

Predation on native birds in New Zealand beech forests: the role of functional relationships between Stoats *Mustela erminea* and rodents

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In the Holarctic, predation by mustelids on birds is often linked to population cycles of rodents (especially voles and lemmings) because birds may be buffered against mustelid predation at high rodent densities. By contrast, interguild relationships between introduced mustelids and rodents can have very different consequences for native birds in ecosystems where mustelids have been introduced. Here, we consider the interactions between Stoats *Mustela erminea*, feral House Mice *Mus musculus* and native birds in New Zealand beech *Nothofagus* spp. forests. We conclude that buffering to protect birds from Stoat predation normally fails in these systems, because peak populations of mice in these forests are low by Holarctic standards, and mice usually do not become sufficiently abundant to distract increased numbers of Stoats from preying on birds. However, temporary buffering is possible during rare episodes of extreme mouse abundance.

Worldwide, invasive alien species constitute one of the foremost causes of species extinctions and population declines (Atkinson 1996, Vitousek *et al.* 1997, Mack *et al.* 2000). Birds on islands are particularly susceptible to the effects of invasive mammalian predators (Courchamp *et al.* 2003), as they frequently lack pre-adaptation to predation (Dickman 1996, Short *et al.* 2002).

New Zealand was the last major land mass to be colonized by humans. The Polynesian ancestors of the Maori arrived in about 1250–1300 AD, accompanied by the Pacific Rat *Rattus exulans* and domestic dogs *Canis familiaris* (Hogg *et al.* 2003). The long geographical isolation of the islands prior to this resulted in high levels of endemism; birds were the largest land animals, and mammals were represented by only a few species of bats and seals (Clout & Lowe 2000, Craig *et al.* 2000, King 2005). Predation by human hunters on large endemic species, and by *R. exulans* on the small ones, produced a catastrophic extinction event between the 13th and 18th centuries (Holdaway 1999). Since European colonization 200 years ago, additional predatory mammals from the Holarctic have caused the extinction of more endemic bird species (Clout & Lowe 2000).

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Before human colonization, the forest ecosystems that covered almost all of New Zealand supported a diverse avifauna dominated by large, sometimes flightless, birds, rather than by the mammals found in other parts of the world (Craig *et al.* 2000). The establishment of 32 species of invasive land mammals in New Zealand over the last 700 years has resulted in a radical shift in the taxonomic structure of the animal communities in these forests. In some respects, the ecosystems that emerged have mirrored those in which these same species were found in their native environments, but in other respects they are quite different. This paradox can be observed in the three-way predator–prey interaction between mustelids, rodents and birds.

In the Holarctic, rates of predation by native predators on native birds fluctuate between years. Lack (1954) suggested that the changes in predation rates on birds could be linked to population cycles of small rodents, if predators switch between birds and rodents through the cycle. Early studies in Wytham Woods, UK, confirmed that the rate of predation by Common Weasels *Mustela nivalis* on Paridae in nestboxes was inversely correlated with the density of the woodland rodents: Bank Vole *Clethrionomys glareolus* and Wood Mouse *Apodemus sylvaticus* (Dunn 1977). Similarly, Common Weasels on agricultural

land took fewer birds in years when Field Voles *Microtus agrestis* were abundant (Tapper 1979). During these two studies, rodent densities varied through a wide range, equivalent to 17–140 and 12–194 rodents/ha, respectively. The rates of predation on birds in the two studies were substantially reduced when rodent densities exceeded 75/ha (Dunn 1977) and 150/ha (Tapper 1979). Similar variations in predation rate on birds by predators that normally feed mainly on small rodents and Rabbits *Oryctolagus cuniculus* have been documented since then, in response to both natural and human-induced changes in mammalian prey populations (Hogstad 1995, Murphy *et al.* 1998, Haselmayer & Jamieson 2001, Blomqvist *et al.* 2002, Norbury *et al.* 2002, Sharp *et al.* 2002, Huhta *et al.* 2003).

Common Weasels and Stoats *Mustela erminea* were introduced into New Zealand in the mid 1880s, supposedly to control Rabbits, and they (especially Stoats) rapidly spread into the native forests. In the absence of any native small mammals, the niche for a small (mean < 150 g) forest rodent had been occupied, from the 13th to the 19th centuries, by *R. exulans*, introduced by Polynesian settlers, replaced in the mid to late 19th century by non-commensal House Mice *Mus musculus* and rats (first *Rattus norvegicus*, then *R. rattus*: only *R. rattus* is now common in forest), introduced by Europeans (King 2005).

Nothofagus forest is marginal habitat for introduced Stoats except in mast years (autumns with heavy seedfalls) (Murphy & Dowding 1994). In three *Nothofagus* forests in the South Island of New Zealand (described by King 1983), the masting years of 1976 and 1979 stimulated an increase in feral House Mice over winter. In one of these three areas, the Eglinton Valley, a seedfall in 1990 was described by Murphy and Dowding (1995), and another in 1999 by Ruscoe *et al.* (2001). The only absolute density estimates available for House Mice in forest come from this area after the 1999 seedfall, when peak mouse densities in August 1999 ranged from 27 to 50 mice/ha (Ruscoe *et al.* 2001). This was a substantial increase by New Zealand standards, although low by comparison with the range of densities for rodents recorded by Dunn (1977) and Tapper (1979) in the UK.

The pattern common to all these events was as follows. By spring, 6 months after a seedfall, high numbers of House Mice supported unusually large litters and high juvenile survival of Stoats, which allowed female Stoats to reach their maximum productivity over very large areas of forest (King *et al.* 2003). The consequent large cohort of young

Stoats appearing during the summer, 9 months after a seedfall, accounted for a temporary increase in the local Stoat population, to levels usually 5–6 times higher than during a normal summer (King 2002).

The frequency of occurrence of House Mice in Stoat guts collected in post-seedfall summers was positively correlated with an index of mouse abundance (King 1983). There was no reciprocal decline in frequency of occurrence of birds eaten, and no indication that a higher availability of mice might distract Stoats from eating birds. On the contrary, the greater abundance of Stoats in mouse peak years, and lack of any buffering effect, suggested that total predation pressure on birds would be higher during the peaks of the mouse irruptions, rather than during the decline period after them (King 1983). Subsequent studies in the same and comparable areas recorded similar results (Murphy & Dowding 1995), so the hyperpredation risk to native birds in *Nothofagus* forests during the summer after a seedfall, in contrast to the buffering effect usually observed in the Holarctic, is now regarded as predictable (O'Donnell & Phillipson 1996).

In this study, we introduce new data from two additional areas where, for unknown reasons, post-seedfall mouse irruptions can span a higher range of abundance than had previously been recorded (King *et al.* 2003). Including data from these additional areas, the total dataset spans a greater range of rodent abundance in *Nothofagus* forests, closer to the range commonly observed in the Holarctic. We use this dataset to examine whether the abundance of mice in the emerging ecosystems of New Zealand ever reaches levels sufficient to permit the same predation-buffering process found in native ecosystems in the Holarctic. If predation buffering of birds by mice is occasionally possible in New Zealand beech forests, we would expect a negative correlation between the frequency of bird and mouse predation, a positive relationship between mouse predation and mouse abundance, and a negative relationship between bird predation and mouse abundance, over the full range of mouse abundance indices recorded.

METHODS

This paper presents a meta-analysis of data from several studies conducted across five areas over a period of 25 years, as summarized in Table 1. Comparisons over such a long period are necessary to collect repeat examples of rare events (*Nothofagus* masting years recur at 3- to 5-year intervals). The field methods in

Table 1. Data on Stoat diet in relation to mouse abundance, in peak and post-peak years in four study areas.

Study area	Summer season	Peak mouse abundance index (corrected % trap success)	No. of Stoat guts analysed	Percentage guts containing birds	Percentage guts containing mice	Reference
Eglinton	1976/77	24.0 (F)	63	70	35	King (1983)
	1977/78	3.9 (F)	17	71	6	King (1983)
	1979/80	12.8 (N)	88	52	48	King (1983)
	1990/91	21.9 (A)	54	57	54	Murphy and Dowding (1995); O'Donnell and Phillipson (1996)
	1991/93	0.7 (1991)	42	55	0	Murphy and Dowding (1995); O'Donnell and Phillipson (1996)
Hollyford	1976/77	25.4 (F)	44	52	45	King (1983)
	1977/78	0	8	50	0	King (1983)
	1979/80	21.4 (N)	74	59	27	King (1983)
Craigieburn	1974/75	13.1 (F)	17	65	41	King (1983)
	1975/76	0	39	69	0	King (1983)
	1976/77	23.4 (F)	40	37	40	King (1983)
Borland	1979/80	69.2 (N)	5	0	100	C.M. King unpubl. data
Grebe	1979/80	77.5 (N)	6	17	100	C.M. King unpubl. data
Borland	1999/2000	62 (N)	36	5	87	R.A. McDonald and D.H.V. Smith unpubl. data
Grebe	2000/01	0 (N)	59	47	10	Purdey <i>et al.</i> (2004)

(F), February; (N), November; (A), August. For comments on the data, see text.

regular use until recently were unsophisticated by contemporary standards, but were applied consistently. Populations of rodents and Stoats were monitored by a simple abundance index, calculated as the number of animals of the target species killed in standard lines of traps (expressed as captures per 100 trap-nights or C/100TN), corrected for the number of traps unavailable by subtracting half a trap-night for each trap sprung or blocked by any capture. In each area, between 30 and 40 traps were set for Stoats at 400-m intervals and operated monthly; for House Mice and Black Rats, 36 pairs of rodent traps were set at 50-m intervals and operated quarterly, always according to the same routines explained in more detail by King (1983).

The highest values of the index are likely to be underestimates, for two reasons. (1) Beyond a trap capture rate of 20 C/100TN the trap-success index is less reliable (Tanaka 1960). (2) Indices for Black Rats and House Mice usually vary together, although when rats are abundant, they can depress the abundance index for mice (Brown *et al.* 1996). Rats were scarce in all areas except after seedfalls (King & Moller 1997, Dilks *et al.* 2003, Purdey *et al.* 2004). Nevertheless, our assumption, that abundance indices can track the real changes in abundance of both mice and Stoats reasonably well, is supported by parallel studies documenting variations in repro-

ductive success and survival of both species (King 1982, King & McMillan 1982, Powell & King 1997).

In three *Nothofagus* forests, each monitored through two heavy seedfall years (Eglinton and Hollyford valleys 1976, 1979, Craigieburn Forest Park 1974, 1976, mapped in King 1983), House Mouse abundance indices normally varied from 0 to 25 C/100TN. Birds were found in 40–70% of guts at all values of the abundance indices for mice across this range. This conclusion was confirmed in the Eglinton Valley during a Stoat irruption after the seedfall of 1990, when Murphy and Dowding (1995) also found no reduction in consumption of birds per Stoat when mice were abundant (birds found in 57% of Stoat guts) compared with the following 2 years when mice were scarce (birds found in 55% of guts) (Table 1).

The mouse abundance indices used in our calculations were taken according to a standardized protocol, implemented in the same way in all samples except two (Eglinton 1990/91 and 1991/93). Stoat gut analyses were done by standard protocols summarized by King and Moody (1982). Percentage data were arcsine-transformed prior to analysis (Zar 1984). We used summer data only, from peak seedfall years and the following year, to test the relationship between Stoat diet and House Mouse abundance index across all study sites using linear regression analysis. The comparison necessarily assumes that

traps and Stoats are equally good at tracking variations in the number of House Mice, whereas we suspect that rodents at low density tend to be distributed patchily in the forest, and that Stoats are somewhat better at locating the last few mice than are traps (Purdey *et al.* 2004).

Stoats can be harder to catch when mice are extremely abundant (King & White 2004). For example, in the Grebe and Borland valleys, which are linked across a low alpine pass, only six and five Stoats, respectively, were caught during the massive mouse irruption of 1979/80. During the next mouse irruption we observed in 1999/2000, a larger sample of Stoats was collected ($n = 36$) by intensive trapping in a smaller area in the Borland Valley only. In the crash year of 2000/01, rodent trap lines in both valleys registered zero captures, but a few mice remained in the Grebe Valley several kilometres from the trap lines, and many of the surviving Stoats were trapped there (Purdey *et al.* 2004). All but three of 62 non-empty Stoat guts collected on the transect that year came from the Grebe Valley, so the Borland sample is not shown for that year in Table 1.

We use linear regression models to investigate the relationship between predation rate and mouse abundance because we have few data relating to intermediate mouse abundance indices (c. 30–50 C/100TN), on which the form of a curvilinear or threshold relationship could be based. However, the relationships between rodent predation rate and rodent abundance shown by Dunn (1977) and Tapper (1979), based on a more even distribution of rodent abundances, were also linear.

RESULTS

The frequency of occurrence of birds eaten was inversely correlated with the frequency of occurrence

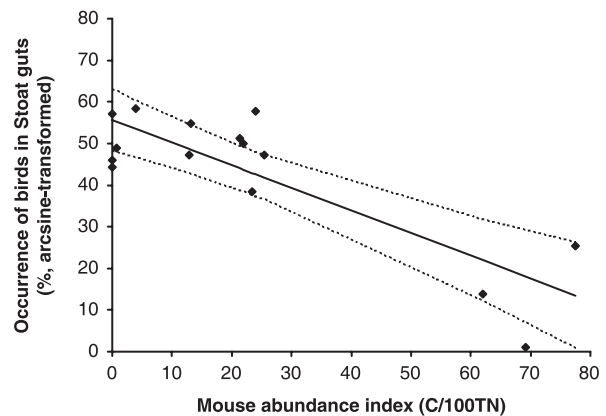


Figure 1. Relationship between the consumption of birds by Stoats and mouse abundance indices in New Zealand *Nothofagus* forests. Summer data only, from peak years and the following year. The graph shows the best-fit line (solid line) with 95% upper and lower confidence intervals (dotted lines) for the linear regression model $y_i = 55.63 - 0.54x_i$, where y_i is the percentage occurrence of birds in Stoat guts (arcsine-transformed) and x_i is the mouse abundance index (C/100TN). Data are from sources listed in Table 1.

of mice eaten ($r_s = -0.55$, $n = 15$, $P \leq 0.05$). There was a statistically significant inverse relationship between the frequency of occurrence of birds eaten (arcsine-transformed) and the mouse abundance index (Fig. 1, Table 2 model I). Conversely, there was a significant positive relationship between the occurrence of mice in Stoat guts and mouse density (Fig. 2, Table 2 model II). On all but one occasion (Grebe Valley, 2000/01), the frequency of occurrence of birds in summer samples of Stoat guts exceeded 40% when mouse abundance was low to moderate (within the normal range of 0–25 C/100TN), and the frequency of occurrence of mice varied from 0 to 50%. However, at the highest levels of mouse abundance, of at least 60 C/100TN after the 1979 and 1999 seed-falls in the Grebe and Borland valleys, the frequency

Table 2. Model fit, parameter estimates and significance test statistics for variables in the linear regression model $y_i = \alpha + \beta x_i$, where x_i is the mouse abundance index (C/100TN) and y_i is the percentage occurrence of birds in Stoat guts (Model I) and the percentage occurrence of mice in Stoat guts (Model II), both arcsine-transformed.

Variable	Estimate	se	<i>t</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>R</i> ² (adjusted <i>R</i> ²)	<i>P</i>
Model I								
α	55.63	3.42	16.28	< 0.001				
β	-0.54	0.10	-5.46	< 0.001				
					29.79	1, 13	0.70 (0.67)	< 0.001
Model II								
α	13.21	3.59	3.69	< 0.01				
β	1.06	0.10	10.20	< 0.001				
					103.99	1, 13	0.89 (0.88)	< 0.001

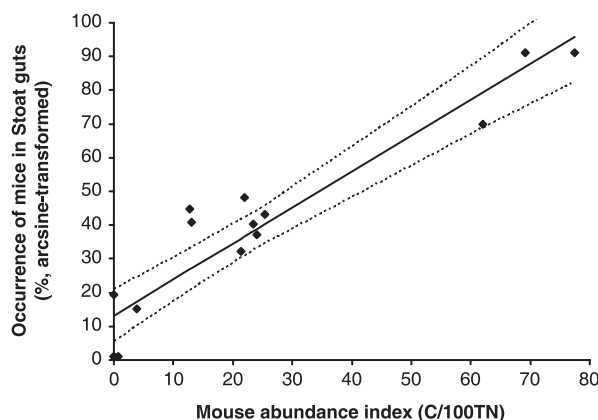


Figure 2. Dietary response showing the consumption of mice by Stoats in relation to mouse abundance indices in New Zealand *Nothofagus* forests. The graph shows the best-fit line (solid line) with 95% upper and lower confidence intervals (dotted lines) for the linear regression model $y_i = 13.21 + 1.06x_i$, where y_i is the percentage occurrence of mice in Stoat guts (arcsine-transformed) and x_i is the mouse abundance index (C/100TN).

of occurrence of birds in Stoat guts dropped to < 20%, whereas that of mice rose to > 85% (Table 1).

Plots of the residuals against the predicted values showed that both models met the assumptions of normality and homoscedasticity of variance (Tabachnick & Fidell 1996). None of the data points in either Model I or Model II had a Cook's distance greater than 0.91, a Mahalanobis distance greater than 4.37 or a leverage value exceeding 0.31. Therefore, none of the data points exerted undue influence over the parameters of the models (Field 2000), indicating that they are stable across the sample and not unduly affected by the highest mouse abundance points.

DISCUSSION

Predator-prey relationships between Stoats and mice

Heavy seedfall (mast) years recur only at 3- to 5-year intervals on average, and the two exceptional mouse irruptions were recorded 20 years apart. Data concerning rare events such as these are therefore scarce. The abundance indices used are only approximations of true abundance. In particular, variations in trap success resulting from heterogeneous distributions of mice, particularly at low mouse densities, will lower their accuracy. However, these types of error would be expected to decrease the likelihood of patterns emerging from data gathered over several different sites and several time periods. Therefore,

the coincidence of new observations of an unprecedented change in Stoat food habits with periods when mouse abundance indices were exceptionally high increases the chances that these are real events, and that they are connected. The relationships we have documented probably underestimate the true functional responses (Boutin 1995), but indicate a clear, although rare (two areas, two summers), buffering effect of mice reducing bird predation, as is typical of northern hemisphere systems.

The use of standard abundance indexing protocols means that the New Zealand figures can be compared with each other, but they cannot be converted to absolute density. The highest mouse densities recorded in the Eglinton Valley were 27–50 mice/ha (Ruscoe *et al.* 2001). The two mouse irruptions in the Grebe/Borland area reached abundance indices 2–3 times higher than the highest observed in the Eglinton Valley by the same methods (24 C/100TN in February 1976: King 1983). These irruptions are therefore likely to have represented densities substantially greater than 27–50 mice/ha, and perhaps well into the range of densities observed by Dunn and Tapper in the UK.

In general, the abundance, body sizes and distribution of small mammal prey are much less favourable for Weasels and Stoats in New Zealand than in Europe (King & Moors 1979, King 1991). Masting of woodland trees in Europe is typically followed by massive population irruptions of several long-resident and well-adapted native rodent species, often reaching several hundred individuals per hectare (Jedrzejewski *et al.* 1995). Such abundance of food for mustelids cannot easily be matched in New Zealand by introduced species of commensal rodents that have recently invaded unfamiliar forest habitat. Indeed, Raymond *et al.* (1990) and Vaudry *et al.* (1990) observed that Stoats were more successful at hunting Meadow Voles *Microtus pennsylvanicus* and Deer Mice *Peromyscus maniculatus* than House Mice, and that they obtained the lowest net energy gain from House Mice.

Consequences for native birds

Inappropriate management of invasive species may lead to adverse changes, such as potential extinctions or the expansion of other invasives (Courchamp *et al.* 1999, 2000, 2003, Crooks & Soulé 1999, Mack & Lonsdale 2002). For example, it is not clear to what extent, if at all, the extremely high numbers of *R. rattus* after an unusual double beech mast year in 1999 and 2000 were influenced by the Department

of Conservation's permanent (since 1997) year-round Stoat trapline in the Eglinton Valley (Dilks *et al.* 2003). There is therefore a need for increased understanding of the functional relationships between native and introduced species.

Only after an exceptionally heavy seedfall, and then only in the Grebe and Borland valleys (thus far), has the abundance of mice been sufficient to reduce the number of birds eaten per Stoat (Fig. 1) – and probably then only for a short time. Such easy hunting for Stoats surrounded by abundant live mice also helps to explain why Stoats become more difficult to trap at very high densities (60–70 C/100TN) of mice (King & White 2004) – the very time that efficient control of Stoats is most needed to protect remnant populations of endemic birds in *Nothofagus* forests, such as the Yellowhead *Mohoua ochrocephala* and the Kaka *Nestor meridionalis* (O'Donnell *et al.* 1996, Wilson *et al.* 1998).

The very different community structure of small mammals and birds in New Zealand *Nothofagus* forests compared with the Holarctic (King 2005) is part of the reason that mast-seeding events usually have different consequences for birds in the two ecosystems. The Stoat's two key prey items in its native habitats (McDonald *et al.* 2000) are absent (voles) or scarce (Rabbits) in *Nothofagus* forests. In most study areas so far examined in detail, House Mice (especially when unaccompanied by rats) are not an adequate substitute for voles, so cannot protect native birds against hyperpredation. However, our analyses suggest that, where post-seedfall irruptions of House Mice in New Zealand do reach sufficiently high levels, the same predator–prey interactions can emerge, buffering birds against the impact of Stoat predation. The problem is that the period of very high numbers of House Mice lasts for a shorter period than that of Stoats (King 1983), so any protection will be merely a brief temporary respite. The consequences for birds of mast seeding depend therefore not only on those species most directly affected by the masting event, but on the species composition and interrelationships of the total ecosystem.

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