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Why is eradication of invasive mustelids so difficult?

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ABSTRACT

We conducted two field experiments to explore the reactions of feral ferrets (*Mustela furo*) to traps and bait dispensers set on pastoral farmland in central North Island, New Zealand. First, in 2004 we showed that only six of 13 radio-collared ferrets resident near four observation stations approached to within 8 m of two stations, and only three of the six entered over 8 days of observation. Five of the 15 ferrets available on the 6000 ha study area eluded recapture, although all remained present. Second, in 2006 we monitored the survival of 23 radio-collared ferrets before, throughout and after a 5-week field experiment, using toxic bait deployed in 20 automated bait dispensers distributed over 2554 ha. Eight ferrets entered a bait dispenser: four entered but did not take the bait; two did not visit but were killed by secondary poisoning; and nine never entered a bait dispenser. After the experiment, intensive live trapping guided by repeated radio-location surveys retrieved only two of 13 collared ferrets that were definitely still alive on the study area. Inefficiency of trapping wide-ranging mustelids such as ferrets, stoats (*Mustela erminea*) and mink (*Neovison vison*) is probably commonplace, due to lack of opportunity (if animals take longer to find or enter a trap than it remains available) and/or to active avoidance (refusal to enter traps or to take bait). Our results provide confirmed examples of both, and help explain why short-term or seasonal control of invasive mustelids is often very inefficient, and eradication unlikely.

1. Introduction

Invasive predators have reached almost every country, and the consequences for biodiversity vary from negligible to catastrophic (Macdonald et al., 2007). An enormous literature describes attempts to halt biodiversity losses by various forms of predator control, although a surprising proportion of these efforts do not benefit protected species for long, if at all (Cote and Sutherland, 1997; Keedwell et al., 2002). Field experience shows (Crouchley, 1994; Russell et al., 2005) that finding the last (or first) predator, essential for eradication, can be unexpectedly difficult. Many different theoretical models have explored alternative removal strategies (Barlow and Norbury, 2001; Barlow and Choquenot, 2002; Choquenot, 2006; Baxter et al., 2008) and their potential unplanned consequences (Tompkins and Veltman, 2006). By contrast, there is very little conclusive evidence on what encourages or prevents the success of any real predator control operation (Sutherland et al., 2004; Tyler et al., 2005).

The problems of controlling invasive predators can be addressed two ways, according to whether the main objective is to reduce the density of the target population or prevent

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damage to protected resources (King, 1981). The ideal, but more difficult, option would be to eradicate or at least reduce the long-term numbers of predators year-round, whether or not unacceptable levels of damage are expected in all seasons and years, but this is feasible only if every individual is at risk and reinvasion impossible (Parkes and Murphy, 2003). Failing that, a less demanding option (but more expensive over the long-term) is to minimise damage during sensitive periods (say, throughout the nesting season of protected fauna, or the dispersal period of young predators), whether or not future population densities of predators are also affected. The challenge for managers is to decide which of these is most appropriate in given circumstances, and meet its demands at minimum cost.

Both the theory and planning of effective predator removal operations need realistic estimates of the probability of success, which is influenced by, among many other factors, the aims of the operation and the extent to which the target population is resistant to the control technology employed. Among intelligent, wary carnivores such as ferrets (*Mustela furo*), stoats (*M. erminea*) and mink (*Neovison vison*), the most common forms of resistance are avoidance of traps and toxic bait (Cross et al., 1998; Morley, 2002; King et al., 2003; Zuberogoitia et al., 2006), and rapid replacement of the individuals removed. The efficacy and cost of a control programme depend on the probability of killing a resident pest with 1, 2, 3, etc. control stations in its home range (Moller et al., 1996, but this function is usually unknown.

For eradication, but not for damage control, the last few individuals are the most important and the most difficult to catch (Gosling and Baker, 1989), but their survival can seldom be detected without considerable investment in monitoring the fates of marked animals, so available data are few. In the absence of other information, users of traditional control methods usually assume that the target species has been removed, at least locally and temporarily, when no further individuals are detected by independent means. Both here and in a previous study (King et al., 2007a) we used automated bait dispensers to test this assumption during a conventional trapping operation.

The invasive mustelid of greatest concern in Britain and Europe is the American mink, whose accidental arrival has had serious consequences for native species (Macdonald and Harrington, 2003). In New Zealand during the late nineteenth century, ferrets and stoats were deliberately released on pastoral farmlands in an attempt to control rampant populations of European rabbits (*Oryctolagus cuniculus*) (Clapperton and Byrom, 2005). This early attempt at biological control failed, and instead, both have become significant pests. Ferrets carry bovine tuberculosis and both ferrets and

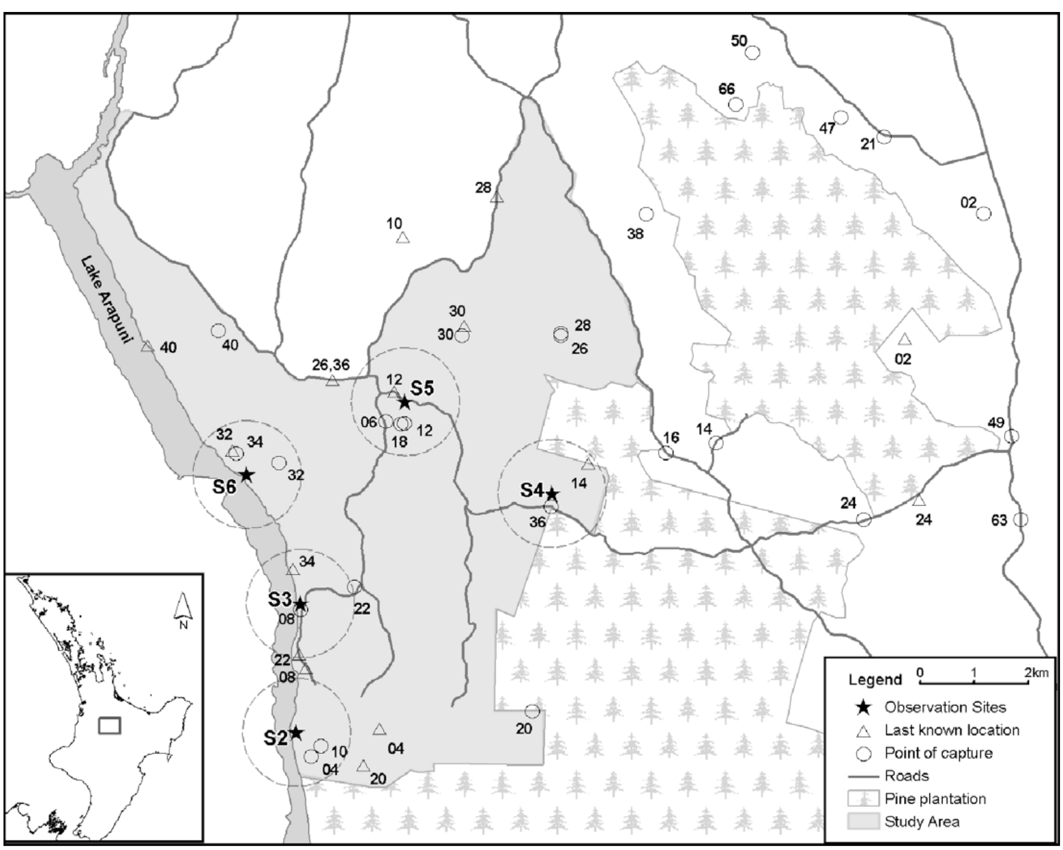

Fig. 1 – Observation stations (stars within 1-km-radius circles) for monitoring ferret reactions to recording devices in 2004. Most land cover not shown as pine forest is improved pasture. Ferrets were later trapped throughout the 6000 ha shaded area bordering Lake Arapuni, but not in the adjacent farmland. First and last known ground locations (in traps) of radio-collared ferrets (TX numbers 02–66) refer to 2004 season only; some are separated by considerable distances. Fates of all animals shown in Supplementary Table 1. Aerial locations and 2005 recoveries not precise enough to map.

stoats destroy many native birds. Monitoring and control of invasive mustelids in New Zealand now costs millions of dollars a year (Parkes and Murphy, 2003).

Mink, ferrets and stoats are small, intelligent, fast-moving and wide-ranging carnivores, difficult to observe directly in the wild. Routine landscape-scale monitoring of any small mustelid is difficult and expensive. Field research and associated modelling studies on American mink in Europe is of great interest to the agencies in New Zealand responsible for management of ferrets. Conversely, here we present data on New Zealand ferrets that should interest European agencies concerned with management of mink.

The objectives of this study were to document, by means of two linked field experiments: (1) the behaviour of unrestrained feral ferrets toward novel objects (traps, bait dispensers) placed on familiar ground, and (2) the impact of behavioural trap/bait avoidance on the efficacy of control operations against low-density populations of feral ferrets in New Zealand.

First, in autumn 2004 we observed how radio-collared individuals reacted to traps and non-toxic bait dispensers, and estimated how often they approached novel devices without interacting with them (Experiment 1). Second, in autumn and early winter of 2006, we observed the survival of a known population of radio-collared ferrets through a toxic baiting operation (Experiment 2). Both experiments were followed by intensive live trapping to retrieve survivors.

2. Methods

Both experiments began during the normal ferret-trapping season (late southern summer and autumn, February–May),

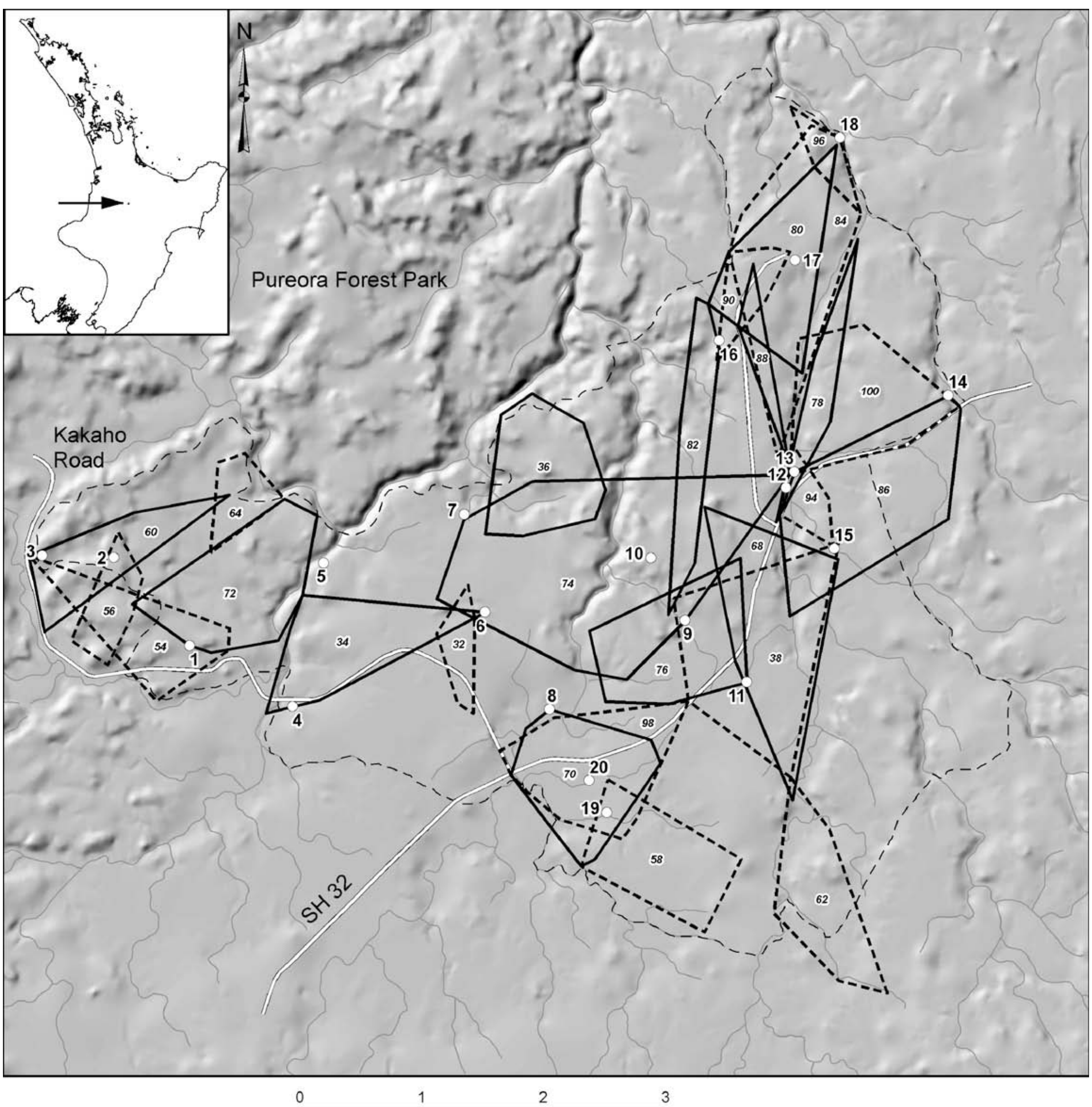

Fig. 2 – Distribution of locations of radio-collared ferrets (with collar numbers in italics) released in April 2006; fates of all individuals listed in Supplementary Table 2. Solid lines, males; dashed lines, females. Numbered white dots show the positions of automated bait dispensers with RFID loggers. Faint dashed line encloses the study area (2554 ha). Distribution of those that survived the toxic baiting can be deduced from data listed in Supplementary Table 2.

on privately-owned improved pastoral farmland grazed by beef and dairy cattle or sheep, with scattered patches of bush, small wetlands, and a few farm buildings. The first study area covered 6000 ha near Tokoroa (38°10′S, 175° 40′E), partially isolated by Lake Arapuni and by exotic pine forests (Fig. 1). The second was a 2550-ha site west of Taupo (38° 55′S, 175° 75′E) (Fig. 2). The topography of both study areas ranged from sloping to steeply dissected, crossed by several precipitous, scrub-filled gullies. Ferrets had been live-trapped for routine monitoring of bovine tuberculosis on both study areas during previous years, but reinvasion was always very rapid (King et al., 2007a).

The two experiments were part of a longer-term programme developing a new automated bait dispenser, the Scentinel® (King et al., 2007a–c), designed to achieve landscape-scale control of invasive mustelids at minimum cost in human effort.

For Experiment 1, we set up ten widely-spaced (2 km) observation stations spread throughout an area scheduled for a routine ferret control trapping operation (Fig. 1), and another ten on adjacent farmland not scheduled for trapping (total 8861 ha). We intended the stations to be independent, so spread them more widely than the 1-km spacing recommended by Moller et al. (1996). We live-trapped and radio-collared ferrets living around each station, by standard methods summarised in the Electronic Supplementary Material. We made no attempt to mark all resident animals in either area, but aimed merely to identify the best locations for intensive observations. From this preliminary survey we chose to concentrate on five stations (Fig. 1), where we could best conduct replicate observations of the behavioural reactions of known individual ferrets to bait dispensers and traps. Afterwards, we examined all ferrets collected by the trappers.

For Experiment 2, we used an experimental design slightly modified from that of Dilks and Lawrence (2000). We trapped and radio-collared ferrets by the same methods as in 2004, except that in 2006 we made a serious effort to locate and mark all ferrets living on a study area of 2554 ha. We set out 20 bait dispensers equipped with PIT tag readers, distributed across the study area such that every resident ferret should have access to at least one unit within its home range. For the 26 ferrets most often recorded, we estimated the extent of bait avoidance by calculating how many and which bait dispensers were potentially within the ranges of individual ferrets, compared with how many and which were actually visited. Finally, we made an intense effort to retrieve surviving collared ferrets, using traps set at a density ten times higher than that of the bait dispensers.

3. Results

3.1. *Experiment 1*

We captured and released 16 ferrets with both radio-collars and eartags in mid-February 2004 (Fig. 1), plus another six with eartags only (Supplementary Table 1). In order to check the source and speed of potential immigration into a cleared area (the so-called ‘sink effect’), we also released 10 ferrets with collars and eartags, plus three with eartags only, on a roughly equivalent area of adjacent farmland.

3.1.1. *Behavioural reactions of ferrets to recording devices*

Thirteen radio-collared ferrets were confirmed to be alive on the study area on 31 March (Supplementary Table 1), and their approximate positions were shown by our aerial radio-tracking survey on that day. Six of the 13 approached within c.8 m of two of the four observation sites. Three of these six (TX 12, 34 and 40) approached but never entered a detection device, and three (TX 8, 20 and 22) eventually entered a device, but not before visiting the site several times over the previous 2–3 days (Table 1). When these ferrets did enter a device they remained for only a few seconds, just long enough to lunge for the meat and then back out immediately.

The position of Site 2, on the bank of Lake Arapuni, must have been on a frequently-used ferret runway, because it was visited disproportionately often both in 2004 and in 2005 (see map in King et al., 2007b). Three of the six ferrets visited only Site 2; TX 12 and TX 40 made trips of 6 and 7.6 km, respectively to pass within range, although without entering (Fig. 1). TX 20 visited both Sites 2 and 3 on different nights, and TX 22 visited both these same sites on a single night.

Table 1 – Visits by ferrets to observation stations from 30 March to 8 April 2004. At each station, a Holden trap tunnel containing footprint tracking papers, and an automated bait dispenser with tracking paper and internal still camera, were continuously monitored by external video cameras. Radio-collared ferrets were detected by automated radio frequency identification (RFID) loggers programmed to sweep through 8 specified radio frequencies every 4 s, and record the dates/times when each frequency was detected within range (c. 8 m). Loggers were active at sites 2–5 throughout, but not at site 6 until after the period of observations reported here. Visits by uncollared ferrets were not individually distinguishable.

Ferret collar (TX) number	Observation stations visited (site numbers)	Number of nights a collared ferret came within RFID range (number of separate visits)	Number of times a ferret entered a bait dispenser or Holden trap	Number of nights a ferret was seen by the video cameras
08	Site 3	2 (2)	1	0
12	Site 2	2 (4)	0	0
34	Site 2	2 (3)	0	0
40	Site 2	2 (4)	0	0
20	Sites 2 and 3	3 (5)	1	0
22	Sites 2 and 3	3 (4)	1	1
Total visits by collared ferrets	Sites 2 and 3	22	3	1
Un-collared	Sites 2, 3, 5 and 6	–	9	4

Only one of a total of 13 visits, all known from the timestamp on the RFID logger records to have been made when the video cameras were operating, was observed by the cameras. That was the only night, April 6, when the presence of a radio-collared ferret (TX 22) was detected by all four devices at Site 3 (RFID logger, both external video cameras and the footprint papers in the trap tunnel), although not by all of them simultaneously. This ferret was within range of the RFID logger for most of the night, but came close enough to be seen by the video cameras only twice.

The remaining seven of the 13 ferrets available were never detected by the RFID loggers or video cameras during the 8 days of our observations, or by manual scanning around the observation stations. Our radio-tracking records were not detailed enough to show whether any of these animals ever found an observation station during the 8 days of our recording. However, since the average maximum distance between locations of all the radio-collared ferrets released was 4.3 km ($n = 25$), these animals were clearly moving about widely. Therefore, we cannot rule out any as being potentially unavailable. All 13 ferrets remained resident till the end of our observations, so all were potentially at risk of detection had they approached the RFID station programmed to search for their channel number.

Uncollared ferrets were detected by the bait dispenser cameras and footprint tracking papers on nine occasions, of which four were also detected by the video cameras (Table 1). Uncollared ferrets could not be detected by the RFID loggers, so we cannot tell how often these animals approached the devices without entering, but they visited four of the five sites. Only three of 22 known visits by collared animals resulted in an entry (of which only one was seen on video): by proportions, nine entries by uncollared animals could represent >100 visits, unless uncollared ferrets were much less cautious than collared ones.

3.1.2. *Retrieval trapping*

During the autumn trapping season of 2004 immediately following our observations, commercial contractors working over the entire 6000-ha study area (about twice the area sampled by our observation stations) killed 37 ferrets (0.62/100 trapnights), including 10 of the 15 collared, two of six tagged, and 25 unmarked ferrets. In the following trapping season (autumn 2005), they captured 61 ferrets (1.2 per 100 trapnights) in 5070 trapnights (18 March–30 April) (King et al., 2007a).

The 2005 operation recovered three ferrets marked in 2004, all still living close to their last known locations within the study area. (1) TX04 was photographed 12 times by automatic cameras before the 2005 trapping began, but killed as soon as the trapping reached its home range (King et al., 2007a), and (2) TX06 was caught without its collar but still with its ear tag. In addition, TX 30, listed at the end of the 2004 season as ‘unaccounted’, was trapped in July 2005 by a farmer about 7 km from where we last recorded it. It was still wearing its collar, so our loss of contact in 2004 was probably due to transmitter failure. Contrary to our expectations, none of the 13 ferrets marked on the adjacent farmland ever appeared on the trapped area.

All nine ferrets that were never detected at any of the observation stations in 2004 were eventually trapped (TXs 10, 14, 26, 28, 32, 36 in the 2004 trapping season, and 04, 06 and 30 in 2005: Supplementary Table 1). Among the six that had visited the observation stations in 2004, four were caught (TXs 20, 22, 34 and 40). The only two ferrets released on the study area but never recovered, TXs 08 and 12, had visited the stations on two nights each (Table 1), yet they survived two consecutive trapping operations. If there is any predictable relationship between individual trapping history and the probability of further capture, it was not strong enough to be detected in these data.

3.1.3. *Age structure*

We classified the ages (in year-classes beginning in October, the average month of birth) of 71 ferrets recovered in March/April of both years: 60% were 0-1 years old; 30% were 2 years old; and 10% were 2–3 years old.

3.2. *Experiment 2*

3.2.1. *Release of marked ferrets*

During the 12 days of initial live trapping, we caught 31 ferrets (16 males, 15 females), in 1674 trapnights (average 1.85 new captures per 100 trapnights). All were released alive and then relocated at least once. If the 31 individuals represented the total population on 2554 ha, the local density was *c.* 1.2/km^2.

The ages of the collared ferrets were unknown, but most of the 11 we recovered had gained weight (Supplementary Table 2), suggesting either that they were not full-grown when first captured, or that ferrets commonly put on weight in preparation for winter (we suspect the latter).

3.2.2. *Relocation records*

We collected a total of 309 location records (trap captures plus radio fixes) in 35 days (Fig. 2). The success of the 18 radio-location surveys depended both on the behaviour of the animals and on the weather, so not every animal thought to be present was detected every time (Supplementary Table 3). Ferrets usually stay in dens during the day, which simplified the location procedure, but radio reception from those that had chosen a den in a deep hole was poor to undetectable. This is the main reason why, during the five radio surveys of the undisturbed population between 26 April and 16 May 2006, we never located more than 20 of the 23 collared ferrets we knew were still alive within the study area, and most surveys detected only 14–16 individuals. After the toxin was deployed, we used radiolocations to retrieve carcases for analysis.

The bait dispensers operated continuously between 16 May and 20 June 2006. Eight of the 31 ferrets released had died or moved away from the study area by May 16, leaving 23 potentially at risk from toxic bait (Supplementary Table 2). Eight of these entered a bait dispenser and took bait directly (one sublethal and seven lethal doses); two did not visit but were killed by secondary poisoning; four visited a bait dispenser without taking bait; nine never visited a bait dispenser or accessed the bait indirectly.

About the same median number of reliable (ground) locations were recorded for those ferrets that accessed toxin ($n = 10$) and those that did not ($n = 8$), but they did not all have equal opportunity to find bait. From our approximate estimates of home range area, we calculated the number of bait dispensers available in each home range, and the number of nights during which each resident ferret was exposed to the risk of encountering toxin. The 14 ferrets which reached the toxin (the 10 males and four females that either entered bait dispensers, with or without taking bait, or scavenged poisoned carcases) tended to have more opportunity to find toxin (68 bait dispenser-nights per ferret) than the nine (three males and six females) that did not (21 bait dispenser-nights per ferret). This gender bias is probably related at least in part to the generally smaller home ranges of females (Clapperton and Byrom, 2005).

On the other hand, there was also great variation in individual willingness to enter the bait dispensers and take bait from them, even among ferrets that had plenty of opportunities. Three males among the eight ferrets that took bait directly (seven males, one female) entered a dispenser within 48 h of deployment (two of them twice each). Conversely, among the nine ferrets that never accessed the toxin over the entire 5 weeks of the trial, one (M86) entered dispensers seven times, but always refused the bait.

The cameras photographed a total of 24 visits by collared ferrets, but none by an uncollared ferret until June 18, after the toxic bait had been out long enough (34 days) to remove up to half the resident ferrets and so, presumably, make room for immigrants.

3.2.3. *Modelling of location data*

The total number of ground locations recorded by traps, bait dispensers and ground radio searching for each of the 26 most frequently recorded ferrets (Supplementary Table 2) ranged from 3 to 16 (median = 9, inter-quartile range (IQR) = 8–15, not normally distributed). When repeat locations were removed, the number of remaining locations per ferret ranged from 3 to 14 (median = 8, IQR = 6–11).

Minimal individual range lengths varied between 0.8 km and 3.2 km (median = 1.4 km, IQR = 1.1–2.0 km). Minimum convex polygon range areas varied between 16.3 ha and 307.5 ha (median = 84.8, IQR = 33.5–132.8). The bootstrap analysis of MCP range areas (Fig. 3) shows that no individual home range area was fully revealed, so the median estimate of 85 ha is a substantial underestimate. Nevertheless, this information is useful for interpreting our results because it shows the *minimum* possible relationship between the distributions of the animals and the bait dispensers. It also warns us not to dismiss individuals we thought could have been out of range of a bait dispenser, because they might in fact still have been exposed to the toxin.

3.2.4. *Fates of radio-collared ferrets*

Six ferrets died before the deployment of the toxic bait, one left the area, and one lost contact soon after release, leaving 23 available for the study (Supplementary Table 2). Ten of these 23 (43%) died after accessing the toxin. We recovered the carcases of 9 of them, which all contained high levels of 1080 residues.

Identifying marks remained reliable throughout. One (M78) shed its collar, which was retrieved from under a woolshed, severely damaged but still transmitting a mortality signal. One (M84) lost the PIT tag from its collar, but was identified from photographs and eartags; one (M86) lost one of its two eartags.

3.2.5. *Retrieving survivors*

After the bait dispensers were withdrawn on June 20, radio-tracking confirmed that the last 13 collared ferrets were all still alive in the study area. The retrieval operation collected

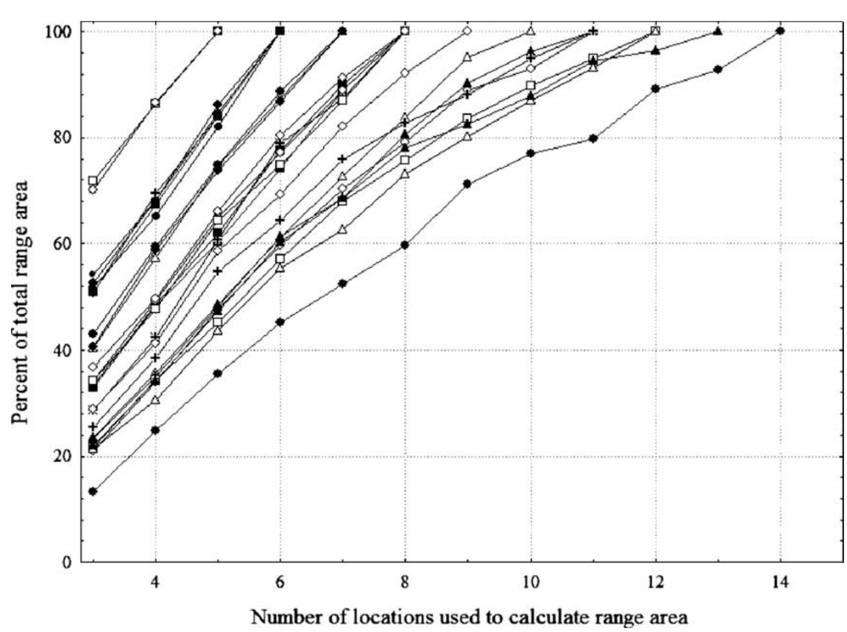

Fig. 3 – Minimum convex polygon (MCP) bootstrap analyses of the records of the 26 most frequently located ferrets monitored in 2006, scaled to percentages of the total calculated range area. No individual home range was fully revealed.

only two of them (M86, which had often visited bait dispensers but refused to take it, and M36, which had never visited a dispenser) in 1300 trap nights over eight nights (Supplementary Table 2). Neither of these carcasses contained 1080 residues. Two unmarked ferrets were also caught, both near a dispenser which had photographed an uncollared ferret ten days earlier. A third, F98, also escaped the next trapping season (February 2007), and was finally caught on 12 May 2008, about 2 km north of its previous range and in excellent condition, still with collar and eartags.

4. Discussion

This study was designed to quantify the risk of imperfect removal of a target population, because that strongly affects the choice of optimum control strategy (Baxter et al., 2008). Reduction of pest populations requires long-term removal at a high level every year, estimated at between 50% of the population for ferrets (Barlow and Norbury, 2001) and 80% for mink (Bonesi and Palazon, 2007; Bonesi et al., 2007). A 50% cull is the minimum required to suppress the long-term density of ferrets if repeated annually (Barlow and Norbury, 2001), but the probability of achieving that level of removal in practice is unknown.

Approved humane kill traps for mustelids can be left indefinitely set if they meet certain specifications (Warburton et al., 2008). Where this is not possible, or where fresh samples are required for analysis, the only alternative is to use live traps and inspect them daily, as the law requires. This necessarily makes the operations labour-intensive, time-consuming, limited in land coverage, and expensive, especially if often repeated (Moore et al., 2003; Parkes and Murphy, 2003).

The usual technique to cover large areas with live traps is to operate a 'rolling front', using each site for a limited time before shifting the trap to a new location. Efficient predator control depends on finding the most economic balance between costs (minimising the number of traps and the time they are serviced at a given site), and benefits (maximising the number of target animals caught at that site) before moving on. The primary unknown factor is the assumption that the traps will catch (or bait stations deliver toxin to) enough resident animals in a short time to meet the aim of the operation. Well-documented, successful eradication campaigns show that such high targets get more elusive as density declines and any given control method gets less effective with familiarity (Gosling and Baker, 1989; Bloomer and Bester, 1992; Veitch, 2001). Our results show that a large number of opportunities for detecting the presence of a pest may be missed by conventional equipment. It is hardly surprising that trapping of ferrets, mink, and other wary, intelligent carnivores (including stoats, mongooses and cats) is so difficult anywhere that control operations have to be short-term or seasonal.

4.1. *Causes of imperfect removal*

The results of our experiments are summarised in Table 2. The most common reasons for imperfect removal are probably lack of opportunity (if individuals take longer to find a trap or bait dispenser than it remains available), and active avoidance (if individuals find but refuse to enter a trap or take bait), or both, in unknown proportions. Our results include confirmed examples of both, so have significant implications for the results of routine control operations and for estimating population densities from trap results.

4.1.1. *Lack of opportunity: unable to find a trap*

Marked individuals, especially those resident at the edge of a study area, may move back and forth across the boundary and so are not always at risk. However, that does not explain our poor retrieval rate, because we could account for all marked individuals in both our study areas, and discount those we knew were absent.

Theoretical models assume that the minimum operating density of bait dispensers should be one per ferret home range (Moller et al., 1996). Ensuring that all resident ferrets are exposed to traps or toxic bait therefore depends on reliable knowledge of home range areas and movement patterns in the local area (Bonesi et al., 2007). If some individuals are unable to find a control device, decisions about cost-effective device spacing can be quite wrong, and that would seriously undermine a minimum-effort operation.

The home ranges we observed in 2006 (Fig. 2) were consistent with previous estimates of ferret home range summarised by Clapperton and Byrom (2005); yet bootstrap analyses (Fig. 3) showed that not one was fully revealed. But we can say definitely that the areas of the ranges of these animals were *at least* as large as shown, and could have been larger. We disagree with the statement by Caley and Morriss (2001) that home ranges can be calculated from a minimum of five relocation records.

4.1.2. *Lack of opportunity: traps/bait not available for long enough*

The proportion of a resident population affected by control operations depends on the season and the amount of control

Table 2 – Summary of the results of our two experiments and of the trapping operations that followed them.

	Experiment 1, 2004		Experiment 2, 2006	
Methods	Observation stations	Commercial trapping	Toxic bait dispensers	Intensive trapping
Dates	30 Mar–7 April	29 Mar–27 April	16 May–20 June	26 June–7 July
Study areas	Four sites *ca.* 2 km apart	6000 ha	2554 ha	Focussed on known survivors
Number of radio-collared ferrets available	13	15	23	13
Number of radio-collared ferrets detected or trapped	Six detected, of which three entered	10 trapped	12 Detected, of which eight took bait, plus two killed by secondary poisoning	Two trapped

effort invested. In autumn, the peak of the trapping season, Cross et al. (1998) estimated that a normal four staff-day operation could remove only 50% of a South Island (5.3/km^2) population; removal of 80% would take 7 staff-days, and 95%, 11 staff-days. The 36 staff-days' effort we made (1674 trapnights) seems to have been enough to ensure that the 31 animals marked comprised virtually all of the resident population, but it required much more effort than commercial trappers can normally afford. Most routine operations keep traps in any given location for only a few days, which could help explain the unexpected inefficiencies of Experiment 1 (Table 2).

The automated bait dispensers used in Experiment 2 were continuously available for 5 weeks, at the theoretical minimum density (<1/km^2). Extended availability could: (1) give resident ferrets time to overcome their neophobia, and/or; (2) increase the chances of their encountering a control device. Both are plausible hypotheses. Neophobia by ferrets towards new objects placed on familiar ground takes up to 10 days to pass (A.E. Byrom, unpublished data). Time to find a device is also a likely limitation on short-legged animals searching home ranges of about 100–200 ha, below ground as well as above (Clapperton and Byrom, 2005). More intensive radio-tracking would be needed to distinguish these explanations.

4.1.3. *Active resistance: seasonal variation in susceptibility to trapping*

According to the simplest method of calculating trapping efficacy (the number of tagged ferrets killed expressed as a percentage of the total number of tagged individuals known to be at risk), standard autumn trapping of the abundant ferret populations in the South Island may recover between 19% and 76% of marked individuals (G. Norbury, unpublished data), with a median of 51%. In 2004 our recovery rate during early autumn was within this range (55% of 15), and in late autumn 2006 the poison bait removed or incapacitated 10 (43%) of 23 ferrets at risk (Table 2).

On the other hand, during the winter (June 26–July 6, 2006) we caught only two of 13 (15%) ferrets known to be still available. All these ferrets had a history of previous captures, and we could direct our trapping effort precisely to their known locations. Was this population reduced by natural winter mortality, or was there seasonal inactivity of living, resident individuals? Our experimental design provided an unusual opportunity to separate these explanations.

Experienced trappers assert that ferrets die off quickly when the weather turns severe. We expected to find evidence of that in Experiment 2, during which there were frosts on 22 nights, yet the ferrets were still active during that period (Supplementary Table 3). But mortality-sensing radio-collars confirmed that all the animals we failed to recover in late June and early July 2006 were in fact still alive on the study area. Our poor retrieval rate must therefore have been more to do with reduced activity or increased neophobia than accelerated seasonal mortality. Similar conclusions have been reported previously. Spurr et al. (2005) killed only five (29%) of 17 radio-collared ferrets available in July 1997. In winter/spring 2000, A.E. Byrom (unpublished data) caught 16% of 19 known ferrets over three nights in newly placed traps, compared with 60% of 15 in traps that had been in place for three months.

4.1.4. *Active resistance: individual variability in trap/bait response*

We present clear records of individual variation in willingness of ferrets to enter traps or bait dispensers, as did Cross et al. (1998). This variability is probably an unavoidable and complex matter related to gender, activity, and experience. There was no simple explanation assuming a general deterrent effect of trapping and handling; on the contrary, Moller et al. (1996) suggest none should be expected, because the long history of domestication of the ferret should make them generally more tractable. The simplest explanation is that some ferrets were more confident about artificial devices and baits than others, even though all individuals were treated the same. Spurr et al. (2004) also reported finding signs (footprints or scats) of ferrets that had approached a trap but declined to enter.

Pre-baiting is the standard method of reducing this problem, and often works well by giving resident individuals experience of find free food in live traps and getting out again afterwards. On the other hand, the great behavioural flexibility of mustelids allows some, especially females, to learn from experience to *avoid* traps, even a complete array placed right outside a den (Murphy and Dowding, 1995). Two of our marked resident ferrets each escaped two successive trapping operations: TX30, both the 2004 and 2005 trappings (Supplementary Table 1), and F98, both the 2006 and 2007 trappings (Supplementary Table 3). The same applies to bait: M86 refused seven opportunities to try it. Further field trials might help show whether this variation was influenced by the design of our bait dispenser, by our use of anal scent gland lures in 2006 (Spurr et al., 2004) but not in 2004, or both. Perhaps it is just a matter of unpredictable individual choice of reaction to experience of confinement. Live-trapping was necessary to equip all residents with radio-collars, even though it may have taught some ferrets to tolerate temporary confinement, and others to avoid it.

The effects of individual learning are well illustrated by the contrasting results of attempts to eradicate stoats from two offshore islands in southern New Zealand. A pregnant female stoat invaded Maud Island (309 ha) in April 1982, and produced seven young there (Crouchley, 1994). Despite intensive trapping, she herself was never caught, and it took 16 months to catch the last of her offspring. In 1989 a second female arrived, and this time the litter included at least five young. This female was also never trapped, but lived on the island for 18 months until she was found dead in February 1991. By then, sibling matings between her offspring had begun to produce the next generation, of whom at least three were included among the total of 16 stoats caught up to July 1994. By contrast, the whole resident population of 16 stoats on Te Kakahu Island (514 ha) was eradicated in a single operation in 1999, 15 of them on the first night (M. Willans, unpublished: King and Powell, 2007, p. 346).

The main difference between these two islands is that the stoats on Maud were experienced with traps, while those on Te Kakahu were not. Maud Island is close enough to the mainland to be at perpetual risk of reinvasion, and conservation officers keep traps set there all the time. The trapping on Te Kakahu was aimed at completely naïve animals, and timed to target them when they were most hungry. The implication is that eradication is possible only by sudden onslaught against naïve populations on islands protected from reinvasion. The same is true of the ferrets we observed, and of that ubiquitous pest, the Norway rat (*Rattus norvegicus*). Individual rats become notoriously wary (Russell et al., 2005), but naïve island populations can be eradicated in a single operation (Towns and Broome, 2003).

Is higher capture success to be expected in populations including more young, unwary animals? Both our experiments confirmed that older ferrets that have learned to avoid traps may remain resident for years. Perhaps there was a higher chance of that happening in our study areas than in the South Island, because only 60% of the ferrets we collected over the 2004 and 2005 seasons were under a year old. In north Canterbury, the proportion of first-year ferrets in a very large sample ($n = 742$) ranged from 93% in February to 89% in May (Caley et al., 2002).

4.1.5. *Active resistance: avoidance of infra-red illumination*

In our first experiment, the combination of RFID loggers and cameras revealed for the first time how reluctant the wild, unrestrained ferrets we observed were to approach the observation stations and how few eventually entered (Table 1). The six collared and up to four uncollared ferrets that did come within camera range investigated the outsides of the tunnels very carefully, trying to find some other means of reaching the bait; half never entered one. The only previous study to have used video cameras inside tunnels came to the same conclusion: on 8 of 45 occasions on which a stoat was seen approaching a tunnel, it merely looked inside, but did not enter (Dilks and Lawrence, 2000). Maloney and Murray (2000) used video cameras to observe from a distance the reactions of ferrets to toxic baits in simple plastic bait hoppers over 577 site-nights. In only one of 15 videoed interactions did a ferret actually eat the bait.

An alternative explanation might be that the animals could see and avoid the pool of infra-red light (wavelengths 840–860 nm) surrounding the objects being filmed. Captive ferrets trained to press a lever for a food reward, in response to a visible light cue, could still reliably see and respond to an infra-red (870 nm) light cue (Newbold and King unpublished). If wild ferrets could also see the infra-red illumination used at our observation stations in 2004, their extreme reluctance to come closer might have been specific to that situation rather than a normal response. Use of internal cameras with infrared flash is different, because ferrets could not detect the flash until after the camera had detected them. In 2005, we ran bait dispensers with internal flash cameras for 11 weeks, and recorded 198 visits by about 20 unmarked ferrets (King et al., 2007a), but we do not know how long they had hesitated outside. New experiments are needed to disentangle the effects on observed trap response in wild mustelids of camera lighting, prior experience, season and opportunity (especially the timing and spacing of recording devices).

4.2. *International implications*

In Europe, trapping of invasive American mink for protection of native fauna is a critically important and expensive management priority (Nordström et al., 2003; Bonesi et al., 2007). New control techniques such as floating rafts (Reynolds et al., 2004) are promising, but applicable only on relatively calm waters. In habitats in which the only available technique is the conventional live trap, the problems of inefficient removal of mink become important (Zuberogoitia et al., 2006). Our results therefore have implications for problems far wider than the control of invasive mustelids in New Zealand, serious though those are.

Our observations are consistent with the experience of trappers (Crouchley, 1994; Murphy and Dowding, 1995), and confirmed by modelling (King et al., 2003; Bartolucci and Pennoni, 2007), that mustelids are cautious and intelligent animals. The two biggest single difficulties in observing them are, first, to get them to approach and enter a recording device, and second, to deal with the statistical implications of strong individual variation in trap response. Heterogeneity in trap response of mustelids seems to be inevitable (King et al., 2003), and explains the difficulty of achieving a high kill rate in most short-term conventional trapping operations.

The variation in individual responses to traps, and the great effort required to account for an entire population, also cast doubt on whether it is feasible to conduct experiments to measure rates of recovery of populations after control, as recommended by Byrom (2002). It is simply too difficult to confirm whether control operations were actually successful. For the same reasons, we caution against uncritical field application of otherwise valuable theoretical models assuming complete removal (Moller et al., 1996) or total enumeration (Efford, 2004).

Our results suggest a warning: models of minimum-effort control strategies (Moller et al., 1996; Baxter et al., 2008) should be applied only with caution to mustelids. Even though conventional methods can reduce numbers of invasive mustelids locally, the extent of reduction is often unknown and the effect is short-lived (King, 1980; Barlow and Norbury, 2001; Nordström et al., 2003). Incomplete removal and rapid replacement of mainland populations should always be assumed, even when trappability is apparently high.

The continuing dilemma for predator-control managers and commercial operators is that, even though it might be desirable to run longer trapping periods during a greater proportion of the year, in practice only short trapping periods during the season of highest trappability are economic. The only exception to this rule seems to be the unusual case of eradication of completely naïve populations on small islands remote from reinvasion. Otherwise, financial constraints and inefficient removal will always make routine control of invasive mustelids less than perfect.

5. Conclusions

Our question was: why is eradication of invasive mustelids so difficult? Our results suggest two main reasons: (1) variation among individual mustelids in opportunity to access traps and bait, interacting with (2) their different individual reactions to them. Neither form of variation is constant, because individuals' reactions can change with experience and with season. The skill of the trappers and the trap layout, spacing and bait used are all important to achieving required capture rates. However, all trapping operations are affected, in unpredictable ways, by the dynamic interaction between the cost-benefit calculations of human pest managers and the behaviour of the animals.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2008.12.010.

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