Rodent and predator population dynamics in an eruptive system

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Received 8 August 2000; received in revised form 13 February 2001; accepted 23 February 2001

Abstract

A computer model of the population dynamics of introduced house mice (*Mus musculus* L.), ship rats (*Rattus rattus* L.) and stoats (*Mustela erminea* L.) in New Zealand forest was constructed, to test the relative importance of food availability and predation in shaping observed small-mammal population dynamics. Ship rats and mice are the two common rodent species present in most New Zealand forests, and exhibit eruptive population dynamics. Stoats are the only common mammalian predator, and undergo large density fluctuations following periodic rodent eruptions. A number of outputs and predictions from the model were developed. The model highlights the overall importance of variation in food availability in determining the timing and amplitude of rodent population eruptions. It indicates that predators can not prevent a prey–species eruption, primarily due to differences in reproductive biology. Predation however, can delay the start of the prey-population increase during the eruption. The role of predators in limiting the peak prey-population size will depend on the size of the energy input. In a full-scale eruption following maximal tree seeding, predators cannot significantly truncate peak prey-population size. Predators should be able to significantly hasten the rate of decline in the prey populations, although the strength of predator limitation will depend on the severity of food limitation and cold-induced mortality over the same period. Predators can limit prey populations during the post-crash low phase. As with the crash phase, the strength of predator limitation in the low phase will depend on the severity of food limitation and natural mortality. The model highlights gaps in current knowledge of predator and prey species biology and ecology. The model highlights key areas where further field study should provide a better understanding of the factors driving small-mammal communities in New Zealand. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: House mouse; Ship rat; Stoat; Model; Population dynamics; STELLA

1. Introduction

Introduced feral house mice (*Mus musculus* Linnaeus) and ship rats (*Rattus rattus* L.) are widespread in native forest ecosystems in New Zealand (Innes, 1990; Murphy and Pickard, 1990). Ship rats are generally more abundant in
broadleaf-podocarp forest than in beech forest (Daniel, 1978), while mice are generally rare in most habitats (Murphy and Pickard, 1990). Both ship rats and mice show periodic population eruptions from sustained low densities, following southern beech (*Nothofagus* spp.) mast seeding (Fitzgerald, 1978; King, 1983b; Fitzgerald et al., 1996), a phenomenon that occurs every 4–5 years. Following mast seeding, several species of introduced mammalian predator, especially the stoat (*Mustela erminea* L.) and weasel (*M. nivalis* Erxleben), subsequently increase greatly in number, apparently in response to increased rodent densities (King and McMillan, 1982; King, 1983b). These large changes in rodent and predator density can lead to increased predation on a number of rare or threatened native species (Moors, 1983; McLennan et al., 1996), and ship rats and stoats have been implicated in recent extinctions in New Zealand (King and McMillan, 1982; Innes, 1990; King, 1990a).

New Zealand forests present a unique system where ship rats and house mice are the only small mammalian prey species present in the environment. Similarly, their only common mammalian predator is the stoat, although weasels are present seasonally in low numbers (King, 1990b). This system has a uniquely simple combination of two small mammalian prey species with one mammalian predator. Thus it provides an ideal system for testing, on a large scale, the role of predators in small mammal population dynamics (May, 1999).

The basic biology of these species and the timing and amplitude of the population fluctuations of small mammals have been well studied in New Zealand, but no attempt has been made to explicitly clarify the role of predators in the eruptive population dynamics of rodents in the New Zealand system. To date, there has been no concerted effort to reconcile small mammal systems in New Zealand with current ecological theory.

In this paper, we present a quantitative computer model of the role of predators in the eruptive small mammal system in New Zealand forests. Using current knowledge on the biology and ecology of predator and prey species, both from published and unpublished accounts, a model of the eruptive population dynamics of house mice, ship rats and stoats is constructed. Key parameters in the model are tested, and the output is compared with current predator–prey theory to generate a number of predictions regarding the role of predators in the eruptive system in New Zealand. The construction of the model has two main functions. It places New Zealand small-mammal communities in the context of current ecological theory and generates predictions regarding the role of predation in the New Zealand ecosystem. These predictions can be tested in either a theoretical or conservation management framework, and can lead to new insights into the role of predators in small-mammal population regulation. Additionally, the construction of the model requires a large number of parameters pertaining to the biology and ecology of the predator and prey species. Therefore, it tests current understanding of, and assumptions in, small-mammal ecology in New Zealand, and serves to highlight deficiencies in current knowledge.

2. Methods

2.1. Model overview

A three-species dynamic model consisting of house mouse, ship rat and stoat populations (termed ERRPTS; Eruptive rodent/predator theoretical simulation) was constructed using the STELLA II modelling package (High Performance Systems, Inc, 1990). The STELLA II programming language uses an iconographic interface to facilitate construction of dynamic system structures (Costanza and Gottlieb, 1998; Anastácio et al., 1999; Angelini and Petrere, 2000).

In order to keep the model as parsimonious and general as possible, a number of assumptions were made in the construction of the model. Each species was separated into juvenile and adult age classes, and the same basic model structure was used for mice and rats, with the insertion of appropriate parameters. It was assumed that immigration and emigration were negligible (or equal), and mortality functions were modified so
that no species went extinct in the model over the course of the simulation. Predation by species other than stoats is known to be minimal in most forest habitats in New Zealand (King, 1990a,b), and was assumed to be zero in the model. An arbitrary area was set at 100 ha, and the model was run for 5 years in each simulation.

2.2. Parameters and model construction

Parameters for the model were gained from the literature on mice, rats, and stoats in New Zealand where available (Table 1), and functions for density-dependent and food-mediated reproduction or mortality were simulated using published parameters if no specific functions were available. A list of variable names and acronyms, their units and a brief description is given in Appendix 1.

2.3. Mouse population

Both mice and rats were divided into juvenile and adult age classes. Numbers of juvenile mice present in the model after each iteration were given by:

\[ M_j(t) = M_j(t - dt) + (bM - rM - mJM)*dt, \]  

where \( M_j \) is the number of juvenile mice, \( bM \) is the mouse birth rate per time \( t \), \( rM \) is the mouse recruitment rate, and \( mJM \) is the juvenile mouse natural mortality rate.

Natural mortality of mice is high in all years, and is largely controlled by food availability (Fitzgerald, 1978; Fitzgerald et al., 1981) and environmental conditions (Bronson, 1979). The carrying capacity and the resulting level of mortality were set by an arbitrary function that allowed a sixfold variation in density between mast and non-mast years. Mortality was set as a function of mouse numbers, with mortality ranging from 1.5% per month at low densities, to 97.5% per month at levels above the carrying capacity (Fig. 1(a)).

Mice were classified as juveniles for two months (Murphy and Pickard, 1990), after which time they entered the adult population and could breed. This was achieved in STELLA II through the use of a conveyor stock for juvenile mice, which keeps mice as juveniles for two iterations before releasing them into the adult population. Adult mice present in the model at each iteration were given by:

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mice</th>
<th>Rats</th>
<th>Stoats</th>
</tr>
</thead>
<tbody>
<tr>
<td>Breeding season</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-mast year</td>
<td>September to March</td>
<td>September to March</td>
<td>September/October</td>
</tr>
<tr>
<td>Mast year</td>
<td>April–January/March</td>
<td>April/May–March</td>
<td>September/October</td>
</tr>
<tr>
<td>Breeding rate</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-mast year</td>
<td>34.2 young/female (2.4 young/mouse/month)</td>
<td>11.1 young/female (0.8 young/rat/month)</td>
<td>2.2 young/female (1.1 young/stoat/year)</td>
</tr>
<tr>
<td>Mast year</td>
<td>57.2 young/female (2.9 young/mouse/month)</td>
<td>28.1 young/female (1.4 young/rat/month)</td>
<td>8.8 young/female (4.4 young/stoat/year)</td>
</tr>
<tr>
<td>Predation rate</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-mast year</td>
<td>12.1 mice/stoat/month</td>
<td>6.1 rats/stoat/month</td>
<td></td>
</tr>
<tr>
<td>Mast year</td>
<td>47.3 mice/stoat/month</td>
<td>23.3 rats/stoat/month</td>
<td></td>
</tr>
</tbody>
</table>

* Sources of values used are listed in the text.
* Breeding in mice may cease earlier (in January) in a mast year, even though food is still available (Murphy and Pickard, 1990).
* Stoats only breed once per year, with a single litter of young produced in late September/Early October (King and Moody, 1982b; King, 1983a). Rats were assumed to be twice as profitable as mice for stoats (Day, 1968). Predation was assumed to switch onto mice if the number of mice was more than twice that of rats.
* Parameter calculated from Day (1968).
Fig. 1. Natural mortality rates for: (a) juvenile mice (jmM) and rats (jmR); and (b) adult mice (amM) and rats (amR), used in the STELLA II ERRPTS model. The same general functions were used for mice and rats, although the densities over which the function acted differed between mice and rats in the model.

\[ M_a(t) = M_a(t - dt) + (r_eM - d_M)dt, \]  

where \( M_a \) is the number of adult mice, and \( d_M \) is the adult mouse death rate per time \( t \). The number of mice initially present in the model was set at 300 individuals.

Breeding rates varied depending on whether the year was a mast year or non-mast year. In a non-mast year, mice breed between September and March (Fitzgerald, 1978), and produce an estimated 34.2 young/female over that period (average litter size 5.72, 6 litters/female). In a mast year, mice start breeding earlier (April–May), stop breeding in January or February (King, 1982), and produce an estimated 57.2 young/female over that period (average litter size 5.72, 10 litters/female; Murphy and Pickard, 1990). The breeding rate of mice ranges from 30% of females breeding in low-density populations, to 10% breeding in high-density populations (Fitzgerald, 1978; King, 1982), so the proportion of mice breeding in the population was scaled to density. Thus, the mouse birth rate per unit time was given by:

\[ b_M = b_sM*(M_a*r_M)*R_{ddM}, \]  

where \( b_M \) is the number of mice recruited into the adult population per time \( t \), \( b_sM \) is a binomial converter that switches from 0 in the non-breeding season to 1 during the breeding season, \( r_M \) is the mouse reproductive rate, expressed as young per mouse, and \( R_{ddM} \) is the proportion of mice breeding each month, and is inversely density dependent on mouse density (Fig. 2).

The rate of mouse recruitment into the adult population depended on the rate of juvenile mouse natural mortality, and was given by:

\[ r_eM = M_j - (mJM), \]  

where:

Fig. 2. The proportion of mice (\( R_{ddM} \)) and rats (\( R_{ddR} \)) breeding as a function of population size for that species. Values for high and low density breeding rates were estimated from published New Zealand studies.
Fig. 3. Functions used to model stoat population dynamics in STELLA ERRPTS model. (a) The number of rodents eaten per stoat (C) as a function of the ratio of Total rodents to Adult stoats. (b) Fecundity of stoats (fS) in the model as a function of the Total rodent: Adult stoat ratio.

\[ m_{JM} = Mj \times jmM. \]

\[ m_{JM} \] is the density dependent proportional rate of juvenile mouse mortality, which ranged from 1.5% of the population at low density, to a high of 97% per month at densities above the carrying capacity (Fig. 1(a)). The adult mouse mortality rate was a function of natural mortality and predation due to stoats, and was given by:

\[ d_M = (Ma \times amM) + pM, \]  

where \( d_M \) is the total monthly adult mouse mortality rate expressed as mice per time \( t \), \( am_M \) is the proportional density dependent adult mouse natural mortality rate scaled to the carrying capacity, with mortality ranging from 6% at low density, to 71.5% at densities above the carrying capacity (Fig. 1(b)), and \( p_M \) gives the rate of mouse removal by stoats per time \( t \).

In Britain, stoats are known to eat c. 23% of their body weight per day for males, and c. 14% per day for females (Day, 1968), although consumption rates in New Zealand are unknown. The average size of stoats in New Zealand is 324.4 g for males, and 207.2 g for females (King, 1990a). Daily food requirements equate to 75 g/food/day for male stoats, and 30 g/food/day for female stoats. Rats make up c. 30% of the diet of stoats in the study area, and mice c. 24% of the diet (King and Moody, 1982a). Therefore, male stoats eat \( \sim 22.5 \) g rat/day, and female stoats eat \( \sim 9 \) g rat/day. Given an average meal size for stoats of 20 g per rat and 10 g per mouse (Day, 1968), this gives an average consumption rate of 1.13 rats/stoat/day for males, and 0.45 rats/stoat/day for females, giving an overall average of 0.79 rats/stoat/day, or 23.6 rats/stoat/month. The same calculation for mice, assuming an average meal size of 10 g, gives a consumption of 47.3 mice/stoat/month.

Mustelids are known to show functional shifts in feeding as preferred foods change in abundance (Tapper, 1979; Hanski et al., 1991; Korpimaki et al., 1991; Murphy and Bradfield, 1992). Therefore, stoat predation was set to switch between low and high rodent consumption rates over a threshold range of 350–450 rodents per stoat (Fig. 3(a)), which allowed maximal predation during a mast year. It was assumed that rats are twice as profitable as mice (Day, 1968), and that mouse numbers greatly exceed rat numbers during an eruption (King, 1983b; Murphy and Pickard, 1990; Murphy, 1992). Therefore stoat predation switched entirely onto mice when the ratio of mice to rats was greater than 2:1. Thus, with mouse:rat ratios greater than 2:1, the rate of mouse removal by stoats was given by:

\[ p_M = 2 \times S_a \times C, \]  

where \( S_a \) is the number of adult stoats, and \( C \) is the per capita consumption rate of mice by stoats,
expressed as mice/stoat/month, and was a function of the ratio of total rodents:adult stoats (Fig. 3(a)). At mouse:rat ratios lower than 2:1, mice and rats were consumed in the ratio of two mice for every rat:

\[
p_M = \frac{2*M_{tot}*S_a*C}{(2*R_{tot} + M_{tot})},
\]

where \( M_{tot} \) is the total number of mice present in the system \((M_f + M_a)\), and \( R_{tot} \) is the total number of rats present \((R_f + R_a)\), where \( R_f \) and \( R_a \) are the numbers of juvenile and adult rats respectively.

### 2.4. Rat population

The rat population was structured in the same way as the mouse population, with the initial number of rats set at 300 individuals. Rats were classified as juveniles for three months (Innes, 1990), at which time they entered the adult population and could breed. Thus the number of juvenile rats present after each iteration was given by:

\[
R_j(t) = R_j(t - dt) + (b_R - r_{deR} - m_{jR})*R_{j},
\]

where \( b_R \) is the rat birth rate per time \( t \), \( r_{deR} \) is the rat recruitment rate, and \( m_{jR} \) is the juvenile rat mortality rate, and the number of adult rats present after each iteration was given by:

\[
R_a(t) = R_a(t - dt) + (r_{deR} - d_R)*R_{a},
\]

where \( d_R \) is the total adult rat mortality rate.

Rat breeding was structured in the same way as for mice. The non-mast breeding season extended from September to March, with an estimated production of 11.1 young/female in that period (average litter size 5.6, 2 litters/female; Innes, 1990). The mast breeding season extended from June to March, with an estimated production of 28.1 young/female (litter size 5.6, 5 litters/female; King, 1990b). The density dependent proportion of rats breeding ranged from 71.6% breeding at low density to 10.8% at high densities (Fig. 2). This breeding proportion was required to generate population fluctuations similar to those seen in the field, given the rat breeding rates used in the model. Thus, the rat birth rate was given by

\[
b_R = b_S*R*(R_a*r_{deR})*R_{ddR},
\]

where \( b_R \) is the rat birth rate per time \( t \), \( b_S \) is a binomial converter, similar to \( b_M \) Eqn. 3, \( r_{deR} \) is the rat reproductive rate, expressed as young/rat/month, and \( R_{ddR} \) is the density dependent proportion of rats breeding (Fig. 2).

Natural mortality of juvenile and adult rats used the same functions as for mice, but was scaled to allow a four-fold variation in the carrying capacity between mast and non-mast years (Fig. 1(a–b)). Thus the rate of juvenile rat mortality was given by:

\[
m_{JM} = R_j*m_{deR},
\]

where \( m_{deR} \) is the density dependent proportional rate of juvenile rat natural mortality.

The rate of adult rat mortality was a function of natural mortality and stoat predation, and was given by:

\[
d_R = (R_a*a_{mR}) + p_R,
\]

where \( d_R \) is the rat death rate per time \( t \), \( a_{mR} \) is the proportional density dependent adult rat natural mortality rate scaled to the carrying capacity (Fig. 1(b)), and \( p_R \) is the rate of rat consumption by stoats. As stated in Eqn. 6, if the mouse:rat ratios were greater than 2:1, stoat predation switched entirely onto mice. Under these conditions:

\[
p_R = 0.
\]

Under field conditions, rats do not become extinct over large areas, due to immigration and prey switching by predators, so a minimum number of 100 rats (1/ha) was set, below which no stoat induced rat-mortality occurred. At rat densities higher than 1/ha, And with mouse:rat ratios lower than 2:1. The rate of rat consumption by stoats was given by:

\[
p_R = \frac{(2*R_{tot}*S_a*C)}{(M_{tot} + 2*R_{tot})}
\]

### 2.5. Stoat population

Adult stoats present in the model after each iteration were given by

\[
S_a(t) = S_a(t - dt) + (r_{deS} - d_S)*S_a,
\]
where $r_S$ is the recruitment rate of stoats per time $t$, and $d_S$ is the adult stoat mortality rate. The initial number of stoats was set at two individuals.

In comparison to the two rodent species, stoat breeding is initiated by day-length (King, 1990a), so that only one litter is produced in late September–early October (King and McMillan, 1982; King and Moody, 1982b; King, 1983b). On average, pregnant female stoats produce 8.8 embryos (King, 1990a). Both the birth and recruitment rates, however, are highly dependent on food availability, and can range from 0–2.6 young/female in a poor-food year to 10–13 young/female in a mast year (King, 1983b). Therefore, the number of juvenile stoats after each iteration was given by:

$$S_j(t) = S_j(t - dt) + (b_S - r_S - m_{JS}) * dt$$ (15)

where $S_j$ is the number of juvenile stoats present, $b_S$ is the stoat birth rate per time $t$, and $m_{JS}$ is the juvenile stoat mortality rate.

The stoat birth rate was given by:

$$b_S = b_sS * (f_S * S_a),$$ (16)

where $b_sS$ is a binomial convertor of the same form as $b_sM$ and $b_sR$ Eqn. 3 and $f_S$ is the fecundity rate, expressed as young per stoat, and was a function that varied from 1.1 young/stoat/month in low food years to 4.4 young/stoat/month in high food years, and was mediated through the total rodent:adult stoat ratio (Fig. 3(b)).

Juvenile mortality is closely correlated with food availability, with mortality of up to 90% recorded in non-mast years (King, 1990a). Thus, the recruitment rate into the adult population was given by:

$$r_S = S_j - (S_j * m_{JS}),$$ (17)

where $m_{JS} = S_j * m_S$, and $m_S$ is the proportional juvenile mortality rate, which is a function of the total rodents:adult stoat ratio (Fig. 4(a)).

Adult stoat mortality was set at 0 at densities below three stoats/100 ha to prevent extinction of stoats in the model. At densities greater than 3/100 ha, the adult stoat mortality rate was given by:

$$d_S = S_a * a_mS,$$ (18)

where $a_mS$ is the proportional adult stoat death rate, mediated by the total rodent:adult stoat ratio (Fig. 4(b)).

A full listing of the ERRPTS model can be obtained from the primary author (G.L. Blackwell).

Variation in mast and non-mast year breeding rates of rodents (mean ± S.D. from published studies) was incorporated into the model to add a
measure of stochasticity into the model, but the model still remained primarily deterministic.

3. Results

3.1. Calibration of the model

Data on population dynamics in pure beech forest in the South Island, New Zealand, were used to calibrate the model (King, 1983b; King and Moller, 1997).

The population trends for mice, ship rats and stoats predicted by the model were compared to population trends from the field data sets for each species. The model correctly predicted the timing and amplitude of the species’ responses to a beech masting, especially for mice (Fig. 5(a)) and stoats (Fig. 5(c)). The correlation for rats was not as tight (Fig. 5(b)), with more variation in the field data than predicted by the model.

The amplitude of fluctuation in peak density between mast and non-mast years from the field data was ~ 6-fold for mice (c.f. 8-fold from the model); 10-fold for rats (c.f. 4-fold from the model); and 8-fold for stoats (c.f. 7-fold from the model).

3.2. Sensitivity analysis

The dynamic nature of the model and the program structure makes multiple tests of parameter sensitivity laborious and time-consuming. Therefore, key parameters (or key parameter pairs in the case of rodent breeding rates in mast and non-mast years) were varied by ± 10 and ± 50% to examine their effects on model performance (Jorgensen, 1986).

Mouse and rat populations were more sensitive to changes in breeding rates than to changes in predation intensity (Table 2). Both rodent species were more sensitive to a decrease in breeding effort than an increase, and rats were much less sensitive to large changes in predation by stoats than mice, as a result of the 2:1 ratio of mouse:rat predation used in the model. An increase of 50% in the predation rate was enough to largely prevent a mouse eruption, while the same increase in predation on rats barely suppressed rat numbers. Both rats and mice were insensitive to changes in the timing of stoat breeding, and would erupt irrespective of the time at which adult stoats appeared in the system.

The model generated sequential increases and declines in mouse, ship rat and stoat populations known to occur during a masting event (Fig. 6). Stoats did not increase in numbers until rodent numbers had almost peaked, and their decline followed the severe population crashes exhibited by mice and rats. The driving of stoat dynamics by rodent density affects the predator:prey ratios throughout the eruption (Fig. 7), so that the ratio is highest in the non-mast years.

3.3. The effect of predation on rodent populations

The effect of stoat removal on mouse and rat populations was investigated by scaling the rate of rodent consumption by stoats (C) in the model from 0 (no stoats present) to 1 (100% stoats present).

As predator:prey ratios peak and then drop following the crash (Fig. 7), predator limitation is reduced, so that populations with and without predator present show little difference. The model predicts that stoats should have a large effect on mouse populations, and may limit their numbers throughout most of the eruptive cycle (Fig. 8(a)). Stoat predation can delay and truncate the eruption of mice following a beech masting, and can potentially hasten the decline. The rate at which the carrying capacity drops, and the amount of natural mortality (Fig. 8(b)) control the severity of predator limitation in the crash and low phase. With a more gradual decline in the carrying capacity following an eruption, predator limitation becomes more important.

The response of rats to stoat reduction is similar to that of mice, but less pronounced (Fig. 9(a)). Predators can limit rat populations in the low phase, and delay the increase during an eruption, but limitation at the peak is much less pronounced than that seen in the mouse population, as a result of buffering of predation on the rat population by mice. Stoat predation can theoretically cause rat populations to crash more
quickly and deeply than food limitation alone would produce (Fig. 9(b)). However, as with the mouse population crash, the importance of predator limitation in the crash phase will depend on the severity of natural mortality over the same period.

The ability of predators to prevent an outbreak was tested by shifting stoat breeding forward, so that adult stoats were present as the rodents started to increase. Neither mouse nor rat population dynamics differed with predator breeding advanced. Both mouse and rat populations
erupted to similar levels with stoat breeding advanced, suggesting it is not the lag in stoat breeding that is the primary reason for the inability of stoats to prevent or truncate a rodent eruption.

The effect of the amount of food supplied to the system was examined by varying the reproductive effort during the population eruption, as a proxy measure of energy input. The breeding rate in the mast period was varied from the non-mast level (0.794 young/rat/month; 2.44 young/mouse/month), to the maximum level used in the model (1.41 young/rat/month; 2.86 young/mouse/month; Fig. 10(a–b)). Stoat predation had a proportionally greater effect on prey dynamics at low breeding rates, than at maximum rates of rodent breeding. However, even at normal (non-mast)

Table 2
Results of sensitivity analysis of the influence of key reproductive and predation parameters on peak eruption density in the ERRPTS population dynamics model

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mice</th>
<th>Rats</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density</td>
<td>S.E.</td>
<td>Range</td>
</tr>
<tr>
<td>Breeding</td>
<td></td>
<td></td>
</tr>
<tr>
<td>+10%</td>
<td>1239.47</td>
<td>14.02</td>
</tr>
<tr>
<td>-10%</td>
<td>960.57</td>
<td>9.93</td>
</tr>
<tr>
<td>+50%</td>
<td>1751.12</td>
<td>8.00</td>
</tr>
<tr>
<td>-50%</td>
<td>73.56</td>
<td>5.27</td>
</tr>
<tr>
<td>Predation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>+10%</td>
<td>1047.67</td>
<td>16.02</td>
</tr>
<tr>
<td>-10%</td>
<td>1132.56</td>
<td>12.60</td>
</tr>
<tr>
<td>+50%</td>
<td>583.40</td>
<td>16.55</td>
</tr>
<tr>
<td>-50%</td>
<td>1264.67</td>
<td>8.12</td>
</tr>
<tr>
<td>Non-treatment</td>
<td>1020.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

* The range in peak densities for each set of manipulations is shown. The model was run 10 times with each set of parameter values.
breeding rates in a mast year (longer, earlier breeding season), predation could not prevent prey populations increasing to significantly higher levels than in non-mast years (Fig. 10).

4. Discussion

The ERRPTS dynamic model of mouse, ship rat and stoat population dynamics generated similar population behaviour during a simulated eruption as seen in field studies (King, 1983b; Innes, 1990; Fitzgerald et al., 1996; King and Moller, 1997). The amplitude of the rat eruption in the model was smaller than that seen in the calibration field data (King and Moller, 1997). While the timing and amplitude of food-driven eruption events in field situations may vary between locations, and temporally within a location, the model serves as a useful generalization of the processes occurring. It provides a framework for investigating the relative importance of food and predation in driving the observed population dynamics.

The model highlights the primary importance of food in driving the eruptive system. Mouse numbers have been shown to be significantly correlated with the size of the beech seedfall in mixed beech/podocarp forest in the Orongorongo valley in the North Island, New Zealand (Fitzgerald et al., 1996), and in pure beech forest in the South Island (King 1983b). Similarly, rat numbers significantly increased following the beech masting in the same South Island study (King and Moller 1997), and are known to increase following heavy winter fruiting in North Island forests (Daniel 1978).

The time lags in the predator response to the rodent eruption appear to be a relatively minor
component in the predator’s inability to prevent a population eruption. Instead, the extended, multiple breeding in rodents (Daniel, 1972; Innes, 1979; King, 1982; Innes, 1990; Murphy and Pickard, 1990), compared to a single breeding effort by stoats (King and Moody, 1982b; King, 1990a), appears to be the main reason why predators cannot prevent a prey outbreak.

It has been suggested that functional shifts in predation rates by year round generalist predators may keep low-density prey populations in a
Fig. 10. The effect of varying the mast-year breeding rate on population dynamics of: (a) mouse; and (b) ship rat populations with predators present or removed. For mice, the low breeding rate was 2.44 young/mouse/month and the high level at 2.86 young/mouse/month. For rats the low and high breeding rates were 0.79 young/rat/month and 1.41 young/rat/month respectively.

1996), the stoat total response may have a greater limiting effect on the rodent populations, but still cannot prevent a significant increase in prey numbers.

In the predator-pit model proposed by Sinclair et al. (1990), Pech et al. (1992) for eruptive systems in Australia, generalist predators (red foxes, Vulpes vulpes, and feral cats, Felis catus) were present in moderate numbers year round, and their numbers were buffered by the presence of alternative prey. In their model, there was a threshold density below which predators could regulate prey populations through shifts in the predator functional response, but above which predation was non-regulating, or inversely density dependent (Sinclair et al., 1990). In comparison, predators (stoats) in the New Zealand system may have little capacity to prevent an eruption; so that, while they can exhibit some population limitation, there may be no threshold density below which they can regulate prey density.

The timing of the stoat population increase in the model suggests that predation will be most important during the crash and low phases following the eruption. A number of field studies of cyclic populations of small mammals have shown that predation is important during the crash and low phases of the cycle (Erlinge et al., 1988;
Korpimaki et al., 1991; Reid et al., 1995), and that the removal of predators may stop the cyclical decline (Korpimaki and Norrdahl, 1998).

In the model, predator:prey ratios were highest late in the crash phase, and stoats were eating the maximum number of rodents per stoat, so that the total predator response was greatest at this time. However, the model highlighted the primary importance of natural mortality over the crash phase. Stoat induced mortality will become relatively more important with a more gradual drop in the carrying capacity, and with less food or cold induced mortality. Both mice and rats have high-energy requirements characteristic of small mammals, and are susceptible to cold stress (Innes, 1990; Berry and Bronson, 1992). As a result, post-mast mortality is high irrespective of predator induced mortality. Therefore, whether the response of rodents to predator removal during the crash phase is detectable under field conditions remains to be seen.

The model also predicts that predators should be able to limit prey populations in the post-crash low phase, through high predator:prey ratios, and such a response has been shown in field experiments with microtine communities in Fennoscandia (Korpimaki and Norrdahl, 1998), and for eruptive rabbit/red fox associations in Australia (Newsome et al., 1989). Once again, the strength of predator limitation in the low phase in the New Zealand forest system will be modified by the relative strength of other limiting factors acting upon rodents at the same time. As predator numbers drop in the period following the eruption, predator limitation should also decline, so that the system becomes reset for the next eruption.

4.1. Future work and model development

While the model generated population dynamics and behaviours similar to those seen in field situations, a number of parameters were ‘best-guess’ estimates, or generalised functions. Clearly a better understanding of the processes occurring in these systems, and the construction of a more robust model, requires the investigation of a number of parameters.

Information is required on the breeding biology of rodents in New Zealand, including the effects of density on reproductive behaviour and fecundity, and the breeding rates of young-of-the-year animals. More information is required on the energy requirements of stoats, and the functional responses of stoats to changes in rodent density and relative species abundance. It is not known to what extent prey switching between rodents occurs in stoats, and consequentially how accurate calculated prey consumption rates are.

The model made no estimates of spatial effects within the system, but rather used average densities in an arbitrary area. Stoats are known to be highly mobile during dispersal (King and McMillan, 1982), but the effect this movement has on predation rates is unclear. Similarly, mice and rats are known to be largely solitary in low-density populations (Daniel, 1972; Fitzgerald et al., 1981; Hooker and Innes, 1995), but the social structure of high-density populations is unknown.

Therefore, while the model is a useful starting point as it stands, and generates testable predictions, the investigation of the points discussed will greatly enhance the validity and applicability of the model, our understanding of New Zealand forest systems, and predator/prey interactions in general.

5. Conclusions

A generalised model of the population dynamics of house mice, ship rats, and stoats in an eruptive system was constructed. The model tested the relative importance of food and predator limitation of rodent populations in New Zealand forests, and generated a number of outputs and predictions that could be tested under field conditions.

Predators can exhibit minor limitation over prey populations prior to an eruption.

Predators cannot prevent a rodent eruption, but may delay the increase in prey populations in response to food.

The inability of predators to stop a rodent eruption is due to the vastly different rates of increase between predators and prey, and the lack
of alternative prey to buffer stoat numbers, rather than the time-lags in predator breeding.

Predators will have relatively more influence on peak prey population density in partial mast conditions. With a full mast eruption, predators should not be able to significantly limit prey population size.

Predators have the potential to significantly hasten the rate of decline in crashing rodent populations. The strength of predator limitation will depend on the severity of the crash in the carrying capacity.

Predators can limit prey populations in the post-crash low phase. The strength of the low-phase predator limitation will depend on the extent of the natural mortality during the crash phase, and on the predator:prey ratios over the crash and low-phases. Predator limitation should decline over the low phase as predator:prey ratios drop.

Acknowledgements

The authors would like to thank Dr Russell Death and Dr Harald Steen, and two anonymous reviewers for comments on earlier drafts of the manuscript. Thanks also to Dr John McLennan, Jonathan Miles, Ray Stevenson, Robert Waiwai, Nick Gillingham, and all those on the Lake Waikaremoana project, for their ideas and support. The project was supported in part by a Massey University Doctoral Research Committee scholarship.

Appendix A. Variables used in the ERRPTS population dynamics model. Listed are the variable acronyms, names, units and descriptions

<table>
<thead>
<tr>
<th>Variable</th>
<th>Name</th>
<th>Units</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mice</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$M_j$</td>
<td>Juvenile mice</td>
<td>Mice</td>
<td>Number of juvenile mice present in the model after each month</td>
</tr>
<tr>
<td>$M_a$</td>
<td>Adult mice</td>
<td>Mice</td>
<td>Number of adult mice present in the model after each month</td>
</tr>
<tr>
<td>$b_M$</td>
<td>Mouse birth rate</td>
<td>Mice/month</td>
<td>The number of mice born per month</td>
</tr>
<tr>
<td>$r_{eM}$</td>
<td>Mouse recruitment rate</td>
<td>Mice/month</td>
<td>Number of juvenile mice recruited into the adult population each month</td>
</tr>
<tr>
<td>$m_{JM}$</td>
<td>Juvenile mouse mortality rate</td>
<td>Mice/month</td>
<td>The monthly rate of natural mortality of juvenile mice</td>
</tr>
<tr>
<td>$d_M$</td>
<td>Adult mouse death rate</td>
<td>Mice/month</td>
<td>The monthly total adult mouse mortality rate; comprising natural mortality and stoat predation</td>
</tr>
<tr>
<td>$b_{sM}$</td>
<td>Mouse breeding season</td>
<td>Binomial</td>
<td>Binomial controller that switches between 0 in the non-breeding season and 1 in the breeding season</td>
</tr>
<tr>
<td>$r_M$</td>
<td>Mouse reproductive rate</td>
<td>Mice/mouse/month</td>
<td>The number of young mice per adult mouse, that varied between mast and non-mast years</td>
</tr>
<tr>
<td>Symbol</td>
<td>Definition</td>
<td></td>
<td></td>
</tr>
<tr>
<td>------------</td>
<td>----------------------------------------------------------------------------</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( R_{ddM} )</td>
<td>Density-dependent proportion of mice in the population breeding</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( f_{mM} )</td>
<td>The density-dependent proportion of juvenile mice that die each month</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( am_M )</td>
<td>The density-dependent proportion of adult mice that die each month</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( p_M )</td>
<td>the number of mice eaten by stoats each month</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( C )</td>
<td>The per capita consumption rate of mice by stoats</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( M_{tot} )</td>
<td>The total number of juvenile and adult mice</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( R_j )</td>
<td>Number of juvenile rats present in the model after each month</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( R_a )</td>
<td>Number of adult rats present in the model after each month</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( b_R )</td>
<td>The number of rats born per month</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( r_{eR} )</td>
<td>Number of juvenile rats recruited into the adult population each month</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( m_{JR} )</td>
<td>The monthly rate of natural mortality of juvenile rats</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( d_R )</td>
<td>The monthly total adult rat mortality rate; comprising natural mortality and stoat predation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( b_{sR} )</td>
<td>Binomial controller that switches between 0 in the non-breeding season and 1 in the breeding season</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( r_R )</td>
<td>The number of young rats per adult rat, that varied between mast and non-mast years</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Symbol</td>
<td>Description</td>
<td>Units</td>
<td>Equation</td>
</tr>
<tr>
<td>--------</td>
<td>------------------------------------------------------------------------------</td>
<td>-------------------------</td>
<td>------------------------------------------------------------------------</td>
</tr>
<tr>
<td>$R_{ddR}$</td>
<td>Density-dependent proportion of rats in the population breeding each month</td>
<td>Proportion/month</td>
<td>The density-dependent proportion of rats in the population breeding each month</td>
</tr>
<tr>
<td>$f_{mR}$</td>
<td>Juvenile rat proportional mortality</td>
<td>Proportion/month</td>
<td>The density-dependent proportion of juvenile rats that die each month</td>
</tr>
<tr>
<td>$a_{mR}$</td>
<td>Adult rat proportional mortality</td>
<td>Proportion/month</td>
<td>The density-dependent proportion of adult rats that die each month through natural mortality</td>
</tr>
<tr>
<td>$P_R$</td>
<td>Rat predation rate</td>
<td>Rats/month</td>
<td>The number of rats eaten by stoats each month</td>
</tr>
<tr>
<td>$C$</td>
<td>Consumption rate</td>
<td>Rats/stoat/month</td>
<td>The per capita consumption rate of rats by stoats</td>
</tr>
<tr>
<td>$R_{tot}$</td>
<td>Total number of rats</td>
<td>Rats</td>
<td>The total number of juvenile and adult rats</td>
</tr>
<tr>
<td><strong>Stoats</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$S_a$</td>
<td>Adult stoats</td>
<td>Stoats</td>
<td>The number of adult stoats present in the model after each month</td>
</tr>
<tr>
<td>$S_j$</td>
<td>Juvenile stoats</td>
<td>Stoats</td>
<td>The number of juvenile stoats present in the model after each month</td>
</tr>
<tr>
<td>$b_S$</td>
<td>Stoat birth rate</td>
<td>Stoats/month</td>
<td>The number of stoats born each month, mediated by food availability</td>
</tr>
<tr>
<td>$r_{exS}$</td>
<td>Stoat recruitment rate</td>
<td>Stoats/month</td>
<td>Number of juvenile stoats recruited into the adult population each month</td>
</tr>
<tr>
<td>$m_{JS}$</td>
<td>Juvenile stoat mortality rate</td>
<td>Stoats/month</td>
<td>The monthly rate of natural mortality of juvenile stoats, mediated by food availability</td>
</tr>
<tr>
<td>$d_S$</td>
<td>Adult stoat death rate</td>
<td>Stoats/month</td>
<td>The monthly rate of adult stoat mortality, mediated by food availability</td>
</tr>
<tr>
<td>$b_{BS}$</td>
<td>Stoat breeding season</td>
<td>Binomial</td>
<td>Binomial controller that switches between 0 in the non-breeding season and 1 in the breeding season</td>
</tr>
<tr>
<td>$f_S$</td>
<td>Stoat fecundity rate</td>
<td>Young/stoat/month</td>
<td>The number of young born per stoat during the breeding season, mediated by food availability</td>
</tr>
</tbody>
</table>
\[ j_{MS} \quad \text{Juvenile Proportional juvenile stoat mortality rate, mediated by food availability} \]

\[ a_{MS} \quad \text{Adult Proportional adult stoat mortality rate, mediated by food availability} \]

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