 3)	$IR = 1042.1[1 - e^{-(S*0.00139)}]$	317.57	11

week of September (week 32 of the simulation), the net reduction in seed availability being subtracted before estimating seed offtake by house mice. This produced a pattern whereby the combined effect of germination and offtake of residual seeds reduced seed availability to zero by mid-November (48 days later).

Results

FUNCTIONAL RESPONSE OF HOUSE MICE TO BEECH SEEDS

To determine the form of the functional response, we first fitted a polynomial model of seed availability (numbers per cage or field enclosure) to the logit-transformed proportion of seeds consumed over the test period. We then plotted the resulting best-fitting models for each data set and examined them for regions of positive or negative density dependence (Appendix I). All regression models predicted a decline in the proportion of seeds eaten (at lower seed availabilities, $N \leq 500$) as seed availability increased from zero. This lack of positive density dependence in the relationship between seed availability and the proportion of seeds consumed indicates that functional responses measured in laboratory and field trials were of Type II form. This suggests that house mice are theoretically capable of consuming all beech seeds to which they have access in beech forests. Addition of an alternative food source did not affect the form of the relationship between seed availability and the number of seeds eaten during 1-h laboratory trials (Appendix I). Therefore the functional response of house mice to beech seeds remained of Type II form,

and the presence of lepidopteran larvae did not cause house mice to switch the focus of foraging away from seed. There was a tendency for house mice to consume more larvae when few seeds were available to them. However, because the biomass of larvae was not varied systematically between replicate trials, the effect of seed availability on intake of larvae could not be tested directly.

Given that seed consumption followed a Type II functional response, Holling's disc equation, Roger's random predator equation and Ivlev's inverted exponential model were all fitted to the data (Table 1; Fig. 2a–d). Seed intake increased steadily with seed availability, approaching an asymptote curvilinearly. While the general form of the functional response and asymptotic levels of seed-intake rate were similar for all three models, Ivlev's inverted exponential equation provided the most parsimonious fit to the data (Table 2), and none of the 95% confidence intervals of the parameter estimates overlapped zero (Table 1). This model estimated maximum seed intake (equivalent to the level of seed consumption where intake by a house mouse was satiated under field conditions) to be 1042 seeds over a 24-h period. In comparison, Holling's disc equation and the Random predator equation gave slightly higher asymptotic intake rates of 1472 and 1126 seeds per 24 h (handling time⁻¹, T_h^{-1}).

Estimates of maximum seed intake during 1-h laboratory trials in which seed only or seed plus lepidopteran larvae were supplied to house mice were 179.92 (95% CI 148.02–211.82) and 136.86 (95% CI 121.65–152.07) seeds h⁻¹, respectively. As such, provision of an alternative food source appeared to reduce maximum seed intake by house mice.

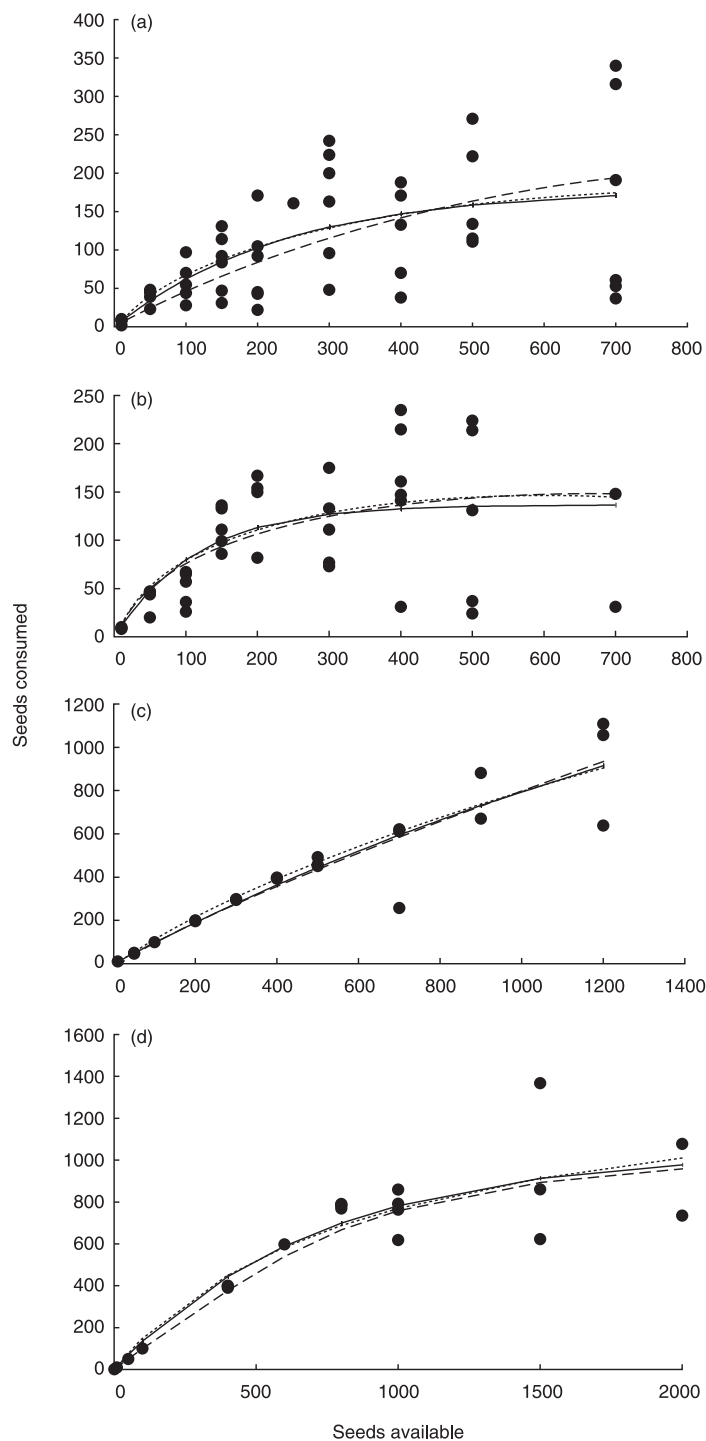


Fig. 2. Variation in the number of beech seeds consumed by house mice during laboratory and field experiments. Single wild-caught house mice were held inside enclosures and presented with a known number of seeds. Points are resultant estimates and lines are three fitted models; Holling's (1959b) disc equation (dotted line), Roger's (1972) random predator equation (dashed line) and Ivlev's (1961) inverted exponential equation (solid line). (a) Seeds only offered for 1 h. (b) Seeds plus an alternative food (larvae) offered for 1 h. (c) Seeds only, offered for 12 h. (d) Seeds offered for 24 h in field trials.

NUMERICAL RESPONSE OF HOUSE MICE TO BEECH SEEDS

The instantaneous rate of change in house-mouse abundance (r) rapidly reached a maximum with beech-seed availability (seeds m^{-2}) for populations monitored in the Eglinton Valley (Fig. 3). The model that included

the additive effects of seed availability, through its influence on seed intake rate, and density dependence (eqn 14), provided the most parsimonious fit to the data (Table 3). Standard errors around the parameter estimates for eqn 14 were $1.57E-2$, $2.55E-5$ and $3.0E-4$, for b , d and g , respectively. None of the 95% confidence intervals of the parameter estimates overlapped zero,

Table 3. Numerical response models describing variation in the instantaneous rate of change in mouse abundance on a quarterly basis (r) as a function of beech seed availability (seeds m^{-2} , S), and prevailing mouse abundance at the start of each quarter (N_t). AIC_C values are measures of parsimony between the fitted models and data, lower scores indicating greater parsimony

Model source	Explanatory variables	Fitted model	AIC _C	Eqn
Caughley & Lawton (1981) (eqn 5)	Seeds m^{-2} (S)	$r = -0.844 + 1.918(1 - e^{-0.001S})$	49.58	12
Caughley & Krebs (1983) (eqn 6)	Seeds m^{-2} (S) Mouse abundance (N_t)	$r = -0.963 - 1.876e^{-0.005S} - 0.005N_t$	46.57	13
Choquenot & Ruscoe (2003) (eqn 7)	Per capita seed intake (IR)† Mouse abundance (N_t)	$r = -0.800 + 0.002IR - 0.0067N_t$	43.72	14
Skalski & Gillian (2001) (eqn 8)	Seeds m^{-2} (S) Mouse abundance (N_t)	$r = -0.866 + 9.48IR$, where $IR = 0.013(S/N)/1 + 0.055(S/N)$	48.18	15

†Per capita seed intake is predicted from beech seed availability using the functional response described in eqn 10.

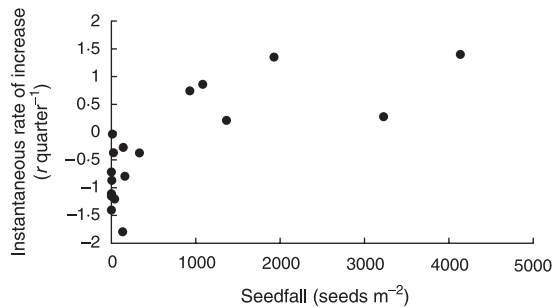


Fig. 3. Variation in instantaneous rate of house-mouse population increase measured on a quarterly basis (r) with variation in beech seed availability (seeds m^{-2}). Data were obtained from two house-mouse trapping grids located in beech-dominated forest in the Eglinton Valley in New Zealand. Measures of r were calculated from sequential quarterly estimates of the minimum number of house mice known to be alive on each trapping grid, over 33 months between 1999 and 2001 (22 measures in total). Seedfall was estimated from the average of four seed traps deployed on each trapping grid.

indicating that r was positively affected by increased seed intake (IR) and negatively affected by increasing house-mouse abundance at the start of the quarter for which r was estimated (N). Expanding this model using eqn 11 to link seed availability (S) to seed intake (IR) gives:

$$r = -0.80012 + (0.00199[1042(1 - e^{-50.00139})] - 0.00665N_t) \quad \text{eqn 16}$$

The effect of increasing seed availability (via seed-intake rate) and house-mouse abundance on r is shown graphically in Fig. 4.

SIMULATING BEECH-SEED CONSUMPTION BY HOUSE MICE

The simulation model used to examine the extent to which house mice could deplete seed reserves in beech forests employed the functional response predicted by Ivlev's inverted exponential equation (eqn 11), and the numerical response predicted from per capita seed intake and prevailing house-mouse abundance (eqn 14).

Figure 5 shows projected changes in house-mouse abundance and seed availability over 52 weeks starting

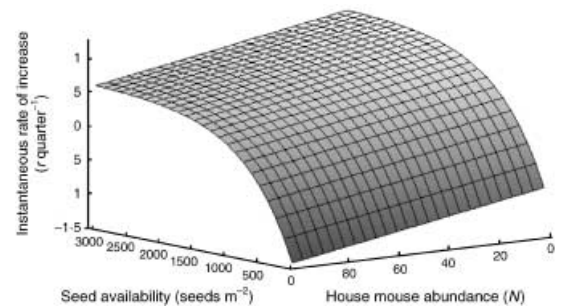


Fig. 4. A model linking instantaneous rate of change in house-mouse abundance on a quarterly basis (r) to beech-seed availability (seeds m^{-2}) and mouse-population size.

at the beginning of seedfall in February, and assuming a starting house-mouse population size of 12 (3.7 mice ha^{-1}) and an annual beech-seed availability of 2000 seeds m^{-2} . The overall patterns shown in Fig. 5 are similar in all simulations that did not result in the elimination of beech seeds prior to germination during spring. Simulated abundance of house mice responded to seedfall by increasing steadily over autumn. Their abundance continued to increase attaining peak densities that reflected their starting density and over-winter seed availability. Following germination of residual seeds during spring, the house-mouse population underwent a rapid decline over summer.

The extent to which house mice deplete beech seeds within a year will depend on the size of the population at the start of the simulation and the magnitude of seedfall. Under conditions where house mice entirely eliminate seed reserves prior to the onset of germination, house mice attain peak densities earlier in the year, and subsequently undergo a more dramatic decline in abundance. Figure 6 shows an isocline of starting house-mouse population size and seedfall that led to complete depletion of seed reserves before germination within the year of the simulation. Combinations of starting house-mouse population size and seedfall that lie to the left of the isocline will lead to complete depletion of seed reserves, while those to the right will result in a residual seed reserve at the point germination starts. This isocline can be used to provide a model that predicts the minimum size of the house-mouse population in

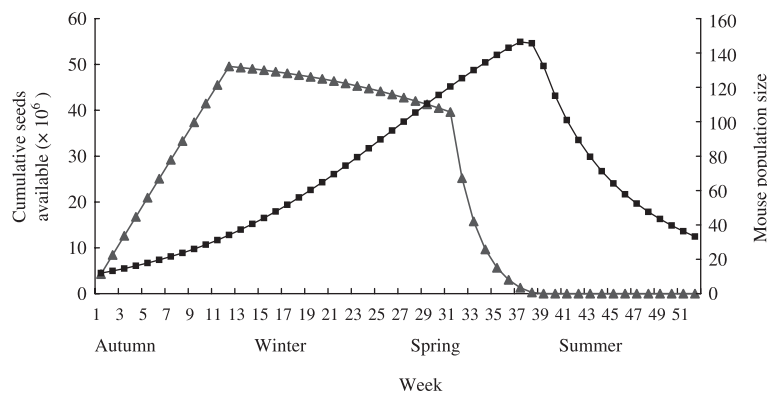


Fig. 5. Simulated changes in seed availability (\blacktriangle) and house-mouse population size (\blacksquare) on a 3.24-ha grid, assuming annual seedfall of 2000 seeds m^{-2} and house-mouse population size of 12 individuals at the beginning of February (week 1 of the simulation).

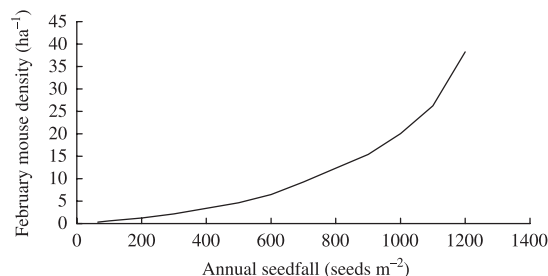


Fig. 6. Isocline linking values of seedfall and house-mouse abundance at the start of February, which in combination yield a residual seed density of 0 when germination begins in the last week of September (week 32 of simulations). Combinations to the left of the isocline lead to complete elimination of seed reserves prior to the commencement of germination, while those to the right do not.

February (N_{Feb} , ha^{-1}) that will lead to complete depletion of any given annual seedfall (S):

$$N_{Feb} = 4 \cdot 10^{-8} \cdot S^3 - 4 \cdot 10^{-5} \cdot S^2 + 0.0218 \cdot S - 1.3886. \quad \text{eqn 17}$$

Discussion

FUNCTIONAL RESPONSE OF HOUSE MICE TO BEECH SEEDS

In studies of how consumer (predator or herbivore) populations interact with their food (prey) resources, a great deal of attention has focused on the role played by Type II and Type III functional responses in stabilizing or destabilizing these interactions (Taylor 1982; Sinclair 1989; Turchin 2003). Because food proportional intake described by a Type II response is high from low levels of food availability, consumers can potentially consume food resources until they are entirely depleted.

We experimentally determined the functional response of house mice to known quantities of available beech seed ranging from 0 to 2000 seeds m^{-2} . This is the only experimental field study we know of where large quantities of natural food have been offered to rodents at levels that exceed daily asymptotic intake (satiation).

In contrast, the vast majority of functional response studies on small mammals have been either entirely laboratory based (Holling 1959a; Price & Heinz 1984; Lundberg 1988) or cafeteria-style field trials where a small number of food items are offered and the proportional removal (of single or multiple foods) analysed (Hulme & Hunt 1999; Li & Zhang 2003; Schnurr *et al.* 2004). While these field studies may reveal the *form* of the total response (functional response of the resident consumer population), and the consumers' *theoretical* ability to deplete a food supply, there is no indication of how these results relate to total annual seed (resource) availability, absolute losses to predation (total response) and consequences for the seed plant's population dynamics. In comparison, the functional, numerical and total responses within carnivore–herbivore systems are well documented (see Dale, Adams & Bowyer 1994; Messier 1994; O'Donoghue *et al.* 1998; Rohner, Doyle & Smith 2001), as both predator and prey populations are jointly monitored in the field.

House mice exhibited a Type II functional response to beech seeds in this study that suggests that beech seed cannot occupy a refuge to which house mice do not have access, or that house mice do not switch their focus to an alternative, abundant food resource when beech seed becomes scarce. The field enclosures did not include substrate such as crevices and deep litter in hollows that may form natural refuges from mice. However, Wardle (1984) suggested that owing to the small size of beech seeds and their limited stored reserves, seeds covered by a deep litter layer lack the energy for the cotyledon to grow sufficiently to reach the surface. This is presumably also the case for nuts lost in deep crevices. As such, these seeds are not capable of establishment and are lost to the seed population irrespective of predation. Collectively, this suggests that mice have the theoretical potential to deplete beech seed reserves entirely in New Zealand forests creating instability in this consumer–resource system (Sinclair 1989; Turchin 2003). The addition of lepidopteran larvae did reduce average maximum rates of beech-seed consumption during 1-h laboratory trials by 24%; however, because house mice in the field trials had access to unmeasured

quantities of alternative food resources including lepidopteran larvae, any tendency for consumption of these to reduce maximum levels of seed intake is presumably already accounted for in the field-parameterized functional response models.

The most parsimonious functional response model derived from field-trial data estimated that on average mice would consume a maximum of 1042 beech seeds 24 h^{-1} when seed availability exceeded about 2000 seeds m^{-2} . Hulme & Hunt (1999) used energetic calculations derived by Grodzinski (1985) to show that the wood mouse (*Apodemus sylvaticus*), a similar-sized rodent to the house mouse, consumed upwards of 1000 wych elm (*Ulmus glabra*, weight 3.5 mg compared with 4.1 mg for beech seed) or 100 ash (*Fraxinus excelsior*, weight 29.3 mg) seeds a day before being satiated.

Miller (1999) estimated that a 15.5-g house mouse would require $86.59 \text{ kJ day}^{-1}$ to maintain energy balance in winter, if living on sunflower seeds alone. Ruscoe *et al.* (2004) reported average energy content of mountain beech seeds to be 30.23 kJ/g . Using this quantity and assuming 90% energy assimilation (Grodzinski 1985 estimated 85–90% for woodmice consuming *Fagus* spp. seed), a 15.5-g house mouse would have to consume 776 seeds day^{-1} simply to maintain energy balance. According to the best-fitting functional response model (eqn 11), this seed-consumption rate would be attained at seed availabilities greater than 982 seeds m^{-2} . When seed availability is below this level, house mice would be unable to achieve energy balance unless alternative energy sources were abundant. When seed availability exceeded this level, house mice would have surplus energy reserves to support reproduction.

NUMERICAL RESPONSE OF MICE TO BEECH SEEDS

While transient or eruptive increases in house-mouse abundance in response to beech-seed abundance has long been recognized in New Zealand (Riney *et al.* 1959; King 1983), only recently have attempts been made to quantify numerically these relationships for predictive purposes. Choquenot & Ruscoe (2000) and Ruscoe *et al.* (2003) estimated rates of change in the abundance of house-mouse populations inhabiting beech-dominated forests at separate locations. Both studies demonstrated a strong demographic response to beech-seed availability between the advent of seed-fall in late summer/autumn and seed germination in the following spring, but not over the remainder of the year. This response was modified by one or more unspecified, negative density-dependent mechanisms that reduced the numerical response of house-mouse populations to seed availability when their prevailing density was high. A similar system (numerical response to food availability modified by density-dependent mechanisms) has been reported for eruptive house-mouse populations in Australian grain-growing areas by Pech *et al.* (1999), and appears to characterize many

other rodent systems (Jensen 1982; Pucek *et al.* 1993; Leirs *et al.* 1997; Lima & Jaksic 1998; Ostfeld & Keesing 2000; Davis, Pech & Singleton 2003).

House-mouse populations inhabiting New Zealand beech forest undergo eruptive increases in abundance when autumn seedfall produces an abundant food supply that allows breeding and recruitment to extend over winter (King 1983; Murphy 1992). While the general availability of energy from beech seed is clearly an important determinant of whether winter breeding and recruitment can occur in any given year, rodent fecundity is also highly sensitive to the level of available nitrogen (Crowley 1983; White 2002). Knapka (1983) reviewed a number of studies on house-mouse nutrition and concluded that a diet consisting of 12–14% 'good quality protein' was adequate for mouse growth, and 17–19% adequate for reproduction. The average protein content of New Zealand beech seed is 24–33%, which exceeds this level (Murphy 1992; Ruscoe *et al.* 2004).

The four numerical response models tested in this study differed in whether or not prevailing population density (either dependently or independently) affected the demographic response of house-mouse populations to increasing seed availability, and whether this demographic response was related to seed-intake rate or seed availability *per se*. The most parsimonious model invoked linear, negative density dependence, and linked r to seed-intake rate projected from seed availability. As such, the data modelled in this study conform to the generalized model of rodent population dynamics proposed by Choquenot & Ruscoe (2000), except that the influence of food availability on rodent demography (the numerical response) was manifested through the influence food availability had on the rate of food intake (the functional response). The need to link directly the functional and numerical response of consumers in dynamic models of resource–consumer interaction was suggested by Rosenzweig & MacArthur (1963) and methods of doing this have been reviewed recently (Turchin 2003).

According to our models, r will be positively related to food intake but density-dependent effects will reduce the rate of population growth achieved as prevailing population abundance increases. When fitted to the data collected in this study, this model (eqn 16) suggested that when house-mouse abundance was low ($0.1 \text{ mouse } 3.24 \text{ ha}^{-1}$), and seed availability high ($3000 \text{ seeds m}^{-2}$), seed intake approached its maximum projected rate ($1026 \text{ seeds mouse}^{-1} \text{ day}^{-1}$) as did the quarterly rate of increase ($r = 1.24$, equivalent to an annual rate of 4.96). The maximum quarterly rate of increase measured in this study was 1.41, which is equivalent to an annual rate of 5.6. This is comparable with the maximum annual rates estimated from house-mouse abundance indices based on kill trapping in a different beech-dominated forest in New Zealand (4.72–9.12; Choquenot & Ruscoe 2000), and estimated for eruptive populations in Australia (7.66; Pech *et al.* 1999).

Increasing the prevailing density of house mice reduces the maximum rates of increase realized by the

population, even though seed availability and per capita seed intake remain high. For example, increasing mouse abundance to 120 house mice 3.24 ha^{-1} while maintaining seed availability at 3000 m^{-2} has no effect on projected seed intake, but reduces quarterly rate of increase by 64% to $r = 0.44$. This implies that the mechanism(s) underlying density dependence operate independently of the direct effect seed availability has on r through variation in seed intake. Choquenot & Ruscoe (2000) suggested that the strong density dependence that characterizes house-mouse populations inhabiting New Zealand beech forests could be due to social processes, predation or parasites and/or pathogens. While the influence that some plausible density-dependent mechanisms have on r may be independent of the relationship between seed availability and seed intake, others will not be. For example, territoriality or other social processes are reported to influence predator consumption rates and produce ratio-dependent functional responses (Abrams & Ginzburg 2000); however, these processes are unlikely to have strong effects on food intake in our system as house mice are socially gregarious at high densities (Singleton & Krebs in press) and are not thought to be territorial (Newsome 1969). In contrast, disease or parasites may reduce the mobility or capacity of house mice to consume and digest seeds when population density is high. In these circumstances, while density-dependent reductions in the capacity of house mice to respond demographically to available seed would directly affect rates of change in house-mouse abundance at high population densities (numerical response), they would also reduce the rate at which house mice could find and assimilate seeds (functional response). However, using model comparison, we found no evidence that a ratio-dependent functional response model fitted the data as well as a simple prey-dependent model (eqn 14). This supports the results of Skalski & Gilliam (2001), who found little evidence for ratio dependence in the functional responses in 13 of 19 predator-prey data sets they examined.

BEECH-SEED CONSUMPTION BY MICE: SIMULATION MODELLING

The model developed to determine the extent to which house mice could deplete seed reserves in beech forest had a number of simplifications that suggest its predictions should be treated cautiously. First, while the functional response experiment used mountain beech seed, the Eglinton Valley where the numerical response of house mice was measured contains silver (*N. menziesii*) and red beech (*N. fusca*) with mountain beech. While all three species have seeds of similar size (5–7 mm seed length), the seeds of red beech tend to be heavier than those of the other two species (Wardle 1984). However, because beech seeds of these species are of similar nutritional value and calorific content (Ruscoe *et al.* 2004), we have ignored the small difference in seed weight. As red beech seed is heavier, maximum daily intake rate of

seeds by house mice may be lower than for mountain beech. Therefore our estimates of seed loss to predation will be overestimated in the simulation model leading to a conservative estimate for seed survival.

Secondly, because the model did not attempt to simulate an age- or stage-structured mouse population, it did not account for the different seed-intake levels that young or reproductive individuals would require to satisfy energetic demands. However, given that young mice will have lower general energy requirements by virtue of their size and lack of reproductive maturity, and reproductive adults have higher energy requirements, we have assumed these differences balance out.

A potentially more problematic assumption is that foraging behaviour of house mice for beech seeds is characterized by scramble competition. That is, the foraging behaviour of each individual corresponds to the functional response used in the model, feeding at the same maximum rate until seed resources become limiting. However, if behavioural mechanisms invoke a spatially moderated or hierarchical exploitation of seeds, the foraging behaviour of different age, size or sex classes within the population may be either more or less efficient than the modelled functional response implies. Because the numerical response used in the model was estimated from data collected under entirely natural conditions, any consequences that predation, disease and behavioural effects had for the foraging efficiency of individual house mice would have been captured in the basic relationship between seed availability, house-mouse population size and rates of change in house-mouse abundance. As such, while the use of a general functional response for all house mice in the population may ignore individual differences in foraging efficiency, these differences will be largely subsumed in the numerical response used.

CAN HOUSE MICE DEplete SEED RESERVES IN NEW ZEALAND BEECH FORESTS?

Because of the widespread threat posed by predators to species with conservation value in beech forest (e.g. avifauna), much work has been carried out to elucidate links between house-mouse populations and higher-order predators (mustelids) and nest predation (King 1983; Murphy & Dowding 1995; O'Donnell & Phillipson 1996; Ruscoe, Norbury & Choquenot in press), but little work has quantified the impacts house mice themselves may have on biodiversity in general and forest regeneration in particular. Seed-eating mammals have only recently been introduced into New Zealand forests, and there has been insufficient time for trees to adapt seeding characteristics that may compensate for any additional seed-predation pressure mammals exert.

House mice inhabiting beech forests appear unable to achieve higher densities than have been observed as (1) they are usually increasing from extremely low densities (O'Donnell & Phillipson 1996), and (2) the period between seedfall and germination is insufficient for a

population to attain densities where all available seed is consumed. As such, while New Zealand beech forests have not evolved in the presence of rodents, variation in interannual seed crop production appears adequate to overwhelm the direct effects of seed predation by house mice. For example, at a seed availability of 1200 m⁻², mice would only be able to entirely eliminate seed reserves if their density in summer (prior to seedfall) exceeded 36 ha⁻¹. In the Eglinton Valley, where the numerical response of mice to seed availability was measured over almost three years, seedfall exceeded 1200 seeds m⁻² in two of three years, while the highest density of mice recorded in any season was 50 ha⁻¹ (Ruscoe *et al.* 2001), and in summers preceding a beech mast, < 10 ha⁻¹. This suggests that either the foraging characteristics of house mice are remarkably similar to those of the depleted native New Zealand beech-seed predators (mostly avian and invertebrate) or seed-masting affords beech trees advantages that are different or additional to seed-predator satiation (Silvertown 1980; Norton & Kelly 1988; Allen & Platt 1990; Kelly & Sork 2002; Richardson *et al.* 2005).

DYNAMICS OF THE HOUSE MOUSE-BEECH FOREST SYSTEM

Caughley & Lawton (1981) identified two general classes of plant-herbivore systems by differentiating systems in which herbivores did not influence the rate at which their food (vegetation) was renewed (non-interactive systems) from systems where herbivores do influence the rate at which food is renewed (interactive systems). They further differentiated non-interactive systems into those where the rate of change in herbivore abundance was tied closely to the rate of renewal in their food resources (reactive systems), and those where rate of change in herbivore abundance was largely independent of the rate at which food resources were renewed (non-reactive). Interactive systems were differentiated into those where herbivores at high densities interfere with each other's capacity to procure food (interferential systems) and those in which they do not (*laissez-faire* systems).

According to this classification, New Zealand house mice and beech trees form a non-interactive system; mice have no immediate influence on the rate at which beech seeds are renewed. If house mice were able to reduce seed reserves sufficiently to affect the recruitment of beech seedlings, they might interact with their food resources over very long periods of time. However, the simulation model developed in this study suggests that such demographically significant levels of beech-seed consumption are probably infrequent. While house mice do not interact with beech trees *per se*, rates of change in their abundance are linked closely to beech-seed availability. As such, house mice and beech trees form an entirely reactive system, with changes in house-mouse abundance being driven largely by variation in beech seedfall, but house-mouse abundance having no influence

on the magnitude of seed fall. Entirely reactive plant-herbivore systems are considered rare in nature, with examples restricted to insects feeding on rot pockets that form in cacti (Fellows & Reed 1972; Stramer *et al.* 1976), and deer limited by canopy leaf fall in forests (Nugent 1990). However, given the number of rodent populations that are limited by seedfall from canopy species (Ostfeld & Keesing 2000), such systems could be more common than is generally thought (Caughley & Lawton 1981).

Acknowledgements

We thank P., D., S. and E. Dinsbacher and S. Richardson for help with mountain beech nut collection. I. and B. Yockney, G. Morris, K. Drew, C. Brausch and B. and H. Ruscoe helped with mouse trapping. L. Clunie identified lepidopteran larvae, K. Minchington and L. Fagan helped collect and sort larvae, G. and L. McElrea built enclosures and K. Drew helped with field trials. Many others helped count eaten/uneaten seeds and larvae following the feeding trials. J. Hone, D. Ramsey, S. Richardson, R. Duncan and an anonymous reviewer provided useful comments on previous drafts of the manuscript. This study was funded by the Foundation for Research, Science and Technology, New Zealand, and conducted with Landcare Research animal ethics approval (AEC 02/04/02) with assistance from the animal facility staff.

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Received 10 November 2004; accepted 22 March 2005

Appendix I.

Results of the polynomial regressions to determine the shape of the functional response for house mice feeding on beech seeds in laboratory and field experiments. Estimates of significant linear and quadratic parameters are reported

Trial	Effect	Estimate	SE	<i>t</i>	<i>P</i>
Seeds only (1 h)	Intercept	1.107	0.293	3.78	< 0.001
	Linear	-0.004	0.0008	-4.80	< 0.001
	Quadratic				NS
	Cubic				NS
Seed + larvae (1 h)	Intercept	1.688	0.265	6.35	< 0.001
	Linear	-0.006	0.0008	-7.349	< 0.001
	Quadratic				NS
	Cubic				NS
Seeds only (12 h)	Intercept	17.24	1.77	9.7	< 0.001
	Linear	-0.037	0.0082	-4.52	< 0.001
	Quadratic	2.08E-5	6.89E-6	3.017	0.005
	Cubic				NS
Field trial (24 h)	Intercept	11.35	0.77	14.7	< 0.001
	Linear	-0.0118	0.0022	-5.19	< 0.001
	Quadratic	2.98E-6	1.23E-6	2.42	0.022
	Cubic				NS

*The procedure entailed fitting a polynomial model of seed density (numbers per cage/enclosure) to the logit-transformed proportion consumed over the test period. We began with a cubic model and eliminated any non-significant highest order terms (Juliano 1993).

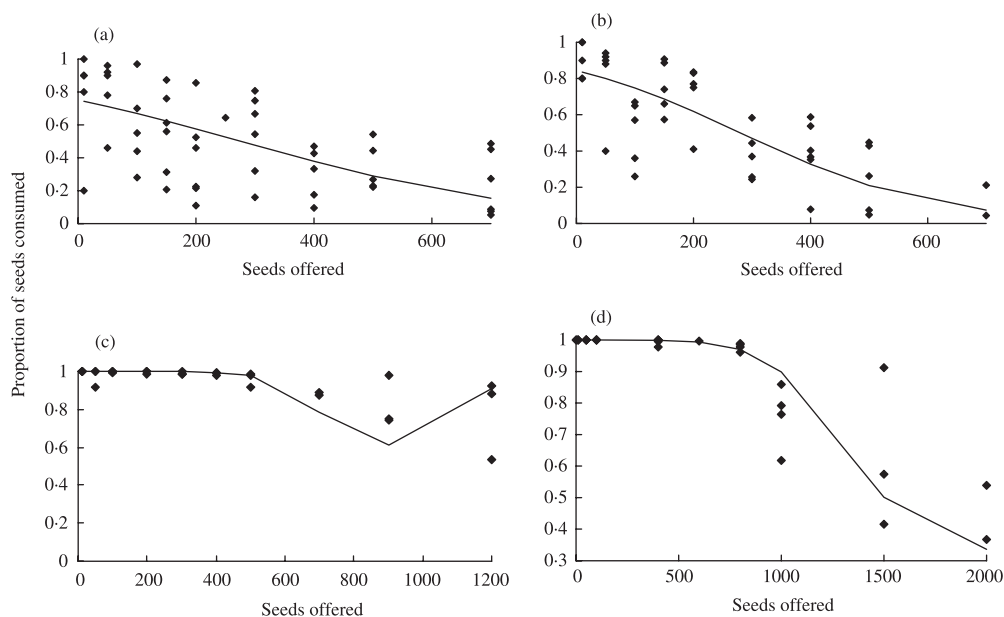


Fig. A1. Variation in the proportion of beech seed consumed by house mice during laboratory and field experiments. Single wild-caught house mice were held inside enclosures and presented with a known number of seeds. (a) Seeds only offered for 1 h. (b) Seeds plus an alternative food offered (larvae) for 1 h. (c) Seeds only, offered for 12 h. (d) Seeds offered for 24 h in field trials. Solid lines represent the back-transformed polynomial regressions from the table above.