Manaaki Whenua
Landcare Research

Impact of Rabbit Control on Predator Ecology

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1. Summary

1.1 Project and Client

The Ministry of Agriculture and Fisheries (Policy Division) commissioned Landcare Research, Alexandra, to investigate the impacts of controlling rabbit populations on the ecology of wild cats and ferrets.

1.2 Objectives

- To determine the effect of rabbit control on predator population size, survival, and recruitment rates.
- To determine the effect of rabbit control on predator movements.
- To determine the effect of rabbit control on predator diet.

1.3 Methods

We monitored the behaviour of wild ferrets and cats for two years before and after rabbit numbers were reduced by 1080 poisoning on two large areas of dry tussock grassland, and on a third site where rabbit abundance remained high. Rabbit populations were monitored every 16 weeks by spotlight counts. Predator populations were monitored every 4-6 weeks by trapping, marking, and releasing animals. The movements and survival rates of 70 radio-collared ferrets and 28 radio-collared cats were measured every 3 weeks. The diet of predators was derived from scats collected from traps.

1.4 Results

- Ferret populations declined gradually over 12 months after rabbit poisoning reduced rabbit spotlight counts by 77% and 99%. We were unable to measure cat population size reliably.
- Recruitment of young ferrets was significantly reduced on the poisoned sites.
- Seven to 15% of radio-collared ferrets died from secondary poisoning after eating poisoned rabbit carcasses. A few ferrets also died from starvation 4-6 months after the poisonings. However, there were no significant differences in survival rates between sites.
- Home range size of ferrets increased from 85 to 230 ha where rabbit numbers were reduced by 99%. While most ferrets at this site remained resident, the proportion of "mobile" ferrets (i.e., those moving > 1.8 km from range centres) in the population increased from 1 of 25 to 6 of 18. Some ferrets dispersed up to 4.3 km from home range centres. For cats, treatment effects were less clear. However, three adult cats dispersed up to 9.2 km from their range centres after rabbit numbers were reduced by 99%. No obvious behavioural changes of predators were observed where rabbit declines were less pronounced or indeed where rabbit abundance remained high.
- Ferrets consumed proportionally less rabbit and significantly more skinks, geckos and invertebrates after the rabbit poisons. Diet change appeared to be greater where rabbit decline was most pronounced. There were no significant changes in cat diet.

1.5 Conclusions

- Major reductions in rabbit populations over large areas of tussock grassland supporting extreme infestations of rabbits cause ferret populations to decline. Declines are gradual because recruitment of young ferrets is reduced.
- Predator dispersal is a small to moderate risk associated with large-scale rabbit control. However, it is impossible to predict effects of dispersal on the bovine tuberculosis (Tb) status of livestock and the population dynamics of fauna already at risk of predation in areas adjacent to rabbit control operations. These predictions require a clearer understanding of the role of ferrets and cats in the epidemiology of bovine Tb, as well as their impact on "at risk" native fauna. Intuitively, however, any consequences are likely to be adverse.
- Predation rates on native fauna increase after rabbit control, at least in the short-term before predator populations decline. Two crucial questions need to be addressed: can native fauna sustain these short-term impacts?; and what are the longer-term effects on fauna of maintaining rabbit populations at low levels in the face of declining predator populations and putative changes in predator guilds?

2. Introduction

In this report, Landcare Research, Alexandra, investigates the effects of controlling rabbit populations on the ecology of wild ferrets and cats to help the Ministry of Agriculture and Fisheries (Policy Division) understand the wider ecological implications of rabbit control in New Zealand.

3. Background

Feral populations of domesticated cats and ferrets are widely distributed across pastoral areas of New Zealand where they prey primarily upon small mammals, particularly feral rabbits (Fitzgerald 1990; Lavers & Clapperton 1990). New Zealand agriculture may benefit from these predators in high rainfall areas (>700 mm) where it appears predation, in combination with drowning of young, suppresses rabbit numbers (Gibb *et al.*1978; Robson 1993). In contrast, in lower rainfall areas of the South Island's high country, rabbit populations can reach very high levels and predators do not appear to suppress their numbers to any great extent. Rabbit control, mainly by poisoning, is therefore required.

However, any benefits predators provide by suppressing rabbit numbers may be largely offset by the fact that cats and ferrets also carry bovine Tb (e.g., Ragg *et al.* 1995) and have localised impacts on protected native fauna (Daniel & Williams 1984; Pierce 1986). Bovine Tb impinges on New Zealand's capacity to trade internationally in beef, dairy and venison products. Introduced predators have also been implicated in the demise of much of New Zealand's endemic fauna. Because cats and ferrets rely primarily upon rabbits as a food source, it is pertinent to ask from a management perspective whether rabbit control may be a means of reducing predator populations, and whether this can assist Tb management and nature conservation programmes. It is possible that rabbit control may cause predators to disperse and spread Tb, and cause changes in predator diet that may increase the rate of predation on indigenous fauna.

Understanding the behavioural responses of predators to declines in rabbit numbers is particularly relevant to the possible arrival of the rabbit biological control agent, Rabbit Calicivirus Disease (RCD), in New Zealand.

4. Objectives

- To determine the effect of rabbit control on predator population size, survival, and recruitment rates.
- To determine the effect of rabbit control on predator movements.
- To determine the effect of rabbit control on predator diet.

5. Methods

5.1 Study design and site descriptions

We monitored ferret and cat behaviour before and after rabbit numbers were experimentally reduced on two large areas of pastoral habitat, and on a third site where rabbit abundance remained high. We chose sites destined for large-scale reductions in rabbit numbers by Regional Councils. In this context, the sites represented standard management units. Further, because Regional Councils seek to reduce rabbit populations by at least 90%, control operations provide potentially dramatic ecosystem disturbances that maximize the chances of producing unequivocal responses of predators. Management action therefore provided the experimentation in this study, a "research by management" approach advocated by a number of authors (Walters & Holling 1990; Nichols 1991). Given the requirement for large management units, it was beyond the resources of this study to monitor more than one control and two treatment sites. Also, because the treatment sites received different levels of rabbit control (see below), it is impossible to use inferential statistics on the treatments. The error terms in this paper relate to the sub-samples within each experimental unit, not to the variation between units. Unless otherwise stated, error terms are standard deviations.

The experiment was conducted between March 1994 and March 1996 in modified short-tussock grassland habitat in New Zealand's South Island. We chose three study sites with similar climate and vegetation: Earnscleugh (1,000 ha) and Bendigo (2,500 ha) stations in Central Otago, and Grays Hills station (6,000 ha) in the Mackenzie Basin. Each site was on pastoral properties extensively grazed by merino sheep. A large hydro-electric dam, which predators were unable to cross, separated the Earnscleugh and Bendigo sites by 24 km. The Grays Hills site was 125 km northeast of the other sites.

Sites consisted of hilly terrain (200-1,060 m above sea level) and deep gullies. Mean annual rainfall ranges from 385 to 456 mm, and mean monthly temperatures range from 3°C in July to 18°C in January. Unusually heavy snowfalls occurred in late June 1995 and snow persisted for 2-3 months. There was record rainfall in the last summer of the study (mean monthly rainfall = 115 mm cf. long-term average of 39 mm). The vegetation consists of native tussock grasses (e.g., fescue tussock and silver tussock), swards of exotic grasses (e.g., browntop and sweet vernal), herbaceous weeds (e.g., viper's bugloss, woolly mullein, hawkweeds), and scattered shrubs of sweet briar and matagouri.

5.2 Rabbit spotlight abundance and poisoning

We estimated the relative abundance of rabbits on each site about every 16 weeks. Each estimate involved the same observer counting rabbits seen on three consecutive nights under spotlight from a slow-moving vehicle driven along permanent 13-19 km transects on farm roads. The only change of observer was a permanent change between the July 1994 and October 1994 counts on Earnscleugh.

At the beginning of the study, rabbit densities on all study sites were 83-155 per km of spotlight transect; Kerr *et al.* (1987) defined rabbit densities > 40 per spotlight km as "extreme" infestation. Rabbits on Bendigo and Grays Hills were poisoned six months into the experiment (September 1994) with sodium monofluoroacetate (1080) in aerially-distributed diced carrot sown at 20–30 kg/ha at a concentration of 0.02% weight/weight. Rabbit carcasses persisted as a potential food source for several weeks, therefore we chose mid-November 1994 as the start of the food-deprivation or "post-poison" period. Rabbit numbers were not reduced on the Earnscleugh site and densities there remained "extreme", hence this site was our experimental control.

5.3 Predator population dynamics

Trapping

On each site, we baited 60-70 cage traps with 30 g of skinned rabbit meat and placed them along farm roads at 300-400 m intervals. Because of the steep terrain, it was not feasible to distribute traps evenly across the sites. Every 4-6 weeks, we set traps for four consecutive nights and predators were captured, ear tagged, some were fitted with a radio collar (see below), and released.

Factors affecting capture probability and survival

Before we could proceed with data analysis we needed to determine whether trapping and radio-collaring affected survival and capture probability of animals. To do this, we fitted a Cormack-Jolly-Seber model (Jolly 1965; Seber 1965) to the ferret mark-recapture data, stratified by study site, sex, and collar status (marked or unmarked). The model was able to detect temporary effects of marking animals on capture probability and survival. Because the data under the most general model with effects due to temporary marking, study site, sex, and collar status were sparse, tests for each effect in the presence of the other effects were carried out using contingency tables. Because capture occasions on each site did not coincide, we did not test for site effects. The contingency tables were based on partitioning the sets of "minimal sufficient statistics" under the null model according to recapture, radio-collar, or sex class at a particular capture occasion (Pollock 1981; Brownie & Robson 1983). We pooled data across classes if these tests indicated that the classes were not significantly different. Using pooled data, we fitted reduced parameter models using program MARK (White & Burnham in press) and hypotheses tested using likelihood ratio tests.

Cats are notoriously difficult to recapture (e.g., Fitzgerald & Karl 1986), as was the case in this study. There were insufficient recapture data to utilise mark-recapture analyses for cats.

Ferret abundance and recruitment

Abundance and recruitment estimates, and their associated error terms, require capture probability and survival data from marked and unmarked animals. These data were estimated by the mark-recapture program JOLLY (Pollock *et al.* 1990). Data were pooled across sexes. We ignored abundance estimates if their 95% confidence interval exceeded 30 animals. Recruitment estimates were ignored if their 95% confidence interval exceeded 20 animals. Across-site comparisons were therefore restricted to periods when reliable estimates were obtained on all three sites. We obtained reliable abundance estimates in June, July, September, and November of the pre-poison period, and in March, May, and September of the post-poison period. Reliable recruitment estimates were obtained in June, July, September, and October of the pre-poison period, and in March and May of the post-poison period. We analysed differences in abundance and recruitment estimates between sites and the pre- and post-poisoning periods in repeated measures 2-way ANOVAs with standard errors incorporated in the variance-covariance matrix.

Analysis of ferret radio telemetry survival data

Survival estimates from radio-collared animals are more reliable than those derived from mark-recapture data because radio-collar estimates are not biased by potential responses of animals to repeated trapping. Survival estimates were calculated using a modified version of the Kaplan-Meier procedure that allows for new animals to be added after the study has begun (Pollock *et al* 1989). Using MARK, we fitted six models to the radio survival data that included various combinations of sex and time effects, and their interactions. Model selection was carried out using likelihood ratio tests and Akaike's Information Criterion (AIC) (Burnham *et al*. 1995). The AIC corrects for correlation between the deviance of the data and the number of parameters in the model, and is a measure of the models departure from truth. We did not radio-collar enough cats to produce reliable survival estimates.

5.4 Secondary poisoning

We collected nine ferrets and two cats that died within 50 days after the poison bait was applied, and assayed their tissues for 1080 residue. We considered that animals that died after that time were unlikely to have died from secondary poisoning. Retrieved animals were frozen to -18°C within 8 hours of collection to prevent further breakdown of 1080 in their tissues. At a later date, a 10–50 g sample of frozen leg muscle was removed from each animal and analysed. The assay for determining 1080 concentrations in tissue was based on the procedures of Ozawa & Tsukioka (1987, 1989) using gas chromatography with electron capture detection. This technique had a statistically accurate limit of quantification of 0.005 μg/g. Concentrations of 1080 below this level could be detected but not accurately quantified.

5.5 Predator movements

We fitted 70 ferrets (20 on Earnscleugh, 23 on Bendigo, 27 on Grays Hills) with a radio transmitter and mortality sensor, attached to a rubber-coated brass collar (Sirtrack Ltd, Havelock North, New Zealand) that also acted as the antenna. The maximum signal range to an aircraft was 3 km and battery life was 10 months. Most radio-collared ferrets were adults (i.e., > 9 months old) or close to adulthood. Sexual maturity was determined by the external condition of the genitalia, and by measuring body mass (Moors & Lavers 1981). We only collared ferrets at or near adult body weight (minimum weight of collared females = 630 g; males = 930 g).

We fitted 28 cats (10 on Earnscleugh, 7 on Bendigo, 11 on Grays Hills) with a radio transmitter and whip antenna attached to a nylon webbed collar (Sirtrack Ltd). The maximum signal range to an aircraft was 20 km. Battery life was 14 months. Obvious differences in body weight enabled us to differentiate between juveniles, sub-adults, and adults. We collared sub-adult (4 females, minimum weight = 1390 g; and 3 males, minimum weight = 1830 g) and adult cats.

We tracked predators during the day from a Robinson R22 helicopter equipped with antennae and radio receivers. We recorded locations using a Global Positioning System (GPS) and by marking animal positions on topographic maps. One daytime location was obtained every 7-34 days ($\bar{x} = 19$ days) per animal for 38 male and 32 female ferrets, and for 13 male and 15 female cats.

We estimated home range using the 100% minimum convex polygon (MCP) method (Southwood 1966), which is relatively robust with low sample sizes compared with other analytical techniques (Harris *et al.* 1990). The MCPs include outlying locations, which were important for our study because we anticipated greater movements of predators after reductions in their primary prey.

The minimum number of locations required to describe home range size adequately was determined by plotting the mean cumulative home range size (expressed as a percentage of the total area) against the number of locations for both ferrets and cats; the percentage stabilized from about 10 locations onwards.

We classified ferrets as "resident" or "mobile". Residents remained within discrete home ranges and did not venture far from their home range centre (determined as the harmonic mean centre (Dixon & Chapman 1980; Spencer & Barrett 1984), whereas mobile ferrets moved > 1.8 km from their range centre, some not returning within the study period. The 1.8 km was based on Fig. 4 (see below), which shows nearly all ferret locations during the pre-poison period on Grays Hills were < 1.8 km from the range centre. Cats were also classified as resident or mobile, but all mobile cats dispersed > 4 km from their range centre, and did not return within the study period. Fisher's exact test was used to compare the proportion of mobile to resident animals.

We tested dependent variables for normality and equality of variances and, where necessary, data were log-transformed for parametric testing. Where analysis of variance (ANOVA) tests are indicated in the results, multiple comparisons were made using the Student Newman-Keuls method.

5.6 Predator diet

We collected predator scats from traps only on the first night an animal was caught during a given trapping session. This reduced the chance of scats containing bait. Fewer cats were caught than ferrets, and cats tended to defecate in traps less often than ferrets. Therefore the number of cat scats collected from traps was supplemented by collecting fresh cat scats found at random throughout each site. We collected a total of 999 ferret scats, of which 79% contained identifiable prey. The remainder contained mainly mucous and were not included in the analysis. Of the 159 cat scats collected, 97% contained identifiable prey.

We soaked scats in water over night, washed them into a 250 μm sieve, and macroscopically sorted them into taxa *viz.* rabbit, skink, gecko, bird, invertebrate, hedgehog, and mouse. We determined the minimum number of skinks and geckos per scat by counting the number of left and right front or hind feet. It was not possible to count accurately the number of individuals for other prey taxa.

We divided the post-poison period into two parts: the initial eight month period after the poison operation from early November 1994 to June 1995; and the 11 month period from July 1995 to May 1996. We calculated the amount of a given prey in the diet as the number of scats containing that taxon, expressed as a percentage of the total number of scats containing prey (i.e., percentage frequency of occurrence). Differences in diet between sites and times were tested using multi-way contingency tables. Ferret diet was analysed separately for each sex. For cats, the sexes were combined because of small sample sizes and because a number of scats were from cats of unknown sex.

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6. Results

6.1 Effects of poisoning on rabbit abundance

There was a 76.5 ± 4.2 % (± SE) decline in rabbit abundance on Bendigo, and a 99.4 ± 0.2 % decline on Grays Hills (Fig. 1). The poison was less successful on Bendigo because of technical difficulties encountered during the baiting.

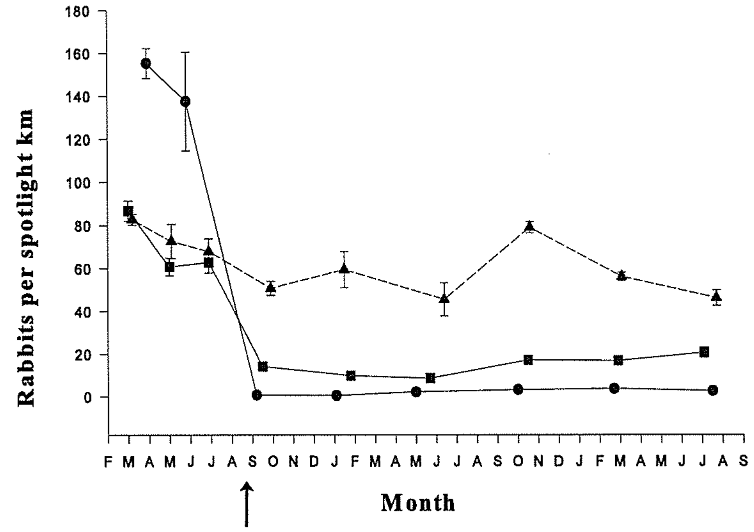

Fig. 1 Numbers of rabbits counted under spotlight. ● = Grays Hills. ■ = Bendigo. ▲ = Earnscleugh. Error bars ± 1 SE of the mean. Arrow indicates rabbit poisoning on Grays Hills and Bendigo.

6.2 Predator population dynamics

Factors affecting capture probability and survival

Trapping and radio-collaring did not appear to bias ferret population parameters derived from the mark-recapture data. There was no evidence of a temporary marking effect ($\chi_{16}^2 = 17.30$, $p = 0.36$) or of a collar effect ($\chi_{28}^2 = 25.59$, $p = 0.60$) on capture probability and apparent survival of ferrets. However, there was very strong evidence of an effect due to sex on capture probability and apparent survival ($\chi_{36}^2 = 158.76, p < 0.0001$) (see Fig. 3).

Ferret abundance

Ferret numbers on Earnscleugh declined from July to November, increased during the following recruitment period between January and May, and declined again thereafter (Fig. 2). Reliable estimates of ferret numbers on Earnscleugh were not available beyond then. Compared with Earnscleugh, the other sites contained more ferrets before the rabbit poisonings. Numbers similarly declined from May to November, however, unlike Earnscleugh, ferret numbers did not increase again during the following recruitment period. There were marked increases in ferret numbers on Bendigo and Grays Hills after record rainfall during the final summer of the experiment.

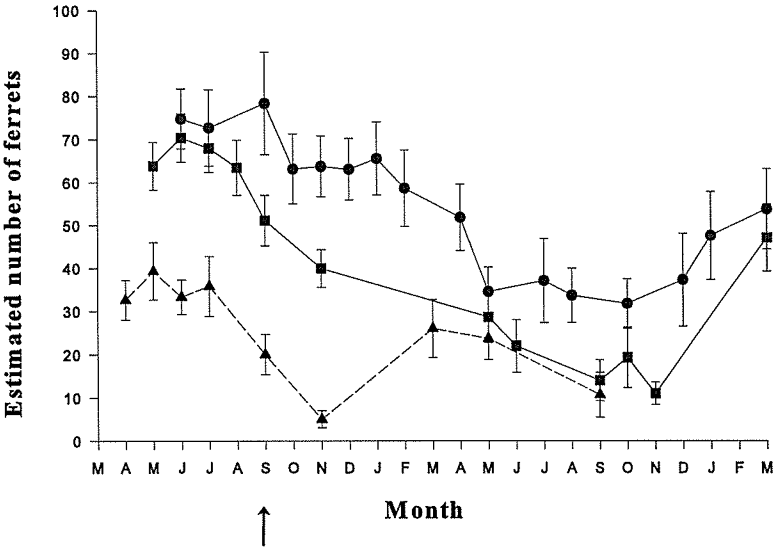

Fig. 2 Reliable estimates of ferret numbers. ● = Grays Hills. ■ = Bendigo. ▲ = Earnscleugh. Error bars ± 1 SE of the mean. Arrow indicates rabbit poisoning on Grays Hills and Bendigo.

Across-site comparisons of ferret abundance were restricted to periods when reliable estimates were obtained on all three sites (Table 1). Proportional declines in abundance on Grays Hills and Bendigo between these periods were greater than the decline on Earnscleugh. Significant differences were detected at the 10% significance level ($F_{1,1} = 39.47$, $P = 0.100$). Given the lack of replication in this study, and only one degree of freedom of the variance, very large treatment differences would have been required to detect differences at the 5% significance level.

Table 1 Estimated numbers of ferrets in the effective trapping area on each study site before and after rabbit poisoning on Grays Hills and Bendigo.

Site	Before poisoning June, July, September, November)	After poisoning (March, May, September)
	Mean (SE)	Mean (SE)
Grays Hills	72.39 (4.45)	40.86 (3.08)
Bendigo	57.37 (2.70)	31.65 (5.46)
Earnscleugh	23.52 (2.37)	20.11 (3.25)

Ferret recruitment

Across-site comparisons of ferret recruitment were restricted to periods when reliable estimates were obtained on all three sites (Table 2). Recruitment increased on Earnscleugh compared with little to moderate declines on the other sites. Significant differences were detected at the 10% significance level ($F_{1,1} = 52.53$, $P = 0.087$).

Table 2 Estimated numbers of new ferrets recruited on each study site before and after rabbit poisoning on Grays Hills and Bendigo.

Site	Before poisoning (June, July, September, October)	After poisoning (March, May)
	Mean (SE)	Mean (SE)
Grays Hills	4.89 (2.90)	4.52 (3.33)
Bendigo	2.44 (1.22)	0.69 (3.10)
Earnscleugh	0.45 (0.55)	7.32 (2.46)

Ferret survival

Despite the fact that some ferrets died from starvation 4-6 months after rabbit poisoning on Bendigo and Grays Hills, ferret survival on Earnscleugh (where rabbit numbers remained high) was lower. Annual survival on Earnscleugh was only 19.0% (SE = 5.4, $\bar{x}$ = 12 animals), while on Bendigo it was 47.0% (SE = 9.5, $\bar{x}$ = 18 animals) and on Grays Hills it was 54.0% (SE = 8.4, $\bar{x}$ = 22 animals) (Fig. 3).

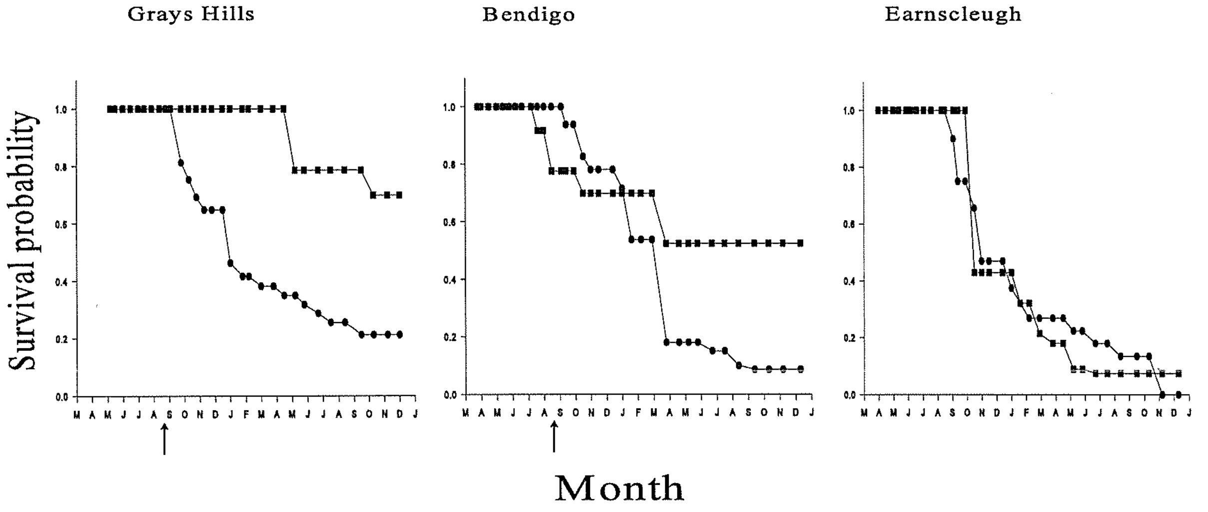

Fig. 3 Survival rates of male (●) and female (■) ferrets. Arrows indicate rabbit poisoning.

For all three sites, a pre-poison, post-poison, male, and female separation of survival data appeared necessary in the minimal model because male survival was less than female survival. To test for a site effect we used the pre- and post-poison survival estimates (weighted for the inverse of the sampling variance) in a repeated measures 2-way ANOVA with standard errors incorporated in the variance-covariance matrix, carried out separately for each sex. In neither case could site account for apparent differences in survival rates over time (males, $P = 0.261$; females, $P = 0.518$).

Based on survival rates, males have an estimated life-span of 309 days beyond their age at capture. Females have a longer life-span of 802 days beyond their age at capture.

6.3 Secondary poisoning

Seven to 11% (minimum and maximum estimates, $n = 28$) of radio-collared ferrets on Bendigo and 8-15% ($n = 26$) of ferrets on Grays Hills, apparently died from secondary poisoning, presumably by scavenging poisoned rabbit carcasses. No radio-collared cats died from secondary poisoning during the study, although we have observed it elsewhere (unpubl. data).

6.4 Predator movements

Ferrets

Home range: We determined the position of each radio-collared ferret on at least 10 occasions. The maximum number of locations was 30 and the average 17.0 ± 0.7 (± SE). Average home range size for ferrets was calculated for the pre- and post-poison periods on each site (Table 3). Home ranges (including those of ferrets monitored only during the pre- or post-poison period) nearly tripled in size during the post-poison period on Grays Hills where rabbit populations had been reduced by 99%, but did not change at the other treatment site where rabbits remained in low numbers, or at the non-treatment site where rabbit numbers remained high (2-way ANOVA: site effect, $F_{2,68} = 7.56$, $P = 0.001$; poison-period effect, $F_{1,68} = 1.54$, $P = 0.218$; site x poison-period interaction, $F_{2,68} = 5.00$, $P = 0.009$).

Table 3 Average home range size (ha) of ferrets before and after rabbit poisoning.

Site	Before poisoning		After poisoning	
	Mean (SD)	n	Mean (SD)	n
Grays Hills	85 (51)	19	230 (202)	12
Bendigo	70 (32)	18	67 (22)	6
Earnscleugh	71 (34)	13	61 (39)	5

Distance from range centre: Ninety percent of ferret locations from the control and Bendigo populations remained within 1 km of the range centres for the entire study, as was the case before poisoning on Grays Hills (Fig. 4). However, on Grays Hills we recorded locations up to 4.3 km from the range centre from February 1995 onwards, 5 months after the rabbit poisoning.

Proportion of resident and mobile animals: The majority of ferrets on all study sites were residents. The remainder made occasional forays or dispersed > 1.8 km from their range centre (mobiles). For the control and Bendigo sites, there were no differences between the pre- and post-poison periods in the proportion of mobile to resident ferrets (Table 4; $\chi^2_1 = 0.11$, $P = 1.000$ for the control site; $\chi^2_1 = 1.33$, $P = 0.539$ for the Bendigo site). On Grays Hills, the proportion of mobiles to residents was greater after rabbit control ($\chi^2_1 = 6.63$, $P = 0.015$). Two females of the 6 mobile ferrets on Grays Hills made small excursions from their home ranges after poisoning, and one returned 20-75 days later and the other 90-130 days later.

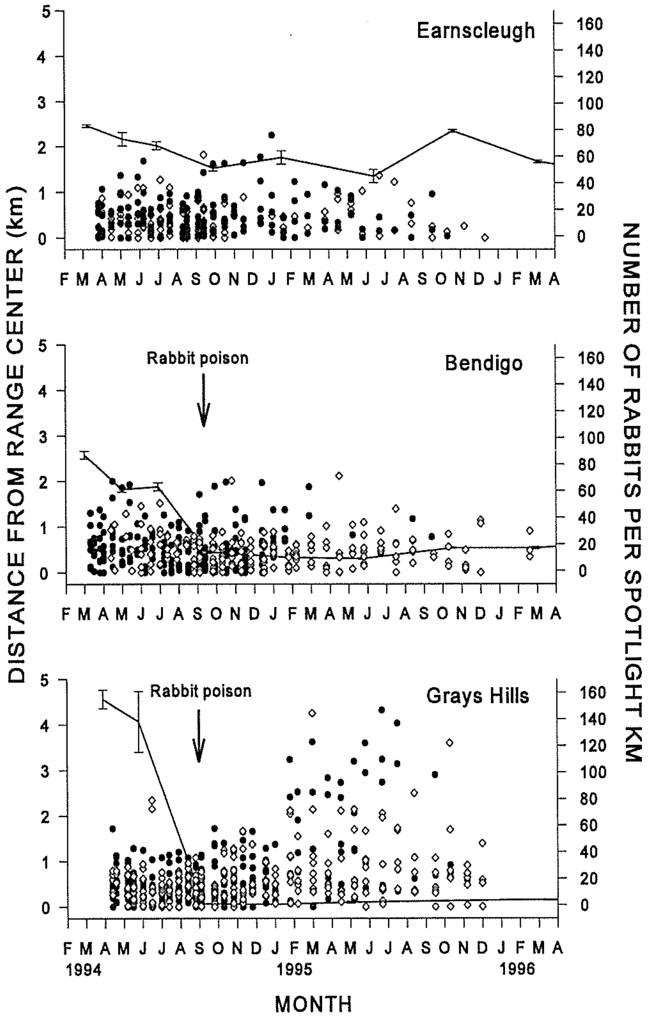

Fig. 4 The distance of all ferret locations from their respective home range centres during each radio tracking period. ● = males. ◇ = females. Solid line = rabbit spotlight counts as in Fig. 1.

Table 4. Number of radio-collared ferrets that were 'mobile' (see text). Pre-p = pre-poison. Post-p = post-poison.

	Earnscleugh		Bendigo		Grays Hills	
	Pre-p	Post-p	Pre-p	Post-p	Pre-p	Post-p
No. Ferrets	14	9	23	13	25	18
No. 'Mobiles'						
Males	0	1	1	1	0	3
Females	1	0	0	1	1	3
Total	1	1	1	2	1	6

Two mobile males (AM1426 and AM1401) dispersed up to 4.3 km from their range centres to areas outside the study site that contained more rabbits (D. Maxwell, pers. comm.) (Fig. 5A, 5B). Adult male 1401 returned 90-195 days later, but the fate of AM1426 is unknown because its transmitter expired. Data collection was curtailed for the other 2 mobile ferrets (AF1666 and AM1405) because 1 slipped its collar and the other died (Fig. 5A, 5B). There was no evidence of dispersal from the control or Bendigo sites.

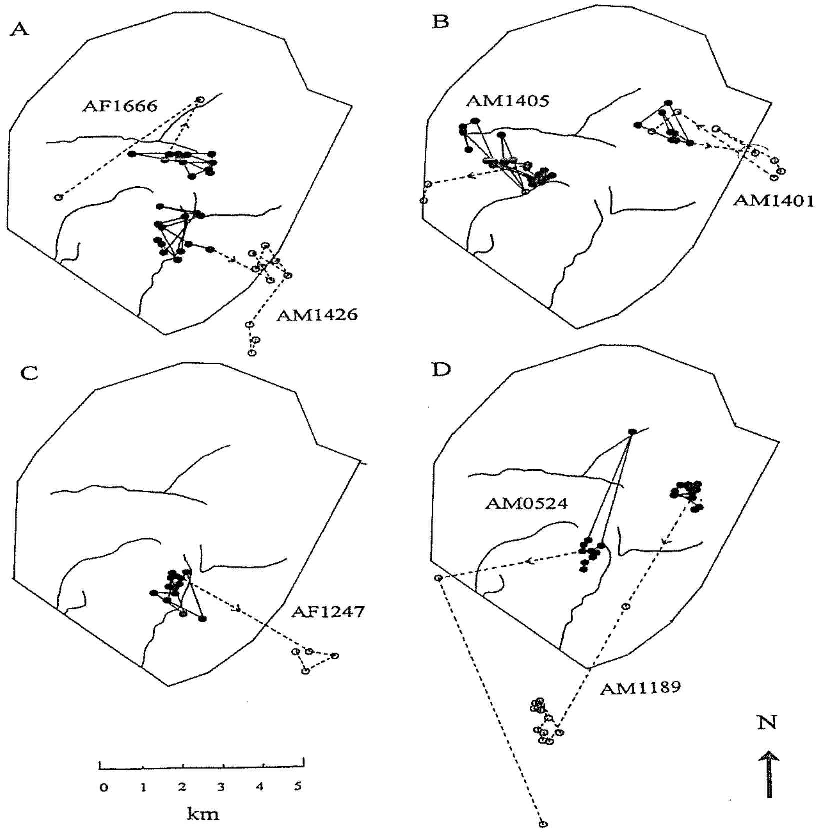

Fig. 5 Consecutive movements of four ferrets (A & B) and three cats (C & D) on Grays Hills. Study site boundary, major gullies, pre-poison locations (●), and post-poison locations (○) are indicated. The direction of movement in the post-poison period is indicated by an arrow head.

Cats

Home range: We determined the position of each radio-collared cat on at least 10 occasions. The maximum number of locations was 26 and the average 17.1 ± 1.0 (± SE). Home ranges of cats (excluding 3 dispersing subadults, see below) were averaged for the pre- and post-poison periods on each study site (Table 5). Rabbit poisoning had no effect on home range size, nor were there site or site x poison-period effects (2-Way ANOVA: poison-period, $F_{1,25} = 0.51$, $P = 0.485$; site, $F_{2,25} = 0.98$, $P = 0.391$; site x poison-period, $F_{2,25} = 0.46$, $P = 0.636$). However, the power of the test was low because the data were highly variable and the sample sizes small.

Table 5 Average home range size (ha) of cats before and after rabbit poisoning.

Site	Before poisoning		After poisoning	
	Mean (SD)	n	Mean (SD)	n
Grays Hills	155 (140)	7	497 (903)	8
Bendigo	1250 (2515)	5	291 (388)	3
Earnscleugh	179 (212)	7	124 (79)	4

Distance from range centre: Most cats remained within 4 km of their range centres for the duration of the study. However, within 2 months of initial capture, 3 subadult cats (2 males and 1 female) dispersed up to 15.3 km from their range centres on the control and Bendigo sites. At Grays Hills, 3 adults dispersed up to 9.2 km from their range centres (Fig. 5C, 5D above) to areas with higher rabbit densities (D. Maxwell, pers. comm.), 1-7 months after rabbit control. The transmitters of these 3 adults eventually expired, but at least 1 cat (AM1189) appeared to settle outside the study area. These 3 cats had been relatively sedentary before rabbit control, occupying well-defined home ranges.

Proportion of mobile and resident animals: For each site, the proportion of mobile to resident cats did not differ between the pre- and post-poison periods (control, $\chi^2_1 = 0.01$, $P = 1.000$; Bendigo, $\chi^2_1 = 1.11$, $P = 1.000$; and Grays Hills, $\chi^2_1 = 3.69$, $P = 0.100$). Excluding subadults (because of a strong innate tendency to disperse, independent of prey abundance), the only mobile cats were observed at Grays Hills after rabbit control.

6.5 Predator diet

Ferrets

Before the rabbit poisonings, 80-100% of ferret scats from each site contained rabbit. On the treatment sites, most of the diet still consisted of rabbit for 4-6 weeks after the poisons, which was presumably mostly carrion. As the availability of carrion declined, the diet changed to secondary prey species (Fig. 6). Secondary prey was mainly common skinks and geckos, birds, hedgehogs, mice and invertebrates. Occasional prey included rats, weasels, and possums. Invertebrates varied considerably between scats and seasons. The most common invertebrates were grasshoppers (Orthoptera) and porina moth larvae (Lepidoptera). There was usually only one or two invertebrates found in each scat, however some scats contained considerable numbers. Less common taxa were blow flies (Diptera), earwigs (Dermaptera), moths (Lepidoptera), large weta (Orthoptera), grass beetles (Coleoptera), and spiders (Aranae). There were significant changes in the frequency of skinks (χ_4=17.28, P=0.002), geckos (χ_4=12.26, P=0.016) and invertebrates (χ_4=23.30, P<0.0005) in the diet, which were unrelated to sex. A minimum of 19 skinks was found in one scat after the poisons. The diet did not significantly change on the Earnscleugh site.

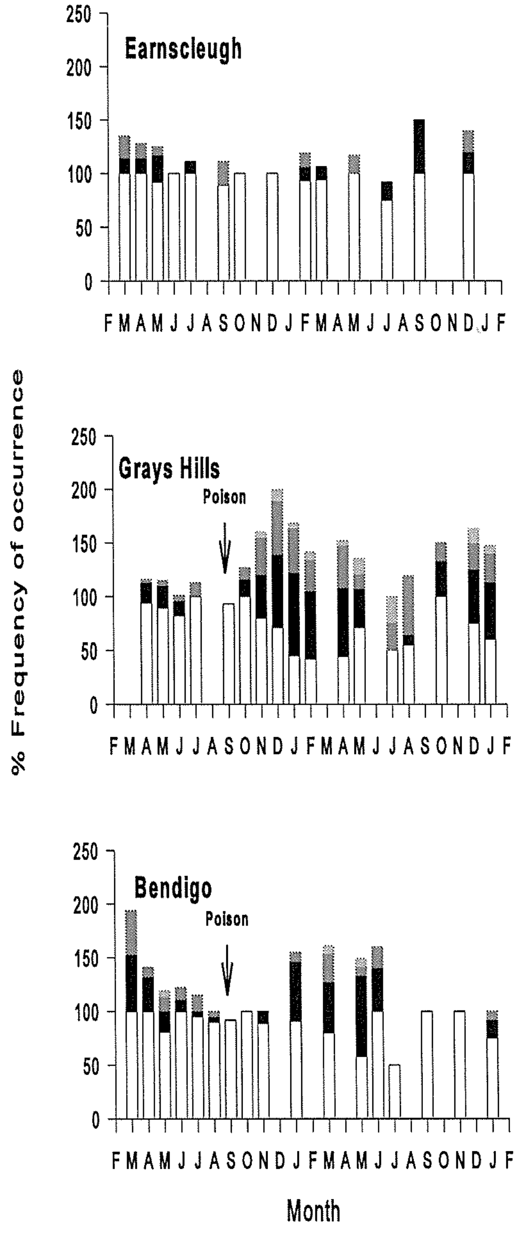

Fig. 6 The main food items in the diet of ferrets. Open bars = rabbit, black = lizard, dark grey = invertebrate, light grey = hedgehog.

Cats

Cat scats contained a greater proportion of secondary prey before the rabbit poisonings (e.g., up to 69% skinks) compared to ferrets (up to 25% skinks). Rabbit occurred in 94-100% of scats before the poisons, with birds and skinks occurring frequently in the diet, and occasionally mice, hedgehogs, geckos and invertebrates. After the rabbit poison on Grays Hills, there was a trend for more secondary prey and less rabbit in the diet, but this was not significant ($P > 0.05$). A minimum of 35 skinks was found in one scat after the poisons. One cat consumed considerable amounts of mushroom on several occasions.

7. Discussion

7.1 A cautionary note

We stress that the conclusions from this work are qualitative. Without replication of the experiment, we cannot reliably determine the power and therefore the probability of predators' responses to rabbit control. We therefore do not know the extent to which observed changes in predator behaviour were influenced by the rabbit control treatments or by inherent differences between sites. The conclusions about rabbit control effects are, by necessity, weakly inferred.

Moreover, the conclusions are relevant only to major reductions in rabbit populations over large areas of tussock grassland supporting extreme infestations of rabbits. Predator-prey relationships are likely to differ in wetter, lowland areas of New Zealand (e.g., Robson 1993). Similar experiments need to be conducted in the lowlands.

7.2 Predator population dynamics

Ferret numbers gradually declined over 12 months on the two sites subjected to rabbit control because numbers failed to increase during the recruitment period between January and May. However, this effect was short-lived as ferret numbers recovered during the following recruitment period after record summer rainfall. Declines in predator numbers after rabbit control have been observed elsewhere in New Zealand using mark-recapture techniques (Pierce 1987) and spotlight counts (Norbury & McGlinchy 1996).

The abundance of primary prey affects the population dynamics of a number of predator species around the world, mainly by reducing recruitment (e.g., Macpherson 1969; Mech 1977; Ward & Krebs 1985; Zabel & Taggart 1989; White & Ralls 1993). Failed recruitment appeared to be the main cause of ferret declines after rabbit poisoning in this study, and is the most likely reason why ferret declines were gradual and not sudden.

7.3 Predator movements

Across all study sites and throughout the study, only a minority of ferrets and cats were mobile. However, most ferrets on Grays Hills expanded their home range size after a 99% decline in rabbit numbers, and proportionally more became mobile. The home range sizes of cats were more variable than those of ferrets but, because of low sample sizes, we could only weakly infer that the three adult cats that dispersed from Grays Hills did so in response to dramatic declines in their primary prey. No ferrets or adult cats dispersed from the study sites where declines in primary prey were less pronounced or indeed where primary prey remained abundant. Unless our results reflect some unexplained peculiarity of the Grays Hills site, we believe that gross changes in predator movements occur only after very large reductions in numbers of their primary prey; smaller reductions cause little or no change. This explanation is supported by the absence of any gross changes in adult predator behaviour at any study site during the 6 months before the treatments were imposed.

Most of the predator dispersals occurred during late summer and autumn, 5-7 months after the rabbit poisoning, which suggests that food did not become critically low until that time. Delayed dispersal also has been shown for lynx in response to natural declines in snowshoe hares (Poole 1994). Summer and autumn may be critical periods of primary prey availability in our study area because survival of young rabbits in the nest (the preferred prey, especially of ferrets) is usually lowest during this period (Gibb *et al.* 1985).

7.4 Predator diet

Ferrets significantly changed their diet to lizards and invertebrates about two months after rabbit control. Diet changes appeared to be greater where rabbit control was most successful. The inherently more diverse diet of cats may have partly obscured any diet changes after the rabbit poisonings. Other work in New Zealand also has shown the composition of predator diet to be largely a function of rabbit density (Mills 1994; Pierce 1987; Norbury & Murphy 1996). Predator diet changes after rabbit declines are corroborated by increased predation of birds' nests in braided riverbeds during the breeding season immediately after rabbit poisonings (Pierce 1987; Rebergen 1993; Sanders unpubl. data).

On their own, diet changes of individual predators (i.e., the functional response) are not sufficient to predict predator impacts on native fauna. Diet changes need to be combined with the population response of predators (i.e., the numerical response) to determine whether overall predation rates on native fauna increase, decrease, or remain unchanged. Only then can one estimate the proportion of a prey population that is taken by predators. While we detected a decline in ferret numbers after rabbit control, we are unable to calculate changes in predation rates on native fauna without more detailed information. Even then, further information is required on the rate of recruitment of fauna in the absence of predation. Clearly, these are difficult parameters to measure in the field. Based on available information, Norbury & Murphy (1996) were unable to predict the likely impacts of rabbit declines on native fauna.

A more straight-forward way of measuring the indirect effects of rabbit control on native fauna is to compare key population parameters of fauna with and without rabbit control. We made some attempt at this in our study by recording the numbers of pipits, skylarks, quail, and chukar along fixed transects. We found no significant change in abundance for any species before and after the rabbit poisonings (unpubl. data).

Predator impacts research needs to separate short- and longer-term effects. Pierce (1987), Rebergen (1993), Sanders (unpubl. data), and this study, showed that at least in the short term (i.e., 2-10 months after rabbit poisoning) predator impacts on native fauna are likely to increase because predator diet shifts occur more rapidly than declines in predator numbers. Longer-term impacts are harder to predict because it depends on the numerical response of predators and the possibility of changes in predator guilds. Based on available evidence from tussock grasslands, semi-improved pastures, and open forest valleys, stoats or ship rats are likely to increase in abundance after population declines of most rabbit predator species such as ferrets and cats (Norbury & Murphy 1996). The overall effect on native fauna is unknown, but early indications are that stoats and rats are more serious conservation pests than ferrets and cats.

7.5 Management implications

Major reductions in rabbit populations over large areas of tussock grassland supporting extreme infestations of rabbits appears to reduce ferret populations. While some of the reasons ferret numbers declined took effect immediately (i.e., secondary poisoning) or within 7 months (i.e., starvation and dispersal), the main reason ferrets declined appeared to be failed recruitment. Because ferrets are seasonal breeders, population declines were gradual.

Some ferrets dispersed up to 4.3 km from home range centres. Rabbit population declines also may have caused some adult cats to disperse 4-9 km from home range centres. This increased dispersal is potentially important because some ferret populations, in particular, have high rates of bovine Tb infection. Depending on the extent to which ferrets are capable of spreading bovine Tb among themselves, and to other wildlife and domestic stock, these dispersal events could increase the rate of spread of the disease beyond the boundaries of rabbit control operations. However, because the two Tb-infected areas in New Zealand that contain extreme rabbit infestations are very large (approx. 13,000 and 21,000 km^2), most induced dispersal of ferrets will be within infected areas. Induced dispersal of hungry ferrets and cats may also impose additional (and as yet unquantified) predation pressure on native fauna adjacent to rabbit control areas.

There is clear evidence that predation rates on native fauna increase, at least in the short term, after rabbit control. However, there are two crucial questions that need addressing: can fauna sustain these short-term impacts?; and what are the longer-term impacts on fauna? There has been no attempt to address these questions in New Zealand. Landcare Research has recently begun some preliminary work, funded by the Foundation for Research, Science and Technology.

8. Conclusions

- There is increasing evidence that major reductions in rabbit populations over large areas of tussock grassland supporting extreme infestations of rabbits cause ferret populations to decline. Declines are gradual because recruitment of young ferrets is reduced.
- Predator dispersal is a small to moderate risk associated with large-scale rabbit control. However, it is impossible to predict effects of dispersal on the Tb status of livestock and the population dynamics of fauna already at risk of predation in areas adjacent to rabbit control operations. These predictions require a clearer understanding of the role of ferrets and cats in the epidemiology of bovine Tb, as well as their impact on "at risk" native fauna. Intuitively, however, any consequences are likely to be adverse.
- There is clear evidence that predation rates on native fauna increase, at least in the short-term, after rabbit control. However, two crucial questions need to be addressed: can native fauna sustain these short-term impacts?; and what are the longer-term effects on fauna of maintaining rabbit populations at low levels in the face of declining predator populations and putative changes in predator guilds?

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10. References

Brownie, C.; Robson, D.S. 1983: Estimation of time-specific survival rates from tag-resighting samples: a generalization of the Jolly-Seber model. *Biometrics 39:* 437-453.

Burnham, K.P.; White, G.C.; Anderson, D.R. 1995: Model selection strategy in the analysis of capture-recapture data. *Biometrics 51:* 888-898.

Daniel, M.J.; Williams, G.R. 1984: A survey of the distribution, seasonal activity and roost sites of New Zealand bats. *New Zealand journal of ecology 7:* 9-25.

Dixon, K.R.; Chapman, J.A. 1980: Harmonic mean measure of animal activity areas. *Ecology 61:* 1040-1044.

Fitzgerald, B.M. 1990: House cat. *In:* King, C.M. *ed.* The handbook of New Zealand mammals. Auckland, Oxford University Press. Pp. 330-348.

Fitzgerald, B.M.; Karl, B.J. 1986: Home range of feral house cats (*Felis catus* L.) in forest of the Orongorongo Valley, Wellington, New Zealand. *New Zealand journal of ecology 9:* 71-81.

Gibb, J.A.; Ward, C.P.; Ward, G.D. 1978: Natural control of a population of *rabbits, Oryctolagus cuniculus* (L.), for ten years in the Kourarau enclosure. *Department of Industrial and Scientific Research bulletin 223.* 89 p.

Gibb, J.A.; White, A.J.; Ward, C.P. 1985: Population ecology of rabbits in the Wairarapa, New Zealand. *New Zealand journal of ecology 8:* 55-84.

Harris, S.; Cresswell, W.J.; Forde, P.G.; Trewhella, W.J.; Woollard, T.; Wray, S. 1990: Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. *Mammal review 20:* 97-123.

Jolly, G.M. 1965: Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika 52:* 225-247.

Kerr, I.G.C.; Williams, J.M.; Ross, W.D.; Pollard, J.M. 1987: The classification of land according to degree of rabbit infestation in Central Otago. *Proceedings of the New Zealand Grassland Association 48:* 65-70.

Lavers, R.B.; Clapperton, B.K. 1990: Ferret. *In:* King, C.M. *ed.* The handbook of New Zealand mammals. Auckland, Oxford University Press. Pp. 320-330.

Macpherson, A.H. 1969: The dynamics of Canadian arctic fox populations. Canadian Wildlife Service Report Series No. 8. 52 p.

Mech, L.D. 1977: Productivity, mortality, and population trends of wolves in northeastern Minnesota. *Journal of mammalogy 58:* 559-574.

Mills, R.G. 1994: Rabbit predators in the semi-arid high country of the South Island of New Zealand. Masters thesis, Lincoln University, Lincoln (unpublished).

Moors, P.J.; Lavers, R.B. 1981: Movements and home range of ferrets *(Mustela furo)* at Pukepuke Lagoon, New Zealand. *New Zealand journal of zoology 8:* 413-423.

Nichols, J.D. 1991: Science, population ecology, and the management of the American black duck. *Journal of wildlife management 55:* 790-799.

Norbury, G.; McGlinchy, A. 1996: The impact of rabbit control on predator sightings in the semi-arid high country of the South Island, New Zealand. *Wildlife research 23:* 93-97.

Norbury, G.; Murphy, E. 1996: Understanding the implications of rabbit calicivirus disease for predator-prey interactions in New Zealand. Landcare Research Contract Report LC9596/61 (unpublished) 28 p.

Ozawa, H.; Tsukioka, T. 1987: Gas chromatographic determination of sodium monofluoroacetate in water by derivatization with dicyclohexylcarbodiimide. *Analytical chemistry 59:* 2914-2917.

Ozawa, H.; Tsukioka, T. 1989: Determination of monofluoroacetate in soil and biological samples as the dichloroanilide derivative. *Journal of chromatography 473:* 251-259.

Pierce, R.J. 1986: Differences in susceptibility to predation during nesting between pied and black stilts (*Himantopus* spp.). *Auk 103:* 273-280.

Pierce, R.J. 1987: Predators in the MacKenzie Basin: their diet, population dynamics, and impact on birds in relation to the abundance and availability of their main prey (rabbits). Report for the Wildlife Service, Department of Internal Affairs (unpublished). 110 p.

Pollock, K.H. 1981: Capture-recapture models allowing for age-dependent survival and capture rates. *Biometrics 37:* 521-529.

Pollock, K.H.; Winterstein, S.R.; Bunck, C.M.; Curtis, P.D. 1989: Survival analysis in telemetry studies: the staggered entry design. *Journal of wildlife management 53:* 7-15.

Pollock, K.H.; Nichols, J.D.; Brownie, C.; Hines, J.E. 1990: Statistical inference for capture-recapture experiments. *Wildlife monographs No. 107,* 97 pp.

Poole, K.G. 1994: Characteristics of an unharvested lynx population during a snowshoe hare decline. *Journal of wildlife management 58:* 608-618.

Ragg, J.R.; Moller, H.; Waldrup, K.A. 1995: The prevalence of bovine tuberculosis (*Mycobacterium bovis*) infections in feral populations of cats (*Felis catus*), ferrets (*Mustela furo*) and stoats (*Mustela erminea*) in Otago and Southland, New Zealand. *New Zealand veterinary journal 43:* 333-337.

Rebergen, A.L. 1993: Factors influencing the predation of eggs and young of the banded dotterel (*Charadrius bicinctus*) on some braided rivers in the Mackenzie Basin. Diploma of Wildlife Management thesis, University of Otago, Dunedin (unpublished).

Robson, D.L. 1993: Natural mortality of juvenile rabbits (*Oryctolagus cuniculus*) in north Canterbury, New Zealand. *Wildlife research 20:* 815-831.

Seber, G.A.F. 1965: A note on the multiple-recapture census. *Biometrika 52:* 249-259.

Southwood, T.R.E. 1966: Ecological methods: with particular reference to the study of insect populations. London, Methuen & Co. Ltd.

Spencer, W.D.; Barrett, R.H. 1984: An evaluation of the harmonic mean method for evaluating carnivore activity areas. *Acta Zoologica Fennica 171:* 255-259.

Walters, C.J.; Holling, C.S. 1990: Large-scale management experiments and learning by doing. *Ecology 71:* 2060-2068.

Ward, R.M.P.; Krebs, C.J. 1985: Behavioral responses of lynx to declining snowshoe hare abundance. *Canadian journal of zoology 63:* 2817-2824.

White, G.C.; Burnham, K.P. in press: Program MARK - survival estimation from populations of marked animals. *Bird study:*

White, P.J.; Ralls, K. 1993: Reproduction and spacing patterns of kit foxes relative to changing prey availability. *Journal of wildlife management 57:* 861-867.

Zabel, C.J.; Taggart, S.J. 1989: Shift in red fox, *Vulpes vulpes,* mating system associated with El Nino in the Bering Sea. *Animal behaviour 3:* 830-838.