

Population dynamics of the ship rat *Rattus rattus* L. in the Orongorongo Valley, New Zealand

M. G. Efford , B. M. Fitzgerald , B. J. Karl & P. H. Berben

To cite this article: M. G. Efford , B. M. Fitzgerald , B. J. Karl & P. H. Berben (2006) Population dynamics of the ship rat *Rattus rattus* L. in the Orongorongo Valley, New Zealand, New Zealand Journal of Zoology, 33:4, 273-297, DOI: [10.1080/03014223.2006.9518457](https://doi.org/10.1080/03014223.2006.9518457)

To link to this article: <https://doi.org/10.1080/03014223.2006.9518457>



Published online: 30 Mar 2010.



Submit your article to this journal [↗](#)



Article views: 1163



View related articles [↗](#)



Citing articles: 4 View citing articles [↗](#)

Population dynamics of the ship rat *Rattus rattus* L. in the Orongorongo Valley, New Zealand

M. G. EFFORD*

Landcare Research
Private Bag 1930
Dunedin 9054, New Zealand
murray.efford@stonebow.otago.ac.nz

B. M. FITZGERALD

Ecological Research Associates of New Zealand
PO Box 48147
Silverstream
Upper Hutt 5142, New Zealand
bmfitzgerald@ezysurf.co.nz

B. J. KARL

Landcare Research
Private Bag 6
Nelson Mail Centre
Nelson 7042, New Zealand
karlb@landcareresearch.co.nz

P. H. BERBEN

Landcare Research
Private Bag 11052
Manawatu Mail Centre
Palmerston North 4442, New Zealand
berben@landcareresearch.co.nz

*Present address: Zoology Department, University of
Otago, PO Box 56, Dunedin 9054, New Zealand.

Abstract The population dynamics of ship rats (*Rattus rattus* L.) were studied in podocarp/hardwood and hard beech (*Nothofagus truncata*) forest in the Orongorongo Valley, near Wellington, from 1971 to 1998. Rat density (indexed by captures in 116 snap traps over 3 nights per quarter) varied up to five-fold between consecutive years. Fruiting of hinau (*Elaeocarpus dentatus*) and hard beech did not drive the fluctuations as had been suggested. Average density increased over the first 15 years of the study

(from 2.3 ± 0.3 to 7.5 ± 0.8 per 100 trap-nights (mean \pm SE)), and then declined; this mirrored a trend in cat density driven by external factors. Breeding was largely restricted to spring (November) and summer (February). Breeding rate (proportion pregnant or lactating) was density-dependent, particularly in older rats. Litter size (based on live embryos and new uterine scars) increased between spring (4.4 ± 0.4) and summer (5.5 ± 0.3) (mean \pm SE), but did not vary with density or age. Winter breeding was rare (2% pregnant or lactating in August). Hinau fruitfall did not predict the proportion breeding in autumn (May), or survival in winter-spring (i.e., population change between August and November). Varying predation intensity was the most likely explanation for the population trend. We review other New Zealand studies and question the assumption that ship rat populations are “eruptive”, except possibly when predation is eliminated.

Keywords *Rattus rattus*; *Elaeocarpus dentatus*; *Nothofagus*; frugivory; predation; phenology; seasonal breeding; masting; feral cat; stoat; eruptive dynamics

INTRODUCTION

Invasive species, of which the ship rat (*Rattus rattus* L.) in New Zealand forests is a classic example, frequently require active management, and improved ability to predict their dynamics will assist conservation. Long-term studies provide data that are useful in at least two distinct ways for predicting population dynamics. Prediction may be approached by statistical extrapolation of patterns in historical data. Prediction may also be based on quantitative biological understanding of population change, especially the determinants of breeding and survival, and patterns in long-term data can provide strong indications of these determinants. Furthermore, any model must stand the test of reproducing historical patterns, and full documentation of historical patterns increases the power of this test.

Ship rats are widespread in New Zealand indigenous forests, but are generally more common in podocarp/hardwood forests than in southern beech (*Nothofagus*) forests (e.g., King & Moller 1997; Innes 2005). Their diet in podocarp/hardwood forests consists predominantly of fleshy fruits, large seeds, and large invertebrates (especially lepidopteran larvae and weta (Stenopelmatidae, Rhaphidophoridae)) (Best 1969; Daniel 1973; Innes 1979; Clout 1980; Gales 1982; Miller & Miller 1995; Rickard 1996). Ship rats are a substantial part of the diet of introduced mammalian predators (feral cats (*Felis catus* L.) and stoats (*Mustela erminea* L.)) in forests (Gillies & Fitzgerald 2005; King & Murphy 2005).

Ship rats are of concern as opportunistic predators of bird eggs and nestlings, and for sustaining populations of other introduced predators that prey on birds, particularly feral cats and stoats (Innes 2005). They probably also have large effects on populations of their invertebrate prey and, by seed predation, may gradually change forest composition (e.g., Beveridge 1964; Campbell 1978; Wilson et al. 2003).

Ship rat population density in New Zealand forests was first addressed by Daniel (1972, 1978). He attributed the natural variation of rat population density in podocarp/hardwood forest in the Orongorongo Valley, Wellington, to both the size of the autumn and winter food supply and predation. Rats reached higher density in autumn and winter 1971 (a year of exceptional fruit production) than in 6 other years. He suggested "...both the length of the breeding season and the over-winter survival of ship rats are directly controlled by the size of the autumn seed and fruit crops" (Daniel 1978, p. 146). His findings are still widely cited (e.g., Innes 2005).

Since Daniel's studies, long-term investigations of various other components of the Orongorongo Valley forest ecosystem have been undertaken (Fitzgerald & Gibb 2001). The measurements of the fruit production of forest trees (hinau *Elaeocarpus dentatus* (J. R. Forst. & G. Forst.), and hard beech *Nothofagus truncata* (Colenso)), initiated by M. J. Daniel in the late 1960s have continued (Daniel 1978; Cowan et al. 1992; Fitzgerald et al. 2004). Rodent numbers have been indexed with a standard line of snap-traps, established by BMF and BJK in 1971, through 4 km of mixed beech and podocarp/hardwood forest (see Fitzgerald & Karl 1979, fig. 2). Traps were operated each season and provided indices of ship rat and house mouse (*Mus musculus* L.) density from 1971 to 1993 (Fitzgerald

et al. 1996, 2004). Animals caught were autopsied, providing information on breeding and age structure. Seedfall measurements and trapping were continued from 1994 until 1998 by J. C. Alley, PHB, and others. Sightings of predators (feral cats and mustelids) provided an index of their density, supported by periodic live-trapping. The diet of feral cats was studied from 1970 to 1973 and again from 1984 to 1988 (Fitzgerald & Karl 1979; Gibb & Fitzgerald 1998). Changes in the numbers of rats and predators were summarised briefly by Fitzgerald & Gibb (2001). Here we analyse these long-term records from the Orongorongo Valley, including the data on breeding and age structure obtained from autopsies, and re-examine the roles of food supply and predation in the population dynamics of ship rats in New Zealand forest.

METHODS

Study area

The Orongorongo Valley is a steep-sided valley on the western slope of the Rimutaka Range, 18 km east of Wellington, with a field station at 41°21'S, 174°58'E. A research area of 1200 ha extends for 4 km along the valley and to the crests of the ridges on either side. The valley floor at the field station is 100 m a.s.l. and the eastern ridges reach 843 m a.s.l. (Campbell 1984; Fitzgerald & Gibb 2001). The research area is covered in evergreen temperate rain-forest, comprising southern beech, podocarp (Coniferales) and hardwood species (Campbell 1984).

Terraces near the river and some lower slopes have a mixed forest of podocarps, mainly rimu (*Dacrydium cupressinum* Lamb.), miro (*Prumnopitys ferruginea* (D. Don) and matai (*P. taxifolia* (D. Don)), and hardwoods, including northern rata (*Metrosideros robusta* A. Cunn.), mahoe (*Melicactus ramiflorus* J. R. Forst. & G. Forst.), hinau, pigeonwood (*Hedycarya arborea* J. R. Forst. & G. Forst.), rewarewa (*Knightia excelsa* R. Br.), pukatea (*Laurelia novaezelandiae* A. Cunn.) and nikau palm (*Rhopalostylis sapida* Wendl. et Drude). Understorey shrubs include *Macropiper excelsum* (Forst. f.), horopito (*Pseudowintera axillaris* (J. R. Forst. & G. Forst.)) and *Coprosma* spp. Many of the trees carry epiphytes, (especially *Astelia solandri* A. Cunn. and *Collospermum hastatum* (Col.) Skottsb.), and lianes, including *Metrosideros* spp., supplejack (*Ripogonum scandens* J. R. Forst. & G. Forst.) and kiekie (*Freycinetia baueriana* Endl.) (Daniel 1972; Fitzgerald 1976).

Ridges and old alluvial fans from the valley floor to about 300 m a.s.l. have hard beech forest, with some black beech (*N. solandri* var. *solandri* (Hook. f.)) on steeper slopes. The understorey in beech forest is more open, and epiphytes and lianes less common than in podocarp/hardwood forest. Silver beech (*N. menziesii* (Hook. f.)) is present above 480 m a.s.l. and is dominant above 600 m a.s.l.

The mean summer temperature (December–February) at the field station (130 m a.s.l.) is 15.9°C and mean winter temperature (June–August) is 7.5°C; frosts are uncommon. The annual rainfall over 30 years averaged 2370 mm, with monthly averages ranging from about 100 mm in January to 275 mm in July. Cloud frequently covers the mountain range above about 550 m a.s.l., making the silver beech forest cooler and moister than the lower forest (Campbell 1984). Snow rarely falls on the valley floor and does not settle, but may lie for several days each winter in the silver beech forest (Fitzgerald & Gibb 2001).

Ship rats and house mice are the only rodents present. Ship rats are more common in areas of podocarp/hardwoods than in beech, whereas mice are more evenly distributed (Fitzgerald et al. 2004). Feral cats and stoats are the main predators of rats in the Orongorongo Valley. Weasels (*M. nivalis* L.) are rare, and they and moreporks (*Ninox novaeseelandiae* (Gmelin)) are unimportant as predators of rats (Daniel 1972; Fitzgerald & Karl 1979).

Hinau and beech phenology and seedfall

M. J. Daniel initiated measurement of the annual seedfall of hinau and hard beech in 1968, because he considered them to be important foods for rodents; measurement is continuing (Daniel 1978; Cowan et al. 1992; Fitzgerald et al. 2004). Hinau flowers in late spring and summer (November–January); fruit ripen in early autumn (March) and fall during autumn and winter (Fitzgerald 1976). The fruit is an ovoid purplish drupe weighing on average 1.05 g (Williams 1982). Hard beech flowers in spring (peak in October) and the ripe nuts are shed from their woody cupules in autumn (February–April). The nuts weigh on average 0.016 g (Alley et al. 1998).

Seedfall was measured under mature trees within 500 m of the field station, using Beveridge traps with a collecting area of 0.28 m² (Daniel 1978; Cowan et al. 1992; Alley et al. 1998; Monks & Kelly 2006). The numbers of traps under hinau and hard beech were increased from three (1971–73) to 15 (1974–78) and later 21 (1979–93). In later years, the mean seedfall of the three hinau traps in

use throughout predicted the average from the remaining traps well ($r = 0.90$). The three hard beech traps predicted the count from other traps very well ($r = 0.96$) (Fitzgerald et al. 2004). For consistency we therefore used the mean of the three traps as our measure of hinau fruitfall and beech seedfall.

Rat trapping and autopsy

Rats and mice were trapped on a line of 116 trap sites at 50 m intervals in the forest along the valley and no more than 350 m from the river (Fitzgerald & Karl 1979, fig. 2). At each trap site one rat snap-trap and one mouse snap-trap was set under a metal cover with wire mesh across the ends to exclude brushtail possums (*Trichosurus vulpecula* Kerr). Traps were baited with a mixture of peanut butter and rolled oats for 3 consecutive nights late in February, May, August, and November (summer, autumn, winter, and spring) from August 1971 to May 1998. Trapping was carried out by BMF and BJK between August 1971 and November 1993, and by J. C. Alley and PHB from February 1994 to May 1998. Capture data from 1994 to 1998 were included in the analyses whereas autopsy data were excluded, as explained later.

There was considerable variation in the forest along the trap line. Podocarps, and hardwood species such as hinau and pukatea, often with heavy loads of lianes and epiphytes, dominated at 82 trap sites classed as “podocarp” sites. Beech trees were present at the remaining 34 “beech” trap sites (Alley et al. 2001). Species composition was highly variable within both classes of site.

Another line, of 36 trap sites, in silver beech forest (>600 m a.s.l.) above the field station, was operated quarterly from November 1973 to August 1978 (Fitzgerald et al. 2004). Only 16 rats were caught on this line, and never more than two in a 3-day trapping session; we do not consider them here.

Rodents were collected and autopsied each day. Animals were measured and the skull was saved for determining tooth wear. Weight was recorded before and after removing the stomach (mean 6.6 g, SD 3.7 g), and again after removing the uterus (mean 5.9 g, SD 7.6 g) of visibly pregnant females. Analyses used the “core weight” (body weight minus the stomach and minus uterus if pregnant). Males were classed as sexually mature if tubules were visible in the epididymis. Females were classed as sexually mature if they were visibly pregnant, lactating, or had uterine scars. Females were recorded as lactating if milk could be expressed from the nipples.

The number of live and resorbing embryos in the uterus, and the crown-rump length of live embryos, was recorded. Uterine scars were counted; new scars, consisting of swellings on the uterus, were distinguished from old scars (small pigmented areas). Uterine scars are reliable indicators of parity in captive *Rattus norvegicus* (Davis & Emlen 1948) and presumably also in *R. rattus*. The number of old scars is less useful as a measure of the production of young because of errors in counting and uncertainty over whether resorbed embryos leave scars. Females were considered to have bred if they were visibly pregnant or carried uterine scars (all lactating females had uterine scars except for one that was doubtful). Length of nipples in millimetres was also recorded. Sixty of 76 females with enlarged nipples (>2 mm) were visibly pregnant or lactating, but 74 visibly pregnant or lactating females did not have enlarged nipples, so we did not consider nipple size a useful indicator of breeding. Autopsy information was recorded differently after 1993, so we have not included data for the later period (1994–98) in the analyses.

Toothwear ages

Rats were assigned to Karnoukhova's (1972) toothwear classes (see also Innes 2005). These classes have not previously been calibrated to chronological age in New Zealand. Eleven rats caught and tagged as juveniles (≤ 100 g) during live trapping studies (Daniel 1978; BMF & BJK unpubl. data) were re-trapped in this study after 25–677 days. Their initial ages (38–98 days) were estimated from an approximate growth curve based on wild *R. rattus* in Venezuela (Gomez 1960). Bentley & Taylor (1965) recorded slightly faster growth in captive *R. rattus*, and it is possible that we overestimated initial age. We did not use data of Hirata & Nass (1974) from captive *R. rattus* in Hawaii because these reached average body weights at 20 weeks that were much greater than we generally recorded. Our limited data (Appendix 1) provide the following range of chronological ages within toothwear classes (class 3, 63–332 days, $N = 5$; class 4, 273–472 days, $N = 5$; class 5, 738 days, $N = 1$). The estimated age at final capture of the two animals that weighed 100 g at first capture is less reliable than the others (34–85 g at first capture). The wide range of chronological ages within toothwear classes 3 and 4 mean that animals born in one breeding season cannot be distinguished reliably from those born in the next breeding season.

Predators

Sightings

We have used the number of reported sightings of feral cats and mustelids in the research area as an index of their population density. Active research on predators and rodents was undertaken throughout the period 1971–93, and people working at the field station were diligent in recording their sightings of predators in a card file. Whenever possible, records of cats included a description: coat colour (striped or blotched tabby, grey, black, ginger) and white pattern, and whether it had short or long hair. Patterns were sufficiently varied that known individuals could be identified from the descriptions (Fitzgerald & Karl 1979). Sightings of mustelids were usually identified as a stoat or a weasel.

The field station was used less in later years, particularly after 1987, and we adjusted the predator index for the number of days that the station was occupied, although this had little effect on the overall pattern (Gibb & Fitzgerald 1998). Rather than arbitrarily combine the counts of cats and mustelids we focus on cats, which diet studies showed to be the more significant predator of rats. Counts of cat sightings varied erratically, we presume because of sampling error, so we constructed a smoothed series by fitting a Poisson regression in which temporal variation was represented by a spline curve with 10 equivalent degrees of freedom. Field station occupancy was included as a covariate. For the smoothed index we used the predicted number of cat sightings per 3 months, adjusted to the median occupancy of the field station (50 days per quarter).

Trapping

Cats were live-trapped during three periods of the study. In addition, cats caught incidentally during possum or rabbit live-trapping programmes were tagged and released. For all cats trapped, tagged and released, detailed notes were kept of their coat colour, white pattern, and hair length.

From January 1971 to April 1972, trapping was carried out during daylight hours, using twin-cage possum traps set in forest in about 14 ha around the field station. Further trapping, using large cage traps (illustrated in Veitch (1985)), was carried out by BJK from January 1975 to December 1976 on grass and scrub covered flats along the edge of the riverbed. From April 1981 to May 1983 cats were live-trapped and fitted with radio-transmitters for a study of their home ranges (Fitzgerald & Karl 1986). Subsequently, from 1983 to 1987, cage traps were

set along the vehicle track through the research area to capture and remove predators.

C. M. King live-trapped for stoats during three periods in 1972, and again in 1974–75 (King & Edgar 1977; C. M. King unpubl. report 1975). Different models of traps and areas were used during the three trapping periods. Between January and February 1972, 30 Whitlock traps were used in about 14 ha around the field station. They were set again in March–April and November–December 1972, and 20 Edgar Mark II traps on 4 km of the vehicle track through the research area. Between August 1974 and January 1975, 51 Edgar traps Mark III were set at 100 m intervals on a line through the research area, mainly along the vehicle track.

Diet

Diet of predators was determined from scat analysis. Cat scats were collected from walking tracks in the forest and the vehicle track between 1969 and 1973 (Fitzgerald & Karl 1979), and again from August 1984 to December 1988. Here we present the data on diet from January 1971 to December 1973 and from August 1984 to December 1988. Stoat scats were collected from the live-traps (C. M. King unpubl. report 1975, quoted in Fitzgerald & Karl 1979). Remains of vertebrate prey in the scats were identified from bones, teeth, hair, and feathers.

Analysis

Results are given as mean \pm SE except as indicated. We used χ^2 tests of homogeneity, linear regression, *t*-tests, Pearson correlation, and one-way analysis of variance to indicate the statistical support for simple comparisons.

The capture rate of rats (number caught divided by number of rat traps set) was adjusted to a linear index of density by fitting a Poisson hazard model that also allowed for sprung traps and non-target captures (Linn & Downton 1975; Fitzgerald et al. 2004; program *Indextr* available from MGE). At the low capture rates that we mostly observed, this index is numerically close to the more familiar “captures per 100 corrected trap nights” (e.g., Nelson & Clark 1973; King 1982; Efford et al. 1988). The method has the major advantage that it provides an estimate of sampling variance, although this may have been underestimated because of overdispersion, which we could not measure. Our use of trapping data to index density also assumes that trappability, the per capita probability of capture, is constant over time. This is not directly testable with the present data, and breaches of the assumption

should be considered as a possible explanation for observed patterns.

We estimated the instantaneous rate of population change $r_t = 4 \times \ln(N_{t+1}/N_t)$ from the seasonal indices N_p and $SE(r_t)$ as described by Fitzgerald et al. (2004). The factor of four adjusted seasonal rates to an annual rate (per year). For annual population change we used successive spring (November) density indices ($r_y = \ln(N_{y+1}/N_y)$).

Breeding data were analysed by fitting generalised linear models (logistic regression for proportions and Poisson regression for counts) (e.g., Venables & Ripley 1999). Models were compared by means of Akaike’s Information Criterion (AIC); small values of AIC indicate an acceptable tradeoff between model fit and number of parameters. Models were fitted with the *glm* function in S-Plus and AIC values were obtained using the *extractAIC* *glm* function of the MASS library (Venables & Ripley 1999). The small-sample correction recommended by Burnham & Anderson (2002) was applied routinely (AICc). Values (Δ AICc) are reported relative to AICc of the best model. Autopsy records with missing data in any predictor were deleted before analysis of a particular response variable to ensure comparability of AICc between models with different predictors.

Logistic regression was used to predict the head and body length and core weight at which 50% of rats were sexually mature, separately for each sex using breeding season data (November and February). A logistic regression model was also fitted to describe variation in the proportion of females breeding. The main analysis examined the possible effects of population density, temperature, and rainfall (all continuous predictors) while controlling for season (spring versus summer) and age (toothwear class 3 versus older). Density was measured by the trapping index at the time of sample collection. Weather variables were based on the 2 calendar months prior to sample collection (September and October for spring (November) samples, December and January for summer (February) samples), because these appeared most likely to have affected the measured breeding rate. Rainfall was recorded at the field station. Temperature was the mean daily temperature at the Kelburn climate station, Wellington, 18 km to the west.

Litter size and the number of uterine scars in parous females were modelled by Poisson regression. Predictors were season (spring versus summer), density index and maternal age (toothwear class 3 versus older). We ignored the inherent zero-truncation of the data (females with no embryos or scars did not

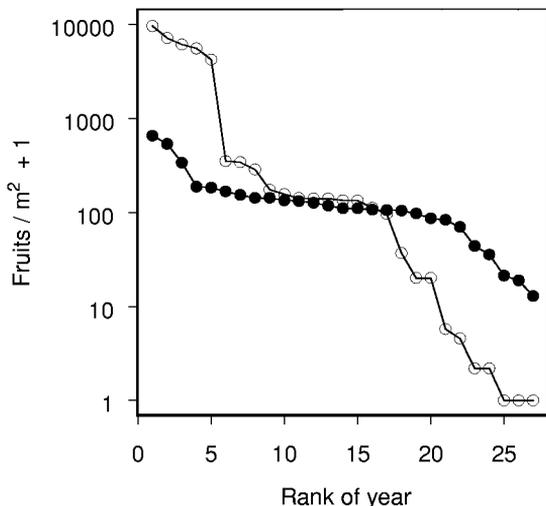


Fig. 1 Annual variation in fruitfall of hinau (●) and seedfall of hard beech (○) in the Orongorongo Valley 1971–97. Mean of (total number of fruits per $m^2 + 1$) from three collecting trays, ranked by magnitude. For hard beech see also Fitzgerald et al. (2004).

appear in the sample of parous females) but this had negligible effect because zero values were predicted to be rare under the fitted Poisson models.

RESULTS

Rats were caught in all 108 trapping sessions except in February 1978 (range 0–56). In total (August 1971–May 1998) 1636 rats were caught, although 35 of these were caught in mouse traps and were excluded from the density index based on rat traps. Traps caught single rats except for a pair in May 1996. We analysed autopsy data on 1301 rats caught between August 1971 and November 1993, including those caught in mouse traps. The great majority of rats were of the pale-bellied frugivorous morph (97.0% $N = 1282$); the others were of the *rattus* morph (e.g., Innes 2005). The sex ratio did not deviate from parity overall (51.1% male, $N = 1281$, $\chi^2 = 0.56$, 1 d.f., $P = 0.55$), nor did it vary significantly by season ($\chi^2 = 6.36$, 3 d.f., $P = 0.10$) or toothwear class ($\chi^2 = 1.07$, 6 d.f., $P = 0.98$).

Seedfall

For the period 1971–97, hinau fruitfall was more than 50% above average (148 ± 28 fruit per m^2) only in 1971 (533), 1979 (650), and 1995 (337), but it fell 50% below average in 6 years (1973 (35), 1981 (18), 1984 (12), 1987 (69), 1992 (43), and 1997 (20)) (Fig. 1; see also Appendix 2). Using data from all traps rather than only the three original traps, 1971, 1979, and 1995 remained the 3 years with the highest fruitfall, and 1973, 1981, 1984, 1992, and 1997 the 5 years with the lowest fruitfall.

Data for hard beech seedfall from 1971 to 1994 were given in Fitzgerald et al. (2004); corresponding figures for 1995–97 were 6394, 19, and 1 seeds per m^2 (86, 25, and 0% viable, respectively). The 3 highest hinau seed years were among the 5 mast years for hard beech in 1971–97 (1971, 1979, 1986, 1990, 1995), and seedfall in the two species was correlated ($r = 0.73$, $P < 0.001$). Hard beech seedfall showed a much clearer distinction between mast years and other years (Fig. 1). We used the coefficient of variation (CV) of the total number of seeds per trap to measure the annual variability of seedfall. The CV was 2.06 for hard beech and 0.98 for hinau ($N = 27$; CV 2.09 and 0.76 respectively if based on the average across all trays instead of the three original trays).

Rat density

Fluctuations in the rat density index showed high-frequency seasonal and annual variation (including sampling error) overlaid on a longer-term trend (Fig. 2A). The general trend was positive over the first 15 years, followed by a decline to intermediate levels at the end of the study, as indicated separately by data from the seasonal peak (winter) and trough (spring) (Fig. 3). Rats were caught 2.5 times more often at “podocarp” trap sites (mean density index 5.9 ± 0.4) than at “beech” sites (2.4 ± 0.2). The mean density index over 7 years at the peak (1983–90, 7.5 ± 0.8) exceeded by a factor of 3.2 that at the start of the study (1971–78, 2.3 ± 0.3). In some subsequent analyses we contrast the demography of rats in these “low” and “high” phases.

The mean density index in winter (August) was nearly double that in spring (November) (Table 1). The estimated quarterly log population change varied over 1971–98 in the range -10.3 per year to $+7.2$ per year (Fig. 2B) (mean 0.06 per year, SD 3.43, $N = 107$). Mean rate of population change was strongly positive only between summer and autumn, and between autumn and winter (Table 1). The density index generally increased in winter

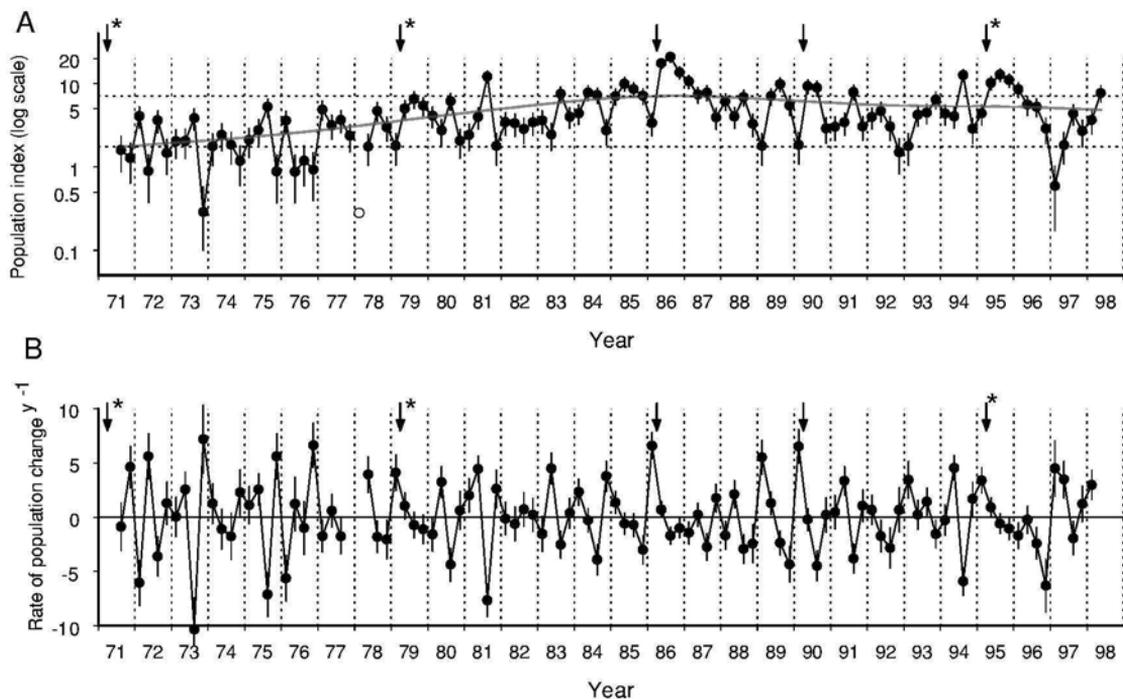


Fig. 2 Variation in the density and rate of population change of rats in the Orongorongo Valley indexed by snap trapping. Arrows show years in which hard beech masted, and asterisks years in which hinau fruitfall exceeded 150% of the mean. **A**, Density index $N_t \pm 1$ SE. The curve is a smoothing spline with 4 equivalent degrees of freedom, fitted with the “gam” function in S-Plus. Dashed horizontal lines indicate minimum and maximum of curve (1.7, 7.1). Zero catch (open circle) in February of 1978 could not be displayed on the log scale and is shown as 0.28, corresponding to one capture in 348 trap nights. **B**, Instantaneous annual rate of population change $r_t = 4 \ln(N_{t+1}/N_t) \pm 1$ SE.

Table 1 Seasonal population statistics for rats snap-trapped in the Orongorongo Valley, August 1971–May 1998.

	Population index		Rate of population change (per year)	
	Mean \pm SE	<i>N</i>	Mean \pm SE	<i>N</i>
Spring	3.61 \pm 0.58	27	0.39 \pm 0.69	27
Summer	3.68 \pm 0.45	27	1.18 \pm 0.65	27
Autumn	5.05 \pm 0.71	27	1.61 \pm 0.40	26
Winter	6.72 \pm 0.82	27	-2.88 \pm 0.50	27

(May–August; 17 years out of 26) and almost always declined in spring (August–November; 25 years out of 27). Spring decline was unrelated to density in August ($r = -0.14$, $P = 0.48$). Annual population change (November–November) varied between –

1.63 per year ($\times 0.20$) and +1.45 per year ($\times 4.3$) (mean 0.029 per year, SD 0.848, $N = 26$). Residuals from the quadratic trends were not noticeably auto-correlated in either winter or spring ($|r| < 2/\sqrt{N}$ for all lags, Chatfield 1984).

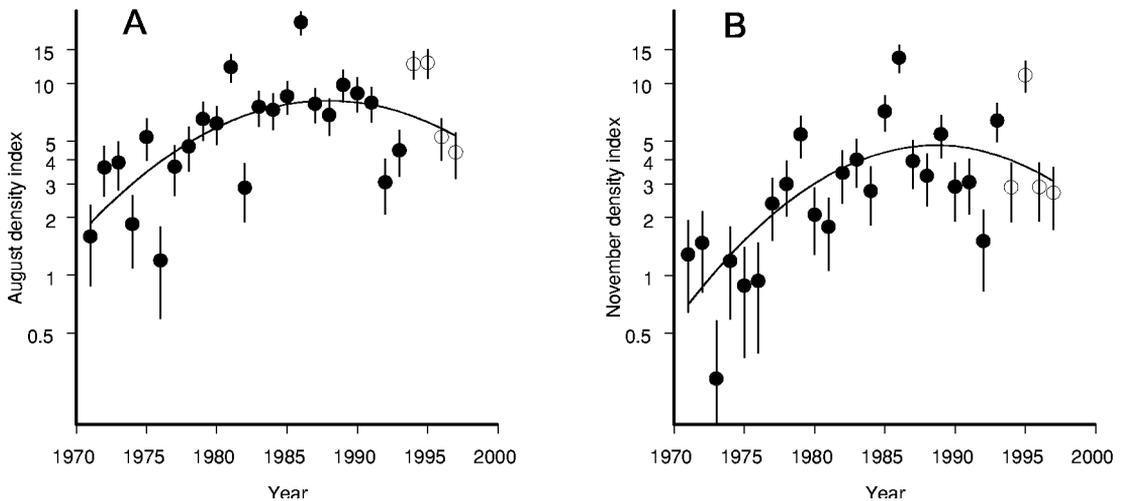


Fig. 3 Long-term trend in density of rats in the Orongorongo Valley indexed by snap trapping \pm 1 SE. Open circles indicate data collected by J. C. Alley and PHB. Quadratic curves fitted by Poisson regression to count data. A, August; B, November.

Table 2 Uterine scar status of adult female rats (toothwear class > 2).

Season	Percentage classified as					<i>N</i>
	No scars	New scars only	Old scars	New and old scars	Scars present (age uncertain)	
Spring	57.8	7.3	18.3	5.5	11.0	109
Summer	38.3	3.5	18.3	19.1	20.9	115
Autumn	66.4	1.3	16.4	3.9	11.8	152
Winter	63.3	0.5	25.1	0.5	10.6	199
Total	58.1	2.6	20.2	6.1	13.0	575

Rat breeding and recruitment

Sexual maturity was analysed for rats caught during the main breeding season (November and February; see below). No rats were mature in toothwear class 2. The great majority of both females and males were mature by toothwear class 4 (Fig. 4). Intermediate proportions of males (53.1%) and females (62.2%) in toothwear class 3 were mature. The predicted head and body length at which 50% of rats were sexually mature was 161.0 ± 1.9 mm for females and 163.5 ± 1.3 mm for males. The corresponding core weights were 96.6 ± 3.3 g for females and 102.8 ± 2.6 g for males.

Status with respect to uterine scars was recorded for 606 females. In Table 2, we summarise scar status by season for 575 adult females (toothwear class > 2). The majority of females were nulliparous except in summer when the population was

actively breeding, but still dominated by over-wintered animals, judging by the preponderance of females with old scars. Autumn and winter samples were generally similar with respect to parity, although there was negligible evidence of recent breeding in winter (only 1% with definite new scars). The lightest female with scars weighed 100 g (core weight 95 g), and the heaviest without scars 177 g (core weight 144 g). In spring or summer, the core weight at which 50% of females were predicted to carry scars was 122.8 ± 2.7 g (0% in toothwear classes 1–2 ($N = 17$), 22% in class 3 ($N = 69$), 62% in class 4 ($N = 122$), and 79% in class 5 and over ($N = 33$)). In autumn and winter the equivalent statistics were 123 ± 1.4 g (0% in toothwear classes 1–2 ($N = 12$), 9% in class 3 ($N = 214$), 69% in class 4 ($N = 98$), and 95% in class 5 and over ($N = 39$)).

Fig. 4 Sexual maturity of rats in spring (November) and summer (February) in relation to toothwear class; Orongorongo Valley 1971–93. Males (○) were considered mature when tubules in the epididymis were macroscopically visible; females (●) were considered mature when they were pregnant or lactating or carried uterine scars from a previous pregnancy.

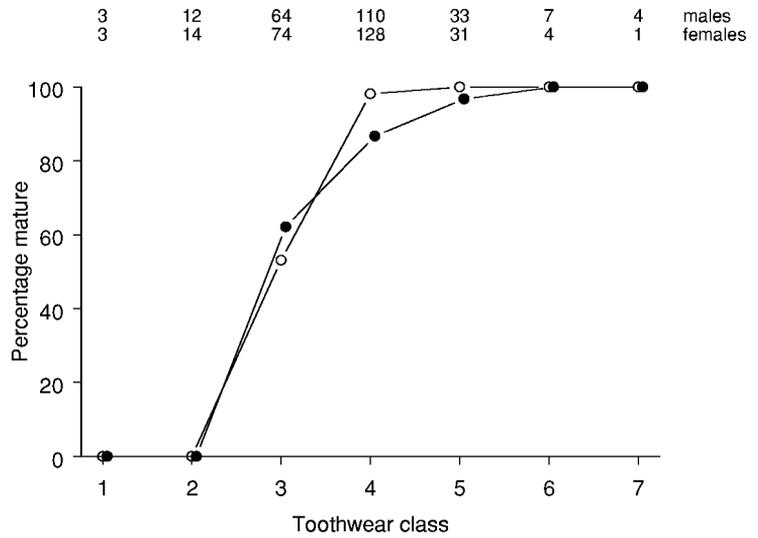
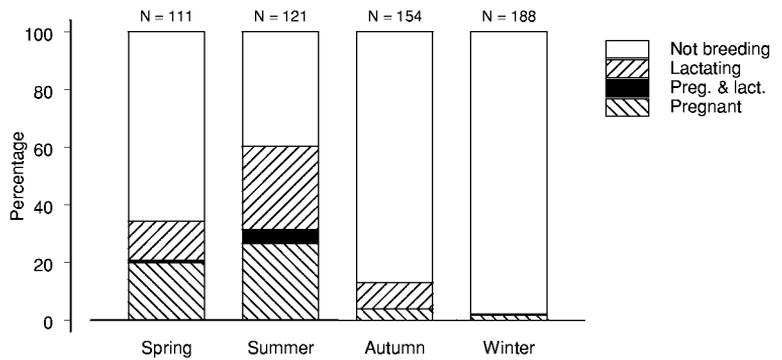


Fig. 5 Breeding by female rats in relation to season; Orongorongo Valley, 1971–93. Restricted to rats in adult age classes (toothwear class > 2). The combined proportion pregnant or lactating varied significantly between seasons ($\chi^2 = 154$, d.f. = 3, $P < 0.001$).



Rates of both pregnancy and lactation among adult rats (toothwear class > 2) varied seasonally and were high only in spring and summer (Fig. 5). In spring 19.8% of female rats were visibly pregnant, 13.5% lactating, and 0.9% both pregnant and lactating ($N = 111$); in summer 26.4% were pregnant, 28.9% lactating, and 5.0% both pregnant and lactating ($N = 121$). The proportion breeding (pregnant or lactating) differed significantly between spring and summer ($\chi^2 = 14.8$, 1 d.f., $P < 0.001$). In autumn, few adult rats were pregnant (3.9%) although some were still lactating (9.1%) ($N = 154$); by late winter, only 1.6% were pregnant and 0.5% lactating ($N = 188$). Rats may conceive at a postpartum oestrus, but in our total sample of lactating females only 10% were also visibly pregnant ($N = 72$).

The best logistic regression model for breeding rate included the categorical covariates toothwear class and season (spring versus summer), and their interaction, as well as a seasonal effect of density (Table 3). No evidence was found for any effect of temperature or rainfall in the preceding 2 months on breeding rate. Breeding decreased with increasing density, particularly among older females (toothwear class ≥ 4) (Fig. 6).

Litter size (number of live embryos) ranged from 0 to 13 (Table 4). Five females were resorbing all their embryos, and only two females had more than eight live embryos (litters of 12 and 13). Resorbing embryos were present in 34.7% of pregnant rats ($N = 72$), and 22.0% of all embryos were being resorbed ($N = 295$). On average, 0.90 ± 0.21 embryos were

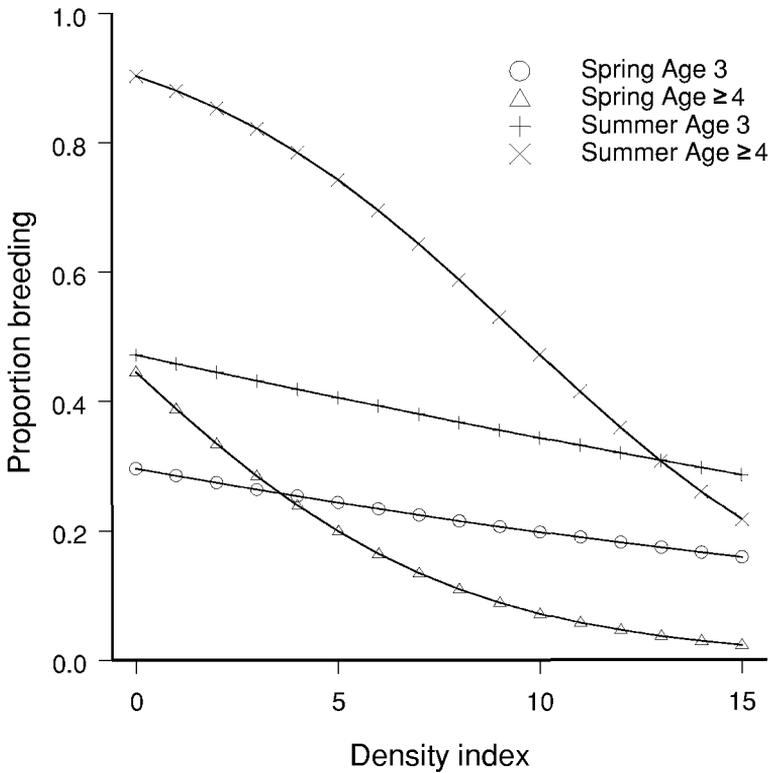


Fig. 6 Proportion of female rats pregnant or lactating in relation to season (spring versus summer), age (toothwear class 3 versus ≥ 4), and a trapping index of density, as predicted from the best logistic regression model (Table 3).

Table 3 Logistic regression models of breeding by female rats in spring and summer in relation to two measures of weather over the previous 3 months, a trapping index of density, and age as indicated by toothwear class (3 versus ≥ 4). In model notation, + indicates an additive effect on the logit scale, and \times an interaction. The best model includes season-specific effects of both density and age. K is the number of parameters estimated and LL is the log likelihood of the fitted model. $\Delta AICc$ is $AICc$ relative to the best model.

Model predictors	K	LL	$\Delta AICc$
None	1	-162.63	47.17
Season	2	-155.00	33.95
Age	2	-148.85	21.65
Season + age	3	-141.22	8.44
Season \times age	4	-138.15	4.37
Season + temperature	3	-154.91	35.81
Season + rainfall	3	-155.00	36.00
Season + density	3	-151.75	29.49
Season \times density	4	-150.33	28.73
Season + age + temperature	4	-141.21	10.49
Season + age + rainfall	4	-140.85	9.76
Season + density + age	4	-138.46	4.98
Season \times density + age	5	-137.12	4.39
Season \times density + season \times age	6	-133.87	0.00

Lack of evidence for a demographic shift between low-and high-density phases

The large change in the density index between 1971 and 1977, and between 1983 and 1989 (Fig. 2, 3) raised the possibility of a shift in other demographic parameters between these two periods. We tabulate a number of comparisons (Table 5). No significant differences were found in breeding parameters. The only possible exception concerned the head and body length at which females matured, but it is based on a particularly small sample of young rats in the low-density period (only four were less than 160 mm). We found no sign of a change in the overall sex ratio of the trapped sample, nor of changes in age structure (Table 5).

We further examined the pattern of within-year population change in the two periods. Rate of population change did not differ systematically between the low and high density periods in any season (t -tests, all $P > 0.08$). In particular, there was no evidence for a change in August–November ($P = 0.40$). Recruitment of young rats is slight or non-existent over this period, so change in the density index may be attributed to mortality.

The influence of fruit and seedfall on rat density and breeding

Hinau fruitfall did not predict annual population change (linear regression $F_{1,24} = 3.07$, $P = 0.09$). The rat population showed a modest increase (0.60 ± 0.35

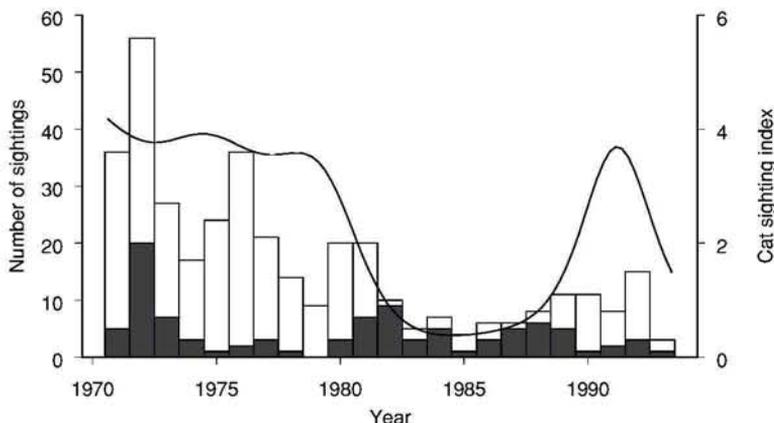
Table 5 Demographic comparisons between initial period of low density (November 1971–August 1978) and later period of high density (November 1983–August 1989). P is the probability of rejecting a null hypothesis of equality, based on either a χ^2 -test for proportions or t -test for means. Sample size for proportion breeding is number of females in toothwear class 3 or over.

	Low density	High density	P
Density index	2.32 \pm 0.27	7.45 \pm 0.83	<0.001
Proportion of captures at "beech" sites	15.4% ($N = 214$)	13.9% ($N = 646$)	0.67
Predicted head and body length at maturity			
Females	149.8 \pm 7.1	164.7 \pm 2.6	0.05
Males	162.9 \pm 2.2	164.0 \pm 2.5	0.74
Breeding			
Proportion in spring, summer	53.8% ($N = 39$)	44.4% ($N = 108$)	0.41
Proportion in autumn	11.1% ($N = 18$)	9.3% ($N = 86$)	0.84
Litter size	4.53 \pm 0.41	4.80 \pm 0.28	0.65
Pregnant females with resorbing embryos	40% ($N = 10$)	35% ($N = 34$)	0.92
Age composition			
Proportion in class 1–3			
Spring, summer	27.0% ($N = 89$)	37.8% ($N = 233$)	0.09
Autumn, winter	61.5% ($N = 122$)	67.9% ($N = 399$)	0.23
Proportion in class 5 or older	14.2% ($N = 211$)	12.5% ($N = 632$)	0.60
Sex ratio (males/total)	55.2% ($N = 212$)	51.7% ($N = 633$)	0.42

Table 6 Comparative variability of ship rat density between consecutive seasonal samples (e.g., spring–summer) and between years (e.g., spring–spring) 1971–98. Values are the mean of $|\ln(N_{t+1}/N_t)|$, where t is either quarterly or annual (SE in parentheses).

Season of initial sample	Mean absolute change to:			
	Next season		Same season in next year	
Spring	0.85	(0.25)	0.67	(0.10)
Summer	0.87	(0.23)	0.65	(0.12)
Autumn	0.49	(0.08)	0.63	(0.08)
Winter	0.76	(0.11)	0.59	(0.09)
Seasons pooled	0.74	(0.09)	0.64	(0.05)

Fig. 8 Sightings of predators (cats and mustelids) in the research area 1970–93. Bars represent the number of mustelid sightings (filled) and cats (open) in the 12-month period starting in December of the labelled year. The line shows the smoothed quarterly index of cat sightings adjusted for field station occupancy as explained in the Methods.



per year) in 1979, the year of greatest hinu fruiting, and a large increase (1.34 ± 0.33 per year) in 1995, another year of high hinu fruiting. As Daniel (1978) suggested that a large fruit crop reduces mortality in the non-breeding season, we tested for an effect of hinu crop on rat population change between August and November, with negative results ($F_{1,24} = 0.01$, $P = 0.91$). Rate of increase was not elevated in beech mast years (1979, 1986, 1990, 1995) compared to other years ($t = 1.19$, d.f. = 24, $P = 0.25$).

Only four females were recorded as pregnant or lactating in winter (August) (one in each of 1976, 1979, 1983, and 1989). We therefore restricted analyses of the effects of fruiting to autumn (May) samples. One of 10 female rats (toothwear class > 2) caught in autumn 1979 was pregnant and the others were not breeding. The comparable figure for 5 poor years for hinu fruiting was two females breeding out of 40. (We did not analyse autopsy data from the high seedfall year of 1995 or the low one of 1997.) If rats bred in autumn and winter in years of high fruitfall then we would also expect high frequencies of young animals in the winter and spring of these years. We recorded 11 rats in toothwear classes 1 and 2 in winter and spring, only two of them in a year when hinu or beech fruited heavily (1979). These data fail to support an effect of hinu or beech seedfall on breeding.

Predators

Predator sightings

The annual number of sightings of feral cats decreased greatly between the start of the study in

1971 and the early 1980s (Fig. 8). Cats were seen frequently in the early years of the study (101 sightings for December 1970–November 1974) and then gradually declined to a low in the early 1980s to mid 1980s (eight sightings for December 1981–November 1985). Fewer mustelids were seen, with 94 sightings over the whole period, 1971–93. They comprised 82 stoat, 4 weasel, and 8 unidentified mustelid sightings (Gibb & Fitzgerald 1998; BMF unpubl. data). Stoats were seen commonly only in 1972.

The smoothed index of cat sightings correlated strongly and inversely with the rat density index in November ($r = -0.67$, $P < 0.001$).

Cat and stoat trapping

Data from intermittent trapping of cats supports a large shift in cat density between the 1970s and the 1980s. Seven cats were trapped, marked, and released near the field station between January 1970 and December 1973. Also, two dens of four young kittens (weighing < 500 g) were found and two of the kittens survived to join the adult population. Half of the records of sightings included descriptions that matched known, tagged cats and the other half “were apparently of animals that had not been trapped” (Fitzgerald & Karl 1979). This suggests that there may have been about 14 cats whose home ranges included the vicinity of the field station.

In 1975 and 1976, 21 individual cats were caught on a trap-line that extended the 4 km length of the research area. From April 1981 to May 1983 nine cats were trapped and fitted with radio-transmitters (Fitzgerald & Karl 1986). Three had been caught

previously, two as kittens in 1976 and 1979, and one as an adult in 1979. By May 1983 four of the radio-tagged cats were dead. Most of the sightings were of the radio-tagged cats, suggesting that these nine cats were most, if not all, of the cats present (Fitzgerald & Karl 1986; Gibb & Fitzgerald 1998). From 1983 to 1987, traps were set along the vehicle track through the research area to capture remaining predators; five cats and four stoats were trapped and killed. From 1984 to 1991 most of the sightings were of just two cats.

From January to April 1972, five stoats were captured or recaptured 29 times (most of them in February and March), but between November and December 1972 no stoats were caught. From August 1974 to January 1975, three stoats, including a male first captured in February 1972, were caught but none was recaptured (King & Edgar 1977; C. M. King unpubl. report 1975).

A few stoats were caught in rat snap-traps on the rodent line. None was caught in early 1972, when stoats were common, but between February 1982 and May 1997 seven stoats (1 male, 4 females, and 2 of unknown sex) were caught.

Cat and stoat diets

Cat scats were collected from 1969 to 1973 and remains of prey identified (Fitzgerald & Karl 1979). Few scats were collected in 1969 and 1970; here we present the data on diet from January 1971 to December 1973, together with the smaller sample of scats from August 1984 to December 1988 (Appendix 3). During both periods about half the scats on average contained remains of rats, even though the trapping index indicated substantially higher numbers of rats from 1984 to 1988 (Table 3). However, the 17 scats collected between August 1985 and August 1986, when rats were at their highest numbers, all contained remains of rats. From 1971 to 1973 rat remains were recorded most frequently (>50% occurrence) from February to June, and in October. The small samples collected from 1984 to 1988 were consistent with this pattern (Appendix 3).

Mice were less frequent in the scats from 1984 to 1988, perhaps because on average there were fewer mice available then (a mean index of 2.6 compared with 3.6 from 1971 to 1973), but also because from 1984 to 1988 the few cats present were eating substantially more rabbit (Gibb & Fitzgerald 1998). Cats hunted and caught rabbits whenever possible, in preference to other prey, and killed most of the young rabbits soon after they emerged from their natal burrows (Gibb & Fitzgerald 1998).

DISCUSSION

Ship rat population dynamics

The density of ship rats fluctuated seasonally, but appeared to be regulated between years. The pattern was neither essentially stable, as in the brushtail possum (Efford & Cowan 2004), nor subject to repeated multi-annual fluctuations, as in the house mouse (Fitzgerald et al. 2004).

Innes (2005, p. 197) reported that "...seasonal changes [in ship rat density] are small compared with annual changes", which he based in part on the account of Daniel (1978) from the Orongorongo Valley (see also Innes et al. 2001). The relative magnitude of within-and between-year variation is significant because it has been used to argue for the importance to rats of annual variation in fruit production (e.g., Innes 2005). To evaluate the claim we compared population change (i) between consecutive quarters, and (ii) between consecutive years, starting in each of the four quarters (Table 6). Seasonal fluctuations tended to be as large or larger than between-year changes, despite the four-fold greater interval between annual samples. This points to population regulation between years, and undermines rather than supports the case for an external driver of between-year variation.

The snap-trap data provide limited insight into possible mechanisms of regulation: breeding rates were significantly reduced in high-density years, but did not differ on average between the extended phases of low and high density. Spring decline, the only seasonal component of change due entirely to mortality, was not density-dependent. The feedbacks that maintain density within bounds require investigation. We speculate that breeding may be controlled by competition for food, particularly large invertebrates (weta) which are important in the breeding-season diet (Daniel 1973). Below we discuss food and predation effects as limiting factors (Sinclair 1989), putting to one side their possible role in population regulation.

Trapping index of population density

We relied on snap trapping for an index of density. This assumed that individual capture probability did not vary systematically with respect to variables of interest (year, season), and that the number removed was too small to have affected the overall population dynamics. The trapping system (layout, trap maintenance, personnel) was constant through November 1993, and largely so thereafter. On the same trap line, Fitzgerald et al. (2004) noted "apparent recruitment"

of house mice (increasing density index between August and November when no young were being recruited) that pointed to a spring increase in capture probability in some years. We did not find evidence of this sort for seasonally changing trappability of ship rats (the index decreased between August and November in all but 2 years, 1982 and 1993 Fig. 2B). Increase in the population index between May and August (Table 1) most likely reflected the increasing trappability of autumn-born rats, rather than weaning of additional young by the small number of females still pregnant or lactating in May. In a Northland study, overwintered immature male ship rats enlarged their home ranges when they became mature in spring (Dowding & Murphy 1994), which might be expected to increase their trappability, but in spring the Orongorongo snap trap index decreased strongly (Table 1). Detailed seasonal comparisons based on trap success remain problematic, but we expect trap success to be an adequate index of annual changes in population density.

The fraction removed by snap trapping is difficult to estimate. It may be on the order of 10% per quarter, on the basis that the mean catch of 15 rats was drawn from an area of over 50 ha (a strip extending 50 m either side of a 5 km line) with an average density of at least 3 per hectare (Daniel 1972, 1978; D. J. Wilson et al. unpubl. data). However, the declining catches over a trapping session (daily totals 694, 559, 364, all sessions pooled 1971–98) suggest a much larger short-term impact of index trapping on the local population. The Zippin removal estimator (Otis et al. 1978) applied to these counts indicates a reduction of 61% in the immediate population during each trapping session. This estimate includes a large positive bias, possibly on the order of 50%, due to the variation in capture probability among individuals whose ranges overlap the trapline to varying extent (Efford et al. 2004; MGE unpubl. data). Nevertheless, trapping reduced the life expectancy of rats living close to traps, and key results should be checked in future using less intrusive methods. Removal is likely to have been inversely density-dependent, owing to competition for empty traps at higher densities.

Breeding and life history

The key demographic components of breeding are the age or size at which sexual maturity is attained, the seasonal intensity of breeding by mature animals, and the litter size. We compare estimates of each of these parameters with others in the literature and assess evidence for ecologically relevant variation.

Maturation

Innes et al. (2001) also scored toothwear of ship rats from Pureora, North Island, and recorded macroscopic tubules in the cauda epididymis as a criterion of male maturity. They found about half of males in class 3 were mature, and almost all in class 4 were mature, as in our study. Compared to Orongorongo rats, maturation of females appeared to be somewhat delayed relative to toothwear class in their year-round sample (48% with uterine scars in class 4; cf. 65% in the Orongorongo Valley). Both male and female ship rats matured in our study at somewhat lighter body weights (103 g and 97 g core weight) than reported by Best (1973) for a pooled sample from Banks Peninsula and Waimangaroa (112 g and 131 g total body weight), although comparisons may be confounded by the inclusion in the South Island samples of animals from outside the main breeding season. Orongorongo females probably reached the predicted weight at maturity (104 g, including stomach) at 3–4 months of age (Gomez 1960, Bentley & Taylor 1965).

We did not find decisive evidence that females bred before they had overwintered. Of the females in toothwear class 3 in autumn and winter, only 9% had bred. The great majority, if not all, of this group were young born in spring and summer. Some early-born females may already have bred and reached toothwear class 4 by winter, but these were not distinguishable from females born before the previous winter.

Litter size

Litter size in the Orongorongo Valley was at the low end of a fairly narrow range (mean 4.8–6.0 excluding resorbing embryos) from studies in New Zealand forests (Table 7). We found statistical support for a trend noted previously by Innes et al. (2001) towards smaller litters at the start of the breeding season. There was essentially no evidence for variation in litter size by age or population density. Resorption of embryos was common, and limits our ability to infer the actual number of live births per female from data such as these. A laboratory study is needed to establish the precise relationship between the number of new uterine scars and litter size in *R. rattus*, given the frequency of resorption (cf. Davis & Emlen 1948).

Breeding rate

Breeding was seasonal, as in all previous studies (Table 7). Quarterly samples allow only crude determination of the start and end of the season. However,

Table 7 Breeding parameters of ship rats in New Zealand forests.

Locality	Latitude	Year(s)	Percent pregnant (N)				Litter size			Reference
			Spring ¹	Summer	Autumn	Winter	N	Mean	SD	
Pureora	38°31'	1983–87	9 (199) ²	36 (148) ²	21 (186) ²	2 (208) ²	89	5.33	1.2	Innes et al. (2001, pp. 68, 73)
Tiritea	40°26'	1976–77	35 (17) ³	40 (20) ³	15 (20) ³	11 (28) ³	19	4.95	1.31	Innes (1977 fig. 7, 1979)
Orongorongo	41°21'	1966–69	60 (20) ^{3,4}	63 (19) ^{3,4}	19 (21) ^{3,4}	21 (24) ^{3,4}	26	6.10 ⁵	1.79	Daniel (1972, table 8)
Orongorongo	41°21'	1971–93	21 (113)	31 (122)	4 (157)	2 (197)	120	4.75 ⁶	2.01	This study
Waimangaroa	41°44'	1966–67	0 (5) ^{3,4}	46 (13) ^{3,4}	0 (9) ^{3,4}	8 (24) ^{3,4}	7	5.9 ⁵	1.90 ⁷	Best (1973)
Banks Peninsula	43°45'	1966–67	61 (23) ^{3,4}	46 (13) ^{3,4}	20 (10) ^{3,4}	0 (12) ^{3,4}	14	5.9 ⁵	1.61 ⁷	Best (1973)
Hollyford/Eglington	44°47'	1976–78	0 (1)	47 (15)	31 (16)	0 (4)	13	5.99	1.47	King & Moller (1997) ⁸

¹Spring, summer, autumn, and winter correspond to Nov, Feb, May, and Aug samples except where noted.

²Spring, summer, autumn, and winter samples include some Fenn-trapped animals from late Oct, Jan, Apr, and Jul, respectively.

³Snap-trapped samples aggregated over 3-month intervals (Oct, Nov, Dec), (Jan, Feb, Mar), etc.

⁴Includes lactating females and possibly others in "breeding condition".

⁵Includes resorbing embryos.

⁶Includes counts of new uterine scars.

⁷SD calculated from reported SE and sample size.

⁸Pregnancy rates are from their table 5.

we note, for the first time, evidence of geographic variation in the onset of breeding. On Banks Peninsula (Best 1973), in the Orongorongo Valley (Daniel 1972; this study), and at Tiritea (Innes 1977) breeding was well underway by November, whereas at the northernmost site, Pureora, spring breeding was uncommon (Table 7). Spring pregnancy rates differed significantly between Pureora (Innes et al. 2001) and the Orongorongo Valley (this study) ($\chi^2 = 5.6$, 1 d.f., $P = 0.02$; data only from 1983 to 1987, years common to both studies). Recruitment from spring and summer breeding led to dominance of young (toothwear class 3) rats in our autumn sample (68.8%, $N = 337$), whereas this age class comprised only 30% of the autumn sample at Pureora (pooled estimate from Innes et al. 2001, fig. 3, 4). Nearly half of the females in the Pureora sample were from Fenn traps set 2–5 weeks before the regular trapping in late February, May, August, and November, and this will have contributed to the apparent difference in breeding phenology.

Ship rats in New Zealand forests occasionally breed in winter, but we doubt that winter breeding is demographically important. Of the females trapped in August, only 2% were pregnant, both in the Orongorongo Valley (1971–93) and at Pureora (1983–87) (Table 7; Innes et al. 2001). Daniel (1972) recorded three of eight snap-trapped female rats in "breeding condition" in July of 1969 in the Orongorongo Valley, and Daniel (1978) mentioned that rats bred in the winter of 1971, without presenting data. Innes (1979) noted a single pregnant female between mid April and mid September in his study in the Tararua Range. King & Moller (1997) thought that ship rats had bred in the winter of 1976 in the Eglington and Hollyford Valleys, based on the tooth wear of rats caught in the summer of 1976/77. However, the age distribution of these rats (frequencies 6, 9, 5, 1 in toothwear classes 3–6) is now seen to be indistinguishable from that found where there was essentially no winter breeding (Innes et al. 2001, fig. 3, 4; this study, Fig. 7). Published evidence does not support winter breeding as a significant contributor to population growth of ship rats in New Zealand forests.

The relative amplitude of seasonal variation in breeding intensity (2–31%) greatly exceeded the seasonal variation in "young" animals by toothwear (e.g., class 3 rats comprised 29, 27, 69, and 54% of the spring, summer, autumn, and winter samples). Toothwear classes included wide and overlapping ranges of chronological age, although our known-aged sample is small (Appendix 1). It would be

straightforward to improve the calibration of toothwear by releasing marked young rats for later capture to obtain a larger and more representative sample of known-aged animals. However, the variation in our small sample makes it unlikely that toothwear can deliver the precision required, for example, to distinguish seasonal cohorts in demographic studies or to demonstrate winter breeding from summer-caught samples. Toothwear class 3 animals in spring and summer were largely overwintered animals, and hence about 6 months older than recently recruited class 3 rats in autumn and winter.

Diet and the effect of annual variation in fruiting

Diet

Ship rats in the Orongorongo Valley ate both animal and vegetable foods (Daniel 1973). Arthropods predominated in spring and summer, and fruits (drupes, berries, and nuts) in autumn and winter. Of the fruits identified, the more important were pigeonwood in summer (16% of stomachs), *Macropiper excelsum* (18%) and supplejack (14%) in autumn, and hinau (19%) and supplejack (14%) in winter (Daniel 1973). Tree weta (*Hemideina crassidens*) were present in 54% of stomachs in spring, 56% in summer, 34% in autumn, and 14% in winter. The only other arthropods of note were Coleoptera (11% in summer) and cicadas (Cicadellidae) (18% in summer); many other arthropods were recorded at low frequency.

Reliance by ship rats on large invertebrates in summer and on fruits in winter has been recorded elsewhere in mixed podocarp/hardwood forests (Best 1969; Innes 1979; Gales 1982). In simpler systems, invertebrates appear to dominate (pine forest, Clout 1980; *Metrosideros excelsa* forest, Miller & Miller 1995).

Effects of fruit availability on breeding and survival

Daniel (1978) related rat demography to hinau because its fruiting varied substantially between years, the fruit was an important winter food, and hinau was common and widespread in the forest (Daniel 1978; Appendix 2). Hinau was the fruit most frequently recorded in the rat diet in winter, but supplejack and, to a lesser extent, pigeonwood were also important. Captive rats in feeding trials ate hard beech seed, but it was not recorded in the diet by Daniel (1973). In the Orongorongo Valley, hinau is probably the most likely candidate to influence breeding and survival of rats in winter.

Hinau fruit featured in 19% of rat stomachs in winter (Daniel 1973). Much more of his winter sample was collected in June and July 1969 (Daniel 1972), a year of strong hinau fruitfall, than in 1967 (Daniel 1978; Cowan et al. 1992). Females were recorded in “breeding condition” that winter, but the data allow no estimate of the population response over 1969 (Daniel 1978). In our much longer study the hinau fruitfall did not predict breeding in autumn, and winter breeding was rare and unrelated to hinau fruitfall. Any demographic consequences of hinau fruitfall were therefore likely to be through improved winter survival. Daniel (1978) suggested, without data, “...large numbers of [ship rats] starve to death in winters following light forest seed and fruit crops—an event which can occur in three out of every four years”, although this appears to contradict his earlier observation from 1966 to 1968 that fewer rats disappeared in winter than in other seasons (Daniel 1972, p. 331). Our data allowed us to estimate mortality only between winter and spring, a time when very few young rats are recruited and population change can be attributed entirely to mortality. The hinau fruit crop did not predict population change over this period. In summary, there is no evidence either in our study or in previous studies that conclusively relates rat breeding or survival to annual variation in fruitfall.

Effects of fruit availability on population change

Variation in fruitfall has been invoked repeatedly since Daniel (1978) to explain variation in the density of rat populations. He live-trapped rats monthly from September 1969 to August 1974 on a 2.25 ha area. Prior to the start of our study in August 1971, his marked population approximately trebled in density over a 2-month period (March–May 1971) and remained at moderately high density (>5 per hectare) until August 1972 before returning to an average of about 2 per hectare. He attributed the period of higher density to heavy fruiting of hinau and pigeonwood in 1971. Autumn recruitment implies successful breeding in summer 1970/71 (possibly assisted by summer consumption of pigeonwood fruit). Over the period August 1971–August 1972, our snap-trap index fluctuated seasonally over a low to moderate range (0.9–4.1 rats per 100 trap nights; Fig. 2).

Unlike Daniel (1978), we found no overall relationship between rat population change and annual hinau or beech fruitfall. Our trap line spanned about 20 times the width of Daniel’s grid, and the fluctuation he found on 2.25 ha was not apparent at the

larger spatial scale. Seasonal population increase between summer and autumn in our study (Fig. 2, Table 1) was commonly of the magnitude that Daniel observed in 1971 and attributed to exceptional fruiting. This finding leads us to evaluate critically other evidence for fruiting as a controlling influence on ship rat dynamics.

Harper (2005) reported an abrupt (more than tenfold) increase in snap-trap success for ship rats on Stewart Island/Rakiura between June and September 2002, a year in which rimu fruited prolifically. The population declined abruptly after September 2002. These changes are difficult to interpret. He did not observe breeding in the June sample (three adult females), or in September 2002 (17 adult females). If the population increase was real then the recruits were born before June, probably during the usual breeding season, and for unknown reasons were not trapped in June. This is incompatible with the hypothesis that breeding depended on winter consumption of rimu fruit (cf. Ruscoe et al. 2004). It has also been reported anecdotally that ship rat populations in the Okarito kiwi sanctuary erupted after heavy podocarp fruiting in 2002 and 2003 (Innes 2005, p. 197; King & Murphy 2005, p. 278). On the other hand, ship rats were at only average density on both rat trap and Fenn trap lines in Pureora Forest in the spring and summer of 1982/83, after heavy rimu seeding in the previous autumn (Leathwick 1984, p. 15; Innes et al. 2001). We conclude there is not yet any compelling evidence for fruiting as a driver of fluctuations in rat density in podocarp/hardwood forests.

Increases in rat populations have also been reported in beech forests after masting. The amplitude of annual variation in fruit production (mast seeding) by *Nothofagus* spp. is generally greater than in podocarp and hardwood species (e.g., Schauber et al. 2002), but the usual scarcity of rats in beech forests, the small size of beech seeds, and the lack of information on rat diet in beech forests, leaves considerable uncertainty regarding rat-beech interactions. King & Moller (1997) presented data for variation over 1975–78 in the frequency of rats in Fenn traps, snap-traps and stoat guts from the Eglinton and Hollyford Valleys, Fiordland. Fewer rats were caught in 1975 than in other years, but in our opinion the series are too short, sparse, and inconsistent for interpretation, and their inferences about winter breeding were flawed (see “Breeding and life history”).

Heavy masting of silver beech in the Eglinton Valley in 1990 was not followed by a rat eruption

(O'Donnell & Phillipson 1996). Murphy & Dowding (1994, 1995) found no rat remains in 96 guts and 95 scats of stoats from October 1990 to March 1993.

A later study in the Eglinton Valley did provide evidence for masting-related variation in rat density: the weekly tracking rate in baited tunnels in summer was about 10 times higher in the mast years 1995/96 and 1999/2000, than in the 3 intervening non-mast years (Dilks et al. 2003, fig. 3). The mast seeding of both red and silver beech in 1999 was followed by a larger mast of red beech in 2000. Fenn trapping from January 1998 to June 2001 showed that rat density increased through the second half of 2000 before declining in early 2001. To interpret each increase as caused by beech masting it is necessary that the increase follows seedfall (assuming seed is consumed on the ground), and Dilks et al. (2003, p. 3) describe the sequence thus. However, the data in their Appendix 1 shows that the largest relative increase was between summer and autumn in 1999 ($r = 4.9$ per year), relating to breeding before seed ripened and fell. We observed summer to autumn increases of $r \approx 5$ per year in both mast and non-mast years (Fig. 2B). We conclude that seed consumption alone does not explain the Eglinton dynamics, and discuss alternatives in “Predation and ship rat population dynamics”.

Innes (2005, p. 191) also cited the example of Alterio et al. (1999) from red beech forest at Maruia, but this is ambiguous because rat density was greater 15–16 months after significant seedfall than at the only other sample time, 8–9 months after seedfall.

Masting is undeniably associated with strong multi-annual patterns in both the introduced and native fauna of beech forests (King 1983; Wardle 1984; O'Donnell & Phillipson 1996; Ogden et al. 1996; Wilson et al. 1998; Choquenot & Ruscoe 2000; Ostfeld & Keesing 2000; Alley et al. 2001; Fitzgerald et al. 2004). Trophic effects, both direct and indirect, and the external cues (weather) that trigger masting, are almost certain to affect the density of ship rats in these forests. However, well-monitored examples, not complicated by removal of predators (see below), are lacking, and inference of cause-and-effect relationships is inevitably confounded by temporal autocorrelation, sampling error, and seasonality.

Changes in the numbers of predators

The changes in the index of predator sightings in the Orongorongo Valley are supported by the number of individual predators trapped and the number of cat scats collected at different stages of the study. However, trap design and trap-lines were not standardised

and we did not have a standard route on which we collected scats, so the data are not as strong as for the rat density index and the seedfall measurements.

We attribute the decline in both the number of sightings of cats (Fig. 8), and the number of individuals, to increased mortality (Fitzgerald & Gibb 2001). Commercial trappers, using gin traps, caught possums for their skins in forest adjacent to the research area. Possums in the Orongorongo Valley are relatively small, with skins of poor quality, and in the early years of the study trapping was unprofitable (Brockie 1982). When prices for possum skins increased substantially in the late 1970s (from an average of \$4 per skin in 1976/77 to more than \$7 in 1980/81) very large numbers of skins were exported from New Zealand (Clout & Barlow 1982; Warburton et al. 2000). Trapping then became more profitable in the Orongorongo Valley and trappers greatly increased their effort. They continued intensive trapping there until the market collapsed in the late 1980s. With intensive trapping, cats were at greater risk. Our radio-tagged cats all had home ranges extending outside the research area (Fitzgerald & Karl 1986), and it is likely that cats in the research area were at greater risk when possum trapping intensified, than they had been in the early 1970s. Trappers killed and handed in one of our radio-tagged cats in September 1981, and five untagged cats between 1982 and 1987 (1 in 1982, 3 in 1983, and 1 in 1987). Other cats, and some stoats, were almost certainly caught in gin-traps but not given to us.

Predation and ship rat population dynamics

Predator sightings in the Orongorongo Valley were related inversely to long-term change in rat density. Here we consider the possible role of predation in the dynamics of ship rats, both in the Orongorongo Valley and in forests elsewhere in New Zealand.

Rats in the diet of predators

Prey offtake by predators is the product of diet composition, daily food intake, and predator population density. Rats were present in half of the cat scats in 1971–73 and about the same in 1984–88. They were also found in 12% of 33 stoat scats during live-trapping in 1972–75 (C. M. King unpubl. report 1975).

There are few other studies of cat diet in New Zealand forests. Rats were less common in cat gut samples at Pureora, King Country, and Tounoun, Northland (Gillies & Fitzgerald 2005, p. 316) than in the Orongorongo Valley. Studies of stoat diet summarised by King & Murphy (2005, p. 268) report

rat remains in 0–10% of guts in beech forests and in 12–71% in mixed or podocarp forests.

The daily food intake of cats in the Orongorongo Valley was probably about 170 g wet weight of prey (Fitzgerald & Karl 1979). Stoats fed meat in captivity consume about 50 g daily (non-breeding females) to 90 g daily (males); King & Murphy 2005). Evidence from both sighting and trapping indicates a greater population density of cats than stoats, with the possible exception of the mid 1980s, although precision is impossible. We conclude that offtake of rats by cats substantially exceeded that by stoats in the Orongorongo Valley. Fitzgerald & Karl (1979) estimated the offtake by cats at 1–2 times the average rat population over 1971–73. This estimate could be refined by accurate measurement of rat and predator population densities with simultaneous studies of predator diet.

Rat responses to predator control

King et al. (1996, p. 233), discussing results of the 5-year (1982–87) kill-trapping study of small mammals in Pureora Forest Park, commented “we have no explanation for the increased numbers of ship rats on all lines in 1985”. Later, Innes et al. (2001, p. 72) noted for the same study “the increase in density indices for rats in all habitats in 1985 followed a substantial reduction in density indices for stoats and cats over the first two years of the study”. Given that rats did not respond to rimu fruiting at Pureora (above), this is consistent with our interpretation of rat dynamics in the Orongorongo Valley: reduction in predator density as the primary reason for a long-term increase in the rat population.

In many conservation programmes, removal of predators, especially stoats, has been the primary goal, with ship rats as by-catch. Stoat trapping in the Eglinton Valley during 1973–78 (King 1983) and 1990–94 (O'Donnell & Phillipson 1996) was limited in scale and provided only local stoat control. In contrast, intensive trapping of stoats throughout the valley over 1998–2001 removed many more individuals and greatly lowered predation rates on kaka and mohua (Dilks et al. 2003). Increasing rat density in the later period, including much of the apparent response to mast seeding, may have been due to very much lower predation rates, a possibility acknowledged by Dilks et al. (2003, p. 6). We cannot use rat capture rates to index rat density in the Eglinton Valley over 1973–2001 because of wide variation in the number, distribution, and spacing of traps. However, we note that the ratio of rat to stoat captures in Fenn traps shifted radically from 0 to 0.4

under the earlier, less intensive regimes, to 1.0–3.8 under the more intensive regime (1998–2001) (annual March–February statistics compiled from the sources given above). This is consistent with a population response of rats to stoat removal. It may also reflect more complete removal of stoats than rats in 1998–2001, given that the large home ranges of stoats place more of the population at risk of capture on the trap line along the valley-floor.

Another hypothesis treats predation as a secondary effect, moderating “eruptions” driven by fruiting. Blackwell et al. (2003) described ship rats together with house mice as “eruptive” species, although they did not define the term. Stoats at Okarito were suggested to “truncate peak ship rat population size” (Innes 2005, p. 197). The hypothesis was addressed experimentally in beech and podocarp/hardwood forest at Lake Waikaremoana by Blackwell et al. (2003, p. 610). They used tracking tunnels and Fenn traps to index ship rat populations for 3 years on two peninsulas of the lake, one of 750 ha where they killed predators and another of 400 ha where they did not. Some rat tracking rates increased at the beginning of the study, and the increases were attributed to beech masting of which there had been anecdotal reports. They concluded that “predators do not truncate peak rodent population size during a full eruption”. We do not find these results entirely convincing, because responses of rodents were not consistent, and interpretation is hampered by habitat differences and inadequate monitoring.

We also draw attention to a more fundamental problem in the way rat dynamics are viewed. The “eruptive” model suggests that rat density is low except for transient “peaks” driven by fruiting. This is not the Orongorongo pattern: our plot of the logged density index (Fig. 2) showed high-amplitude seasonal and annual variation largely unrelated to fruiting. We question whether well-documented population time series at other sites without predator control would support the “eruptive” model; for the moment we note that no such series exist.

CONCLUSION

Our analyses of the data from the rat population in the Orongorongo Valley over 27 years showed a positive trend in the density index over the first 15 years, followed by a decline to intermediate levels that persisted to the end of the study. Seasonal changes were as large or larger than changes between years. Density-dependence of breeding, possibly due

to competition for invertebrate foods, may regulate annual density. Variations in autumn breeding, winter survival, and annual population change were not related to fruitfall of hinau or seedfall of hard beech. The long-term changes in the population density of rats were related inversely to the changes in the number of predators. Our review of previous studies in New Zealand indicates that their patterns are consistent with the more detailed account from the Orongorongo Valley. However, there is a significant body of anecdotal evidence for ship rat “plagues” and “eruptions” correlated with fruiting (see Discussions of King & Moller 1997; Harper 2005), and the hypothesis merits further investigation.

Innes et al. (2001) strongly recommended further manipulative tests of predation and food supply as factors limiting the abundance of ship rats, like that of Blackwell et al. (2003). We endorse this, with two further suggestions. Firstly, further work should not be based on the “eruptive” model until it has been established empirically. Secondly, such studies should include the arthropod foods of rats, detailed documentation of their seasonal diet and seasonal demography (survival, age structure, and breeding), and the population density and diet of predators.

ACKNOWLEDGMENTS

We thank the many people who helped with the trapping over the years, especially P. R. Notman, Guo Cong, J. A. V. Tilley, C. M. King, and H. Moller. J. C. Alley collected data over 1994–96. We are indebted to M. J. Daniel and P. E. Cowan for data on hinau and hard beech seedfall. R. M. Fewster, J. G. Innes, C. M. King, and D. J. Wilson provided helpful comments on a draft. MGE and BMF especially thank Alice Fitzgerald whose good humour and cooking sustained them throughout the preparation of this paper. The latter part of this work was funded by FRST, most recently for MGE from FRST contract C09X0209.

REFERENCES

- Alley JC, Fitzgerald BM, Berben PH, Haslett SJ 1998. Annual and seasonal patterns of litter-fall of hard beech (*Nothofagus truncata*) and silver beech (*Nothofagus menziesii*) in relation to reproduction. *New Zealand Journal of Botany* 36: 453–464.
- Alley JC, Berben PH, Dugdale JS, Fitzgerald BM, Knightbridge PI, Meads MJ, Webster RA 2001. Responses of litter-dwelling arthropods and house mice to beech seeding in the Orongorongo Valley, New Zealand. *Journal of the Royal Society of New Zealand* 31: 425–452.

- Alterio N, Moller H, Brown K 1999. Trappability and densities of stoats (*Mustela erminea*) and ship rats (*Rattus rattus*) in a South Island *Nothofagus* forest, New Zealand. *New Zealand Journal of Ecology* 23: 95–100.
- Bentley EW, Taylor EJ 1965. Growth of laboratory-reared ship rats (*Rattus rattus* L.). *Annals of Applied Biology* 55: 193–205.
- Best LW 1969. Food of the roof-rat, *Rattus rattus rattus* (L.), in two forest areas of New Zealand. *New Zealand Journal of Science* 12: 258–267.
- Best LW 1973. Breeding season and fertility of the roof-rat, *Rattus rattus rattus*, in two forest areas of New Zealand. *New Zealand Journal of Science* 16: 161–170.
- Beveridge AE 1964. Dispersal and destruction of seed in central North Island podocarp forests. *Proceedings of the Ecological Society of New Zealand* 11: 48–55.
- Blackwell GL, Potter MA, McLennan JA, Minot EO 2003. The role of predators in ship rat and house mouse population eruptions: drivers or passengers? *Oikos* 100: 601–613.
- Brockie RE 1982. Effect of commercial hunters on the number of possums, *Trichosurus vulpecula*, in Orongorongo Valley, Wellington. *New Zealand Journal of Ecology* 5: 21–28.
- Burnham KP, Anderson DR 2002. Model selection and multimodel inference. 2nd ed. New York, Springer.
- Campbell DJ 1978. The effects of rats on vegetation. In: Dingwall PR, Atkinson IAE, Hay C. ed. *The ecology and control of rodents in New Zealand nature reserves*. Wellington, New Zealand Department of Lands and Survey, Information Series No. 4. Pp. 99–120.
- Campbell DJ 1984. The vascular flora of the DSIR study area lower Orongorongo Valley, Wellington, New Zealand. *New Zealand Journal of Botany* 22: 223–270.
- Chatfield C 1984. *The analysis of time series*. 3rd ed. London, Chapman and Hall.
- Choquenot D, Ruscoe WA 2000. Mouse population eruptions in New Zealand forests: the role of population density and seedfall. *Journal of Animal Ecology* 69: 1058–1070.
- Clout MN 1980. Ship rats (*Rattus rattus* L.) in a *Pinus radiata* plantation. *New Zealand Journal of Ecology* 3: 141–145.
- Clout MN, Barlow ND 1982. Exploitation of brushtail possum populations in theory and practice. *New Zealand Journal of Ecology* 5: 29–35.
- Cowan PE, Waddington DC, Fitzgerald BM, Notman PR, Daniel MJ 1992. Seedfall and litterfall in the Orongorongo Valley: study sites and sampling designs. DSIR Land Resources Technical Record 120.
- Daniel MJ 1972. Bionomics of the ship rat (*Rattus r. rattus*) in a New Zealand indigenous forest. *New Zealand Journal of Science* 15: 313–341.
- Daniel MJ 1973. Seasonal diet of the ship rat (*Rattus r. rattus*) in lowland forest in New Zealand. *Proceedings of the New Zealand Ecological Society* 20: 21–30.
- Daniel MJ 1978. Population ecology of ship and Norway rats in New Zealand. In: Dingwall PR, Atkinson IAE, Hay C ed. *The ecology and control of rodents in New Zealand nature reserves*. Wellington, New Zealand Department of Lands and Survey, Information Series No. 4. Pp. 145–154.
- Davis DE, Emlen JT Jr 1948. The placental scar as a measure of fertility in rats. *Journal of Wildlife Management* 12: 162–166.
- Dilks P, Willans M, Pryde M, Fraser I 2003. Large scale stoat control to protect Mohua (*Mohoua ochrocephala*) and kaka (*Nestor meridionalis*) in the Eglinton Valley, Fiordland, New Zealand. *New Zealand Journal of Ecology* 27: 1–9.
- Dowding JE, Murphy EC 1994. Ecology of ship rats (*Rattus rattus*) in a kauri (*Agathis australis*) forest in Northland, New Zealand. *New Zealand Journal of Ecology* 18: 19–27.
- Efford MG, Karl BJ, Moller H 1988. Population ecology of *Mus musculus* on Mana Island, New Zealand. *Journal of Zoology*, London 216: 539–563.
- Efford MG, Cowan PE 2004. Long-term population trend of *Trichosurus vulpecula* in the Orongorongo Valley, New Zealand. In: Goldingay RL, Jackson SM ed. *The biology of Australian possums and gliders*. Chipping Norton, Surrey Beatty & Sons. Pp. 471–483.
- Efford MG, Dawson DK, Robbins CS 2004. DENSITY: software for analysing capture-recapture data from passive detector arrays. *Animal Biodiversity and Conservation* 27: 217–228.
- Fitzgerald AE 1976. Diet of the opossum *Trichosurus vulpecula* (Kerr) in the Orongorongo Valley, Wellington, New Zealand, in relation to food-plant availability. *New Zealand Journal of Zoology* 3: 399–419.
- Fitzgerald BM, Daniel MJ, Fitzgerald AE, Karl BJ, Meads MJ, Notman PR 1996. Factors affecting the numbers of house mice (*Mus musculus*) in hard beech (*Nothofagus truncata*) forest. *Journal of the Royal Society of New Zealand* 26: 237–249.

- Fitzgerald BM, Efford MG, Karl BJ 2004. Breeding of house mice and the mast seeding of southern beeches in the Orongorongo Valley, New Zealand. *New Zealand Journal of Zoology* 31: 167–184.
- Fitzgerald BM, Gibb JA 2001. Introduced mammals in a New Zealand forest: long-term research in the Orongorongo Valley. *Biological Conservation* 99: 97–108.
- Fitzgerald BM, Karl BJ 1979. Foods of feral house cats (*Felis catus* L.) in forest of the Orongorongo Valley, Wellington. *New Zealand Journal of Zoology* 6: 107–126.
- Fitzgerald BM, Karl BJ 1986. Home range of feral house cats (*Felis catus* L.) in forest of the Orongorongo Valley, Wellington, New Zealand. *New Zealand Journal of Ecology* 9: 71–81.
- Gales RP 1982. Age- and sex-related differences in diet selection by *Rattus rattus* on Stewart Island, New Zealand. *New Zealand Journal of Zoology* 9: 463–466.
- Gibb JA, Fitzgerald BM 1998. Dynamics of sparse rabbits (*Oryctolagus cuniculus*), Orongorongo Valley, New Zealand. *New Zealand Journal of Zoology* 25: 231–243.
- Gillies CA, Fitzgerald BM 2005. Feral cat. In: King CM ed. *The handbook of New Zealand mammals*. 2nd ed. Auckland, Oxford University Press. Pp. 308–326.
- Gomez JC 1960. Correlation of a population of roof rats in Venezuela with seasonal changes in habitat. *American Midland Naturalist* 63: 177–193.
- Harper GA 2005. Heavy rimu (*Dacrydium cupressinum*) mast seeding and rat (*Rattus* spp.) population eruptions on Stewart Island/Rakiura. *New Zealand Journal of Zoology* 32: 155–162.
- Hirata DN, Nass RD 1974. Growth and sexual maturation of laboratory-reared, wild *Rattus norvegicus*, *R. rattus*, and *R. exulans* in Hawaii. *Journal of Mammalogy* 55: 472–474.
- Innes JG 1977. Biology and ecology of the ship rat *Rattus rattus rattus* (L.) in Manawatu (N.Z.) forests. Unpublished MSc thesis, Massey University, Palmerston North.
- Innes JG 1979. Diet and reproduction of ship rats in the northern Tararua. *New Zealand Journal of Ecology* 2: 85–86.
- Innes JG 2005. Ship rat. In: King CM ed. *The handbook of New Zealand mammals*. 2nd ed. Auckland, Oxford University Press. Pp. 187–203.
- Innes JG, King CM, Flux M, Kimberley MO 2001. Population biology of the ship rat and Norway rat in Pureora Forest Park, 1983–87. *New Zealand Journal of Zoology* 28: 57–78.
- Karnoukhova NG 1972. Age determination of brown and black rats. *Soviet Journal of Ecology* 2: 144–147.
- King CM 1982. Age structure and reproduction in feral New Zealand populations of the house mouse (*Mus musculus*), in relation to seedfall of southern beech. *New Zealand Journal of Zoology* 9: 467–480, and Erratum *New Zealand Journal of Zoology* 10(1): 3 unnumbered pages.
- King CM 1983. The relationships between beech (*Nothofagus* sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*), in three New Zealand forests. *Journal of Animal Ecology* 52: 141–166.
- King CM, Innes JG, Flux M, Kimberley MO, Leathwick JR, Williams DS 1996. Distribution and abundance of small mammals in relation to habitat in Pureora Forest Park. *New Zealand Journal of Ecology* 20: 215–240.
- King CM, Murphy EC 2005. Stoat. In: King CM ed. *The handbook of New Zealand mammals*. 2nd ed. Auckland, Oxford University Press. Pp. 261–287.
- King CM, Edgar RL 1977. Techniques for trapping and tracking stoats (*Mustela erminea*): a review and a new system. *New Zealand Journal of Zoology* 4: 193–212.
- King CM, Moller H 1997. Distribution and response of rats *Rattus rattus*, *R. exulans* to seedfall in New Zealand beech forests. *Pacific Conservation Biology* 3: 143–155.
- Leathwick JR 1984. Phenology of some common trees, shrubs, and lianes in four central North Island forests. *Forest Research Institute Bulletin No. 72*. Rotorua, Forest Research Institute.
- Linn IJ, Downton F 1975. The analysis of data obtained from index trappings. *Acta Theriologica* 20: 319–331.
- Miller CJ, Miller TK 1995. Population dynamics and diet of rodents on Rangitoto Island, New Zealand, including the effect of a 1080 poison operation. *New Zealand Journal of Ecology* 19: 19–27.
- Monks A, Kelly D 2006. Testing the resource-matching hypothesis in the mast seeding tree *Nothofagus truncata* (Fagaceae). *Austral Ecology* 31: 366–375.
- Murphy EC, Dowding JE 1994. Range and diet of stoats (*Mustela erminea*) in a New Zealand beech forest. *New Zealand Journal of Ecology* 18: 11–18.
- Murphy EC, Dowding JE 1995. Ecology of the stoat in *Nothofagus* forest: home range, habitat use and diet at different stages of the beech mast cycle. *New Zealand Journal of Ecology* 19: 97–109.

- Nelson L Jr, Clark FW 1973. Correction for sprung traps in catch/effort calculations of trapping results. *Journal of Mammalogy* 54: 295–298.
- O'Donnell CFJ, Phillipson SM 1996. Predicting the incidence of mohua predation from the seedfall, mouse, and predator fluctuations in beech forests. *New Zealand Journal of Zoology* 23: 287–293.
- Ogden J, Stewart GH, Allen RB 1996. Ecology of New Zealand *Nothofagus* forests. In: Veblen TT, Hill RS, Read J ed. The ecology and biogeography of *Nothofagus* forests. New Haven, Yale University Press. Pp. 25–82.
- Ostfeld RS, Keesing F 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology and Evolution* 15: 232–237.
- Otis DL, Burnham KP, White GC, Anderson DR 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monograph* 62: 1–135.
- Rickard CG 1996. Introduced small mammals and invertebrate conservation in a lowland podocarp forest, South Westland, New Zealand. Unpublished Master of Forestry Science thesis, University of Canterbury.
- Ruscoe WA, Wilson DJ, McElrea L, McElrea G, Richardson SJ 2004. A house mouse (*Mus musculus*) population eruption in response to rimu (*Dacrydium cupressinum*) seedfall in southern New Zealand. *New Zealand Journal of Ecology* 28: 259–265.
- Schauber EM, Kelly D, Turchin P, Simon C, Lee WG, Allen RB, Payton IJ, Wilson PR, Cowan PE, Brockie RE 2002. Masting by eighteen New Zealand plant species: the role of temperature as a synchronising cue. *Ecology* 83: 1214–1225.
- Sinclair ARE 1989. Population regulation in animals. In: Cherrett JM ed. *Ecological concepts*. Oxford, Blackwell. Pp. 197–241.
- Singleton G, Krebs CJ, Davis S, Chambers L, Brown P 2001. Reproductive changes in fluctuating house mouse populations in southeastern Australia. *Proceedings of the Royal Society, London, Series B* 268: 1741–1748.
- Veitch CR 1985. Methods of eradicating feral cats from offshore islands in New Zealand. In: Moors PJ ed. *Conservation of island birds*. International Council for Bird Preservation Technical Publication No. 3. Pp. 125–141.
- Venables WN, Ripley BD 1999. *Modern applied statistics with S-PLUS*. 3rd ed. New York, Springer.
- Warburton B, Tocher G, Allan N 2000. Possums as a resource. In: Montague T ed. *The brushtail possum*. Lincoln, Manaaki Whenua Press. Pp. 251–261.
- Wardle JA 1984. *The New Zealand beeches: ecology, utilisation and management*. Christchurch, New Zealand Forest Service.
- Williams CK 1982. Nutritional properties of some fruits eaten by the possum *Trichosurus vulpecula* in a New Zealand broadleaf-podocarp forest. *New Zealand Journal of Ecology* 5: 16–20.
- Wilson DJ, Lee WG, Webster RA, Allen RB 2003. Effects of possums and rats on seedling establishment at two forest sites in New Zealand. *New Zealand Journal of Ecology* 27: 147–156.
- Wilson PR, Karl BJ, Toft RJ, Beggs JR, Taylor RH 1998. The role of introduced predators and competitors in the decline of kaka (*Nestor meridionalis*) populations in New Zealand. *Biological Conservation* 83: 175–185.

Appendix 1 Details of rats trapped and released in the Orongorongo Valley as juveniles (≤ 100 g) and later recovered dead, for calibration of the Karnoukhova (1972) toothwear index. Rats in 1971–73 were caught by M. J. Daniel and BJK, and in 1993 by D. C. Waddington.

Tag	Sex	First capture			Final capture				
		Date	Weight (g)	Estimated age (days)	Date	Elapsed (days)	Weight (g)	Estimated age (days)	Toothwear class
1451	F	22 Jun 1973	50	38	17 Jul 1973	25	—	63	3
1448	F	21 Jun 1973	85	78	26 Jul 1973	35	—	113	3
1447	F	21 Jun 1973	85	78	27 Jul 1973	36	95	114	3
1449	F	21 Jun 1973	100	98	26 Jul 1973	35	80	133	3
1085	M	22 Jan 1971	100	98	16 Jul 1971	175	175	273	4
790	M	16 Feb 1993	62	52	23 Nov 1993	280	162	332	3
772	M	17 Feb 1993	64	54	23 Nov 1993	279	155	333	4
1186	M	16 Feb 1972	55	44	1 Feb 1973	351	150	395	4
1078	M	20 Jan 1971	34	23	25 Feb 1972	401	190	424	4
1127	F	23 Jun 1971	80	72	27 Jul 1972	400	159	472	4
1120	F	21 May 1971	70	61	28 Mar 1973	677	145	738	5

Appendix 2 Breeding of ship rats in relation to annual fruitfall of hinau and an index of population density. Orongorongo Valley, Wellington, New Zealand August 1971–May 1998. Years were defined to start in November of the year preceding fruitfall (i.e., first row refers to November 1970–August 1971). Breeding was calculated as the percentage of pregnant adult females (toothwear class > 2) in the combined spring (November) and summer (February) samples. — indicates not available or could not be calculated.

Year of fruitfall	Density index						Breeding				Hinau (fruit per m ²)
	Nov	SE	Feb	SE	May	SE	Aug	SE	(%)	(N)	
1971	—	—	—	—	—	—	1.59	0.71	—	—	533
1972	1.28	0.64	4.07	1.13	0.89	0.52	3.64	1.05	0	2	105
1973	1.48	0.66	2.04	0.77	2.05	0.77	3.86	1.07	33	9	35
1974	0.29	0.29	1.76	0.72	2.43	0.86	1.85	0.75	20	5	82
1975	1.19	0.59	2.10	0.79	2.77	0.92	5.25	1.27	33	3	142
1976	0.88	0.51	3.58	1.03	0.88	0.51	1.19	0.60	20	5	182
1977	0.93	0.54	4.90	1.26	3.16	1.00	3.67	1.06	14	7	106
1978	2.36	0.84	0.00	—	1.76	0.72	4.70	1.21	15	13	131
1979	2.99	0.95	1.79	0.73	5.01	1.25	6.52	1.46	25	4	650
1980	5.42	1.32	4.10	1.14	2.75	0.92	6.18	1.38	27	11	110
1981	2.07	0.78	2.42	0.86	3.99	1.11	12.16	1.97	11	9	18
1982	1.79	0.73	3.44	1.04	3.34	1.01	2.86	0.95	80	5	133
1983	3.41	1.03	3.60	1.09	2.45	0.87	7.54	1.54	25	8	186
1984	4.01	1.11	4.39	1.17	7.85	1.57	7.29	1.52	39	13	12
1985	2.75	0.92	7.06	1.47	9.92	1.78	8.56	1.65	18	11	125
1986	7.14	1.49	3.36	1.01	17.46	2.45	20.80	2.79	32	19	104
1987	13.61	2.18	10.60	1.88	7.38	1.54	7.82	1.56	21	28	69
1988	3.94	1.09	6.13	1.37	4.03	1.12	6.84	1.46	17	18	117
1989	3.29	0.99	1.79	0.73	7.11	1.52	9.83	1.83	50	12	166
1990	5.43	1.32	1.83	0.75	9.35	1.80	8.88	1.78	40	10	110
1991	2.89	0.96	3.04	0.96	3.42	1.03	7.92	1.59	11	9	142
1992	3.05	0.97	3.97	1.10	4.70	1.21	3.05	0.96	20	15	43
1993	1.50	0.67	1.78	0.73	4.23	1.13	4.48	1.20	50	10	96
1994	6.40	1.43	4.35	1.16	4.06	1.12	12.59	2.02	17	12	152
1995	2.87	0.96	4.37	1.17	10.20	1.83	12.82	2.14	—	—	337
1996	11.04	1.99	8.51	1.70	5.57	1.39	5.26	1.28	—	—	86
1997	2.88	0.96	0.59	0.42	1.83	0.75	4.36	1.17	—	—	20
1998	2.69	0.95	3.66	1.16	7.69	1.64	—	—	—	—	26

Appendix 3 Diet of cats in the Orongorongo Valley, from scat analysis in 1971–73 when rats were at low density and in 1984–88 when rats were at high density.

Percentage occurrences of prey in 1971–73 ($N = 650$ scats) and in 1984–88 ($N = 143$ scats)

Prey category	1971–73	1984–88
Rat	50.0	52.4
Mouse	42.9	22.4
Rabbit	20.6	46.8
Stoat	0.5	0.7
Possum	19.4	9.1
Bird	12.1	11.2
Lizard	0.3	0.7
Fish	3.1	6.3
Insect	56.8	28.7
Freshwater crayfish	3.1	0.0

Monthly occurrence of rats in the cats diet.

Month	1971–73		1984–88	
	(%)	(N)	(%)	(N)
Jan	48.5	33	44.4	9
Feb	59.3	54	75.0	4
Mar	65.3	49	66.7	3
Apr	69.2	26	60.0	5
May	56.0	25	90.0	10
Jun	70.7	41	50.0	10
Jul	43.0	79	70.6	17
Aug	39.7	68	60.6	33
Sep	30.8	91	25.9	27
Oct	61.4	70	28.6	7
Nov	49.1	59	33.3	15
Dec	41.8	55	100.0	3