Decline in capture rate of stoats at high mouse densities in New Zealand *Nothofagus* forests

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Abstract: We present two statistical models documenting variations in density indices of stoats and of mice in New Zealand southern beech (*Nothofagus* spp.) forests. They confirm previous, simpler correlations showing that the summer capture rate of stoats increases with spring mouse density index up to about 20–25 mouse captures per 100 trap-nights (C/100TN). However, at much higher mouse densities (60–80 C/100TN), observed in the Grebe and Borland Valleys in southern Fiordland in 1979/80 and again in 1999/2000, fewer stoats were caught than expected. These models quantify a serious decline in capture rate of stoats during periods of high mouse abundance over the range 25-80 C/100TN. At such times, management strategies aiming to protect threatened birds by intensive lethal trapping of stoats during the nesting seasons may be least effective just when they are most needed.

Keywords: beech forests; capture rate; conservation of birds; mouse density; *Mustela erminea;* population irruptions; predator control; seedfall.

Introduction

Long-term monitoring in southern beech (*Nothofagus* spp.) forests in New Zealand has documented a recurring sequence of events, set off by periodic heavy seedfalls in autumn (March–June) (King, 1983; O'Donnell and Phillipson, 1996; King, 2002). Mice (*Mus musculus*) (Murphy and Pickard, 1990; Ruscoe, 2001) and (if present) ship rats (*Rattus rattus*) (King and Moller, 1997; Dilks *et al.*, 2003) breed over winter and are captured in very high numbers in spring (September–November). Nine or ten months after the seedfall, the cohort of young stoats (*Mustela erminea*) born in summer (December–January) is also much larger than usual (Murphy and Dowding, 1995; Powell and King, 1997; King, 2002).

The sequence of events correlated with a heavy seedfall is variable in detail but reliable in general. In areas where threatened fauna are vulnerable to stoat predation, the risk to conservation values can confidently be predicted to rise dramatically in postseedfall summers (O'Donnell and Phillipson, 1996; Wilson *et al.*, 1998). Increased trapping effort aiming to catch the young stoats as soon as they are independent in summer can reduce predation on vulnerable native birds during a post-seedfall nesting season (O'Donnell *et al.*, 1996), although birds are still at risk of predation if rats also respond to the seedfall (Dilks et al., 2003).

The capture rate of stoats in Fenn (kill) traps in summer (late December-February) is correlated with mouse density, as indexed by mouse capture rates in the previous spring (November) (C/100TN, correcting for unavailable traps) (Nelson and Clark, 1973; King *et al.*, 2003b). Mice may be less trappable in the presence of high numbers of rats (Brown *et al.*, 1996), and increased records of mouse activity often follow removal of rats (Clout *et al.*, 1995; Innes *et al.*, 1995; Miller and Miller, 1995; Gillies and Pierce, 1999; Murphy *et al.*, 1999).

Capture rates of small mammals are usually assumed to be directly correlated with real density up to indices of about 20 C/100TN (Tanaka, 1960; Caughley, 1977). All but four of the 72 data points reported by King (1983) for rodents, and all 61 for stoats, fell below this level. These data have been used to predict the effects of fluctuations in population densities of stoats on birds of conservation importance in different phases of the seedfall cycle, and predatorprey interactions through the cycle (Blackwell *et al.*, 2001). Barlow and Choquenot (2002; p.15) calculated an asymptotic regression model fitting the same data on stoat capture rate (S) to mouse density (M) indices [S=6.8 ($1-e^{-M0.07}$)], which suggests that the increase in stoat capture rate slows somewhat after about 25 mice/ 100TN. They also fitted another model to data of Murphy *et al.* (1998) relating stoat capture rate to a density index (R) for ship rats derived from tracking tunnels [S=18.7(1- $e^{-R0.04}$)], which levels off markedly at tracking indices above 60%.

Alterio *et al.* (1999) have raised some concern that trappability of stoats in live-traps may be increased when mice are scarce. The corollary of their suggestion, that the capture rate of stoats may be reduced when mice are very abundant, is intuitively reasonable and implied by modelling, but it has never been confirmed from stoat and mouse capture data collected at the high end of the range. We here examine the possibility that stoat capture rate might decline at very high mouse densities.

It is important to check for a potential decline in the capture rate of stoats when mice are super-abundant, for two reasons. Firstly, modelling studies which may form the basis of conservation management decisions have so far used mainly the lower range of mouse density data. Secondly, any reduction in real capture rate of stoats during trapping at very high mouse densities will have implications for the practical effectiveness of stoat population control during postseedfall years.

Methods

A long run of data documenting the relationships between stoat capture rates in kill-traps (estimated monthly) and mouse density in snap traps (quarterly) was collected in the Eglinton and Hollyford Valleys, northern Fiordland, and Craigieburn Forest Park, Canterbury, over the period 1972–80 (King, 1983). The relevant subset of these data used here, with confidence intervals (not given in the original) is summarized in Table 1. The best-fit regression line was

$$y_i = 0.30 x_i$$

where y_i is the summer capture rate for stoats and x_i is the previous spring capture rate for mice ($F_{1,10} = 159.19$, $r^2 = 0.94$, adjusted $r^2 = 0.94$, P < 0.001). The standard error of the co-efficient was 0.02. A model including a constant fitted the data less well and the constant was not significant. Both models met the assumptions of normality, linearity and homoscedasticity of variance.

In the present paper, we combine these data with results from other studies in the Grebe and Borland Valleys (including Pig Creek, a tributary of the Borland) in southern Fiordland during 1979/80 and 1999–2001 (all study areas mapped by King 1983). The Grebe and Borland Valleys are linked by a gravel track built to service power pylons, and lie >80 km south of the Eglinton and Hollyford Valleys. In all four valleys and all years, rodent capture rates were monitored by the same methods (Table 1).

For mice, trap lines were set, in the same positions each time and inspected daily, following the standard routine established by Fitzgerald and Karl (1979). Each line had 36 stations at 50–m intervals, with a rat and a mouse snap trap at each, baited with peanut butter and rolled oats, set for three nights in the last week of February, May, August and November. In all years the rodent index line representing the Borland Valley was set along Pig Creek, and the one representing the Grebe Valley was set near the South Arm of Lake Manapouri, both under closed-canopy forest.

Traps for stoats were operated and baited as summarised in Table 1. Single Fenn traps were set in long lines of tunnels (King and Edgar, 1977) in the Eglinton and Hollyford Valleys and at Craigieburn between 1974 and 1978, and in the Grebe and Borland Valleys in the summers of 1979/80 and 2000/01. For further details, see King (1983) and Purdey *et al.* (2004).

In 1999/2000, there was no stoat trapping along the transect through the Grebe and Borland valleys, but the Department of Conservation set traps in a small area (<400 ha) along Pig Creek, to support a remnant population of the endangered mohua (*Mohoua ochrocephala*). There, a grid of 174 Fenn traps at roughly 100–m spacing was established in October 1999, baited with eggs and checked 13 times until March (Riddell and Southey, 2001).

The data points relating to stoat capture rates (dependent variable, y_i) were non-linearly and asymmetrically distributed across the whole range of spring mouse density indices (independent variable, x_i). Stoat capture rate initially increased in a linear fashion towards an upper asymptote, as is common with many numerical responses of predators to prey. However, it then declined exponentially towards an asymptote at zero. We therefore used the following model, which combines a linear increase with an exponential decay, to describe the relationship:

$$y = a \cdot x \cdot e^{-bx}$$

Taking logarithms of the whole equation produces:

$$\ln(y) = \ln(a) + \ln(x) - b \cdot x$$

which is then suitable for linear regression of the form:

$$\ln(y) = \mathbf{K} + \beta_1 \cdot \ln(x) + \beta_2 \cdot x$$

This linear regression generates results for which

$$e^{\mathbf{K}} = a, \beta_1 \approx 1 \text{ and } \beta_2 = -b.$$

Table 1. Trap catch data for mice, rats, and stoats used to construct our models. Data for trapping effort (total trap nights; TN) and capture rate [mean captures per 100 trap-nights; C/100TN (\pm 95% c.i.). Half a trap night subtracted for every trap not still available by morning] are for November for rats and mice, and December–February for stoats. Rats were present in November of some years, but were too few to include in the model, or to affect the mouse density indices (*c.f.* Brown *et al.*, 1996; King and Moller, 1997). Trap regime for rodents was constant throughout (see text); trap regime for stoats using Fenn traps (except as marked, see Methods) given in last column. Data are from King (1983; unpubl.), P. Jamieson (unpubl.), Riddell and Southey (2001) and Purdey *et al.* (2004).

Site	Date	Months		Mice ²		Rats	Stoats		Trap station	
		since	TN	C/100TN	TN	C/100TN	TN	C/100TN	spacing	bait
		seedfall1								
Eglinton	1974–1975	45	210	4.3 (1.9–7.9)	102	0	1983	1.46 (1.0-2.1)	1 × 400 m	FBCF
	1975-1976	57	210	3.8 (1.6-7.4)	101	2.0 (0.2-6.9)	1993	0.70 (0.4-1.2)	$1 \times 400 \text{ m}$	FBCF
	1976-1977	9	191	20.9 (15.4-27.4)	83	1.2 (0.03-6.5)	1362	5.43 (4.3-6.7)	$1 \times 400 \text{ m}$	FBCF FBCF FBCF FBCF ⁴ FBCF
	1977-1978	21	207	6.8 (3.7–11.1)	106	0	1411	1.42 (0.9–2.2)	$1 \times 400 \text{ m}$	FBCF
	1979-1980	9	195	12.8 (8.4–18.3)	97	0	1183	5.49 (4.3-6.9)	$1 \times 400 \text{ m}$	FBCF
Hollyford	1975-1976	?	211	2.8 (1.1-6.1)	103	0.97 (0.02-5.2)	1654	1.63 (1.1-2.4)	$1 \times 400 \text{ m}$	FBCF
	1976-1977	9	189	14.3 (9.6-20.1)	80	1.2 (0.03-6.7)	1124	4.45 (3.3-5.8)	$1 \times 400 \text{ m}$	FBCF
	1977-1978	21	212	1.9 (0.5-4.8)	107	0	1186	0.84 (0.4-1.5)	$1 \times 400 \text{ m}$	FBCF
	1979-1980	9	187	21.4 (15.7-28.0)	89	0	1179	6.19 (4.8-7.7)	$1 \times 400 \text{ m}$	FBCF
Craigieburn	1973-1974	9	208	6.3 (3.4–10.4)	107	0	1108	0.72 (0.3-1.4)	$1 \times 400 \text{ m}$	none
	1974-1975	21	215	0.5 (0.01-2.5)	105	0	1260	1.35 (0.8-2.1)	$1 \times 400 \text{ m}$	none
Borland	1979-1980	9	146	69.0 (61.0-76.5)	67	5.9 (1.6-14.6)	623	0.80 (0.3-1.9)	$1 \times 400 \text{ m}$	FBCF
	1999-2000	9	110	62.0 (52.1-70.9)	57	0	24 267 ⁵	$0.45 (0.4-0.5)^6$	$5(0.4-0.5)^6$ 1 × 100 m egg	egg
	2000-2001	21	213	0	106	0	527	0.57 (0.1-1.6)	$4 \times 1000 \text{ m}$	egg
Grebe	1979-1980	9	142	77.4 (69.7-84.0)	61	0	612	0.98 (0.36-2.1)	$1 \times 400 \text{ m}$	FBCF
	2000-2001	21	202	0.5 (0.01-2.7)	107	0	808	7.40 (5.7–9.4)	$4 \times 1000 \text{ m}$	egg

¹ Seedfalls were classified as binary events (heavy or not) by Powell and King (1997).

² Spring mouse density estimates for 2000–2001 were taken in the first week of December.

³ Fish-based cat food.

⁴ Live traps; first captures only.

⁵ Stoat trapping in 1999–2000 was done only on a grid in Pig Creek (a tributary of the Borland River), whereas in all other years stoat traps were set along the length of the transect through the Grebe and Borland Valleys.

⁶ Plus 20 rats, 0.08 (0.05–0.13) C/100TN, even though none were caught on the standard index line.

Rats were caught in 2 of 4 summers in the Hollyford, 2 of 5 in the Eglinton, 1 of 3 in the Borland/ Pig Creek and never in the Grebe. Table 1 provides the data on rats even though they were not included in the models, to check the assertion of Brown *et al.* (1996) that, when rats are abundant, activity indices tend to underestimate the density of mice. In these data the highest capture rate for rats (Borland, November 1979) coincided with very high density indices for mice.

Results

Grebe/Borland data

In 1979/80, the November mouse capture rates in the Grebe and Borland valleys exceeded all previous records (Table 1). From the positive correlation between stoat and mouse density indices previously established from the Eglinton and Hollyford data, stoat densities were expected to be high in summer 1979/80. In fact only 9 young and 2 adult stoats were caught in the two

valleys from December 18–21 1979 to January 18–31 1980, over 1 235 trap nights.

Twenty years later, on the standard rodent line in the Borland (P. Jamieson unpubl.), mouse density indices in November 1999 were again very high (Table 1). By February 2000 these density indices had fallen to 32.9 C/100TN (95% CI 25.2-41.0) in the Grebe and 31.9 (24.7–40.0) in the Borland, only half the November average but still exceeding the highest peak recorded in northern Fiordland, and well over twice the highest figure ever recorded in the Orongorongo Valley (Choquenot and Ruscoe, 2000; Fitzgerald et al., 2004). No rats were caught on the Borland rodent index line at Pig Creek in November 1999 (Table 1), but nearby, the massive effort by Department of Conservation trappers (24 267 trap nights) caught 108 stoats and 20 ship rats in Fenn traps between November 1999 and March 2000 (Riddell and Southey, 2001) (Table 1).

In the following summer (2000/01), only one mouse was trapped on the standard mouse density

index line run in the Grebe on 5–8 December 2000 and none in the Borland, but between 16 and 28 January 2001, 63 stoats were caught along the transect through the two valleys (3 in the Borland and 60 in the Grebe) in 1335 trap nights. All these stoats were adults, most born during the mouse peak of 1999/2000 (King *et al.*, 2003b; Purdey *et al.*, 2004).

Analysis

Capture rate of stoats is influenced by trap spacing and length of trap line (King, 1980), so we first ran the model excluding the 1999/2000 stoat data from the grid at Pig Creek. This relationship was not significant. Further inspection showed that one point (Grebe Valley, 2000/01) had a residual twice as great as any other point. Activity of stoats in the Grebe Valley that summer was concentrated around a central section of the transect line (stations 14-22 of 30) distant from the rodent index lines but still supporting a few mice (Purdey et al., 2004). The point representing the Grebe Valley in summer 2000/01 is a statistical outlier because, although the index lines recorded nearly zero mice, unexpectedly high numbers of stoats still survived on patchy remnants of the 1999/2000 peak mouse population.

Without the Grebe outlier, the model was significant (Model I, $F_{2-11} = 6.56$, P = 0.013, Table 2). The addition of the Pig Creek stoat data for 1999/2000 had no significant effect on the parameter estimates, and marginally improved its significance (Model II, $F_{2-12} = 6.59$, P = 0.012, Table 2). Plots of the residuals against the predicted values showed that both models met the assumptions of normality and homoscedasticity of variance (Tabachnick and Fidell, 1996). None of the data points in either Model I or Model II had a

Cook's distance greater than 0.20, a Mahalanobis distance greater than 6.45 or a leverage value exceeding 0.50. Therefore, none of the data points (other than the Grebe one already excluded) exerted undue influence over the parameters of the model, indicating that the model is stable across the sample and not biased by any of the data points included (Field, 2000). The fit of Model II, including 95% confidence intervals about the mean, is shown in Figure 1.

A multiple regression including dummy variables for various site combinations, and for the number of months since the last seedfall, did not improve the fit of either model.

Discussion

Validity of the model

The reasons for the extremely high post-seedfall density indices for mice in the Grebe and Borland valleys are unknown, but the chances that they are due only to human error are diminished by their four-fold replication in these results, recorded by identical field procedures in two valleys sampled at the same sites >30km apart, and in two post-seedfall summers 20 years apart. Perhaps they indicate some basic contrast between the ecology of the stoat-mouse interactions in the study areas correlated with, for example, the difference in distribution of rats. On the other hand, lack of interference from rats might explain the very high capture rates of mice (Brown *et al.*, 1996), but not the low capture rates of stoats.

It could be argued that incorporating data from different stoat trap arrays and baits (Table 1) will invalidate our model. We agree that such variation



Figure 1. Relationship between stoat summer and mouse spring capture rates (C/100TN). The graph shows the best fit curve (solid line) with 95% upper and lower confidence intervals (dotted lines) for the linear regression Model II. Original data points are shown as diamonds. The statistical outlier (Grebe Valley 2000/01) is shown with a clear symbol, but excluded from the regression (see text).

	Variable	β	t	Р	F	d.f.	r^2 (adjusted r^2)	Р
Model I	$x x (\ln x)$	-0.029 ± 0.009 0.623 ± 0.172	-3.20 3.62	0.008 0.004	6.56	2, 11	0.54 (0.46)	0.013
Model II	$x x (\ln x)$	-0.031 ± 0.009 0.624 ± 0.176	-3.50 3.54	0.004 0.004	6.59	2, 12	0.52 (0.44)	0.012

Table 2. Model fit, parameter estimates (\pm standard error) and significance test statistics for variables in the linear regression model ln (*y*) = *K* + $\beta_1 \cdot \ln (x) + \beta_2 \cdot x$, where *y* is the stoat summer capture rate and *x* is the mouse spring capture rate. Model I excludes the Pig Creek 1999/2000 and Grebe Valley 2000/01 data (see text); Model II excludes only the Grebe Valley 2000/01 data.

must introduce error in a regression, especially if the differences in trapping effort and area covered are large. The data point for stoats most different in origin from the others in our model was derived from Pig Creek in 1999/2000, where the very intense local concentration of closely spaced traps in a grid must have sampled the stoat population differently from the much more extensive trap lines set along the transect through the Grebe and Borland Valleys. However, the significance and stability of our model were unaffected by whether or not we included the Pig Creek stoat data. This suggests that the similarities between the stoat samples (e.g. season, time since last seedfall, no previous stoat trapping) outweighed the difference in trap spacing.

Some unknown proportion of the stoat population will never enter a trap even at normal prey densities (Dilks and Lawrence, 2000; King et al., 2003a). When prey are superabundant it is likely that more stoats than usual will be uninterested in artificial baits of any sort. Then, neither trappability nor capture rate will be related to stoat density. Riddell and Southey (2001; p.3) commented: "Catch rates probably relate at least as much to catchability as they do to overall population densities. Mouse numbers were at plague levels along Pig Creek at the time. Anecdotal reports indicate stoat numbers were also high. In all probability, mice were such easy prey that a potentially risky new food source such as hens eggs in trap tunnels held insufficient appeal for the well fed predators". Stoat catch rates in Pig Creek increased in late summer and early autumn 2000, and Riddell and Southey assumed this was because the numbers of mice were declining. Our records confirm that the mouse density index in Pig Creek had fallen substantially by February 2000 (King et al., 2003b).

Proof of an inverse link between prey abundance and trappability requires an independent estimate of real stoat density when prey are very abundant, such as capture-mark-recapture data. But these are subject to the same underestimate in capture rate as are killtrap data, and for the same reasons. For example, Cuthbert and Sommer (2002) live-trapped a high-density population (about 17 stoats per 100 ha in summer) living in a large breeding colony of Hutton's shearwaters (100 000 pairs) in the Kowhai Valley, South Island. Stoats could easily enter the nesting burrows, and they took adults, eggs and chicks (Cuthbert *et al.*, 2000). Surrounded by such superabundant food, these stoats were hard to catch (summer capture rate 0.82/100TN) (Cuthbert and Sommer, 2002).

More recent rodent and stoat monitoring programmes in the Eglinton Valley and elsewhere have used methodologies different from ours. Capture rate is influenced by habitat and sampling strategy (O'Donnell and Phillipson, 1996), so density indices collected by these methods cannot be added to our model. Nevertheless, comparisons can still be made between years with high and low density of mice within the same dataset. For example, in November 1990 after a heavy seedfall in the Eglinton Valley (Deer Flat), a line of tunnels set 25 m apart with two mouse traps in each caught 18 mice/100TN (O'Donnell and Phillipson, 1996). Stoat traps set nearby over a 50 ha grid, with 56 tunnels at 100-m intervals, caught five times more stoats (0.38 C/100TN) in the summer of 1990/91 than after an average non-mast year. We know of no data indicating that November mouse capture indices for the Eglinton, estimated with our methods, ever reach levels beyond the middle of the curve shown in Figure 1.

Year-round trapping has an important influence on catch rate, as illustrated by a set of unpublished data from the Dart Valley. In November 2000 after a heavy seedfall, B. Lawrence (*unpubl. data*) set two lines of tunnels 25 m apart with two mouse traps in each, and caught 40.5 mice/100TN and 74.5 mice/100TN respectively. Stoat traps set nearby at 200–m spacing caught 0.20, 0.29 and 0.42 stoats per 100TN in the three summer months December, January and February 2000/01. Trapping of stoats continued throughout the winter. By November 2001, 18 months after the seedfall, mice were down to 0.3 C/100TN (averaged across both lines), and the capture rate for stoats in the three months December–February 2001/02 was 0.075 stoats/100TN. These data show that, as in the Eglinton/ Hollyford Valleys during the 1970s, but in contrast to the Grebe Valley in January 2001 (Table 1), winter trapping after a large irruption of mice and stoats substantially reduced the number of stoats surviving in the Dart Valley 18 months after the seedfall.

By contrast, where there is no winter trapping, stoats can remain more numerous than usual for some time after the mice have declined. For example, in the Eglinton in 1991/92, the year after the five-fold increase mentioned above, trappers caught 0.18 stoats/100TN (O'Donnell & Phillipson 1996), although by then the mouse density index was down to zero. The first Fenn trapping session in the Hollyford Valley in February 1975, where stoats had never been trapped before, produced a capture rate index of 9.28 stoats/100TN, by far the highest recorded there and much higher than expected from the first (February) mouse index (8.4 C/ 100TN) (King, 1983).

Implications

Stoats evolved in the cool climates of the far north, where their tight energy budgets often restrict the amount of time they can spend foraging per day (Sandell, 1989). Individuals that can fulfil their daily food requirements in a very short time are predicted to gain an important advantage (e.g. by saving energy for breeding and avoiding hazards) by travelling short distances on each hunt, maintaining small home ranges, and soon returning to their dens (King, 1989). The second part of this prediction has been confirmed in New Zealand, in the Eglinton and Kowhai Valleys, where stoats do maintain small home ranges at high densities of prey (Murphy and Dowding, 1995; Cuthbert and Sommer, 2002).

The implication is that, where easy prey are very abundant, this combination of disinterest in baits and reduced home range size and activity must also reduce the rate at which stoats encounter traps and other monitoring devices. In such circumstances, control of stoats to prevent damage to conservation values will be extremely difficult. At present the Kowhai Valley shearwaters are too abundant to be much affected by stoat predation (Cuthbert and Davis, 2002). By contrast there were, at least until recently, small remnant populations of the endangered mohua in both the Grebe and Borland Valleys, which may not indefinitely survive the recurring post-seedfall stoat irruptions unless they can be protected.

The decline in stoat capture rate we observed at very high mouse densities is statistically valid and biologically reasonable for the particular study areas we modelled, but it is not possible to predict how widely our model would apply, since few other areas have recorded mouse densities above 30 C/100TN (Murphy, 1992; Choquenot and Ruscoe, 2000; Ruscoe, 2001). Nevertheless, our results might have implications for the modelling studies on which decisions about management of stoat populations for conservation are based. The rates at which stoats are recorded in traps or tracking tunnels are usually assumed to act as direct indices of stoat density, and to be reliably predictable from mouse density indices. Models have therefore used winter and spring mouse density indices to predict sudden increases in stoat density over the following summer (Barlow and Choquenot, 2002), and the consequent predation pressure on birds of conservation importance such as the mohua. However, our analysis suggests that the correlation between stoat capture rates and spring mouse density index increases only up to a point (so far unidentified), beyond which it goes into reverse. Because stoats are actually very abundant during the summers of highest mouse densities, stoat capture rates therefore cannot be accurate indices of stoat density in all circumstances.

Our results also raise questions for management strategies for bird conservation in these forests, which rely on stoat control by lethal means requiring artificial baits. If a major control effort is applied in the spring and early summer 6-8 months after a seedfall, when rodent density indices are very high, stoat numbers are rising rapidly, and protection for nesting birds is most needed, removing stoats by single-catch traps does work but is slow and inefficient. In the Eglinton, Dilks et al. (1996; p.305) pointed out that "the rate of predation on forest birds might have been even further reduced if the adult females could have been caught before they produced independent young". In a comparable but different situation, Cuthbert and Sommer (2002; p.158) concluded: "The very low rates of trapping success in this area with a very high density of stoats... indicates that any control programme [to protect Hutton's shearwaters] would be of limited success without a huge degree of effort".

The same relationships may be observed in podocarp forests supporting unusually high numbers of rats. In the Okarito Forest, South Westland, 353 stoats and 577 rats were caught in the summer after a heavy rimu mast, compared with 124 stoats and 61 rats the year before. Despite this effort, none of the 14 kiwi chicks that were being monitored in the Okarito sanctuary survived (Department of Conservation, *unpubl. data*).

These and other results therefore reinforce the argument that management of irruptive populations of stoats would be greatly assisted if we could prevent or minimise the production of the large peak-year cohorts of young stoats by more efficient removal of fertilized females or by fertility control (Norbury, 2000), rather than waiting till the young appear and removing them individually. Attempts to remove the adult females by conventional means during the autumn and winter, 1-5 months after the seedfall, are often inefficient, especially if trappability of stoats declines as soon as the rodent populations begin to irrupt. A recently developed alternative method, using trained dogs to find breeding dens (Theobald and Coad, 2002) during the late winter and spring, 5–8 months after the seedfall, is more hopeful, although very labour-intensive. In the future, an integrated control strategy for stoats involving trapping, dogging and fertility control would be most effective.

Acknowledgements

We are grateful to the Royal Society (London) and the Universities of York and Waikato for funding the exchange visits that led to this paper. We also thank Barry Lawrence, Dan Purdey, Paul Jamieson, David Riddell and Ian Southey for trapping data; Jim Smart and Ian Westbrooke for advice on the statistical analysis; and Nigel Barlow, Murray Efford, Barry Lawrence, Robbie McDonald, Henrik Moller, Elaine Murphy, Des Smith and two anonymous referees for helpful comments on previous drafts of the manuscript.

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