

Advances in New Zealand mammalogy 1990–2000: Stoat and weasel

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27. STOAT

Mustela erminea Linnaeus, 1758

For a searchable database of stoat references, see King, C.M. (2000) Stoat bibliography. [online] Available: <http://www.invasive-mammals.org.nz/stoats/> [retrieved *Insert Date of Retrieval*].

Description

After combining several phylogenetic analyses, Bininda-Emonds (1999) reached the conclusion that the stoat is most closely related to the mountain weasel *M. altaica*, but is also very close to the common weasel (*M. nivalis*) and the long-tailed weasel (*M. frenata*). The next closest relatives are New World species, the Colombian weasel *M. felipei* and the tropical weasel *M. africana*, both previously considered to be part of the sub-genus *Grammogale*.

The change to a white winter coat, typical of stoats living where winters are predictably cold, is controlled both by genetic and by environmental factors (Feder 1990). Stoats are well adapted to climates much colder than New Zealand, and were among a handful of species to survive in Britain throughout the last (Devensian) glaciation (Yalden 1999).

Body fat is deposited at several sites in succession, first along the spine and kidneys, then on gut mesenteries, in cavities under limbs, and finally around shoulders. Even very fat stoats thereby retain their tubular shape (King 1989b).

In Nearctic populations, long-term geographic variation in size is correlated with climatic variables, but variation in shape is more likely to be related to the history of recolonisation of northern lands from different glacial refugia (Eger 1990). In the Palaearctic, geographical variation in size is more complex and apparently related to the distribution of prey sizes (Erlinge 1987; Meia & Mermud 1992). In New Zealand, there is significant short-term variation in size, due to nutritional conditions during the period from implantation to independence (Powell & King 1997). Growth of young stoats born in beech forest populations after a good seed year, when mice are abundant, is temporarily enhanced. In large samples from Fiordland and Craigieburn collected in the 1970s, the difference was detectable in skull length, which is fixed early, but not in body weight, which is changeable throughout life.

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Individuals >3 years old were similar in skull size regardless of birth year. Since well-fed young stoats of both sexes grow larger, early nutrition does not affect sexual dimorphism, which is still best explained by a model incorporating the different ecological energetics and reproductive strategies of the two sexes (Sandell 1989).

Field sign

Ratz (1997) provides a key from which the footprints of stoats may be distinguished from those of other small mammals in New Zealand, and Ratz & Moller (1997) describe a technique to help distinguish predators from bite marks on carcasses.

Distribution

The list of islands with stoats has changed somewhat since the one given by King (1990). Deletions include Te Kakahu (Chalky Island); additions include Great Island, both in Fiordland (Willans 2000). Stoats have been eradicated from Maud Island twice (Crouchley 1994), and from Otata Island (I. McFadden, unpubl. data). Reports in the *Southland Times* of 13 December 1999, claiming that stoats had been sighted on Stewart Island, have not so far been confirmed from carcasses, despite an extensive trapping campaign.

Stoats are generally considered uncommon in the Mackenzie Basin, an opinion largely confirmed by an intensive trapping programme done from November to January 1996/97, except in the valleys of the Tasman and Godley Rivers, where stoats were caught in similar numbers to cats and ferrets (Keedwell & Brown 2001).

Food

Diet

Stoats are flexible and opportunist in their diet, so a change in abundance of their normal prey can be expected to cause a rapid shift to alternative resources. In mixed podocarp-hardwood forest at Mapara and Kaharoa, for example, rats were the main prey of stoats in 175 and 27 guts, respectively, examined between 1989 and 1995 (Murphy & Bradfield 1992; Murphy et al. 1998b). After successful poison operations against rats, there were strong and consistent functional responses by stoats to the loss of their primary prey. Overall, the frequency of occurrence of rats in the diet (the proportion of guts examined containing the prey item) was positively correlated ($r^2=0.90$) with rat density, whereas the frequency of occurrence of birds was strongly negatively correlated ($r^2=0.72$) with rat density.

Comparing the diet of stoats in beech (*Nothofagus*) forest in a post-seedfall year (1990/91), when mice were at a population peak, with that in the following years when mice were scarce (1991/93), Murphy & Dowding (1994, 1995) confirmed the changes in frequency occurrence of prey categories through the irruption documented in the same areas through the 1970s.

Cuthbert et al. (2000) collected 788 scats from stoats living in a Hutton's shearwater (*Puffinus huttoni*) colony in the Seaward Kaikoura Mountains. Remains of shearwater eggs, chicks and adults were found in 785 (99%) of scats, plus invertebrates in 7.9% and skins in 7.7%. Mouse and hare remains were infrequent (1.5% and 0.9% respectively).

Rickard (1996) collected 44 guts from stoats living in a lowland podocarp forest in South Westland, and found in them remains of considerable numbers of invertebrates (frequency of occurrence 81.8% of guts, 44.3% of total volume). Rats were the next most frequent prey item, found in 29.5% of guts, then birds in 15.9%, mice in 9.1% and fish in 9.1%.

In the rabbit prone Mackenzie Basin, 63% of 49 stoats examined contained bird remains, 53% lagomorph, 29% lizard and 25% invertebrates, but no rodent remains (Murphy et al.

1998a). Birds and lagomorphs were also an important component of stoat diet in coastal grassland on the south-eastern coastline of the South Island (Alterio & Moller 1997b). Of 75 stoats examined, lagomorphs were found in 47%, birds in 41%, and mice in 31%.

Rodents (both rats and mice) were the most important prey of 57 stoats collected from three habitat types (forest, forest/pasture and coastal) in Northland, followed by invertebrates and birds (Gillies 1998). Lagomorphs were absent from the guts of stoats from forest habitat, but they were an important component of the diet in the forest/pasture habitat.

A recent large study of the diet of stoats from throughout Britain by McDonald et al. (2000b) demonstrated an increase, starting in the mid 1990s, in the importance of rabbits compared with the early 1960s, especially in spring. British rabbits are now strongly recovering from myxomatosis, and comprise over 50% of diet of stoats throughout the year. British stoats also commonly eat ground-nesting birds, and their chicks and eggs (Robson 1998).

Eggs are a favourite food of stoats, which have been observed stealing eggs by rolling them along with their noses or carrying them under one arm (King 1989b:221). Eggs are often used as bait for traps, and videos of stoats removing eggs from trap tunnels were important in showing that tunnels had to be modified to stop poison eggs from being stolen and cached, becoming a potential risk to non-target species.

There are similarities and differences between the feeding niches of the two sexes (Murphy & Dowding 1994; King et al. 1996a; Alterio & Moller 1997b) which could be governed either by an evolved behaviour pattern, or by the availability of prey of different sizes in each habitat, or both. In general, males take a higher proportion of larger prey such as rabbits than do females, which depend to a greater extent on small rodents (King 1989b; McDonald et al. 2000b). Observations on captive stoats of both sexes show that females gain more net benefit from hunting voles than do males (Raymond et al. 1990).

The effect of predation by stoats on populations of their prey varies widely. In Britain, stoats have been estimated to eat >43 million field voles a year, contributing 4.4% of the total annual numerical impact of predators on vole populations in Britain (Dyczkowski & Yalden 1998), though it is not known what effect this rate of removal has on the population dynamics of the voles. In pristine forest in Poland, stoats contributed <1% of the total consumption of prey by a diverse community of predators (Jedrzejewska & Jedrzejewski 1998). Predation by stoats has apparently not limited the post-myxomatosis recovery of rabbit populations (Sumption & Flowerdew 1985). Stoats can have a substantial impact on populations of wild game birds, but they are not usually regarded as a serious problem for reared game (McDonald & Murphy 2000). On a kept grouse moor in Teesdale, curlew populations were found to suffer from high levels of predation of eggs and chicks and, in a simulation model, observed levels of predation resulted in a negative population growth rate (Robson 1998). However, the community dynamics and predator-prey relationships governing predation rates by stoats in the northern hemisphere are very different from those in New Zealand.

In New Zealand, the total impact of stoats on avian prey populations can be very high in beech forests during the post-seedfall years when rodent populations are highest, and is due mainly to the substantial numerical response of stoats to increased food supply (Lawrence 1997; O'Donnell et al. 1996), rather than to prey switching by a stable number of stoats. Several threatened beech forest species are seriously damaged by predation for short periods during such peak years, principally by stoats, including, kaka, mohua, and yellow-crowned parakeet (O'Donnell 1996; McDonald & Murphy 2000), and see further below. In non-beech habitats in New Zealand, populations of stoats are generally lower and more stable, but the consequences of their predatory activities cause concern for much longer periods of the year, most years. They are especially damaging to the comparatively rare bird species such as kiwi

and New Zealand dotterels (see below), even though these may form only a small part of their diet.

In Nordic regions, predation by small mustelids is reckoned to be the force that drives microtine population cycles (Korpimäki et al. 1991; Sittler 1995). Removal of predators, mainly small mustelids, can reverse the crash phase of rodent cycles (Korpimäki & Norrdahl 1998) and increase the growth rate of *Microtus* populations (Klemola et al. 1997). The predator-prey interactions producing vole cycles may include, not only the direct effects of predation, but also predator-induced breeding suppression (Ylönen 1989; Ylönen & Ronkainen 1994). However, some of the experiments used to test this hypothesis have been flawed (Mappes et al. 1998), so the role of predation and predation risk in population dynamics of voles remains a contentious area (Lambin et al. 2000). An alternative hypothesis proposes that the key to vole cycles is not predation but the mean standing crop of ground vegetation (Jedrzejewski & Jedrzejewska 1996). In contrast to New Zealand, the immediate impact on northern hemisphere bird populations of temporary increases in numbers of small mustelids tends to be buffered by the functional response of mustelids to the rodents (King 1989b).

Behaviour and social organisation

Activity

Stoats can be active at any time of the day or night (Alterio & Moller 1997a). They have a rapid metabolism and need to eat frequently, up to five or six times per day (King 1989b). Their usual pattern of alternating periods of hunting, eating and resting around the clock was documented in Québec, where Samson & Raymond (1995) recorded an average of five expeditions averaging 40 minutes long during the day and one at night, plus 17 bouts of stationary activity in the day and six at night. The total activity budget was correlated mainly with ambient temperature, and secondarily with reproductive condition (Robitaille & Baron 1987). The first radio-tracking study of stoats in New Zealand, in South Island beech forest, confirmed that stoats were often active during the day (Murphy & Dowding 1995).

Home range

The rapid improvement in radio-tracking technology over the last decade has produced many new data on home ranges (Table 1), although stoats are still difficult to work on and samples are sometimes small. Stoats generally have larger home ranges in New Zealand compared with the northern hemisphere. For example, on farmland in Québec, one study reported that 11 live-trapped male stoats had mean range of 19.8 ha, and 12 females 4.8 ha (Robitaille & Raymond 1995), and another study radio-tracked a male and a female across 35.3 ha and 15.6 ha respectively (Samson & Raymond 1998). In New Zealand beech forest, in 1990–91 three males had mean ranges of 93 ± 7 ha, and four females, 69 ± 8 ha (Murphy & Dowding 1995), and in the same area in 1991–92, four males had mean ranges of 206 ± 73 ha, and five females, 124 ± 21 ha (Murphy & Dowding 1994).

However, these differences are not easy to interpret. On the one hand, Murphy & Dowding (1994) suggested that, in most years, New Zealand beech forest might be marginal habitat for stoats. On the other hand, stoats in Canada are much smaller than in New Zealand, a difference that would in itself affect home range size even if all else were equal. In beech seeding (mast) years, all else is definitely not equal: higher densities of potential prey (mice & birds) are quickly followed by higher densities of stoats. Then they either live on smaller home ranges (Murphy & Dowding 1995), or are non-territorial (Alterio 1998).

Home ranges often overlap, particularly between sexes (Murphy & Dowding 1994; 1995; Alterio 1998), but many individual stoats have separate core ranges that do not overlap

(Young 1998). Scent marking behaviour is well known but not well understood. At the very least, scent marks convey information on social and reproductive status, and probably also individual identity.

Dens

Den sites may include holes up the trunks and in roots of trees through forest habitat (Murphy & Dowding 1994), or in piles of logs, ditches and isolated patches of scrub in open habitat (King 1989b). In the Eglinton Valley, of 29 stoat dens found, 22 were obvious holes in the ground under tree roots, three were up trees and four were in the middle of a grass plain (Murphy & Dowding 1995). In Ireland, of 19 dens belonging to three radio-tracked individuals, 15 were in underground burrows (nine rat, four rabbit, one mouse and one unknown), three in piles of sticks or stones and one up a tree (Sleeman 1990). In arctic and montane regions, access to sub-nivean tunnels and the nest sites they provide are essential for the survival of small mustelids, and may limit their body size in that environment (King 1989a). The well-known habit of northern stoats to line their nests with the fur of their prey, an especially useful trait allowing the identification of their subnivean nest sites after snow melt, is being used to track population changes through the lemming cycle in a long term study in Greenland (Sittler 1995).

Female stoats move about less during the breeding season (Robitaille & Raymond 1995), and females with small young are likely to stay close to their dens except when it is necessary to shift their young between den sites. In the Eglinton Valley, Murphy & Dowding (1995) observed an adult female moving her young 500 m to a new den.

Table 1 Home ranges of New Zealand stoats

Source	Habitat, year	Season	Sex	n	Home range (Hectares)	Comments
Murphy & Dowding 1994	Beech forest, 1991/92	Su/Au	M	4	206 ± 73	2 years after last mast year, mice scarce
			F	5	124 ± 21	
Murphy & Dowding 1995	Beech forest, 1990/91	Su/Au	M	3	93 ± 7	Post-seedfall year, mice abundant
			F	4	69 ± 8	
Alterio 1998	Beech forest, 1996	Sp	M	4	223 ± 45	18 months since last seedfall, mice scarce
			F	7	94 ± 13	
Gillies 1998	Kauri/podo-carp/hard-wood forest		M	3	108 ± 19	
			F	1	49.5	
Moller & Alterio (1999)	Ungrazed grassland	Sp/Au	MM	3	110 ± 28	
				3	158 ± 31	
Miller et al. (2001)	South Is. Podocarp forest		M	1	94	
			M	8	256 ± 38	
			M	3	171 ± 14	
			M	2	145 ± 35	
			F	2	123 ± 6	
			F	5	79 ± 21	
			F	3	102 ± 36	
F	2	75 ± 5				

Sp=Spring; Su=Summer; Au=Autumn; Wi=winter; M=Male; F=Female; n= Sample size. Mean home range is in hectares ± one standard error, calculated by the minimum convex polygon method.

Reproduction and development

Preliminary data suggested that fecundity might be related to female age (King & Moody 1982a), but this effect disappeared when the data were controlled for inter-annual variation in food availability (Powell & King 1997). The adult male serves the breeding female and her precocious juvenile females in the den at the same time. The lack of pair bonds, the variable mating strategies of males of different social status (Sandell & Liberg 1992), and the rapid turnover of the population, reduce the chances that any given male is serving his own young (King 1989b), but the levels of inbreeding within local populations have not been tested. Recent records from Britain take the total known mean embryo count to 8.9, $n = 50$, range 6–13 (McDonald 1998).

Population dynamics

Delayed implantation means that productivity can not be related to fecundity. Maximum potential fecundity is set during the mating season of one year, while productivity cannot be realised until the following year, when conditions may be very different (King 1989b). Resorption and nestling mortality cut down the potential litter size by 0–100% of ova released, depending on food supplies during the season of implantation and lactation. In New Zealand beech forests, productivity rates in the 1976 and 1979 cohorts, born when mice were abundant, were higher than in cohorts born when mice were scarce (Lawrence 1997; Powell & King 1997).

Similar food-dependent mechanisms probably caused the population decline of stoats in Britain after myxomatosis (1953–55), which was clearly documented by gamekeeper's records (Tapper 1992). After 1970, stoats recovered their numbers until 1975, but then appeared to begin a second, slower decline continuing to 1998. However, when allowance is made for the reduction in trapping effort by gamekeepers over the last 25 years, the overall population of stoats in Britain, roughly 462 000 before breeding (Harris et al. 1995), is probably not declining (McDonald & Harris 1999). In New Zealand, the average number of stoats killed per 100 km of road has been relatively stable for the last 34 years, whereas rabbits, cats and ferrets have increased (Flux 1995).

The numbers and distribution of stoats can be affected by interference competition from larger predators (King 1989a). In Europe, increases in foxes tend to be associated with declines in stoats (Mulder 1990; Tapper 1999); in the McKenzie Basin, New Zealand, Pierce (1987) suggested that stoats might increase after ferrets and cats were removed. Since stoats are considered to be more serious conservation pests than ferrets or cats (Norbury & Murphy 1996), this shift in the local predator guild could be one of the less desirable consequences of the illegal introduction of rabbit hemorrhagic disease (Norbury & Murphy 1996). Over the last three years, however, predator trapping by Department of Conservation staff in four Mackenzie Basin rivers has not indicated any changes in the predator guild (Cook & Maloney 1999; Cook et al. 2000; Keedwell & Brown 2001).

Methods of age determination applicable to stoats were reviewed by King (1991c). Survival rates are generally correlated with food supplies. In three New Zealand beech forests in the 1970s, where rodent populations were variable and other food scarce, first year mortality rates varied from 0.55 to 0.92 (Powell & King 1997); in mixed podocarp and exotic forests at Pureora in the 1980s, it was 0.76 (King et al. 1996a).

Mortality rates due to disease are largely unknown, but the incidence of diseases and pathogens in British stoats was reviewed by McDonald et al. (2000a). They identified *Bartonella* sp. in 73% and *Borrelia burgdorferi* sensu lato in 22% of the 45 carcasses examined. None of 33 stoats examined in Britain between 1971 and 1986 tested positive for

Mycobacterium bovis (Anon 1987), but one of 62 stoats from an area in New Zealand with endemic tuberculosis showed tuberculous lesions (Ragg et al. 1995). Stoats can carry tularaemia and canine distemper, with unknown effects. They do not transmit *Neosporium caninum* to cattle (McAllister et al. 1999). The intermediate host of *Skrjabinogylus nasicola* in New Zealand is unknown, but circumstantial evidence suggests that stoats pick up the invasive larvae from mice (King 1991a). A comprehensive list of the ectoparasites carried by stoats has been compiled by McDonald & Larivière (in press).

Adaptation to New Zealand conditions

Erlinge (1987) pointed out an apparently regular cline in size of stoats in Europe (smaller in the north, from far northern Scandinavia to Britain, contrary to Bergmann's Rule), and showed a correlation between body size and prey size in European stoat populations. Independently, King & Moody (1982b) had already concluded that adult New Zealand stoats collected from beech forests in the 1970s had become significantly larger in average condylobasal length than their British ancestors (Mann-Whitney U-tests $P < 0.001$ in both sexes). The same comparison pooling adults from all sample areas for both countries was significant for females (Britain 44.8 ± 1.36 SD, $n=23$; New Zealand 45.7 ± 1.19 SD, $n=378$; $P < 0.001$) but marginal for males (Britain 49.6 ± 1.60 SD, $n=45$; New Zealand 50.1 ± 1.59 SD, $n=350$; $1.87 > P > 0.05$). King (1991b) suggested that New Zealand stoats should be able to offer a test of Erlinge's hypothesis, since the distribution of prey sizes in New Zealand is different (fewer small prey) than in Europe. The point for the mean body weight of stoats in New Zealand neatly extends Erlinge's correlation with a prey size index (King 1991b). Paradoxically, in a large new collection of British stoats made in 1995–97 by McDonald (1998), the mean condylobasal lengths of males and females were 51.01 ± 1.38 SD, $n=164$ and 46.99 ± 1.24 , $n=61$ respectively, not smaller than in New Zealand. New collections currently being made in New Zealand, more sophisticated modern tools for statistical analysis, and more recent data on other, previously undocumented factors that can affect body size such as early nutrition (Powell & King 1997) or intra-guild competition (Dayan & Simberloff 1994, 1998), should allow further investigation of the physical adaptations of stoats to the New Zealand habitat (McDonald & King, unpubl. data).

Significance to the New Zealand environment

Damage

The Department of Conservation predator research strategy (Murphy 1997) lists the following category A species (Molloy & Davis 1994) as potentially at risk from stoat predation: Haast tokoeka [kiwi] (*Apteryx* "Haast tokoeka"), NI brown kiwi (*Apteryx* "North Island"), Okarito brown kiwi (*Apteryx* "Okarito brown"), orange-fronted parakeet (*Cyanoramphus malherbi*), black stilt (*Himantopus novaezealandiae*), takahe (*Porphyrio mantelli hochstetteri*) and fairy tern (*Sterna nereis davisae*).

Predation has obviously been a hugely significant factor in the historic decline in New Zealand's native fauna (Innes & Hay 1991). Planning of cost-effective control operations to prevent further losses requires certain critical evidence, which has grown rapidly over the last decade. The key is to make quantitative measurements of the mortality of particular protected species, definitely due to an identified species of predator, in relation to all forms of natural mortality or failures in recruitment. This is very hard to deduce from comparative estimates of the population density of adult birds. In Fiordland, periods of high stoat numbers, such as in 1976, were not always clearly correlated with periods of high losses of takahe (*Porphyrio mantelli*) (Mills 1990), although since then stoats have been identified as a key predator of

adult takahe, and stoat control has been identified as a required management action to protect the surviving breeding stock (Crouchley 1994). Three years of regular bird counts during and after intensive stoat trapping could not demonstrate any predictable benefit to populations of common bush birds (Efford & Morrison 1991), but low intensity stoat trapping in the same valley has provided enough protection to markedly reduce stoat predation on breeding adult mohua and kaka (Department of Conservation 2000).

Techniques concentrating on measuring the effects of predation on productivity and mortality of eggs and chicks are much more likely to succeed, but have been employed only since the mid 1980's. Elliott & O'Donnell (1988) hypothesised that birds which nest in tree-holes, such as the yellowhead or mohua (*Mohoua ochrocephala*), are at particular risk from stoats, which are common in forests and are adept tree climbers. The productivity and mortality of mohua is significantly affected by predation in years of high stoat densities (Elliott 1996; O'Donnell et al. 1996), and this effect can be reversed by intensive stoat trapping (Dilks 1999). Likewise, the survival and nesting success of kaka (*Nestor meridionalis*) were known to be seriously affected by predation on eggs, chicks and nesting females (Beggs & Wilson 1991) for some time before the main culprit was shown to be the stoat (Wilson et al. 1998). Catastrophic failures in recruitment of young kiwi (*Apteryx* spp.) chicks, which are very vulnerable to predation up to the age of about 14 months (McLennan et al. 1996), are due largely to stoats. A model developed from systematic field observations concluded that "the persistence of kiwi on the mainland is now largely dependent on the development of new technology for controlling stoats" (Basse et al. 1999). Monitoring of kiwi populations has confirmed that effective local reduction in the numbers of stoats can increase productivity and survival rates of juveniles. On the Puketukutuku Peninsula on Lake Waikaremoana, the proportion of young kiwi to reach stoat-resistant size (800 g) increased from 4% to 44% in the 1995/96 and 1996/97 seasons (McLennan 1998), rising to 58% by the third year of trapping (J. McLennan unpubl. data).

Predation by stoats continues to assist the declines of several other mainland species, e.g. the yellow-eyed penguin (*Megadyptes antipodes*) (Moller et al. 1995), some burrowing seabirds (Lyver 2000), and the New Zealand dotterel (*Charadrius obscurus aquilonius*) (Dowding & Murphy 1996). In 1999 the New Zealand Government accepted the argument that an extensive state-funded campaign is required to protect endangered ground and hole nesting birds from stoats (Hackwell & Bertram 1999), and instigated a five-year programme to find more cost-effective and sustainable approaches to controlling them (Department of Conservation 2000).

Species long resident in New Zealand are especially vulnerable to predation because they have insufficient innate anti-predator behaviour compared with similar species adapted to avoid predation, e.g. black stilt compared with pied stilt (Pierce 1986), and takahe compared with pukeko (Bunin & Jamieson 1996). Large size is their only effective defence, but few of the surviving species are safe from stoats on that account (Holdaway 1999).

The conservation status of stoats in Britain and New Zealand was compared and contrasted by McDonald & Murphy (2000). In Britain, stoats have been commonly regarded as vermin at least since the 16th century. Their predation on game birds, including nesting females, makes them a pest, less serious than foxes, feral cats, mink and corvids, but more serious than polecats, rats, hedgehogs (Packer & Birks 1999) or weasels (McDonald & Harris 1999).

On the other hand, they are native to Britain, and therefore are regarded as having an intrinsic value there that they do not have in New Zealand. Stoats have no protection under UK conservation legislation, and are not being considered for it (Tapper 1999; McDonald &

Murphy 2000), but they are protected in Eire. Stoats are included in Appendix III of the Bern Convention, hence their status and exploitation is subject to consideration by signatory states.

Potentially large numbers of stoats are exposed to anticoagulant rodenticides, though the population-level effects are unknown (McDonald et al. 1998). They may also suffer from intra-guild predation from increasing fox populations in UK (Tapper 1999).

Control

There has been an explosion of new research on the control of stoats over the last decade, much more than can be cited here. For extensive summaries, see Sim & Saunders (1997), Griffiths (1999) and Department of Conservation (2000).

The great difficulty of achieving effective, long-term control of small, short-lived mammals with high annual productivity (“*r*” strategists), is that the control measure(s) must exceed the mortality rate, which in stoats is naturally high at around 70% (King 1994). Recruitment rates are variable but can also be very high, depending on the success of the previous breeding season. Because stoats are polygynous and the young females are fertilised before they leave the nest, reducing only male stoats to very low levels (e.g., in widely spaced traps) will have no effect on the young of the year, or on the next years’ population. Individual stoats can learn to become very wary of traps and resistant to capture even by intensive operations conducted over a limited area, e.g., on Maud Island (Crouchley 1994). An ideal control measure would bring the female population to very low levels before they have given birth, but is at present very difficult or, in many places, unattainable. These aspects of their population dynamics make management of stoats a severe challenge. Monitoring is essential (King 1994), but must be done in ways that ensure statistical validity (Brown & Miller 1998). Models are now available to predict the number of tracking tunnels required to detect new invasions and/or given levels of population change (Choquenot et al. in press).

Trapping Effective control operations with current technology are labour intensive, and therefore costly, so it is important to maximise trap efficacy by selecting the correct trap type, bait, layout, seasonal timing and length of operation to suit the purpose of the operation (King 1994; O’Donnell & Phillipson 1996; Griffiths 1999). Kill trapping with the Fenn trap, set in tunnels and baited with hen’s eggs or meat, is still, at present, the only proven and safe method applicable over wide areas (Dilks et al. 1996; Lawrence & O’Donnell 1999). The gin trap (Bateman 1979), banned in Britain since 1958, is still legal, but discouraged, in New Zealand.

Until recently the single most severe limitation on the area that could be covered by traps was the Animals Protection Act 1960, s.6, requiring that “*any* trap, noose or similar contrivance” must be inspected daily (King et al. 1994). However, the Animal Welfare Act 1999 s.36 specifies that “A person who, for the purposes of capturing *alive* a mammal, bird, reptile or amphibian, sets or causes to be set a trap, must inspect that trap...within 12 hours after sunrise on each day the trap remains set”. The Department of Conservation’s current interpretation of the new legislation is that, since the Fenn trap is not designed to catch animals alive, the requirement for daily inspections does not apply, so the usual practice now is to set Fenns and inspect them weekly or even monthly, as necessary. The cost-effectiveness of such continual low-level trapping is currently being trialed in several areas.

The most commonly used baits at present are hens’ eggs, which may last up to a month in cool climates, or rabbit meat. Electronically produced sound lures have produced equivocal results, and seem worth further investigation (Spurr & O’Connor 1999). Synthetic lures have been so far less successful (Clapperton et al. 1994) than natural lures made from anal scent glands (Clapperton et al. 1999). In one study the most effective lures for captive stoats were

freshly dead animals (such as mice and chickens), fresh meats and eggs. The artificial odours and flavours tested (e.g. trappers' lures, food flavours, trimethylamine and synthetic fermented egg) were all relatively unattractive (Spurr 1999). The best baits to offer may differ with location and with the natural diet of stoats in that location (L. Robbins, pers. comm.). Trappability may also vary with the density of live prey (Alterio et al. 1999; King et al. unpubl.).

Poisoning Poisoning will become a viable alternative as better delivery methods are developed (Dilks & Lawrence 2000; Spurr 2000; D. Purdey, unpubl.). For directly poisoning stoats, three toxins have been tried, with mixed results. These are 1080 (sodium monofluoroacetate), cholecalciferol and diphacinone, a second-generation anticoagulant (Miller & Elliot 1997; Spurr 1999; Department of Conservation 2000; Dilks & Lawrence 2000). All trials to date have used hens' eggs as a bait in which to carry the poison. Full instructions for using poisoned hens' eggs are given by Spurr & Hough (1997).

Stoats are vulnerable to secondary poisoning when they are exposed to dead or sub-lethally poisoned prey containing concentrations of poison, which may happen accidentally in the UK (Shore et al. 1999) but is more likely to be deliberate in New Zealand. Studies documenting the secondary effects of 1080 suggest that the routine use of 1080 to control possums and rats may have been affecting carnivore populations over several decades (Gillies & Pierce 1999; Murphy et al. 1999; Alterio 2000). More recently, brodifacoum has been widely used against rodents (Innes et al. 1995). The secondary effects of brodifacoum kill many predators (Alterio 1996; Alterio et al. 1997; Brown et al. 1998; Murphy et al. 1998b), but there are snags. Operations targetting species already at low density may produce insufficient carrion for stoats to accumulate lethal levels of poison (Gillies & Pierce 1999); and the long-term effects of accumulating a persistent poison such as brodifacoum in the ecosystem have recently been under review (Eason & Spurr 1995; Murphy et al. 1998b; Eason et al. 1999; Eason & Murphy 2000).

Other potential methods of reducing losses to stoats, such as predator proof fences (T. Day unpubl. data), repellents (Spurr 1997), fertility control (Norbury 2000), and manipulation of diseases (McDonald & Larivière in press) are under investigation. Control by habitat manipulation, e.g. the "grass wall" hypothesis to protect nesting yellow-eyed penguins (Alterio et al. 1998; Ratz 2000) proved ineffective.

28. WEASEL

Mustela nivalis vulgaris Erxleben, 1777

For a searchable database of weasel references, see King, C.M. (2000) Weasel bibliography. [online] Available: <http://www.invasive-mammals.org.nz/weasels/> [retrieved *Insert Date of Retrieval*].

The most recent previous review of the weasel literature was compiled by Sheffield & King (1994).

Description

There is still no agreement on the relationship between the two closely related species, the Palaearctic *Mustela nivalis* and the Nearctic *M. rixosa*, but *rixosa* is generally regarded as a subspecies of *M. nivalis* (van Zyll de Jong 1992; Reig 1997). Geographical variation in skull size among European weasels is extensive (Schmidt 1992).

Distribution

Besides New Zealand, weasels have also been introduced to various Mediterranean islands and the Azores (Mitchell-Jones et al. 1999). Local distribution and habitat use is determined by habitat and prey density (see below).

Food

McDonald et al. (2000b) document extensive new data on the size and diet of British weasels. British rabbits have now largely recovered from myxomatosis, and juvenile rabbits are widely available in spring, a time when rodents tend to be scarce. The male weasels surveyed had eaten a higher proportion of rabbits, especially juveniles, whereas the females still depended almost entirely on small rodents. In captive trials done with *M. n. rixosa* in enclosures, weasels showed no preferences for any particular type of prey (Derting 1989). All offered prey was attacked when encountered, as expected from the weasel's opportunistic foraging strategy, though they were less efficient in capturing mice (*Peromyscus*) than voles, and caught some species of *Microtus* more easily than others. They spent about the same time searching for, chasing and handling all prey types, but took longer to catch and kill larger prey. In a parallel European study, male weasels *M. n. vulgaris* preferred *Microtus* whereas females preferred *Clethrionomys*, but both sexes selected juvenile *Clethrionomys* as the first prey to eat when given the choice (Pekkarinen & Heikkilä 1997).

The effect of predation by weasels on populations of their prey seems to depend mainly on habitat. In the pristine deciduous forests of Bialowieza National Park in Poland, populations of weasels and rodents increased after periodic heavy seedfalls. Weasels accounted for 2–28% of the autumn standing crop of rodents, or 1.6–9.5 rodents ha⁻¹, each winter (October–April 1985–1992), depending on the phase of the post-seedfall cycle (Jedrzejewski et al. 1995). The effect of the weasels' winter predation on the subsequent population of the rodents was minor at both the top and the bottom of the cycle. When rodents were at low density, weasels were few; when rodents were at high density, they by far exceeded the predatory capacity of weasels; in either case only a small proportion of rodents were eaten by weasels. Only at an intermediate rodent density of about 20 individuals/ha could weasel predation be reckoned as heavy. The timing of the next population increase in rodents was determined by the forest trees; the rodents could not bring on the next seedfall, and weasel predation could not prevent their response to it, since by then the population growth rate of the rodents was much higher than that of the weasels.

In this forest ecosystem, the population fluctuations of both predator and prey are relatively simple and driven by periodic seedfalls, as in the similar cycles of stoats and mice in New Zealand beech forests, except that the details of the reproductive responses of weasels and stoats are different. By contrast, in non-forest habitats the population cycles of voles and lemmings are apparently driven by the internal dynamics of the much more complex three-way relationship between rodents, vegetation and small mustelids, which is still not fully understood. In parts of Fennoscandia, variations in the expected multi-annual cycles have been specifically linked to the local absence of the key predator, *M. nivalis* (Hanski et al. 1993; Hanski & Korpimäki 1995), but alternative explanations are possible (Jedrzejewski & Jedrzejewska 1996).

Weasel scent is avoided by voles, and influences their foraging decisions (Borowski 1998). Scent invokes arboreal escape response and causes reduced mobility in bank voles (Jedrzejewska & Jedrzejewski 1990; Jedrzejewski et al. 1993) affecting the distribution of some individuals for several days after a visit by a weasel.

In New Zealand, weasels are scarce and hard to study (King 1990). At Pureora Forest Park

over the five years 1983–87, only 16 weasels were collected in 24 272 Fenn trap-nights (King et al. 1996b). All came from areas of disturbed vegetation, along roadsides and in an exotic plantation where grass was thick and mice were numerous. As expected, the food items identified in the 15 guts available for analysis were all small species, mostly mice, insects, and a lizard (King et al. 1996a). Mice accounted for the majority of weasel diet, both by frequency of occurrence (72%) and by weight (64%), analysed from 28 weasels collected from Mapara and Kaharoa (Murphy et al. 1998c). Birds, lizards and invertebrates were also important. Stoats collected from the same areas ate significantly more rats and lagomorphs and fewer mice than the weasels.

On the Puketukutuku Peninsula, in Lake Waikaremoana, 11 weasels were caught in 66 000 Fenn and Conibear trap nights in 1994–96, mostly along the shoreline where mice were abundant in the thick grass and shrubs recolonising areas of old lake bed exposed by hydroelectric power works (McLennan 1997).

Social organisation and behaviour

Weasels have to extend their home ranges during periods of food shortage. In Poland the mean ranges of radio-tracked male weasels expanded from 24.2 ± 11.9 ha ($n=5$) to 117 and 216 ha ($n=2$) during a vole crash year (Jedrzejewski et al. 1995). Small rodents are usually scarce in New Zealand, so the home ranges of weasels here might need to be large most of the time. A key survival strategy of weasels in cold climates, surplus killing and caching, does not work in warmer conditions (Jedrzejewska & Jedrzejewski 1989). The consequent unfavourable energy equations for weasels in New Zealand might help to explain their general rarity here. In addition, weasels suffer from interference competition from stoats (Erlinge & Sandell 1988).

Reproduction and development

The mean litter size of weasels is lower than that of stoats (ovulation rate 7.1, range 4–11, $n = 32$; embryo count 5.7, $n = 44$, range 4–9; number of young born 6.2, range 4–8, in 17 litters) (King 1989b; McDonald 1998). On the other hand, when food is abundant (but not otherwise) female weasels can breed in the year of their birth: of 77 female weasels examined by McDonald (1998), six were pregnant, and one of these was less than six months old. By contrast, female stoats cannot produce their first litter until they are 12 months old however well fed they are.

Populations

Local populations of weasels are subject to rapid fluctuations in numbers and distribution, including frequent local extinctions, correlated with the distribution and abundance of food. At Pureora, the mean density indices for mice in four study areas in native and exotic forest ranged from 0–0.14 C/100TN over five years, but in one area after a short-lived irruption of mice (to 41.4 C/100 ha in May 1984), the density index for weasels briefly reached 1.15 C/100TN over the following summer (King et al. 1996a).

In Britain, weasels are not regarded as a serious pest by most gamekeepers, but are regularly caught in Fenn traps set primarily for stoats and Norway rats (McDonald & Harris 1999). Gamekeepers' records, a useful means of monitoring the numbers and distribution of both species, apparently show that there has been a downward trend in number of weasels caught since 1961 (Tapper 1992). Explanations considered include: a return to the lower pre-myxomatosis population density of weasels (King 1989b); the widespread use of persistent rodenticides on farmland, which can cause secondary poisoning in weasels (McDonald et al. 1998); or a consequence of the reduction in trapping effort made by the reduced national

force of gamekeepers. McDonald & Harris (1999) have concluded that the third of these explanations is the most likely one.

The common excess of males in trapped samples can be variously (or in combination) ascribed to the greater ranges of males and their higher chances of finding a trap; the lighter weight of females and their lower chances of setting off a trap; and the differences between the sexes in activity and behaviour (Buskirk & Lindstedt 1989). A sample of 38 British weasels aged by cementum analysis produced no new records for longevity; the maximum age was two (McDonald 1998). In northern countries, raptors kill many small mustelids and may affect their populations (Korpimäki & Norrdahl 1989a, b).

None of 33 weasels examined in Britain between 1971 and 1986 tested positive for *Mycobacterium bovis* (Anon 1987). American weasels may be infested with helminths, including the trematode *Alaria*, the nematodes *Capillaria*, *Filaroides*, *Trichinella*, and the cestode *Taenia* (Svendsen 1982).

Significance to the New Zealand environment

In New Zealand, weasels are much less common than stoats, and are less important as pests, except locally when they damage small populations of, e.g., Whitaker's skink (Miskelly 1997). In Europe they are listed under Appendix III of the Bern Convention, but are not protected under UK conservation legislation. They are susceptible to secondary poisoning, by warfarin (Townsend et al. 1984) and by the second-generation rodenticide brodifacoum (Alterio et al. 1997).

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