Estimating density of ship rats in New Zealand forests by capture-mark-recapture trapping

Deborah J. Wilson[1]*, Murray G. Efford[1,3], Samantha J. Brown[2], John F. Williamson[2] and Gary J. McElrea[1]
[1] Landcare Research, Private Bag 1930, Dunedin 9054, New Zealand
[2] Landcare Research, Private Bag 11 052, Palmerston North 4442, New Zealand
[3] Present address: Department of Zoology, University of Otago, PO Box 56, Dunedin 9054, New Zealand
* Author for correspondence (Email: wilsond@landcareresearch.co.nz)

Published on-line: 30 April 2007

Abstract: We developed a capture-mark-recapture protocol for measuring the population density (*D*) of ship rats (*Rattus rattus*) in forest. Either mesh cage traps or Elliott box traps were set at each of six sites (48 traps per site for 5 nights) in the Orongorongo Valley on two occasions in autumn 2003. Cage traps only were set at three sites in autumn 2004. Rats were caught much more readily in cage traps than in Elliott traps and none were recaptured in Elliott traps. Additional food, bedding and trap covers reduced mortality and interference with traps. To estimate density we fitted a spatial detection model; this method avoids the need to estimate effective trapping area. Estimates were based on both a model assuming equal capture probability ($\hat{D}_0$) and a model incorporating temporal and individual variation ($\hat{D}_{th}$). Our target for precision was CV($\hat{D}$) ≤ 20%, but when data were pooled from multiple sites with cage traps, CV($\hat{D}_{th}$) was ~30%. Estimated density of rats ($\hat{D}_{th}$) was 5 ha^{-1} in 2003 and 9 ha^{-1} in 2004; these estimates did not differ significantly. The overall capture index in 2004 was 31 rats per 100 corrected trap-nights on snap-trap lines set after live trapping. House mice were caught in both types of live trap, but at rates high enough for density estimation only where Elliott traps were used.

Field estimates of detection functions for rats captured with cage traps allowed us to simulate the performance of alternative trapping systems. We predict that a 64-trap layout at three sites with five trapping occasions would yield acceptable precision of $\hat{D}_{th}$ (20–23%) at the observed rat densities. Our use of $\hat{D}_{th}$ was conservative; slightly higher precision may be achieved by assuming constant trappability ($\hat{D}_0$), and future work may justify this assumption.

Keywords: density estimation; inverse prediction; *Rattus rattus*; small mammals

Introduction

Introduced ship rats (*Rattus rattus*) are widespread and common in New Zealand lowland podocarp–broadleaved forests, where they prey on invertebrates and birds (Innes 2005). Methods are needed to estimate the density of ship rat populations in forests to describe, model and predict the population dynamics of rats for conservation management and ecological research. Indices of the relative density of ship rats based on kill trapping or on tracking rates in ink tunnels are commonly used in New Zealand (Cunningham & Moors 1996; C. Gillies and D. Williams, Department of Conservation, pers. comm., 2002), requiring the strong assumption that each index bears a constant relationship to density. In fact, the relationship between these indices and density is not known. Snap traps and tracking tunnels are usually placed on lines, and rats must (1) encounter the device and (2) interact with it in order to be recorded. Index values therefore depend on both these behavioural processes, although neither is usually observed. Encounter rates potentially vary with home-range size, habitat structure, and activity; home ranges of ship rats in New Zealand forests appear highly variable in size (Dowding & Murphy 1994; Pryde et al. 2005). Interaction rates probably depend on weather, hunger, experience (age), and perhaps other unknown factors. These complexities may explain why index values are often confusing and contradictory (Blackwell et al. 2002).

The formal alternative to relative index methods for cryptic small mammals has long been to estimate absolute population size N (Otis et al. 1978; McKelvey & Pearson 2001) by removal trapping or capture-mark-recapture (CMR) live trapping (Otis et al. 1978), usually on a grid of traps. However, the population on a trapping grid is usually not closed, because animals routinely move back and forth across the edge, and the size of the population at risk of capture is therefore defined only vaguely (White et al. 1982). Recently it has been shown that the problem of edge effect can be solved by fitting a spatially explicit detection model allowing for the home-range movements of animals (Efford 2004). In addition to absolute density (D, the expected number of animals per unit area), the model has parameters that correspond to the two behavioural components of detection mentioned above: encounter and interaction.

The density of ship rats has been estimated in New Zealand forests by relating an estimate of the population of nearby animals (N) to an effective trapping area (A) calculated as the trapped area plus a boundary strip equal to average home-range radius (Dice 1938). To estimate N, New Zealand researchers have used the minimum number known to be alive (MNA; Krebs 1966) from live-trapping studies (Daniel 1972; Innes 1977; Hickson et al. 1986) or from combined live and kill trapping (Hooker & Innes 1995), or a Zippin estimate [the maximum likelihood estimator for capture-recapture model M_b, where 'b' indicates a behavioural response to trapping (Otis et al. 1978)] from removal trapping (Brown et al. 1996; Blackwell et al. 2002). Home ranges were estimated by radio tracking or from capture locations. The methods used to estimate N and A have known limitations that compromise the estimate of $D = N/A$. MNA underestimates N (only exceptionally will the entire population be caught), and the Zippin estimator tends to underestimate N because it is not robust to heterogeneous capture probability between individuals (Otis et al. 1978; Pollock et al. 1990). Trapping data provide a biased measure of home-range size because movements outside a trap grid are not detected, and estimates from radio tracking depend on details of sampling and analysis (White & Garrott 1990). A more fundamental problem is that home-range size varies over time and between habitats. Density estimates that assume a constant boundary strip will therefore be unreliable (Efford et al. 2004).

Spatially explicit analysis of CMR data (Efford et al. 2004) estimates density without calculating an effective trapping area. A further advantage is that the parameters of the detection model may be used to simulate the performance of alternative trap layouts. The capture probability of an individual in a particular trap is modelled as a decreasing detection function $g(r)$, where r is the distance of the trap from the animal's home range centre. The shape of the fitted function appears not to be critical, and a half-normal curve seems adequate. An indirect computer-intensive method (simulation and inverse prediction) has been used to fit the detection function and the density D to trapping data (Efford 2004).

The small samples often obtained in small-mammal trapping pose difficulties for CMR analysis (Slade & Blair 2000; McKelvey & Pearson 2001). Ship rat studies are no exception, and study design is key to their success. Our aim was to establish a capture-mark-recapture protocol that will enable the density of ship rats to be estimated efficiently in small areas of forest (c. 10 ha) with greater rigour and reliability than the methods used previously. This protocol could then be used repeatedly to sample larger areas as required. The capture rate of rats was compared between two types of trap in a configuration that would enable fieldworkers to cover a given area quickly. We tested whether capture and recapture rates were high enough to estimate D from spatial CMR data (Efford 2004). We considered that a coefficient of variation of the density estimate, $\hat{D}$, of ~20% would indicate acceptable precision, i.e. $\mathrm{CV}(\hat{D}) = \mathrm{SE}(\hat{D})/\hat{D} \approx 20\%$. Finally, we used computer simulation to predict how alternative trap layouts and different numbers of trapping occasions would affect the precision of $\hat{D}$ in populations with the estimated parameters.

Methods

The field component of this research was done in mixed forest in the Orongorongo Valley, Rimutaka Forest Park, North Island, New Zealand (41°21' S, 174°58' E). This location, used for brushtail possum (*Trichosurus vulpecula*) and rodent research for many years (Fitzgerald & Gibb 2001), was chosen because rats were plentiful and we could place rodent traps on existing surveyed possum-trapping grids. The grids we used were located in mixed podocarp–broadleaved forest, except for one site used in 2003 only that was in podocarp–beech forest. Ship rats and house mice (*Mus musculus*) were the only rodents present.

Rats were trapped in metal mesh cage traps (27 × 17 × 13 cm; 19RT10, Pest Management Services, Kapiti, NZ) or Elliott sheet aluminium box traps (32 × 9 × 10 cm; Elliott Scientific, Upwey, Victoria, Australia), arranged in open 3.2-ha squares of 48 traps 15 m apart (Fig. 1). These trapping arrays were separated by at least 180 m in 2003 and 600 m in 2004; rats were never recaptured on a different array from where they had been marked. Traps were set for 5 nights and checked each morning. Traps contained synthetic batting for warmth; cage traps were fitted with metal covers and Elliott traps were enclosed in plastic sleeves to keep

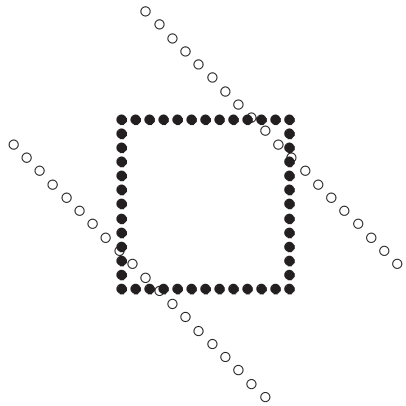

Figure 1. Layout of traps used to estimate the population density of ship rats in the Orongorongo Valley, 2003–2004. Filled circles: live traps (spacing 15 m); open circles: snap traps used after live trapping in 2004 (spacing 20 m).

them dry. Rats were lightly anaesthetised with halothane and marked with numbered metal fingerling tags in both ears. Morphometrics and reproductive condition were recorded, and animals were released at point of capture. In 2003 a large number of house mice were caught; they were tagged in one ear without anaesthetic.

Trapping was repeated in April 2003, May 2003 and April 2004. In April 2003, six trapping arrays were used, with a single trap type randomly assigned to each trapping array. In this first session, traps were baited only with carrot and peanut butter. In May 2003, the assignment of trap types to trapping arrays was reversed and cage traps were provided with additional food and shelter in the form of commercial rat pellets inside a plastic tunnel (made from a 1-litre milk bottle) wired into the trap; the batting was placed in this tunnel. Rat pellets were added to Elliott traps also. In April 2004, only three trapping arrays were used, all with cage traps modified as above and protected from possums by A-frame wire-mesh covers (500 × 390 × 500 mm) pegged to the ground. Apple (which was easier than carrot to push onto bait hooks), peanut butter and rat pellets were used as bait in this final session.

After the final live-trapping session in April 2004, we set Ezeset Supreme rat snap traps for 3 nights, in order to compare kill-trapping indices with the density estimates. These traps were arranged to cover the area of the live-trapping arrays as well as possible, at spacing recommended by C. Gillies (Department of Conservation, pers. comm.). Two lines of snap traps, 380 m long and separated by 200 m, each with 20 traps 20 m apart, crossed each square of live traps diagonally (Fig. 1; 360 trap-nights in total). Snap traps were shielded from non-target species (birds and possums) with the wire-mesh covers described above. Traps were baited with peanut butter and oatmeal and checked daily. The capture rate of rats was expressed as the number caught per 100 trap-nights corrected for sprung traps, including traps that had caught rats and non-target species (rats $100TN^{-1}$) (Nelson & Clark 1973).

Analysis of capture-mark-recapture data

Because only small numbers of animals were captured and recaptured on most trapping arrays (Table 1), it was necessary to group data for analysis. We pooled data within each year over the three (in 2004) or six (in 2003) trapping arrays with the same type of trap. To compare rat density between years, we made a separate estimate for 2003 by pooling data over the three trapping arrays that had cage traps in both years.

The aim of the analysis was to estimate three parameters:

D	density of population (animals ha^{-1})
g_0	daily probability of capture when trap is at the centre of home range (day^{-1})
σ	spatial scale (standard deviation of half-normal detection function) (m).

The detection parameters g_0 and σ are explained diagrammatically in Efford (2004, fig. 1).

For estimation we used simulation and inverse prediction (Carothers 1979; Pledger & Efford 1998; Efford 2004; Efford et al. 2004). This method matches values of statistics calculated directly from the field data to values of the same statistics calculated from data simulated with known parameter values. 'Matching' uses multivariate linear multiple regression. We used the following statistics as predictors of D, g_0 and σ, respectively:

$\hat{N}$	estimate of closed population size,
$\hat{p}$	capture probability corresponding to $\hat{N}$ (day^{-1}), and
$RPSV$	root pooled spatial variance (m), defined as:

$$RPSV = \sqrt{\frac{\sum_{ij}(x_{ij}-\bar{x}_i)^2 + \sum_{ij}(y_{ij}-\bar{y}_i)^2}{\sum_i (n_i - 1)}},$$

where (x_{ij}, y_{ij}) are the coordinates on the trapping array of the j-th capture location of the i-th animal, and the summations are over animals with at least two captures ($n_i \geq 2$).

The statistic $RPSV$ is a measure of the scale of trap-revealed movements, pooled across individuals. We used $RPSV$ in preference to mean distance between

Table 1. Numbers of first captures, recaptures and mortalities of ship rats caught in cage traps in three trapping sessions in the Orongorongo Valley.

Trapping session	Site	Captures	Recaptures	Mortalities
April 2003	1	34	27	4
	2	13	2	3
	3	17	2	1
May 2003	4	14	2	1
	5	4	1	0
	6	7	1	1
Total 2003	6 sites	89	35	10
April 2004	1	21	7	0
	2	55	15	1
	3	32	5	2
Total 2004	3 sites	108	27	3

captures, $\bar{d}$ (Efford 2004), as it is more robust to serial correlation (MGE, unpubl. results). A caret or 'hat' (ˆ) above a symbol indicates that it is an estimate.

Each of these statistics has a monotonic relationship to one parameter when other parameters are held constant; e.g. $\hat{N}$ is expected to increase with D (Efford 2004, fig. 2a). Here we treat $\hat{N}$ as a convenient summary of the data rather than as an estimate of a population parameter, thus avoiding any consideration of effective trapping area. The choice of statistics to estimate $\hat{N}$ may affect the results, but there is at present little experience or theory to guide this choice (Efford 2004; Efford et al. 2004). We therefore compared results with two estimators for $\hat{N}$ corresponding to different capture-recapture models:

(1) The maximum likelihood estimator for the null model (M_0), which assumes that the probability of capturing an animal is constant between individuals and between different trap-nights (Otis et al. 1978).

(2) Chao's second coverage estimator for model M_{th} in which capture probability differs both between individuals and over time (Lee & Chao 1994).

The respective population and density estimates are denoted $\hat{N}_0$, $\hat{N}_{th}$, $\hat{D}_0$ and $\hat{D}_{th}$. We chose these models for their contrasting assumptions. The estimator for M_{th} is expected to have lower bias, given that capture probabilities vary between individuals ('h' for heterogeneity), and between days ('t' for time) with different weather conditions. Previous comparisons using data from brushtail possums have suggested the effect of varying the *N*-estimator on the density estimated by inverse prediction depends primarily on whether or not the *N*-estimator allows for heterogeneous individual capture probability (Efford 2004; Efford et al. 2005). However, the estimator for M_0 is expected to have greater precision because it relies on fewer parameters, and maximising precision might be more important than minimising bias when the goal is to compare populations over time (cf. Davis et al. 2003). The capture histories of rats that died before the last day of the trapping session were removed before analysis, and an equal number of rats was added to the estimate of *N* (Otis et al. 1978).

We used program DENSITY 3.3 to estimate density and detection parameters from $\hat{N}$, $\hat{p}$ and *RPSV* (Efford et al. 2004). The simulated home-range centres were assumed to follow a Poisson distribution. The simulated population of potentially trappable individuals was considered within the trapping array plus a 150-m buffer, chosen arbitrarily to far exceed the observed mean distance between captures (about 30 m). We analysed pooled data from *k* arrays, where $k = 3$ or $k = 6$. Simulating captures on *k* separate arrays in their correct geographic configuration was time-consuming because we must consider individuals located in the gaps between arrays with little chance of being trapped. As all arrays shared the same geometry, we instead treated the pooled data as simultaneous captures on a single array, with no constraint on the number of rodents that could be caught in one trap (i.e. traps were 'multi-live' devices in the terminology of DENSITY). Thus, we did not model local saturation of traps by animals, but this omission had negligible effect on the estimates, based on preliminary simulations. Average density was then estimated as $\hat{D} = \hat{D}'/k$, where $\hat{D}'$ was the density estimate on the *k* pooled arrays. Simulations spanned ±20% of the initial parameter values, determined as described in Efford et al. (2004); statistics were

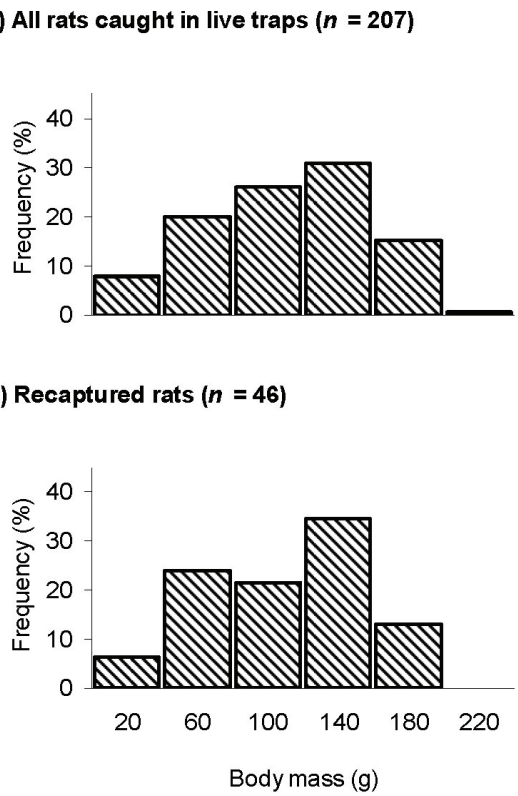

Figure 2. Frequency distributions of body mass of (a) all rats caught in live traps and (b) recaptured rats. *x*-axis labels indicate the midpoint of each category. Small discrepancies in sample sizes between numbers of rats caught and body mass data are due to missing values.

averaged from 2000 simulations with each combination of parameter values. The variance-covariance matrix of the estimates was estimated by conducting 1000 further simulations at the fitted parameter values, and used to calculate asymmetric confidence intervals under the assumption that the estimates were log-normally distributed (Burnham et al. 1987; Chao 1987; Rexstad & Burnham 1991). The precision of density estimates was expressed as CV(*estimate*) = SE(*estimate*)/*estimate*.

Simulating alternative trap layouts, numbers of trapping occasions, and detection variability

We used DENSITY's power analysis facility to predict the precision obtainable with alternative trapping protocols. We simulated captures of rats from populations with density and detection parameters based on those estimated from each year's pooled data. For each combination of population parameters and trapping protocols simulated, 100 random populations were generated and sampled ('trapped'), and estimates were obtained from the sample as described above. Although our data analyses gave no information on the variability between individual rats in values of g_0 and σ, considerable variation is likely to exist (e.g. based on age, sex, condition, experience, home range characteristics, and weather). To test the impact of potential variability on precision of estimates, we simulated scenarios with both (1) constant detection parameters and (2) detection parameters allowed to vary among individuals with a CV of 30%. In the latter case, values of g_0 were randomly chosen from a beta distribution and values of σ from a log-normal distribution, with the mean in each instance equal to values estimated from field data, assuming zero covariance.

Three replicate arrays of traps in four different layouts were simulated: (1) our field layout: 48 traps 15 m apart in an open square, (2) 64 traps 20 m apart in an 8×8 grid, (3) 64 traps 15 m apart in two concentric squares, (4) 96 traps 7.5 m apart in an open square. These layouts were chosen from many possible arrangements of traps because they were of specific interest. The second arrangement has been used in other studies of New Zealand rodents (e.g. Ruscoe 2004; Ruscoe et al. 2004). The third arrangement has been found efficient for trapping house mice in Elliott traps, and simulations predicted more recaptures of mice with two concentric squares of traps than with a single open square (Wilson et al. 2006). The fourth arrangement was chosen in order to test the effect of doubling the number of traps in our field trapping arrays.

To further test how additional trapping effort would affect precision, we compared results from three, five and seven simulated trapping occasions (an 'occasion' equates to a trapping day). Finally, we compared scenarios with no interference by non-target species (defined as the percentage of traps sprung and empty or with non-target captures), and with 10% interference. In summary, the following sets of simulations were done:

(1) D, g_0, and σ based on estimates from data collected in (a) 2003 and (b) 2004
(2) With and without variation in g_0 and σ
(3) Four alternative layouts of cage traps in three replicate arrays
(4) Three, five and seven trapping occasions
(5) With and without 10% interference by non-target species.

Results

Comparison of the two types of live-capture trap

Rats were caught much more readily in cage traps than in Elliott traps and the reverse was true of mice. In April and May 2003 combined, we caught 89 individual rats in cage traps (Table 1) and 48 mice in Elliott traps. We also caught 12 rats in Elliott traps, with no recaptures, and 8 mice in cage traps, with only one recapture. Several European hedgehogs (*Erinaceus europaeus*) were caught in both types of trap, a few juvenile possums were caught in cage traps, and one weasel (*Mustela nivalis*) was caught in an Elliott trap. In May 2003, possums often disturbed the cage traps (interference, i.e. traps that were sprung and empty or caught non-target species, was 75%), with the result that there were few recaptures of rats in that trapping session. The rate of interference with Elliott traps was also high in May 2003, at 39%. In May 2004, 108 rats (Table 1) and no mice were caught in cage traps with covers that successfully reduced interference to only 10%.

After the first trapping session we revised the protocol because of an unacceptably high mortality rate. In April 2003 eight rats (8%) died in the cage traps, and one rat (8%) in an Elliott trap. All the bait in these traps had been eaten, and bait was missing from many empty cage traps, some of which remained set. We suspected that bait had sometimes been taken from cage traps before animals were caught, and that perhaps the metal mesh provided insufficient insulation from cold. Therefore, for subsequent trapping sessions we provided additional food in all traps and additional shelter in cage traps (see Methods; rats chewed the plastic shelters provided, and metal may have been better). In May 2003 two rats (7%) died in cage traps and none in Elliott traps. In 2004, with apple, peanut butter and rat pellets provided as bait and food, only two rats (1.5%) died in cage traps, one apparently as the result of entangling the bedding around itself and the bait hook (a third died from the anaesthetic).

Characteristics of rats captured and recaptured in live traps

There were no apparent characteristics distinguishing rats that were recaptured from those that were not. The sex ratios of all individual rats caught in live traps (n = 206) and of recaptured rats (n = 48) were identical at 56 males : 44 females. [Small discrepancies in sample sizes between numbers of rats caught, sex ratios and body mass data (Fig. 2) are due to missing values.] The frequency distributions of body mass of all rats caught in live traps and of recaptured rats were also similar (Fig. 2a, b). All the rats caught were of the 'frugivorus' (Innes 2005) colour morph, with the exception of one 'rattus' morph (Innes 2005), which was not recaptured.

Estimated parameters of rat populations

Rat density and closed population size could be estimated only where cage traps were used (Table 2). (In contrast, house mouse density could be estimated only where Elliott traps were used; unpubl. results.) In order to estimate rat density, it was necessary to pool data from multiple sites with cage traps (in the three instances where there were enough captures and recaptures to estimate site-specific density, precision was very poor). Estimates of density ($\hat{D}$) of rats at the pooled sites (six sites in 2003 and three in 2004) from the two capture-recapture models were within 13% of each other, on average, and estimates of $\hat{N}$ were within 22% of each other (Table 2). Density estimates that allowed for heterogeneity were higher than estimates from the null model ($\hat{D}_{th} > \hat{D}_0$). Precision of $\hat{D}_{th}$ was poor; CV($\hat{D}_{th}$) = 32% averaged over the pooled estimates from both years, and the corresponding CV ($\hat{N}_{th}$) = 22% (Table 2).

Estimated density ($\hat{D}_{th}$) of rats in 2004 at three combined sites was 8.7 ha^{-1} (95% CI 4.9–15.5), compared with density in 2003 at the same three sites (5.4 ha^{-1}; 95% CI 2.7–10.7). These estimates did not differ significantly based on 95% confidence limits. Density estimated by pooling data from the six

Table 2. Estimated population size ($\hat{N}$) and density ($\hat{D}$) of ship rats captured in cage traps in the Orongorongo Valley, pooled over multiple sites within each year, estimated with the null model (M_0) and Chao's second coverage estimator (M_{th}).

			$\hat{N}$		CV($\hat{N}$)		$\hat{D}$		CV($\hat{D}$)	
	Year	Sites	$\hat{N}_0$	$\hat{N}_{th}$	$\hat{N}_0$	$\hat{N}_{th}$	$\hat{D}_0$	$\hat{D}_{th}$	$\hat{D}_0$	$\hat{D}_{th}$
(1)	2003	3 sites	92	127	0.12	0.24	4.1	5.4	0.24	0.37
(2)	2003	6 sites	149	217	0.13	0.24	3.4	4.9	0.29	0.36
(3)	2004	3 sites	231	248	0.15	0.21	8.5	8.7	0.23	0.29
Mean of (2) & (3)			190	232	0.14	0.22	6.0	6.8	0.26	0.32

Table 3. Population parameter estimates of ship rats captured in cage traps in the Orongorongo Valley, pooled over multiple sites within each year. $\hat{N}_{th}$ and $\hat{D}_{th}$ are based on Chao's second coverage estimator (M_{th}). Standard errors are shown in parentheses.

$\hat{N}_{th}$ estimate of population size
$\hat{p}$ estimate of capture probability
RPSV root pooled spatial variance, a measure of animal movement used in the estimation of *D*
$\hat{g}_0$ estimated probability of capture when trap is at the centre of home range
$\hat{\sigma}$ a measure of home range width
$\hat{D}_{th}$ estimated density of population (animals ha–1)

Year	Sites	$\hat{N}_{th}$	$\hat{p}$	*RPSV*	$\hat{D}_{th}$	$\hat{g}_0$	$\hat{\sigma}$
2003	3 sites	127 (31)	0.14	31.5	5.4 (2.0)	0.041(0.005)	29.5 (5.4)
2003	6 sites	217 (52)	0.10	29.6	4.9 (1.8)	0.032 (0.005)	27.8 (4.4)
2004	3 sites	248 (51)	0.11	40.7	8.7 (2.6)	0.023 (0.003)	37.4 (4.9)

Table 4. Number of ship rats caught (*n*) and capture indices from snap trapping; numbers of individuals caught, total captures including recaptures, and estimated population sizes ($\hat{N}_{th}$, with SE in parentheses) based on live trapping of rats, at three different sites in the Orongorongo Valley in April 2004.

	Snap trapping		Live trapping			
Site	*n*	Capture index	Individuals	Total captures	$\hat{N}_{th}$	CV($\hat{N}_{th}$)
1	33	35.5	21	28	37.9 (11.3)	0.30
2	22	23.8	55	70	114.6 (30.7)	0.27
3	32	33.2	32	37	126.0 (65.9)	0.52

site×session combinations where cage traps were used in April and May 2003 was 4.9 ha^{-1} (95% CI 2.5–9.7), but the high level of disturbance by possums in May 2003 may have led to bias in the estimates of $\hat{g}_0$ and $\hat{\sigma}$, and hence of $\hat{D}$, based on the six combined sites. The average effective trapping area of each hollow 3.2-ha trapping square was 7.4–9.5 ha, calculated as $\hat{N}_{th} / \hat{D}_{th}$ / number of combined sites.

The estimated spatial detection parameters $\hat{g}_0$ and $\hat{\sigma}$ were of similar magnitude in the two years (Table 3). At the three combined sites in 2004 $\hat{g}_0$ was 0.023 ± 0.003 (SE) and at the same three sites in 2003 it was 0.041 ± 0.005. The corresponding values of $\hat{\sigma}$ were 37.4 ± 4.9 m and 29.5 ± 5.4 m. In each instance $\hat{\sigma}$ was similar in magnitude to *RPSV* (Table 3). The estimated probability of capture ($\hat{p}$) of rats was 0.11 at the three combined sites in 2004 and 0.14 at the same three combined sites in 2003 (Table 3).

Snap trapping

Eighty-seven rats were caught in snap traps in 360 trap-nights (282 corrected trap-nights or *TN*) in April 2004 (Table 4). Only 25 (29%) of these animals had been tagged. Capture indices were 35.5, 23.8 and 33.2 rats $100TN^{-1}$ at the three sites respectively, with an overall index of 30.9 rats $100TN^{-1}$. These indices were not correlated with $\hat{N}_{th}$ or $\hat{N}_0$ estimated separately at the same sites in 2004, nor with the number of animals caught in live traps, nor with total captures in live traps (Pearson's correlation coefficient $r_3 < -0.55$, $P > 0.68$). Because site-specific $\hat{D}$ could not be calculated, it was not possible to test for correlations between capture indices and $\hat{D}$. One mouse and three hedgehogs were also caught in snap traps.

Simulating alternative trap layouts, numbers of trapping occasions, and detection variability

Two sets of density and detection parameters were taken from the field results for simulating how trapping effort affected precision. Although the density estimates did not differ significantly, we considered them to be realistic alternative densities. First, a relatively high rat density scenario was based on estimates from the three combined sites in 2004 (D = 9 rats ha^{-1}, g_0 = 0.023, σ = 37.4 m; Table 3). Second, a lower rat density scenario was based on estimates from the same three

combined sites trapped in April 2003 (D = 5 rats ha^{-1}, g_0 = 0.041, σ = 29.5 m; Table 3). Detection parameters in the low-density scenario were based on only these three sites because frequent interference by possums on the three sites trapped in May 2003 may have led to bias in $\hat{g}_0$ and $\hat{\sigma}$.

Simulated recapture rates with only three trapping occasions were in most instances too low to obtain useful density estimates. With five or seven trapping occasions, allowing the spatial detection parameters to vary altered CV($\hat{D}_{th}$) by less than 18%, and gave estimates that were neither consistently higher nor lower. Interference by non-target species of 10% (as observed in 2004) altered CV($\hat{D}_{th}$) by less than 5%, again yielding neither consistently higher nor lower estimates. Results are therefore reported below only for five and seven trapping occasions with varying detection parameters and 10% interference by non-target animals.

Simulated precision compared with field estimates of precision

Simulations with 48 traps 15 m apart at three sites and five trapping occasions gave slightly better estimates of precision than those obtained in the field (simulated CV($\hat{D}_{th}$) was ~25% at relatively high density and ~32% at low density, compared with the respective field estimates of 29% and ~37%; Fig. 3a, c; Table 2).

Comparison of different trap layouts

Precision of $\hat{D}_{th}$ improved as increasing numbers of traps were simulated. The simulated effective trapping area ($\hat{N}_{th}/\hat{D}_{th}$) per site varied between 5.2 and 6.3 ha for a grid of 64 traps 20 m apart, and between 8 and 11 ha for the other trapping arrays. Simulations predicted that the goal of CV($\hat{D}_{th}$) ≈ 20% could be achieved in both the high-density and low-density scenarios with either 64 traps and five trapping occasions or 48 traps and seven trapping occasions (Fig. 3). Arranging 64 traps in two concentric squares with 15-m spacing, compared with a grid with 20-m spacing, was predicted to slightly improve precision. Assuming constant trappability also slightly improved the predicted precision of density estimates ($\hat{D}_0$) for equivalent trapping configurations, in all but one instance (Fig. 3), but $\hat{D}_0$ was always more biased than $\hat{D}_{th}$ (Fig. 4).

In most of the simulated scenarios, bias in $\hat{D}_{th}$ was minimised with a grid of 64 traps, slightly higher with 64 traps placed in two concentric squares, and maximised with only 48 traps (Fig. 4). The predicted ratio $\hat{D}_{th}/D$ with 64 traps and five trapping occasions (one of the protocols predicted to achieve the goal of CV($\hat{D}_{th}$) ≈ 20%; see above) was 0.94–0.97 with a grid of 64 traps with 20-m spacing and 0.88 with 64 traps in two concentric squares with 15-m spacing. With 48 traps and seven trapping occasions (see above), predicted $\hat{D}_{th}/D$ was 0.80–0.87.

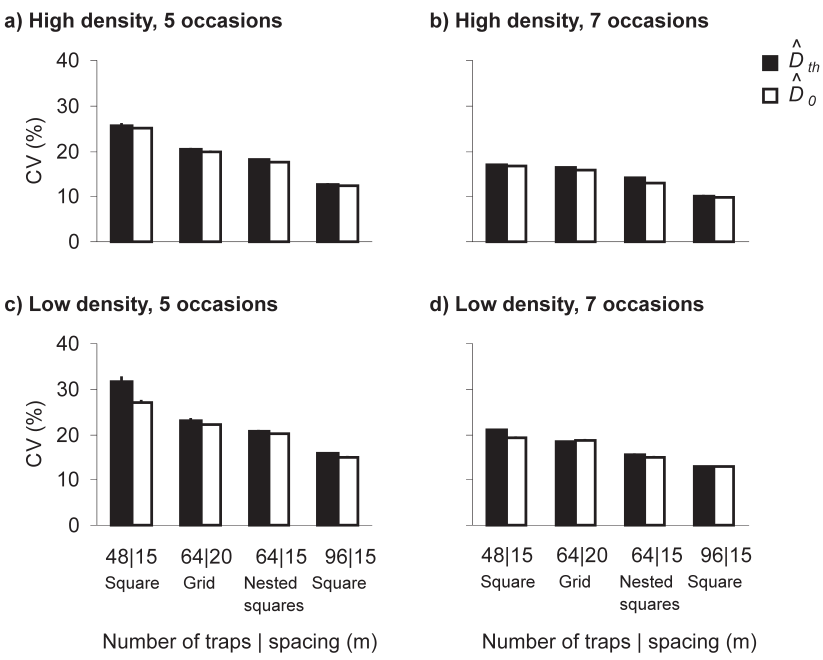

Figure 3. Simulated precision of $\hat{D}$ ($\hat{D}_{th}$ based on Chao's second coverage estimator M_{th} and $\hat{D}_0$ based on the null model M_0) with three replicates of four alternative trap layouts, contrasting scenarios based on field data, and either five or seven trapping occasions. 'High density' scenario D = 9 ha^{-1}, g_0 = 0.023, σ = 37.4 m; 'Low density' scenario D = 5 ha^{-1}, g_0 = 0.041, σ = 29.5 m. Average of 100 simulations; error bars show the standard errors of the estimated CVs (many are too small to show on the graph).

Discussion

We were able to obtain closed-capture estimates of ship rat population size ($\hat{N}$) by using mesh cage traps and combining data from three or six sites, but not by using Elliott traps. The precision of estimates of rat density with the preferred estimator ($\hat{D}_{th}$) was unsatisfactory: at least 29%, compared with our goal of 20%. The precision of estimates that assumed constant capture probability ($\hat{D}_0$) were closer to this goal (23–24% when three sites were combined, but 29% when six sites were combined in 2003).

Evaluating cage traps versus Elliott traps

Both capture and recapture rates of ship rats were much higher in cage traps than in Elliott traps. These results were consistent with those of another New Zealand study, in which snap traps under mesh covers caught more Norway rats than when under solid metal covers (Ji et al. 1999), although in a trial of open-ended covers over Fenn traps set for mustelids in Nelson Lakes National Park, many more ship rats were caught in wooden tunnels than in mesh covers (Butler 2003). In various woodland, grassland and desert habitats in the United States, more species of small mammals and many more individuals were captured in mesh traps than in Sherman box traps with similar cross section but shorter length than the Elliott traps we used (O'Farrell et al. 1994). Most of these results suggest that small mammals are more likely to enter an open cage that they can see through, than they are to enter a closed box. Also, problems with condensation and heat or cold stress can be worse in box traps and may increase mortality (O'Farrell et al. 1994) or reduce the recapture rate.

Both cage traps (Daniel 1972; Innes 1977; Hickson et al. 1986; Dowding & Murphy 1994; Hooker & Innes 1995) and Elliott traps (Ruscoe et al. 2001; Ruscoe 2004) have been used in New Zealand studies aiming to capture ship rats alive, although none of these publications give CMR estimates of *N*. Elliott traps are often used in Australia, where many species of small mammals may be captured in a single study (e.g. Catling et al. 1997; Cox et al. 2004), and other international researchers have used Sherman box traps (Shanker & Sukumar 1999) or cage traps (Tomich 1970; Tamarin & Malecha 1971) for catching ship rats. The use of anaesthetic has varied widely among live-capture studies of ship rats, with ether (Tomich 1970; Tamarin & Malecha 1971; Hooker & Innes 1995), chloroform (Hickson et al. 1986) or none (Daniel 1972; Innes 1977; Cox et al. 2000; Ruscoe 2004) used. Prout and King (2006) achieved a higher recapture rate of ship rats that had been anaesthetised with halothane when first captured, compared with rats that had been handled without anaesthetic. Using anaesthetic in our study may also have improved the chance of recapturing rats, by reducing their experience

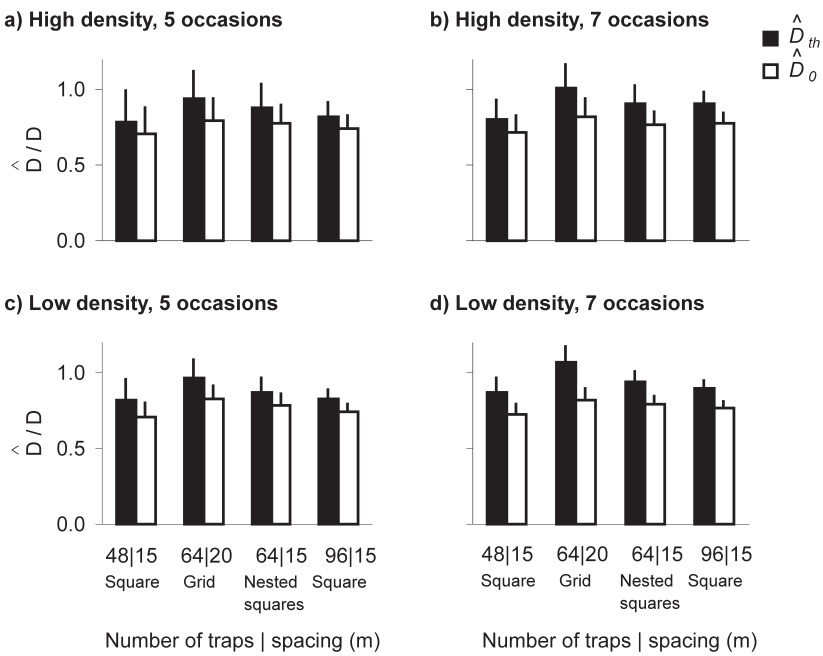

Figure 4. Simulated bias of $\hat{D}_{th}$ and $\hat{D}_0$, given as the ratio of estimated density $\hat{D}$ to simulated density *D*. $\hat{D}_{th}$, $\hat{D}_0$, trap layouts, simulated density scenarios, and trapping occasions are as in Fig. 3. Average of 100 simulations; error bars show the standard errors of the ratios.

and memory of pain or stress when being held tightly for marking and measurement.

In contrast to the result for rats, we found that Elliott traps were better than cage traps for catching mice. The cage traps were not designed to catch mice, which probably often removed peanut butter without springing them. Elliott traps are commonly and successfully used in CMR studies of mice in New Zealand (e.g. Ruscoe et al. 2001, 2004; Wilson et al. 2006) and Australia (e.g. Chambers et al. 2000). Possum disturbance of the Elliott traps could be reduced with the same A-frame mesh covers that we used for the cage traps.

Rat population parameters

The estimated density of ship rats (4.9–8.7 ha^{-1}) at pooled sites in the Orongorongo Valley in 2003 and 2004 was consistent with other estimates based on MNA or removal trapping in New Zealand forests (0.7–6.2 ha^{-1}) (Daniel 1972; Dowding & Murphy 1994; Hooker & Innes 1995; Brown et al. 1996; corrected in Brown et al. 2004). Rat abundance fluctuates irregularly in the Orongorongo Valley: between 1971 and 1992, snap-trap capture indices averaged over four sessions per year varied sixfold (Fitzgerald & Gibb 2001). Our snap-trap capture indices (average 31 rats $100TN^{-1}$) exceeded the maximum recorded there of 20.8 rats $100TN^{-1}$ in August 1986, but some traps in the earlier study were placed in beech forest, where the density of rats was lower (Efford et al. 2006). It is possible that experience with obtaining bait from live traps in our study motivated individual rats to seek out snap traps, increasing the snap-trap index.

The mean home range of ship rats in New Zealand forests has been estimated at between about 0.5 ha and 1.0 ha in winter, with mean range length up to 174 m, and the range of males may more than double in the breeding season (Hickson et al. 1986; Dowding & Murphy 1994). Some individual ranges are much larger (Pryde et al. 2005). Our values of $\hat{\sigma}$, ~30–37 m, give estimated home range radius as 72–92 m and area of 1.6–2.6 ha, based on a 95% activity contour and assuming that utilisation of the area has a circular bivariate normal distribution (using the formula radius = 2.45σ; Jennrich & Turner 1969). However, since this assumption is unlikely to be valid, these should not be considered accurate home range estimates. The capture probability of ship rats in live traps in New Zealand has not been reported previously. In India, the capture probability of this species in Sherman traps baited with coconut and rice, with 49 or 100 traps in grids with 10-m spacing, varied between 0.17 and 0.64 in different habitats and seasons and was unrelated to density, which ranged from 2 to 44 ha^{-1} based on MNA with no boundary strip (Shanker 2000).

Relationship between indices of rat abundance

The high rat-capture index, coupled with the large number of unmarked animals in snap traps, was consistent with the high rat density estimate in April 2004. Other researchers have found that capture indices from snap trapping were also related to tracking rates of rats in ink tunnels – the index of density most often used in New Zealand – when studies were carefully designed (Blackwell et al. 2002; C. Gillies, Department of Conservation, pers. comm., 2004). We were unable to test whether the capture index and $\hat{D}$ at each site were correlated, and there was no correlation between capture index and either number of individuals caught in live traps, total captures including recaptures, or $\hat{N}$. It may be unreasonable to expect these measures to be correlated within a relatively small range of densities, as the indices (capture index, individuals caught, and total captures) may be too insensitive to reflect small differences in density, and the precision of our estimates of N was low (CV($\hat{N}_0$) ≥ 27% and CV($\hat{N}_{th}$) ≥ 19%). However, the correspondence that we recorded between a capture index of about 30 rats $100TN^{-1}$ and a density of about 9 rats ha^{-1} may be useful in interpreting future snap-trapping data.

Recommended trapping protocols based on field results and simulations

The rat-trapping procedures we developed proved satisfactory: cage traps, mesh covers, bait (apple and peanut butter, with rat pellets to provide additional food), shelter and bedding in the traps, and halothane anaesthetic. Bedding with short fibres, such as wood shavings, cotton batting, hay or straw, may be better than the synthetic batting we used, which occasionally became tightly wound around a trapped animal. Also, metal tunnels may be better for providing shelter inside traps than our plastic tunnels, which rats chewed.

The least costly way to increase precision in most field situations will be to increase the number of traps per site, especially if it can be done without adding personnel. The most costly alternative will often be to increase the number of trapping occasions (days), adding to wages and daily living costs. We therefore recommend using 64 cage traps at three replicate sites for five trapping occasions; based on our simulations this protocol should yield precision of $\hat{D}_{th}$ of ~20% at rat densities in the range of those we studied. The best layout of the 64 traps will depend on the goals of the study, since $\hat{D}_{th}$ was predicted to be slightly more precise with two concentric squares of traps and 15-m spacing, but slightly less biased with a grid of traps and 20-m spacing. We found that two people could easily check three 48-trap sites in a day and we believe that three 64-trap sites would have been feasible with the same number of people.

The density of rats may often be much lower than the 5 ha^{-1} in our low-density scenario; e.g. ship rats are often scarce in pure beech forests compared with mixed forests (Innes 2005). If density is expected to be very low and similar precision ($\hat{D}_{th}$ of ~20%) is required, then a minimum of five trapping occasions and either (1) the 96-trap layout on three replicate sites or (2) the 64-trap layout on six replicate sites will be needed. Which alternative is better will depend on the goals of the study, the size and accessibility of the geographical area of interest, and staff available. Option (1) will be faster than option (2), but option (2) will provide better coverage of a large area. The effective trapping area at each site will be about 10 ha. Compared with three 64-trap sites, one additional person might be required for three 96-trap sites, and two additional people for six 64-trap sites, depending on geography, terrain, and experience. If only two people are available, a third option of 64 traps at three sites and seven trapping occasions is recommended.

Because the home-range length of a single male rat may exceed 700 m (measured in beech forest; Pryde et al. 2005), trapping arrays must be at least this distance apart to be independent. However, range lengths were shorter in other studies of ship rats (Hickson et al. 1986; Dowding & Murphy 1994) and so separations of ~400 m may be acceptable if longer gaps between arrays are not logistically feasible. The simulated protocols allowed for 10% of traps being disturbed by non-target species – a level that is probably unavoidable in New Zealand because of the prevalence of possums, other small mammals, and large invertebrates (Wilson et al. 2006).

The trapping effort recommended is the minimum needed to achieve CV($\hat{D}_{th}$) of ~20%, as the simulated precision at low rat density slightly exceeded 20%, and the precision of field estimates of D were poorer than the simulated precision. However, these recommendations are conservative because of our assumption of heterogeneous capture probability both between individuals and through time. Our spatially explicit estimation of $\hat{D}$ accounts for some of the heterogeneity of capture probabilities that exists between individuals, i.e. the spatial heterogeneity that results from variation in the locations of home ranges in relation to traps (Efford et al. 2004). If little heterogeneity remains, then the estimator $\hat{D}_0$, which had slightly better precision compared with $\hat{D}_{th}$, may be satisfactory. However, traditional methods of selecting closed-capture models for estimating N (Otis et al. 1978) do not separate different sources of heterogeneity between individuals, and further research is needed to develop an approach for selecting the best capture-recapture model in the context of spatially explicit estimation of $\hat{D}$.

Patchiness of rat populations may make sampling unnecessarily costly if effort is expended trapping at sites that will not yield density estimates. In 2003, only one of our six trapping arrays yielded more than 20 individual rats; only this site had enough captures for us to fit a spatial model and estimate D at that site. At two sites, fewer than 10 rats were caught, but these data could be combined for analysis with data from the other sites. A form of adaptive sampling may be advisable, to minimise the effort expended on a group of trapping arrays unlikely to yield enough data for combined analysis. A potential rule is: if few rats are captured in 3 days on three arrays that are to be pooled for analysis, cut your losses and move to the next location instead of continuing to trap for 5 days. In order not to bias the overall conclusions of the study, these results must not be discarded but should be recorded as 'density apparently low'. The adaptive cluster-sampling approach proposed by Thompson (1990, 1991) may also be useful, whereby when the number of captures at a location exceeds some limit, nearby locations are also sampled. However, this algorithm will not be helpful if high-density patches of rats are smaller than c. 100 ha, unless very small, high-intensity trapping arrays are used. An alternative or additional approach would be simply to sample at more locations in strata (e.g. forest types) with more captures in preliminary surveys. This strategy assumes that strata likely to have different densities of ship rats can be identified in advance. Although ship rats are highly cosmopolitan, forest composition (King et al. 1996; King & Moller 1997), structure (Harper et al. 2005), and elevation (because ship rats are relatively scarce at high elevations and are not found above treeline; Innes 2005) may be useful strata for stratified sampling of their population density. The best sampling design will depend on the scale and objectives of the study. Even preliminary results may help to improve the design of subsequent studies, and will substantially add to our knowledge of spatial patterns in the distribution and abundance of an important introduced forest predator.

Acknowledgements

We thank Paul Horton, Suzanne Lambie, Mike Fitzgerald and Peter Berben for help in the field, Dave Ramsey for advice and information, and the Department of Conservation for permits to do this research in the Orongorongo Valley. Helpful comments by Adrian Monks, Daniel Tompkins, Christine Bezar and two anonymous reviewers improved earlier drafts. This project was funded by the Foundation for Research, Science and Technology (contract C09X0209) and carried out with Landcare Research Animal Ethics Committee approval (AEC 03/04/01).

References

Blackwell GL, Potter MA, McLennan JA 2002. Rodent density indices from tracking tunnels, snap-traps and Fenn traps: do they tell the same story? New Zealand Journal of Ecology 26: 43–51.

Brown KP, Moller H, Innes J, Alterio N 1996. Calibration of tunnel tracking rates to estimate relative abundance of ship rats (*Rattus rattus*) and mice (*Mus musculus*) in a New Zealand forest. New Zealand Journal of Ecology 20: 271–275.

Brown KP, Moller H, Innes J, Alterio N 2004. Correction. New Zealand Journal of Ecology 28: 312.

Burnham KP, Anderson DR, White GC, Brownie C, Pollock KH 1987. Design and analysis of fish survival experiments based on release-recapture data. Monograph 5. Bethesda, MD, USA, American Fisheries Society.

Butler DJC 2003. Rotoiti Nature Recovery Project Triennial Report 1998–2001. Occasional Publication No. 61. Nelson, Department of Conservation.

Carothers AD 1979. Quantifying unequal catchability and its effect on survival estimates in an actual population. Journal of Animal Ecology 48: 863–869.

Catling PC, Burt RJ, Kooyman R 1997. A comparison of techniques used in a survey of the ground-dwelling and arboreal mammals in forests in north-eastern New South Wales. Wildlife Research 24: 417–432.

Chambers LK, Singleton GR, Krebs CJ 2000. Movements and social organization of wild house mice (*Mus domesticus*) in the wheatlands of north-western Victoria, Australia. Journal of Mammalogy 81: 59–69.

Chao A 1987. Estimating the population-size for capture-recapture data with unequal catchability. Biometrics 43: 783–791.

Cox MPG, Dickman CR, Cox WG 2000. Use of habitat by the black rat (*Rattus rattus*) at North Head, New South Wales: an observational and experimental study. Austral Ecology 25: 375–385.

Cox MP, Dickman CR, Hunter J 2004. Effects of rainforest fragmentation on non-flying mammals of the Eastern Dorrigo Plateau, Australia. Biological Conservation 115: 175–189.

Cunningham DH, Moors PJ 1996. Guide to the identification and collection of New Zealand rodents. 3rd ed. Wellington, Department of Conservation.

Daniel MJ 1972. Bionomics of the ship rat (*Rattus r. rattus*) in a New Zealand indigenous forest. New Zealand Journal of Science 15: 313–341.

Davis SA, Akison LK, Farroway LN, Singleton GR, Leslie KE 2003. Abundance estimators and truth: Accounting for individual heterogeneity in wild house mice. Journal of Wildlife Management 67: 634–645.

Dice LR 1938. Some census methods for mammals. Journal of Wildlife Management 2: 119–130.

Dowding JE, Murphy EC 1994. Ecology of ship rats (*Rattus rattus*) in a kauri (*Agathis australis*) forest in Northland, New Zealand. New Zealand Journal of Ecology 18: 19–28.

Efford M 2004. Density estimation in live-trapping studies. Oikos 106: 598–610.

Efford MG, Dawson DK, Robbins CS 2004. DENSITY: software for analysing capture-recapture data from passive detector arrays. Animal Biodiversity and Conservation 27: 217–228.

Efford MG, Warburton B, Coleman MC, Barker RJ 2005. A field test of two methods for density estimation. Wildlife Society Bulletin 33: 731–738.

Efford MG, Fitzgerald BM, Karl BJ, Berben PH 2006. Population dynamics of the ship rat *Rattus rattus* L. in the Orongorongo Valley, New Zealand. New Zealand Journal of Zoology 33: 273–297.

Fitzgerald BM, Gibb JA 2001. Introduced mammals in a New Zealand forest: long-term research in the Orongorongo Valley. Biological Conservation 99: 97–108.

Harper GA, Dickinson KJM, Seddon PJ 2005. Habitat use by three rat species (*Rattus* spp.) on Stewart Island/Rakiura, New Zealand. New Zealand Journal of Ecology 29: 251–260.

Hickson REH, Moller H, Garrick AS 1986. Poisoning rats on Stewart Island. New Zealand Journal of Ecology 9: 111–121.

Hooker S, Innes J 1995. Ranging behaviour of forest-dwelling ship rats, *Rattus rattus*, and effects of poisoning with brodifacoum. New Zealand Journal of Zoology 22: 291–304.

Innes JG 1977. Biology and ecology of the ship rat *Rattus rattus rattus* (L.) in Manawatu (N.Z.) forests. Unpublished MSc thesis, Massey University, Palmerston North, New Zealand.

Innes JG 2005. Ship rat. In: King CM ed. The handbook of New Zealand mammals. 2nd ed. Melbourne, Oxford University Press. Pp. 187–203.

Jennrich RI, Turner FB 1969. Measurement of non-circular home range. Journal of Theoretical Biology 22: 227–237.

Ji WH, Veitch CR, Craig JL 1999. An evaluation of the efficiency of rodent trapping methods: The effect of trap arrangement, cover type, and bait. New Zealand Journal of Ecology 23: 45–51.

King CM, Moller H 1997. Distribution and response of rats *Rattus rattus, R. exulans* to seedfall in New Zealand beech forests. Pacific Conservation Biology 3: 143–155.

King CM, Innes JG, Flux M, Kimberley MO, Leathwick

JR, Williams DS 1996. Distribution and abundance of small mammals in relation to habitat in Pureora Forest Park. New Zealand Journal of Ecology 20: 215–240.

Krebs CJ 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecological Monographs 36: 239–273.

Lee S-M, Chao A 1994. Estimating population size via sample coverage for closed capture-recapture models. Biometrics 50: 88–97.

McKelvey KS, Pearson DE 2001. Population estimation with sparse data: the role of estimators versus indices revisited. Canadian Journal of Zoology 79: 1754–1765.

Nelson L Jr, Clark FW 1973. Correction for sprung traps in catch/effort calculations of trapping results. Journal of Mammalogy 54: 295–298.

O'Farrell MJ, Clark WA, Emmerson FH, Juarez SM, Kay FR, O'Farrell TM, Goodlett TY 1994. Use of a mesh live trap for small mammals: Are results from Sherman live traps deceptive? Journal of Mammalogy 75: 692–699.

Otis DL, Burnham KP, White GC, Anderson DR 1978. Statistical inference from capture data on closed animal populations. Wildlife Monographs 62.

Pledger S, Efford M 1998. Correction of bias due to heterogeneous capture probability in capture-recapture studies of open populations. Biometrics 54: 888–898.

Pollock KH, Nichols JD, Brownie C, Hines JE 1990. Statistical-inference for capture-recapture experiments. Wildlife Monographs 107: 1–97.

Prout DM, King CM 2006. The effect of handling under anaesthetic on the recapture rate of wild ship rats (*Rattus rattus*). Animal Welfare 15: 63–66.

Pryde M, Dilks P, Fraser I 2005. The home range of ship rats (*Rattus rattus*) in beech forest in the Eglinton Valley, Fiordland, New Zealand: A pilot study. New Zealand Journal of Zoology 32: 139–142.

Rexstad E, Burnham K 1991. User's guide for interactive program CAPTURE. Fort Collins, CO, USA, Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University.

Ruscoe WA 2004. A new location record for kiore (*Rattus exulans*) on New Zealand's South Island. New Zealand Journal of Zoology 31: 1–5.

Ruscoe WA, Goldsmith R, Choquenot D 2001. A comparison of population estimates and abundance indices for house mice inhabiting beech forests in New Zealand. Wildlife Research 28: 173–178.

Ruscoe WA, Wilson D, McElrea L, McElrea G, Richardson SJ 2004. A house mouse (*Mus musculus*) population eruption in response to heavy rimu (*Dacrydium cupressinum*) seedfall in southern New Zealand. New Zealand Journal of Ecology 28: 259–265.

Shanker K 2000. Small mammal trapping in tropical montane forests of the Upper Nilgiris, southern India: an evaluation of capture-recapture models in estimating abundance. Journal of Biosciences 25: 99–111.

Shanker K, Sukumar R 1999. Synchrony in small mammal populations of montane forest patches in southern India. Journal of Animal Ecology 68: 50–59.

Slade NA, Blair SM 2000. An empirical test of using counts of individuals captured as indices of population size. Journal of Mammalogy 81: 1035–1045.

Tamarin RH, Malecha SR 1971. The population biology of Hawaiian rodents: demographic parameters. Ecology 52: 383–394.

Thompson SK 1990. Adaptive cluster sampling. Journal of the American Statistical Association 85: 1050–1059.

Thompson SK 1991. Stratified adaptive cluster sampling. Biometrika 78: 389–397.

Tomich PQ 1970. Movement patterns of field rodents in Hawaii. Pacific Science 24: 195–234.

White GC, Garrott RA 1990. Analysis of wildlife radio-tracking data. San Diego, CA, USA, Academic Press.

White GC, Anderson DR, Burnham KP, Otis DL 1982. Capture-recapture and removal methods for sampling closed populations. LA-8787-NERP. Los Alamos, NM, USA, Los Alamos National Laboratory.

Wilson DJ, McElrea GJ, McElrea LM, Heyward RP, Peach RME, Thomson C 2006. Potential conservation impacts of high-altitude small mammals: a field study and literature review. DOC Research & Development Series 248. Wellington, Department of Conservation.

Editorial Board member: Doug Armstrong