R-10592

Ferret density estimation

Grant Norbury[1] and Murray Efford[2]

[1]Landcare Research
PO Box 69, Lincoln 8152
New Zealand

[2]Landcare Research
Private Bag 1930, Dunedin, New Zealand

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Reviewed by:	*Approved for release by:*
Adrian Monks Scientist Landcare Research	Phil Cowan Science Manager Biosecurity and Pest Management

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Summary

Project and Client

A method to measure the density of wild ferrets was developed by Landcare Research for the Animal Health Board (Project R-10592).

Objectives

1. Develop a method that will accurately measure ferret population density and be capable of differentiating between densities of 2 km^{-2} and 4 km^{-2}, by:
   - evaluating a new simulation-based approach for estimating density using existing capture-recapture data
   - conducting field trials to test the method against a known population determined by removal of ferrets from a large area
   - writing a protocol and software for general use of the new capture-recapture methods, and publishing results in a peer-reviewed journal
2. Calibrate ferret density against a cheaper index of abundance (trap-catch rate)

Methods

- We worked alongside four ferret control operations at Cluden, Tarras, Bendigo, and Poolburn in central Otago between February and May 2003. We divided the operations into 11 blocks (1682–4207 ha). On each block, we captured, ear-tagged, and released ferrets over six consecutive nights of trapping. Contractors then kill-trapped the blocks over 10–13 consecutive nights. The identity and location of every ferret captured was recorded. Ferret density estimates were derived from these data in program DENSITY, a new computer-intensive method of estimating population density from live trapping data that does not suffer from the biases inherent in conventional density estimation methods.
- We conducted simulations with varying trap spacing, trap number, and trapping duration to determine the effect on the precision of density estimates and to provide a basis for a protocol.
- We attempted empirically to verify the DENSITY estimates on four blocks that were partly bounded by natural barriers to ferrets. These blocks received additional kill-trapping for 5–8 nights. The total number of ferrets killed was assumed to be a close approximation of the number actually present. We checked for residual ferrets on two of these blocks using a dog specially trained to find mustelids.
- We attempted to calibrate DENSITY estimates against contractors' trap-catch rate.

Results

- Conventional methods of estimating animal density rely on unreliable methods for estimating the area from which animals are caught. The resulting bias is exacerbated if animal movements vary with density. This was the case for ferrets because they moved greater distances as density declined. Integrating density estimation with animal movements using the methods demonstrated in this report overcomes these problems.
- Ferret density estimates using this new approach ranged from 0.8 to 6.9 km^{-2} between sites. Their precision was largely a function of the number of recaptures of ferrets. Assuming an area of 1000–3000 ha, adequate precision was obtained using at least 100

traps, spacing traps at 150–250 m, and continuing trapping until 40–50 recaptures were obtained (or after 3–4 nights on average).
- Combining capture-recapture data with kill-trapping data did not significantly improve the precision of density estimates. This may have been because our field trials were conducted at a time of high population turnover due to juvenile dispersal.
- New, untagged ferrets continued to be detected and removed at all sites throughout the control phase of the study. This made it very difficult to measure the true size of the populations by removing ferrets. Instead, we advocate the new method over conventional methods based on first principles, and on simulations using known population densities.
- Trap-catch rate performed very poorly as an index of ferret density across sites, regardless of the number of nights used to calculate catch rate.
- The basis and methodological details of program DENSITY are published in peer-reviewed journals (Efford 2004; Efford et al. 2004).
- The software for program DENSITY is available at www.landcareresearch.co.nz\services\software\density.

Conclusions

- Capture-recapture data analysed by simulation and inverse prediction in program DENSITY provide rigorous estimates of ferret population density on a scale relevant to management (e.g., 2000 ha).
- Comprehensive trap coverage of areas to be assessed is required (no part of an area should be further than 500 m from a trap). If only partial coverage can be achieved, consider random placement of trap lines to ensure that the sampled density is representative of the total area.
- Assuming an area of 1000–3000 ha, adequate precision (coefficient of variation of density estimate < 10%) will be obtained by using at least 100 live traps (preferably 150), spacing traps at about 200 m intervals (150–250 m), and continuing trapping until 40–50 recaptures are obtained (this should happen after 3–4 nights on average, unless the density is very low).
- The precision offered by DENSITY is sufficiently high to identify reliably most ferret populations as above or below the putative threshold for ferrets as maintenance or spillover hosts of bovine tuberculosis.
- Combining capture-recapture data with kill-trapping data is unlikely to be a cost-effective way to improve the precision of density estimates.
- Ferret control conducted at times of high dispersal will have a general rather than a local effect on ferret density, and precise measurement of efficacy will be very difficult.
- Trapping of ferrets for density estimation (and possibly also for control) is best done outside the peak period of juvenile dispersal, but when ferret trappability is still high. The months January, April and May provide a good compromise.
- Trap-catch rate does not provide a reliable index of ferret density across sites, presumably because it is vulnerable to other site-specific influences beyond just ferret density.

Recommendations

- Animal Health Board and its contractors should not consider the use of trap-catch indices for estimating ferret density to aid management decisions.
- Animal Health Board should adopt the use of the protocol for estimating ferret density detailed in Appendix 1. This will involve the need for training in the use of program DENSITY.

1. Introduction

Reliable methods for measuring animal densities are an integral part of effective pest management programmes. Such a method was developed for wild ferrets by Landcare Research for the Animal Health Board (Project R-10592) from February 2003 to April 2004.

2. Background

Wild ferrets in New Zealand are potential vectors of bovine tuberculosis (Tb), a disease that poses a significant threat to New Zealand's international beef, dairy and venison industries (Ragg et al. 1995; Lugton et al. 1997). Ferret populations are therefore subject to control.

Modelling predicts a threshold ferret population density for the disease to be able to establish and maintain itself in ferret populations without external sources of infection (Caley & Hone submitted). The threshold density at peak times of the year (February) is estimated to be about 5.0 km^{-2} (2.9 km^{-2} averaged throughout the year). This estimate is imprecise (lower 95% confidence limit 2.1 km^{-2} in February) and has yet to be confirmed empirically, but it nevertheless has guided management decisions on whether a given ferret population should be controlled or not. The problem we address here is how to obtain reliable estimates of ferret absolute density to identify populations that should be controlled.

Unbiased estimation of animal population density is a major problem in animal trapping studies. The conventional way to estimate density from capture-recapture data is first to estimate population size (using one of many established estimators) and then to divide that number by an estimate of the notional 'effective trapping area' (ETA) (e.g., Otis et al. 1978; Moller et al. 2002). The usual way to estimate the ETA is to add a constant-width boundary strip to the area enclosed by the traps. This method lacks rigour because the methods for determining the strip width are *ad hoc*, as acknowledged by Moller et al. (2002: 42). Another way of stating this is that conventional estimates suffer an unknown bias due to edge effect that varies with trap layout and home range size. This is especially relevant to ferrets because their home ranges tend to decrease in size as density increases (G. Norbury unpubl. data, and this report). Failing to allow for this when calculating effective trapping area causes systematic errors in estimates of density.

A further problem with conventional estimates is that, although methods exist for including uncertainty about the trapping area in confidence limits for density (Jett & Nichols 1987), these are seldom used. A possible reason is that the uncertainty in ETA is itself difficult to measure. We believe the confidence limits reported previously for estimates of ferret density have therefore been unrealistically narrow (e.g., those of Moller et al. 2002).

We used a new computer-intensive method for estimating population density from live trapping data (Efford 2004; Efford et al. 2004). The method relates the probability of catching an animal to the distance between its home range centre and a particular trap. The parameters of this relationship (otherwise known as a 'detection function') can be jointly estimated from conventional capture-recapture data by the statistical procedure of simulation and inverse prediction (Efford 2004). The necessary calculations are performed automatically by the program DENSITY, which is available at www.landcareresearch.co.nz\services\software\density. The key advantages of the new method are that it removes the need to calculate the ETA, and that it provides reliable confidence intervals (Efford 2004). The method is explained in more detail in Appendix 2 (see also Efford 2004 and the online documentation for program DENSITY).

We analysed a large ferret capture-recapture data set to obtain estimates of ferret density using the new method. We varied key aspects of the analysis to determine how robust the estimates were to details of how the analysis is performed. We investigated the possibility of combining data from live- and kill-trapping to obtain more precise estimates. We used both the field data and simulations to assess how much trapping is needed to achieve density estimates with a given precision. We expressed our conclusions in a suggested protocol for the use of live trapping to estimate ferret density. We attempted to verify the estimates by intensive removal trapping, and using trained dogs.

Finally, we looked at whether an index of abundance that is cheaper and easier to collect (i.e. trap-catch rate) could be used to predict density. Cross et al. (1998) advocated trap-catch rate as an index of ferret abundance. Contractors collect this information as they undertake kill-trapping, so it comes at little extra cost.

3. Objectives

1. Develop a method that will accurately measure ferret population density and be capable of differentiating between densities of 2 km^{-2} and 4 km^{-2}, by:
    - evaluating a new simulation-based approach for estimating density using existing capture-recapture data
    - conducting field trials to test the method against a known population determined by removal of ferrets from a large area
    - writing a protocol and software for general use of the new capture-recapture methods, and publishing results in a peer-reviewed journal
2. Calibrate ferret density against a cheaper index of abundance (trap-catch rate)

4. Methods

4.1 Field procedures

We worked alongside four ferret control operations at Cluden, Tarras, Bendigo, and Poolburn in central Otago between February and May 2003 (the same operations reported in project R-10591 “Cost-effectiveness of alternative ferret control practices”). We divided the operations into 11 blocks (Cluden 1, 2567 ha; Cluden 2, 2313 ha; Cluden 3, 2061 ha; Tarras 1, 1426 ha; Tarras 2, 1614 ha; Bendigo 1, 2489 ha; Bendigo 2, 2629 ha; Bendigo 3, 1763 ha; Poolburn 1, 2759; Poolburn 2, 2351 ha; Poolburn 3, 3019 ha). On each block, we captured, marked (using numbered ear tags), and released ferrets over 6 consecutive nights of trapping. Each animal was tagged in both ears so that its identity could be determined even if it lost one tag. We set 116–169 Holden traps (Supplier: Michael Holden, Ram Paddock Rd, RD2 Amberley) baited with fresh rabbit meat (replenished if it dried out), and spaced 165–262 m apart. We recorded the identity and location of all ferrets caught.

There are two approaches to estimating density over a large area. One is to position traps (or clusters of traps) at random and to extrapolate from this sample of sites to the larger area. The extrapolation is statistically valid if placement is random. The alternative approach is to position traps so that they sample the larger area, in the sense that all animals are at risk of capture. We used the second approach in our field trials, relying on almost complete coverage rather than extrapolation from a sample of sites. Most traps were set along tracks and along accessible ridges, but we tried to ensure no point within the convex perimeter of the area was more than 300 m from a trap. The fraction of area 'exposed to traps' by this criterion always exceeded 50%. At only one site was more than 5% of the enclosed area more than 500 m from a trap (about 10% at the 'Bendigo 2' site). The project would have been unworkable if we had not taken advantage of easy terrain and tracks for most trap sites. By infilling wherever possible we greatly restricted the potential for selective trap placement to cause sampling bias. The sampling and extrapolation approach may be more appropriate for estimating average density across larger areas (e.g., Efford et al. submitted).

Four days after the live trapping, on average, contractors kill-trapped the blocks over 10–13 consecutive nights. Contractors placed 99–201 traps spaced 172–332 m apart along lines on tracks and accessible ridges. They placed most of their traps within the boundaries of the live-trapped area, but did not know where the live-traps were set. They generally used the same tracks and ridges but there was never precise overlap in where traps were set. Traps were baited with fresh rabbit meat and replenished when needed. Victor traps (placed inside tunnels) were used at Bendigo and Poolburn. Timms traps were used at Cluden and Tarras. Contractors killed every ferret they caught, and recorded tag numbers and the locations of tagged and untagged ferrets.

We attempted to verify empirically the DENSITY estimates on four blocks partly bounded by natural barriers to ferrets. These blocks received additional kill-trapping for 5–8 nights, 2-20 days after the initial kill-trapping. The total number of ferrets killed was assumed to be a close approximation of the number actually present. We checked for residual ferrets on two of these blocks using a dog specially trained for finding mustelids.

4.2 Density estimation

We used program DENSITY to estimate jointly the population density (D ferrets km^{-2}) and two parameters of individual capture probability, magnitude ($g0$) and spatial scale (sigma σ). As this is a new way to analyse capture-recapture data, we therefore first provide some background.

As a trap is moved away from an animal's home range centre it becomes less likely to catch the animal. This relationship is given by the 'detection function'. We mostly fitted a half-normal detection function with parameters $g(0)$ (the probability of capture in a trap at the home range centre) and σ (the spatial scale over which capture probability declines) (Fig. 1). These parameters are not measured directly but are estimated from the field data. The scale parameter σ is related to the home range radius: a circle of radius 2.45σ is expected to include 95% of activity for a circular normal home range.

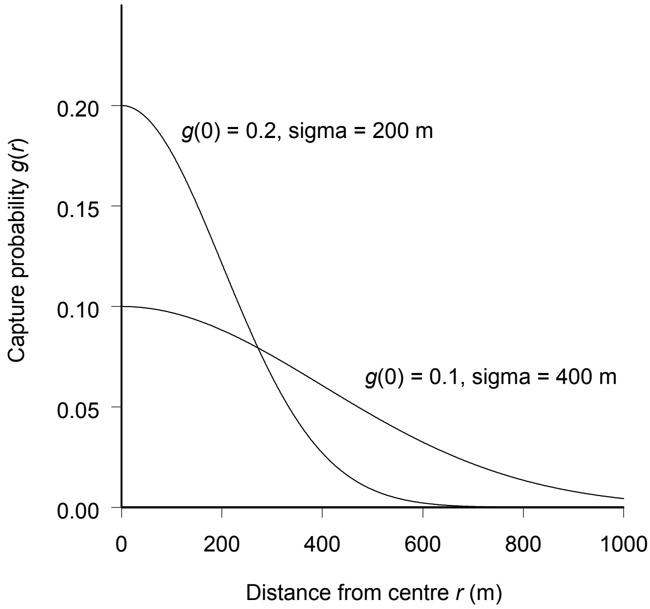

Fig. 1 Examples of half-normal detection functions for two animals with different home range sizes.

To test whether our choice of the half-normal detection function influenced the results, we also calculated density with a step detection function, which has a uniform probability of capture out to a fixed radius and zero probability beyond there. The step function, like the half-normal, has two parameters (‘height’ and ‘radius’).

The three parameters (*D* and the two detection function parameters) were estimated jointly by the statistical method of simulation and inverse prediction in program DENSITY. Inverse prediction uses statistics that are easily calculated from both field data and simulated data as surrogates for the parameters we wish to estimate. Each surrogate has a positive and increasing relationship with a particular parameter throughout its range. We used an estimate of population size ($\hat{N}$, using one of the many established estimators for ‘closed’ populations) as a surrogate for *D*, the corresponding mean capture probability ($\overline{p}$) as a surrogate for $g(0)$, and the square root of the pooled variance of the x and y coordinates of capture locations (RPSV) as a surrogate for σ.

Here we provide technical details of the program settings we used for the ferret analyses. All simulations assumed a Poisson (random) 2-dimensional distribution of the home range centres of a known number of ferrets. Range centres were simulated in an arena extending 2.5 km east, west, north and south beyond the outermost traps. This was likely to contain all potentially trappable animals. The method works by successive approximation and therefore required a set of plausible starting values for the parameters. A multivariate linear model was fitted to simulated data for parameter combinations spanning ±10% of the starting values.

The starting values themselves were obtained by an automatic algorithm in DENSITY, although as the starting value for $g(0)$ tended to be too large it was multiplied by an 'adjustment factor' of 0.3 (Efford et al. 2004). Enough simulations were performed and averaged for each parameter combination so that the CV of the mean of each statistic ($\hat{N}$, $\overline{p}$ and RPSV) dropped below 1%. Choice of a closed population estimator for $\hat{N}$ can affect the final estimate of D, but it is not as critical as in conventional analyses (Efford 2004). We took a conservative approach to estimator selection, and used Chao's second coverage estimator for model M_{th} (Otis et al. 1978). This yielded somewhat larger estimates of D with lower relative precision than was obtained from trials with the maximum likelihood estimator for the null model M_0 (unpubl. results), but it probably protects density estimates from unmodelled temporal and individual variation in capture probability. The mean distance between successive captures of individuals was used as a surrogate for σ in previous work (Efford 2004; Efford et al. 2004), but we substituted RPSV because it appeared to be more robust to breaches of home-range assumptions.

We performed two parallel density analyses for each block: one on the Landcare Research capture-recapture data alone, and the other combining these data with the removal data from the ferret control contractors (next section).

Combining live-trapping and kill-trapping

Kill-trapping by contractors provided an additional source of recapture information on tagged animals in each of our live-trapping studies. In principle, better estimates of absolute density might be obtained by combining the live-trapping and kill-trapping data. DENSITY was modified to accept composite data. However, we discovered technical obstacles to combined analysis. No conventional closed population estimator is strictly applicable to both types of data because of the switch of trap types, trap locations, and release of live ferrets versus removing them. To get around these problems we tried pooling data from each phase into a single sample and applying the 2-sample null model for $\hat{N}$ (known as the Lincoln-Petersen estimator). We also analysed the combined data treating each day as a separate sampling occasion, but using the number of individuals caught instead of the closed population estimates as the surrogate for D for inverse prediction.

Our measure of precision was the standard error of the density estimate, adjusted to remove the expected Poisson spatial variance (SE_{ADJ}; Efford 2004; Appendix 2). This measure of error appears the most useful. The unadjusted standard error would be appropriate for inference about the density of a notional infinite 2-D population of ferrets. But this is of little relevance to ferret controllers whose main interest will be in the density of ferrets in particular areas of about 1000–3000 ha. The adjustment reduced the width of our 95% confidence intervals for local density ($\hat{D} \pm 2SE_{ADJ}(\hat{D})$) by a factor of 0.74 (SE 0.04) compared with intervals that included spatial variance.

Relative precision was estimated as $CV(\hat{D}) = 100 * SE_{ADJ}(\hat{D}) / \hat{D}$. Small values of $CV(\hat{D})$ indicate high precision.

It is possible for estimates to be precise but to lack accuracy because they show a consistent tendency to be higher or lower than the true value. This tendency is called bias. The percent relative bias of a density estimate $\hat{D}$ is given by $RB = 100*(\hat{D}-D)/D$, where D is the true density. Relative bias can be estimated when the true density is known, such as in a simulation experiment.

Assumptions

We detail the assumptions of the inverse prediction method in Appendix 2. In general we believe these are met sufficiently well to justify the use of the method for ferrets. Tests applied to the ferret data revealed a systematic breach of one assumption in the model (Appendix 2: Assumption 7 – 'capture does not affect the probability of recapturing an animal in the same trapping session, or its movement patterns'). Simulations were performed to determine the effect of breaches of assumptions on the estimates. The results were essentially reassuring – effects were minor. The issue is not considered further in this report.

The assumption of population closure during trapping was probably not met in all cases, particularly when we combined live-trapping and kill-trapping. This has consequences for the reliability of the estimates we discuss later.

Inferred strip width

Our method yields a density estimate directly, without first estimating a boundary strip width and an effective trapping area. However, as other workers have used boundary strips and effective trapping areas, it was interesting to ask 'What strip width *W* would have been needed to obtain the estimated densities?' The DENSITY software calculates the 'inferred strip width' numerically (i.e. by searching for the *W* required to give an effective trapping area *A* that would have yielded the measured density with the closed population estimate $\hat{N}$, using $D = \hat{N}/A$).

There are two options for applying a boundary strip to the trap locations. The first option ('convex polygon' in DENSITY) includes a buffer around the convex hull of the outermost traps and all interior points. This may include interior points that are further than *W* metres from a trap. The alternative option ('concave polygon' in DENSITY) is to buffer around the individual trap sites. The resulting perimeter is typically concave in places, and only points that are less than or equal to *W* metres from a trap are included. We used the concave option for all area calculations.

4.3 Empirical verification

We attempted to verify the capture-recapture density estimates empirically on four blocks (two on Cluden, one on Bendigo, and one on Poolburn) partly bounded by natural barriers to ferret movements (lakes and rivers). We did this by asking contractors to return to the blocks for another 5–8 nights, 2-20 days after their initial trapping in order to "mop-up" any remaining ferrets. The total number of ferrets killed was assumed to be a close approximation of the number actually present.

Eleven days later, we tested for the presence of residual ferrets on the two Cluden blocks by using a dog that was specially trained for finding mustelids. Scott Theobald and his dog, "Tui", walked the sites for 9 days and recorded the number of ferrets found. The "effective detection areas" of the dog were calculated by measuring the length of the paths walked (using a GPS held by Scott) and multiplying them by the width of the strip over which the dog worked (about 50 m in this case). The 74-km path walked by Scott and Tui is shown in Fig. 2.

Fig. 2 Dots indicate the 74-km path walked by Scott and Tui on the Cluden 2 and Cluden 3 sites while searching for ferrets after an extended control operation. Grid cells are 1 km^2.

4.4 Calibrating density with the trap-catch index

We regressed our estimates of ferret density against contractors' trap-catch rates (i.e. number of ferrets caught per 100 trap nights). We corrected trap-catch for capture of non-target species, and for traps that were set off (including those that caught a ferret), by assuming that such traps were unavailable to ferrets for half a night and subtracting this from the denominator (the total number of trap nights) (Nelson & Clark 1973). We derived three regressions: ferret density versus trap-catch rate during the first night of trapping, during the first 3 nights of trapping, and during the first 5 nights of trapping.

4.5 Simulations with varying trap spacing, trap number and trapping duration

We conducted simulations with varying trap spacing, trap number, and trapping duration to determine the effect on the precision of density estimates and to provide a basis for a protocol. Trap spacing and number were varied within a fixed area (3 km x 6 km = 18 km^2). The simulated population was randomly (Poisson) distributed at a density of 5 km^{-2} in an arena of 54 km^2 that extended 1.5 km beyond the traps in all directions. The detection function was assumed to be half-normal with $g(0) = 0.1$ and $\sigma = 400$m. The analysis used the RPSV measure of home range and the null model (M_0) closed population estimator. The M_0 estimator was preferred to the Chao's coverage estimator for M_{th} because it could be calculated for all data sets, even when trapping was for only 2–3 days, and because the simulated data did not include extraneous sources of heterogeneity.
The three separate simulation experiments were designed as follows:

Trap spacing

A constant number of traps (120) was arranged in 3, 4, 5, 6, 8, 10, or 20 parallel rows, yielding spacings of 77, 103, 130, 158, 214, 273 and 316 m, respectively. Live trapping was simulated over 5 days.

Trap number

Traps were placed on parallel lines at a constant spacing of 200 m along lines (16 per line). The number of traps (48, 80, 112, 144, 176, 208, 240) was varied by changing the number of lines. Live trapping was simulated over 5 days.

Duration of trapping session

Traps (N = 128) were placed on 8 parallel lines at a spacing of 200 m along lines. Live trapping was simulated over 2, 3, 4, 5, 6, 7 and 8 days.

Ideally, these simulations would use a geometry of trap lines that matched that in the field (i.e. a network of lines mostly running along tracks and open ridges), but we know of no computer algorithm that could generate the required variation in trap number and spacing within a constant area. We believe our idealised rectangular trap layouts captured the major effects on precision of varying trap number and spacing. The geometry of trap lines also influences coverage of the target area and representativeness, which we consider a separate issue.

5. Results

5.1 General

Ferret density ranged from 0.8 to 6.9 km^{-2} between sites (Table 1). Detection parameters were quite variable between sites – the more than 2-fold variation in σ (a linear measure of home range size) indicates a more than 4-fold variation in home-range area. Home range area was negatively correlated with density – ferrets movements were more restricted where densities were high, and vice versa (Fig. 3). There was no relationship apparent between density estimates and the time of year the data were collected.

Table 1 Ferret population density estimated from analysis of 6 days of capture-recapture data in program DENSITY between February and May 2003. *g*(0) and σ are detection parameters explained in the text. Standard errors (in parentheses) and confidence intervals for density were adjusted to exclude spatial variance.

Block	No. animals tagged	No. recaptures	Density (km^{-2})	95% confidence interval for density	*g*(0)	σ m
Tarras 1	52	76	4.7 (0.6)	3.4–6.0	0.105 (0.022)	305 (20)
Tarras 2	46	63	2.6 (0.4)	1.8–3.5	0.049 (0.013)	525 (41)
Bendigo 1	109	187	4.8 (0.3)	4.2–5.4	0.216 (0.031)	327 (13)
Bendigo 2	62	79	1.5 (0.2)	1.1–1.9	0.037 (0.009)	765 (73)
Bendigo 3	73	141	3.9 (0.3)	3.2–4.5	0.163 (0.034)	355 (22)
Cluden 1	118	98	6.9 (0.9)	5.2–8.7	0.048 (0.010)	402 (24)
Cluden 2	64	27	6.4 (1.7)	3.1–9.8	0.030 (0.010)	323 (40)
Cluden 3	43	21	3.8 (1.1)	1.6–6.0	0.014 (0.006)	439 (75)
Poolburn 1	78	73	3.4 (0.4)	2.7–4.1	0.082 (0.016)	392 (24)
Poolburn 2	30	39	0.8 (0.2)	0.5–1.1	0.040 (0.018)	791 (117)
Poolburn 3	63	101	2.0 (0.2)	1.7–2.3	0.087 (0.016)	503 (26)

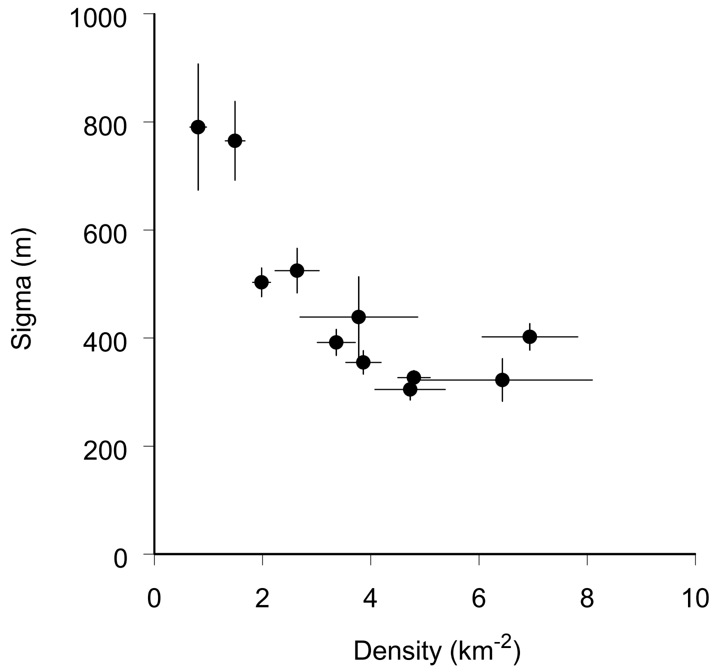

Fig. 3 Relationship between estimates of σ, a linear measure of home-range size (a circle of radius 2.45σ is expected to include 95% of activity for a circular normal home range), and ferret population density (± 1 SE). Each point represents a separate population (data in Table 1).

From the estimated densities we inferred the effective area of each trap layout, and from that area the width of the boundary strip that would have given an unbiased estimate in a conventional calculation of density ($D = \hat{N}/A$). Inferred strip widths W ranged from 170 to 1326 m (mean 627 m, SE 109 m). We report W with the warning that it depends on the closed population estimator (here Chao's second coverage estimator for M_{th}). This is because the retrospective method of calculation effectively uses W to adjust for *all* biases in $\hat{N}$ and A that affect D, not just those in A, and the amount of bias varies between closed population estimators. There was a high correlation between W and σ (r = 0.96), but W was not just a multiple of σ (i.e. the linear relationship $W = 2.05\sigma - 327$ did not pass through the origin).

5.2 Precision of density estimates

The relative precision of the density estimates CV($\hat{D}$) ranged from 6% to 29%. Precision was tightly (and inversely) correlated with the number of recaptures (Fig. 4). The greater the number of recaptures, the greater the precision. Precision improved sharply up to about 40 recaptures (CV($\hat{D}$) = 0.20) and improved more gradually thereafter. There were relatively few recaptures on the second day of each trapping session, when the pool of tagged animals was still small, but from Day 3 to Day 6 numbers were reasonably steady at most sites (Table 2). The total number of tags returned by contractors was usually less than the number of animals recaptured in the final 2 days of live trapping.

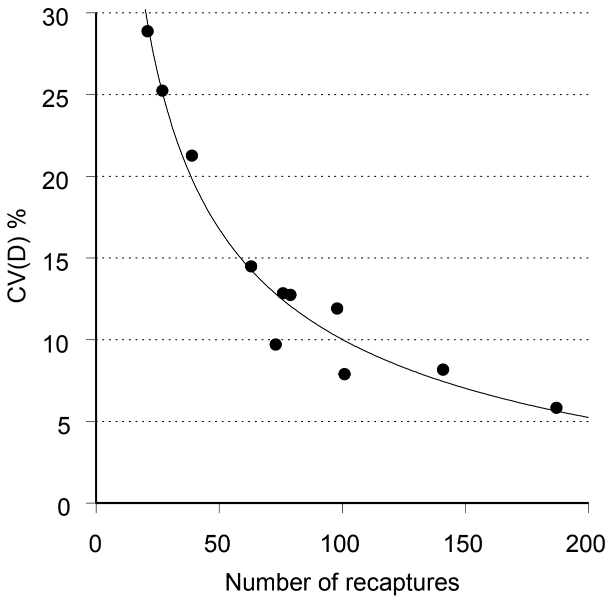

Fig. 4 Precision of ferret density estimates as a function of the number of recaptures over 6 days of live trapping. Curve $y=163x^{-0.5} - 6.3$ was fitted by non-linear least squares (r^2 = 0.96).

Table 2 Daily number of recaptures of previously tagged animals during a 6-day live trapping session and in follow-up control operations. Recaptures during control exclude tagged immigrants. * Incomplete tally.

Block	**Recaptures during live trapping**					**Recaptures during control**
	Day 2	**Day 3**	**Day 4**	**Day 5**	**Day 6**	
Tarras 1	9	19	17	17	14	17
Tarras 2	5	13	12	16	17	27
Bendigo 1	23	35	43	43	43	>48*
Bendigo 2	9	9	14	22	25	35
Bendigo 3	9	21	32	38	41	47
Cluden 1	12	18	20	19	29	46
Cluden 2	1	3	6	7	10	15
Cluden 3	4	2	4	9	2	11
Poolburn 1	4	10	15	25	19	51
Poolburn 2	3	11	11	14	–	17
Poolburn 3	5	18	24	26	28	12
Total	**84**	**159**	**198**	**236**	**228**	**>326***

5.3 Combined live-trapping and kill trapping data

Density estimates derived by combining the live-trapping and contractor kill data exceeded those from live-trapping alone in seven out of ten cases, and the difference was significant overall (paired t-test $t = 2.5$, df = 9, $P = 0.03$) (Fig. 5). We suggest the difference is probably due to a positive bias in estimates from the combined data due to population turnover in the extended period of data collection. Similar indications of positive bias were found in other analyses of the combined data, including those using pooled data (2-sample Lincoln-Petersen estimates) and the null model closed population estimator (unpubl. results).

Relative precision of the combined estimates (mean CV($\hat{D}$) 7.2%, SE 1.3%) was only slightly better than that for the live-trapping data alone (mean CV($\hat{D}$) 8.7%, SE 2.1%). (These estimates are lower than those given previously (Section 5.2) because they were calculated using number of individuals rather than Chao's estimator as the surrogate for D in inverse prediction). Precision of combined estimates based on the 2-sample Lincoln-Petersen estimates was poor (mean CV($\hat{D}$) 20.2%, SE 2.4%).

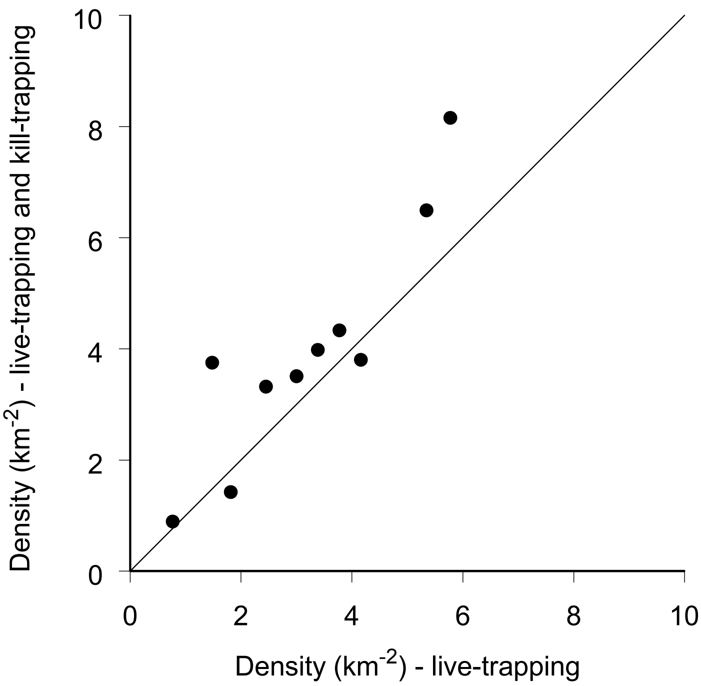

Fig. 5 Relationship between ferret density estimates based on live trapping only and on live trapping followed by kill trapping. Points should lie on the line $y=x$ if estimates are comparable. There was no estimate for the 'Bendigo 1' site because of incomplete tag returns.

5.4 Robustness to choice of detection function

Density estimates based on the step (uniform) detection function did not differ systematically from those obtained with the default half-normal curve (paired t-test $t = 1.28$, df = 9, $P = 0.23$) (Fig. 6). There was a very close correlation ($r = 0.998$) between the two methods.

Although the step function estimates had slightly higher relative precision (mean CV($\hat{D}$) 12.9%, SE 2.4%) compared with half-normal estimates (mean CV($\hat{D}$) 14.4%, SE 2.3%), the difference was not statistically significant. We used the half-normal estimates because these are the default in program DENSITY.

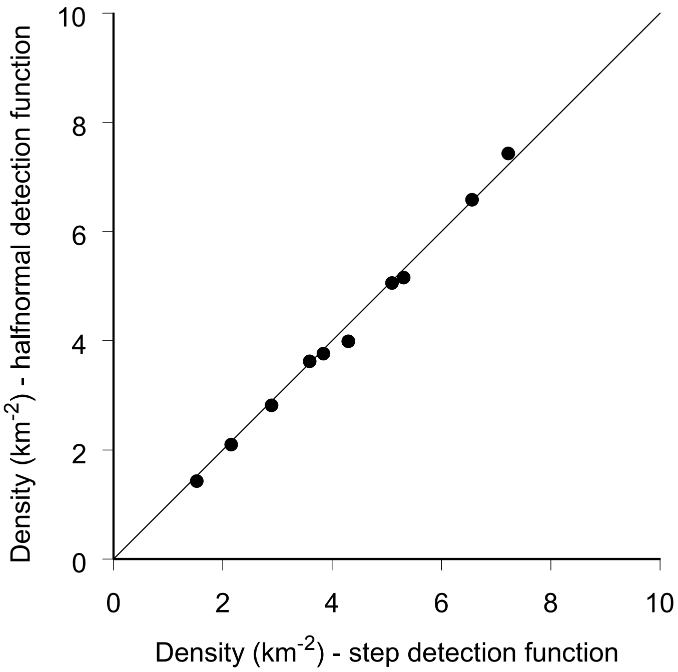

Fig. 6 Comparison of density estimates obtained by fitting half-normal and step (uniform) detection functions. No step function estimate could be obtained for the 'Poolburn 2' site.

5.5 Empirical verification

Four of the 11 sites were subjected to intensive removal of ferrets for 15–20 days. The total numbers removed were converted to approximate densities by dividing them by the contractors' effective trapping areas (calculated by adding a 500m-wide buffer strip (the average home range width of a ferret radio-tracked in this habitat throughout the year – Norbury et al. 1998) to every trap site. Adding a fixed buffer strip is the conventional means of deriving effective trapping area. These estimates were poorly related to those obtained from live trapping and inverse prediction (Table 3). Later, we discuss the problems with this method of verification. The relationship improved overall if we added an inferred buffer strip width which varied between sites according to the equation W = 2.05σ – 327 (Table 4).

Many ferrets were found by the dog after the removal phase. When extrapolated to the area trapped by contractors, the numbers remaining were at least the same as those removed by contractors. Extrapolation is sensitive to our figure for the area swept by the dog.

Table 3. Comparison of ferret densities (km^{-2}) estimated by inverse prediction in program DENSITY (Density 1) with empirically derived estimates of density based on the total number of ferrets removed by exhaustive trapping (Density 2, four sites only), plus the number detected by a trained dog (Density 3, two sites only). The number of ferrets removed by contractors is divided by the contractor's (CON) effective trapping area, *calculated by adding a 500m-wide buffer strip (the average home range width of a ferret radio-tracked in this habitat throughout the year – Norbury et al. 1998) to every trap site*. This produced a 'concave polygon' for each area. * removal period cut short by 2 days.

Block	**Capture-recapture data**	**Removal and detection data**								
	Density 1	No. removed over 9–12 days (A)	No. removed over further 5–8 days (B)	CON effective trapping area (km^2) (C)	**Density 2 (A+B)/C**	No. detected by dog (D)	DOG effective detection area (km^2) (E)	Residual density according to dog (D/E) =F	No. detected by dog, extrapolated over trapped area (F×C) =G	**Density 3 (A+B+G)/C**
Bendigo 2	**1.5**	93	17	21.70	**5.1**	–	–	–	–	**–**
Poolburn 3	**2.0**	14	12*	42.07	**0.6**	–	–	–	–	**–**
Cluden 3	**3.8**	29	28	26.12	**2.2**	6	1.62	3.7	97	**5.9**
Cluden 2	**6.4**	66	42	29.09	**3.7**	8	2.06	3.9	113	**7.6**

Table 4. Comparison of ferret densities (km^{-2}) estimated by inverse prediction in program DENSITY (Density 1) with empirically derived estimates of density based on the total number of ferrets removed by exhaustive trapping (Density 2, four sites only), plus the number detected by a trained dog (Density 3, two sites only). The number of ferrets removed by contractors is divided by the contractor's (CON) effective trapping area, *calculated by adding an inferred buffer strip width (which varied between sites according to the equation $W = 2.05\sigma - 327$) to every trap site*. This produced a 'concave polygon' for each area. * removal period cut short by 2 days.

Block	**Capture-recapture data**	**Removal and detection data**								
	Density 1	No. removed over 9–12 days (A)	No. removed over further 5–8 days (B)	CON effective trapping area (km^2) (C)	**Density 2 (A+B)/C**	No. detected by dog (D)	DOG effective detection area (km^2) (E)	Residual density according to dog (D/E) =F	No. detected by dog, extrapolated over trapped area (F×C) =G	**Density 3 (A+B+G)/C**
Bendigo 2	**1.5**	93	17	40.87	**2.7**	–	–	–	–	**–**
Poolburn 3	**2.0**	14	12*	50.30	**0.5**	–	–	–	–	**–**
Cluden 3	**3.8**	29	28	29.03	**2.0**	6	1.62	3.7	107	**5.7**
Cluden 2	**6.4**	66	42	20.01	**5.4**	8	2.06	3.9	78	**9.3**

5.6 Simulations with varying trap spacing, trap number and trapping duration

The effects of varying trap spacing, trap number, and trapping duration on the precision of density estimates are shown in Figs 7–9. Poor precision at close trap spacings (<100 m; Fig. 7) is slightly counterintuitive. This result is probably a side effect of lower trap coverage. Because total trap number was held constant, layouts with traps close together sampled less of the habitat, marked fewer animals, and provided fewer recaptures. Varying trap spacing in the range 150–300 m had little effect on precision.

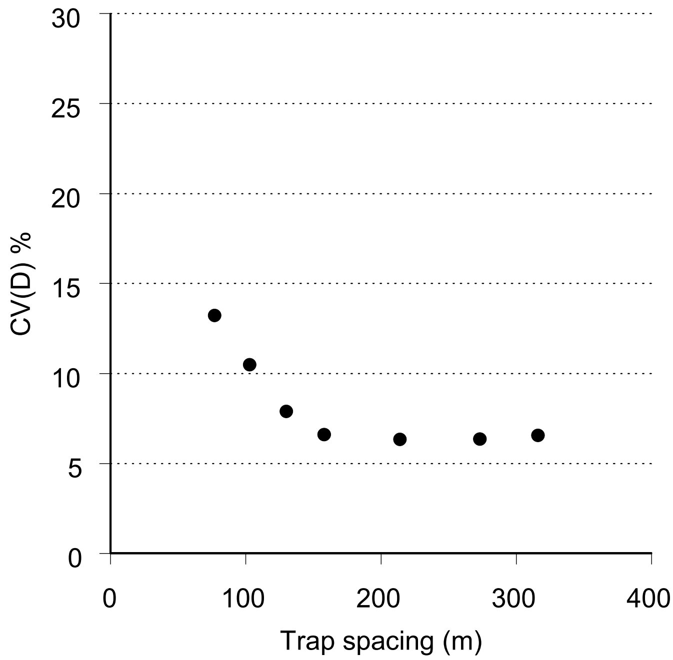

Fig. 7 Effect of simulated trap spacing on the relative precision of estimated ferret density. Population parameters D = 5 km^{-2}, $g(0)$ = 0.1, σ = 400m. We used 120 traps spanning 18 km^{2}. Each point is the average of 100 simulations for a given trap spacing.

Relative precision improved as more traps were used (Fig. 8). Most of the gains in precision were made by using at least 150 traps. High precision (CV($\hat{D}$) < 5%) was achieved when more than 150 traps were used (i.e. about 8 traps km^{-2}).

Relative precision was poor with 2 and 3 days of trapping (CV($\hat{D}$) > 10%), and improved only gradually with more than 5 days of trapping (Fig. 9).

We did not critically evaluate bias as this would have required a much larger set of simulations, but we note that the average relative bias in the three simulation experiments was –2%, –1%, and –2% respectively. These figures are very small and are consistent with the lack of bias in other trials of the method (Efford 2004).

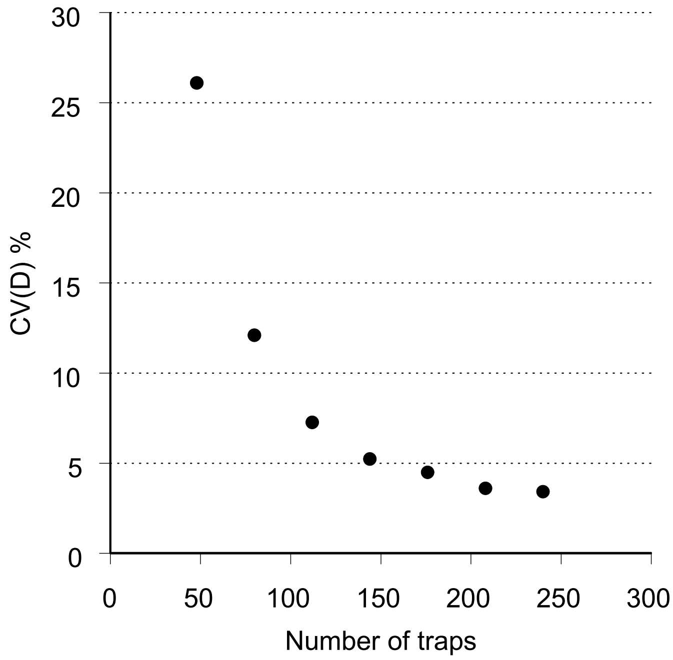

Fig. 8 Effect of simulated trap number on the relative precision of estimated ferret density. Population parameters $D = 5\ \mathrm{km}^{-2}$, $g(0) = 0.1$, $\sigma = 400\mathrm{m}$. Traps were on parallel lines within an 18-km^2 rectangle at a constant spacing of 200 m along lines. Each point is the average of 100 simulations for a given trap number.

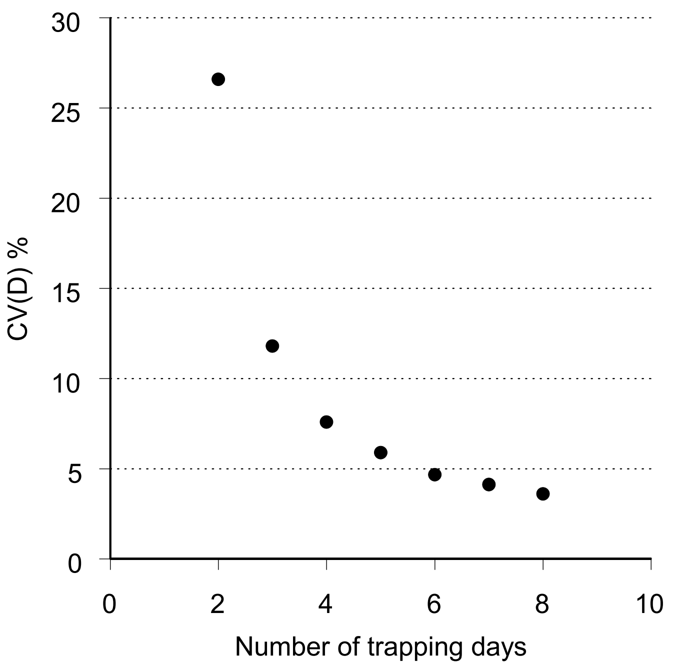

Fig. 9 Effect of simulated trapping days on the relative precision of estimated ferret density. Population parameters $D = 5\ \mathrm{km}^{-2}$, $g(0) = 0.1$, $\sigma = 400\mathrm{m}$. We used 128 traps on parallel lines within an 18-km^2 rectangle at a constant spacing of 200 m along lines. Each point is the average of 100 simulations for a given number of days.

5.7 Calibrating density with the trap-catch index

Trap-catch rate performed very poorly as an index of ferret density across sites, regardless of the number of nights used to calculate catch rate (Fig. 10).

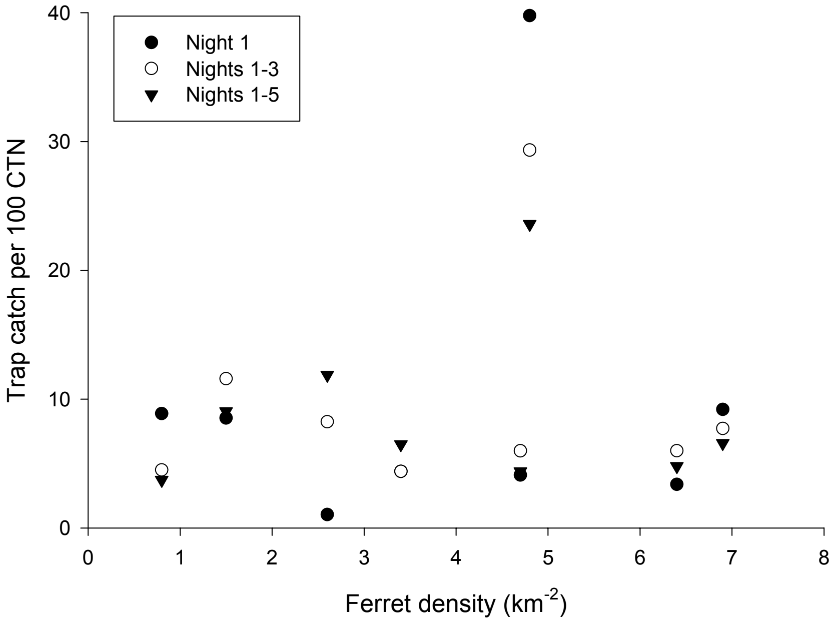

Fig. 10 Trap-catch rate of ferrets during the first night, the first 3 nights, and the first 5 nights of kill-trapping by contractors, versus the density of ferrets estimated beforehand.

6. Discussion

6.1 Accuracy

Accurate measurement of animal density is difficult. The conventional approach is to estimate abundance based on one of many closed population estimators, and to divide this by the area from which animals were trapped. Moller et al. (2002) took this approach for estimating ferret density in New Zealand. Effective trapping area is difficult to define and to measure accurately. It is usually estimated by taking the size of the trapping grid and adding a buffer strip of half an average home-range width (W). While this method has a long history, its theoretical foundations are weak and it cannot be assumed to produce reliable estimates (e.g., Williams et al. 2002). There are usually too few data for an accurate estimate of W and the confidence intervals for density are underestimates because they omit this source of uncertainty. Unreliable estimates are a particular problem when trying to detect small differences at low absolute density, as required by the Animal Health Board for ferrets (e.g., 2 km^{-2} versus 4 km^{-2}).

The home-range size of ferrets in our study varied inversely with density. This means that calculating effective trapping area with a constant boundary strip width is likely to cause a bias that varies with density. This is a strong reason to consider alternative approaches that integrate density estimation and detection function parameters using methods such as those demonstrated in this report.

For estimates of density to be accurate they should be unbiased and precise. From simulations we believe that the density estimates we report are largely free of serious bias (Efford 2004; this study). The more critical question is the cost of obtaining sufficient precision. The precision that can be achieved with a given trapping effort and trap layout may be predicted by simulating with preliminary parameter estimates in DENSITY. Our simulation experiments with various trapping designs suggest the design we chose for the field trials was a good compromise with respect to trap spacing, number of traps and duration. We therefore use our field design as the basis for a draft protocol for estimation of ferret density (Appendix 1).

Varying trap number and varying the number of trapping days gave almost identical patterns of precision in that doubling the number of traps was equivalent to doubling the number of trapping days. However, the difference is that with more traps better spatial coverage of an area can be achieved which protects against spatial variation in density.

Where the true density of ferrets is very low, few ferrets will be recaptured over 3–4 nights. This can lead to two problems: one, the density estimate will have a large coefficient of variation (e.g. 100% – although the estimate may still be less than a putative Tb threshold); and two, in the extreme, so few ferrets may be caught that no calculation may be made (this will often happen when there are <15 recaptures). In this extreme case, it may be necessary to 'borrow' information from other studies or sites. For example, with experience with a range of ‘lowish’ densities, it may be possible to predict $g(0)$ and σ with reasonable certainty. Then DENSITY can be used to simulate the probability of getting the observed (low) number of captures given a true population at the Tb threshold.

We originally proposed that tag returns by contractors might provide a cheap and usable source of recapture data. Two aspects of our results cause us to doubt this. First, density estimates based on the combined capture-recapture and removal data appeared to be biased upwards relative to those from the capture-recapture data alone. This is consistent with the high rates of dispersal movement and resulting turnover of local populations on the time scale of the combined studies (about 3–4 weeks) which, in turn, violated the closure assumption fundamental to our capture-recapture methods. Second, and perhaps related, the overall rate of tag return was low (<50%), again probably related to tagged ferrets dispersing out of the area. Once live traps have been positioned and run for long enough to tag a large sample of animals, the most efficient way of getting more recaptures is probably to continue live trapping for 1–2 days longer. There are also unsolved technical problems in the analysis of combined live and kill data, particularly the choice of closed population estimator.

6.2 Behaviour of the inverse prediction method

Many ferrets were recaptured at the site where they had just been released. This might conceivably be due to a very sharply peaked detection function centred on the site of initial capture, perhaps reflecting concentrated movements within a small core area of the home range. An intuitively more likely interpretation is that ferrets chose to re-visit sites where they had obtained food (bait). Our simulations showed this response must be very strong to explain the observed frequency of zero movements (>10-fold increase in site-specific capture probability (M. Efford unpubl. results). We call the effect a ‘learned site response’ and acknowledge that it is a violation of the model on which our estimates are based. However, simulations show that the effect on density estimates was small (about 1%; M. Efford unpubl. results).

Efford (2004) noted that further work is needed on model selection for the inverse prediction method. In the interim, sample coverage estimators for model M_{th} (Lee & Chao 1994) appear to yield inverse prediction estimates of density with a satisfactory trade-off between robustness and precision in many field situations (M. Efford unpubl. results).

We applied the sample coverage estimator for M_{th} to field data, but we simulated sampling designs with the null M_0 estimator. This potentially causes confusion in comparisons of precision, as estimates from M_{th} are consistently less precise than those from M_0. Our rationale for using M_{th} was that it provided protection from the unmodelled heterogeneity that is likely to be present in field data. The precision we report for field estimates of density (Fig. 4) was in consequence worse than the simulated precision (Figs 7–9). For a given number of recaptures in the range 50–200, the field $CV(\hat{D})$ averaged 64% (SE 3%) greater than the simulated $CV(\hat{D})$ (comparison based on fitted curves as in Fig. 4). Part of this difference is due directly to our use of M_{th} for field data, and part to the unmodelled heterogeneity itself.

Using M_{th} may prove to be unnecessarily conservative, in which case it would be logical to switch to M_0 for the analysis of field data. In the meantime it may be safer to report both estimates. Similarly, we found a step (uniform) detection function provided slightly better precision. If further trials show the coverage of confidence intervals is adequate, and they are narrower, then we would suggest a switch to using the step function rather than the half-normal function.

6.3 Verification of the inverse prediction method

New, untagged ferrets continued to be detected and removed at all sites throughout the control phase of the study. This is further illustrated by some recent data provided by the contractor who re-trapped the Bendigo 2 site last February (2004), 10 months after the site was initially trapped in April 2003. The initial trapping removed 93 ferrets in 10 days (Table 1), and the latest trapping removed another 65 ferrets in 11 days. Similar patterns were reported by Moller et al. (2002) for the Queensbury Hills and Pleasant Valley sites. Some of the later captures would have been residents that were hard to catch initially, but others would have been immigrants. Despite our choice of sites that were partly bounded by natural barriers, we know there was movement into and out of the sites. DENSITY estimates were based on 6 nights of capture-recapture data, and the removal phase involved trapping over an extended period when population 'closure' seems less likely (removal of ferrets may actually stimulate increased ferret movements). This made it very difficult to measure the true size of the populations by removing ferrets. It is also difficult to compare DENSITY estimates with removal estimates based on calculating an ad hoc boundary strip, for the reasons already outlined. Thus we were unable to say confidently whether the inverse prediction method of density estimation revealed true population density. Instead, we advocate the new method over conventional methods based on the arguments already outlined and on simulations using known population densities. Inverse prediction estimates of possum density have been verified by a field trial using a known population size (Efford et al. submitted). Further work is in progress looking systematically at the effects of breaches of assumptions on inverse prediction estimates.

6.4 Density resolution around a putative threshold for Tb maintenance

Caley and Hone (submitted) predicted a threshold density of ferrets that defines them as either spill-over hosts of Tb (where the disease dies out if external sources are removed) or maintenance hosts (where the disease is maintained without external sources). This threshold at peak annual density in February is estimated to be 5.0 km^{-2} (lower 95% confidence limit, 2.1 km^{-2}) but it has not been empirically verified and the value partly depends on the accuracy of the removal method used by Caley and Hone to estimate density. It is therefore premature to make judgements about whether a particular site contains ferrets that are above or below a threshold for Tb maintenance. Instead, we pose a more hypothetical question; if we needed to differentiate between densities of less than or greater than 3 km^{-2}, in how many cases would the precision of the estimates derived by inverse prediction allow us to categorise these densities? The 95% confidence intervals around each density estimate in Table 1 were sufficiently narrow to categorise 3 sites as definitely less than 3 km^{-2}, 5 sites as definitely greater than 3 km^{-2}, and 3 sites as uncertain. Uncertainty is partly because the populations themselves were very close to 3 km^{-2}, and does not necessarily reflect poorly on the method. Overall, this is a good result and shows the precision offered by inverse prediction is useful in an operational context. Future work on putative maintenance thresholds in ferrets should involve capture-recapture data using methods compatible with inverse prediction.

Despite the good result, we are not quite ready to advocate using DENSITY in all areas where ferret control is proposed to determine whether the density is likely to be sufficiently high for Tb to be maintained in the ferret population. Apart from the issue that the putative Tb maintenance threshold is not validated, our research does not provide a basis for answering questions about how the AHB should use the tool. That would require direct knowledge of the costs and benefits, and the acceptable risks of scoring an 'under threshold' population as ‘over threshold’ and vice versa. We do not have that knowledge at this point.

6.5 Trap-catch index

Trap-catch rate bore no relationship to population density when compared across sites. This comes as no surprise because trap-catch takes no account of site differences in trappability of animals. Cross et al. (1998), on the other hand, found a good correlation between trap-catch rate and ferret density. However, this study looked at a single population at one time, so it excludes many of the sources of variation that might undermine an index. The primary use of an index by the Animal Health Board is to detect differences in density across sites and over time. There is no evidence to support the use of trap-catch rate for this purpose. Moller et al. (2002) reached a similar conclusion.

Moreover, there is likely to be little cost efficiency in collecting trap-catch data over capture-recapture data. Although trap catch data are cheaper to collect than capture-recapture data because they are subsumed in control costs, this will only be the case if trap-catch data indicate that ongoing control is warranted.

6.6 Software

A preliminary version of software for density estimation by simulation and inverse prediction is available with documentation on the Landcare Research website (www.landcareresearch.co.nz/services/software/density). Some of the analyses reported here require a new version that will be documented and released in August 2004.

7. Recommendations

- Animal Health Board and its contractors should not consider the use of trap-catch indices for estimating ferret density to aid management decisions.
- Animal Health Board should adopt the use of the protocol for estimating ferret density detailed in Appendix 1. This will involve the need for training in the use of programme DENSITY.

8. Acknowledgements

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10. Appendices

Appendix 1 Density estimation protocol for general use

It is less important to standardise field procedures when estimating absolute density than it is when deriving an index of density. Standardisation is nevertheless useful to ensure that data are suitable for the intended use. We describe procedures to obtain live trapping data to provide inverse-prediction estimates of ferret density that will have sufficient precision to meet AHB's requirements, and that will adequately represent the area sampled.

1. Using a map of the area that indicates access along tracks, ridges and fencelines, assess whether comprehensive coverage can be achieved with the number of traps available. No areas should be further than 500 m from any trap. Special effort should be made to fill in areas that do satisfy this criterion.

2. If comprehensive coverage cannot be achieved, consider the feasibility of random sampling. Procedures for randomly sampling possum populations are outlined in the possum monitoring protocol (National Possum Control Agencies 2002). However, we appreciate that modifications will be required for ferrets, especially for live-capture and release. These modifications need to be built into a protocol for monitoring ferret populations as soon as possible.

3. Assuming an area of 1000–3000 ha:
   - use at least 100 traps (preferably 150)
   - space traps at about 200 m intervals (150–250 m)
   - continue trapping until 40–50 recaptures are obtained (this should happen after 3–4 nights on average, unless the density is very low)

4. Use live traps that are easy to use (we find Holden traps are ideal, although they are bulky). Use fresh rabbit meat as bait.

5. Tag ferrets in both ears (using the tags used for ferret research, available from the Department of Conservation) and release them. Contractors will require approval under the Animal Welfare Act to ear tag ferrets. Some agencies are not listed as exempt from this requirement. Landcare Research is currently looking into this for the Animal Health Board and contractors.

6. Record GPS coordinates of all trap sites, including those that did not catch any ferrets.

7. Record the identity and capture site of all ferrets.

8. Record non-target captures, sprung traps, and traps that were not set on a particular day.

9. Trapping of ferrets for density estimation is best done outside the peak period of juvenile dispersal, but when ferret trappability is still high. The months January, April and May provide a good compromise.

Appendix 2 Methods for estimating density

Conventional estimation of density

In principle, the absolute population density of free-ranging animals may be estimated by counting the number *N* in a known area *A* and forming the ratio $D = N/A$. For mobile animals the meanings of *N* and *A* are unclear. In practice, estimation of *N* by capture-recapture or removal trapping is plagued by problems of differential detection between animals, and we lack a sound theory for estimating *A*. Home-range data may be used informally to estimate *A*, but it is rare for the uncertainty in *A* to be included in the confidence intervals attached to *D*, although this can be done (Jett & Nichols 1987).

Density estimated from a spatial detection model

An alternative and radically different approach is to dispense with *N* and *A*, and to fit a model to trapping data that includes both density *D* and a spatial model of the trapping process (Efford 2004). By 'spatial model' we just mean an equation for the decline in capture probability $g(r)$ as a trap is moved further and further from the centre of an animal's home range. Here we assume that this relationship has two parameters, $g(0)$ and σ. The model is conceptually simple and adaptable to many trap configurations, but estimation is complicated and at present relies on computer simulation.

The detection model $g(r)$ is equivalent to that used in distance analysis (Buckland et al. 1993). However, here it is implicit in the trapping results, as we do not observe a sample of detection distances.

We jointly estimate the three parameters *D*, $g(0)$ and σ by an iterative process. By simulation we 'try out' combinations of *D*, $g(0)$ and σ to see whether they would lead to trapping data that are 'like' what we have observed. We use a standard way of summarising the trapping data (either from the field or from simulations) that captures information about *D*, $g(0)$ and σ (i.e. it can be relied on to change when (D, $g(0)$, σ) changes). The statistics we use to summarise trapping data are a conventional closed population estimate $\hat{N}$, the associated capture probability $\hat{p}$, and RPSV, the square root of the pooled spatial variance.

The search for parameter estimates (D, $g(0)$, σ) that best match the field data is formalised in a procedure called 'inverse prediction' (Pledger & Efford 1998; Efford 2004). We do not describe it here. Software and documentation is available at www.landcareresearch.co.nz\services\software\density. Inverse prediction also provides the variance-covariance matrix of the estimates, from which confidence intervals may be obtained.

Some details of how best to apply the method are still being worked out. In particular, our choice of the statistics ($\hat{N}$, $\hat{p}$ and RPSV) remains *ad hoc*. Although the actual value of $\hat{N}$ is not critical, it is important that it respond to underlying changes in *D* (when $g(0)$ and σ are constant). We have speculated this will best be achieved by a closed-population estimator that is robust to unmodelled (non-spatial) variation in capture probabilities. Our impression is that Chao's second coverage estimator for Otis et al.'s (1978) closed population model M_{th} performs well in most circumstances, although it has lower nominal precision than do models that make no allowance for individual heterogeneity. Model selection appears not to be critical (it causes only modest change in the estimate of density).

Assumptions and goodness-of-fit of spatial detection model for density estimation

The assumptions underlying the estimation of density with the spatial detection model are listed in Table A1.

Table A1. Assumptions of the new density estimation method.

1.	The population is closed (i.e. there are no births, deaths or dispersal events during a trapping session).
2.	Tags are not lost, and the identity and location of each animal is recorded accurately at each trapping occasion.
3.	Traps are set at known locations for a known time.
4.	Trap placement is random with respect to the location of animals.
5.	Animals occupy fixed and randomly oriented home ranges with a known spatial distribution (e.g., spatially random or even).
6.	Capture probability declines with distance from the range centre according to a known function (e.g., half-normal or step).
7.	Captures of an animal within a trapping session are independent events (i.e. capture does not affect the probability of recapturing an animal in the same session, or its pattern of movement).

Assumptions 1–4 are similar to those for any closed-population capture-recapture estimation (Otis et al. 1978). Assumptions 5 and 6 are needed to justify a specific spatial detection model. Assumption 7 is an extension of a common capture-recapture assumption that ensures recaptures provide information on home range size.

These assumptions are mostly satisfied in field studies of small mammals such as ferrets, with some exceptions that we will discuss. No overall goodness-of-fit test is yet available, but some assumptions may be evaluated for a particular dataset by specially designed statistical tests. We warn that such tests have three fundamental weaknesses (i) they are usually non-specific (i.e. they are conditional on other assumptions not being breached); (ii) they often lack power (not all failure is detected); and (iii) when they fail, the effect on the resulting estimates may be insignificant. Nevertheless, tests provide information to help ensure the methods are used appropriately.

Tests of assumptions

Assumption 1. Closure: Otis et al. (1978) provided a test of closure (no population turnover during trapping session). This test is also sensitive to temporal variation in capture probability and to 'learned trap response' in the Otis et al. terminology. An alternative test by Stanley and Burnham (1999) is designed to allow for temporal variation, but it is sensitive to heterogeneity among individuals. We therefore do not consider tests of closure to be useful here.

Assumption 6. Detection function: It is possible in principle to compare the distribution of observed recapture distances to those predicted by the nominated detection function. We expect this test will lack power because the sample size is usually small, and we have yet to implement it.

Assumption 7. Independence: We have devised two Monte Carlo tests for an effect of initial capture on distance to recapture. The first assumes that any effect decays rapidly with time, so the distances of recaptures after at least 2 time steps (days) differ from that of immediate recaptures (1 time step). The second evaluates whether the observed proportion of recaptures in which the animal returns to the same trap (i.e. distance moved = 0) is consistent with predictions from the simulation model. Both tests require estimates of the parameters $g(0)$ and σ, and usually these will be obtained by first fitting the model in DENSITY. More details will be provided in the online help with the next version of DENSITY.

Measure of precision

Inverse prediction yields a variance-covariance matrix for the parameter estimates (Efford et al. 2004). This may be used to obtain both confidence intervals for individual parameters and simultaneous confidence ellipses for pairs of parameters (Pledger & Efford 1998). In the case of density estimation, there is a further complication that some of the estimated sampling variance is due to the spatial variance in whatever 2-D process has been fitted. We used a Poisson model for home range centres. The variance in the number of range centres within some defined area of a Poisson process can be calculated given the area and the density of the process. If our interest is in the density of a particular patch within a notionally infinite 2-D distribution then it is sensible to adjust the sampling error by subtracting the irrelevant spatial variance. The one complication in this adjustment is that we do not initially know the area, and therefore what the Poisson variance in density is likely to be. However, we can infer the effective size of the trapping area (A) retrospectively from the population estimate N divided by the density estimate D ($A = N/D$). The spatial variance in D is then $D^2/\hat{N}$ (M. Efford unpubl. results). We therefore calculate an adjusted standard error for $\hat{D}$:

$$SE_{ADJ} = \sqrt{(\mathrm{var}(\hat{D}) - \hat{D}^2/\hat{N})}.$$