

**Project No: R-10506**

**Effect of Habitat, Season, Trap Shyness and Timing on RTCI**

**Estimates**

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## Summary

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### Project and Client

A series of trials to assess the effects of habitat, season, trap shyness and time following control on RTCI estimates of possum abundance was conducted by Landcare Research, Lincoln, for the Animal Health Board, between February 1999 and June 2003.

### Objectives

Determine the magnitude and predictability of the variation in Residual Trap Catch Index (RTCI) estimates caused by environmental and management factors, by:

- comparing the effects of habitat and season on the relationship between standard RTCI estimates and at least two alternative estimates of possum abundance;
- comparing RTCI estimates measured 1, 3–4, and 6–7 months after control to determine whether changes in trappability are due to induced shyness or neophobia;
- determining whether a radioactive marker can be used to eliminate potential trappability (hereinafter termed ‘capture probability’) biases in mark-recapture estimates of local possum density.

### Methods

- The effects of habitat and season on RTCI estimates were investigated at two sites in the North Island: 3200 ha of indigenous forest at Maungatautari and 6500 ha of farmland at Miranda. Trapping was conducted along one trapline (consisting of 20 traps spaced at 20 m) within each of eight blocks at each site in summer, winter and spring of 1999–2001. Faecal pellet counts and cyanide paste were used to estimate the number of possums remaining on a trapline following trapping.
- We compared RTCI estimates measured 1, 3–4, and 6–7 months after control at two sites in forest and two sites in farmland at Milton and the Catlins in the South Island). There were seven blocks at each site, with one line trapped in each of the three sessions. However, despite informing the contractors of our work, the Milton Farmland area was controlled before we could conduct the third and final session. Faecal pellet counts, cyanide paste and spotlighting were used to estimate the number of possums remaining on a trapline following trapping.
- We analysed the data using a Zippin removal estimator that allowed for sampling error in both local population size and nightly capture probability.
- Fourteen wild-caught adult possums were acclimatised to captivity at the Landcare Research Animal Facility, Lincoln. Four males and three females were given 10  $\mu$ Ci of tritiated progesterone diluted in 1 ml of saline solution by intramuscular injection. All faecal pellets from each possum were collected and counted on day 1, 2, and 3, and every 2 days thereafter, for 16 days following injection. A control group (4 F and 3 M) were fed a diet similar to the injected possums and the number of faecal pellets voided by each possum counted each day. Analysis of marker presence in the faeces was carried out at the IANZ-accredited Landcare Research toxicology laboratory. Samples of non-radioactive faeces were treated in the same way and tested in the scintillation counter at the same time to obtain ‘background’ levels of radiation.
- Two methods for applying the RTCI in tussock country were tested as described in a separate contract report (Warburton & Yockney 2000 unpublished).

## Results

- Faecal pellet counts and spotlighting proved to be ineffective estimators of possum abundance. Cyanide paste, laid along the trapline after trapping had finished, provided an accurate estimate of the number of possums remaining.
- At both Maungatautari and Miranda, individual capture probabilities declined with increasing abundance of possums, generating a non-linear relationship between RTCI and possum abundance. Capture probability varied with season, but not between years. At the forest site, capture probability was highest in summer, followed by winter and then spring, whereas at the farmland site capture probability was highest in winter, but lowest in spring.
- The effects of timing (i.e. the time after control that monitoring is carried out) on RTCI were less apparent than for season. Capture probability increased with time at the Catlins Farmland and Catlins Forest sites, but there was no change in capture probability at the third (Milton Forest) site. The increases in capture probability at the Catlins sites were small, with only the difference between the first and third sessions 'significant'.
- Faecal pellets from days 2 and 3 had a high radioactivity (range 30–103 counts per minute), but the majority of pellets from day 5 onwards gave readings indistinguishable from the unmarked pellets. Pellets from further days were therefore not tested.

## Conclusions

- RTCI does not provide an accurate year-round index of possum abundance when possum densities are high (e.g., > 30% RTCI) due to the combined effects of saturation and seasonal bias. When possum abundance is low (i.e. <10%), the effects of both saturation and season are much reduced. Therefore the RTCI is a useful index in the context in which most possum monitoring is now conducted in New Zealand.
- As a result of the variation in capture probability between seasons (and the difference in this variation between habitats), monitoring of RTCI trends through time are likely to be valid only for assessments made in the same season and habitat, especially for populations at moderate or high density.
- Capture probability increased with time since control at the two Catlins sites (farmland and forest), but not at the Milton forest site, consistent with other evidence of a downward bias in immediate post-control RTCI (i.e. an over-estimation of % kill or under-estimate of 'true' residual RTCI). One implication is that post-control monitoring should be delayed for at least 6 months, but that is not likely to be a practical option for management of possum control contracts. The alternative is to accept that the bias exists and manage populations accordingly (i.e., assume that the apparent rate of increase indicated by changing RTCI will often be higher than is biologically possible in terms of actual possum numbers).
- A statistical technique was developed for estimating the abundance of possums from RTCI monitoring lines trapped for 9–12 days. The technique could be used in other studies where heterogeneous capture probabilities exist.
- Faecal pellet sampling and spotlighting were poor alternative estimators of the abundance of possums at low densities. The number of possums killed with cyanide poison was a useful alternative estimator of abundance for the purposes of our study.
- Possums injected either intramuscularly or intravenously with 10  $\mu$ Ci of tritiated progesterone in saline solution will not consistently void marked faecal pellets after 3 days.

**Recommendations**

- Managers should continue to use the RTCI to monitor control operations that are expected to maintain populations at low abundance.
- Whenever possible, seasonal biases in the RTCI should be minimised by conducting repeat sampling in the same season.
- Further work is required to better define the extent to which time following control affects the RTCI. We do not recommend any changes to current timing of post-control monitoring.
- Further work, possibly including recently developed methods for identifying individual possums from faecal pellets using DNA, is also needed to substantiate the extent of variable trappability within possum populations.

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## 1. Introduction

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A series of trials to assess the effect of habitat, season, trap shyness and time following control on Residual Trap Catch Index estimates of possum abundance was conducted by Landcare Research, Lincoln, for the Animal Health Board (AHB; Contract No. R10506), between February 1999 and June 2003.

Two methods for applying the RTCI in tussock country were tested and described in a separate contract report (Warburton & Yockney 2000 unpublished). That work is not discussed further in this report.

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## 2. Background

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The Residual Trap Catch Index (RTCI) is used throughout New Zealand to monitor the relative abundance of possums (e.g., Sweetapple et al. 2002), and to evaluate the effectiveness of control operations for reducing the abundance of possums for both conservation (e.g., Veltman & Pinder 2001) and Tb-eradication purposes (Coleman & Livingstone 2000). In the 2000/01 year alone, 272 possum population monitoring surveys were undertaken in relation to AHB-funded possum control, involving 10 720 actual RTCI lines (J. McInnes, AHB, pers. comm.).

The RTCI is the product a national protocol aimed at measuring the abundance of possums in New Zealand (Warburton 2000; National Possum Control Agencies 2002). The national trap-catch protocol was developed in 1996 by the National Possum Control Agencies (NPCA) to ensure that the monitoring of possum abundance by regional councils, the Department of Conservation, and researchers was standardised (Warburton 2000).

The RTCI is an *index* of possum abundance. Caughley (1977) defined an index as ‘any measurable correlate of density’. It is often assumed that the index and actual abundance are related through a positive, linear relationship with a slope that is constant across habitats, seasons and time (Gibbs 2000). However, a non-linear relationship may be common when the index becomes saturated at high densities (review in Gibbs 2000).

There has been concern that the RTCI may not be readily comparable between habitats or over time because of three factors systematically affecting the *trappability* (hereinafter termed ‘capture probability’) of possums. First, the RTCI may vary between forest and farmland habitats. Second, possums living in both forest and farmland habitats exhibit seasonal shifts in diet (review in Nugent et al. 2000), and these behavioural changes may affect the seasonal capture probability of possums (Nugent et al. 2001 unpublished). Third, temporary or permanent changes in the mean capture probability of possums that survive control operations could explain the impossibly high rates of increase in RTCI observed after some control operations (Coleman & Coleman 2000 unpublished; Nugent et al. 2001 unpublished; Arthur et al. 2002).

This project sought to quantify how habitat (forest or farmland), season (summer, winter or spring) and timing of monitoring after control (1, 3–4, and 6–7 months) affected the RTCI. The effects of habitat and season were investigated separately from the effects of timing. Initially we also hoped to develop a tool whereby possums caught during RTCI monitoring could be given a marker that was excreted in their faeces over a period of at least 10 days following their release, so that faeces from trapped possums could be distinguished from untrapped possums. Tritiated progesterone injected directly into the bloodstream has previously been used to mark possums for 5 days (T. Fletcher, pers. comm.). A pen trial was therefore conducted to ascertain the feasibility of using tritiated progesterone as this marker.

Two methods for applying the RTCI in tussock country were tested and that work was described in a separate contract report (Warburton & Yockney 2000 unpublished).

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### 3. Objectives

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Determine the magnitude and predictability of the variation in Residual Trap Catch Index (RTCI) estimates caused by environmental and management factors, by:

- comparing the effects of habitat and season on the relationship between standard RTCI estimates and at least two alternative estimates of possum abundance;
- comparing RTCI estimates measured 1, 3–4, and 6–7 months after control to determine whether changes in trappability are due to induced shyness or neophobia;
- determining whether a radioactive marker can be used to eliminate potential trappability (hereinafter termed ‘capture probability’) biases in mark-recapture estimates of local possum density.

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### 4. Methods

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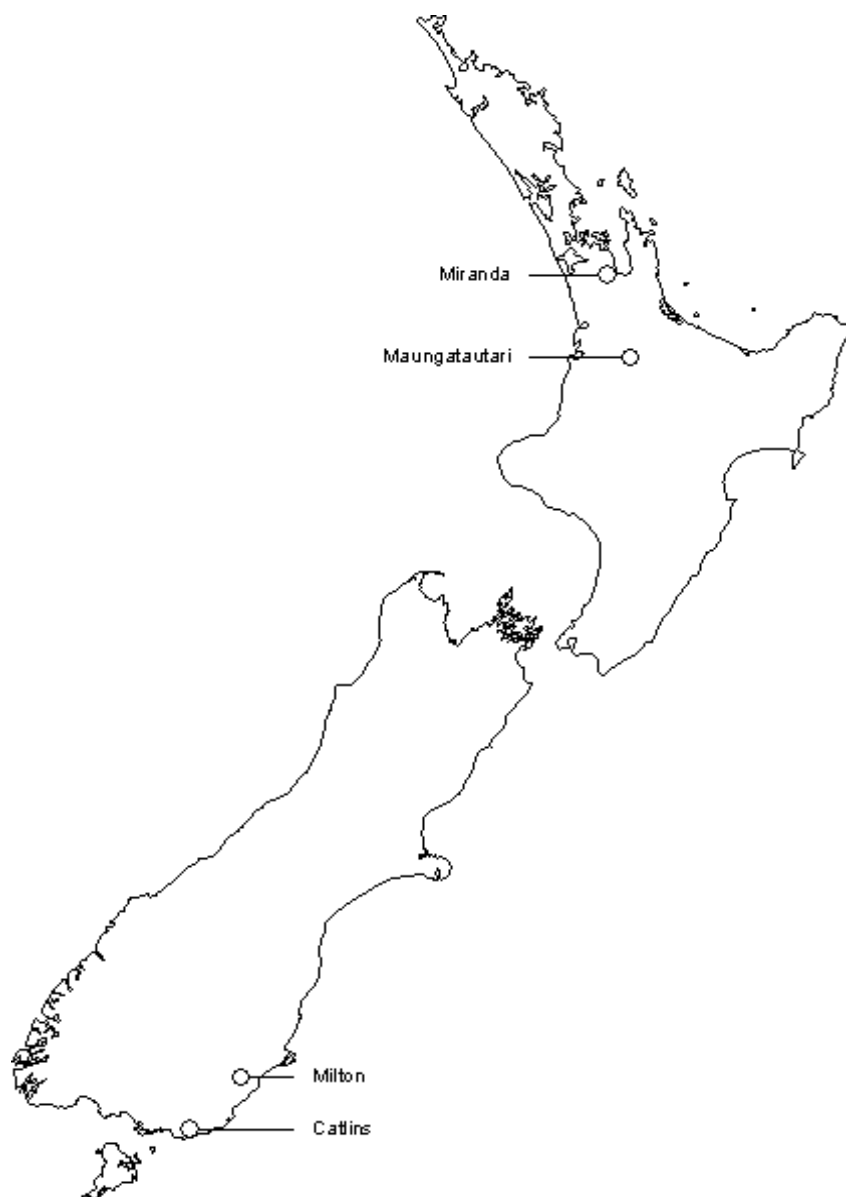
#### 4.1 Effects of habitat and season on RTCI

##### Study areas

Our study was conducted at two sites in the North Island, New Zealand (Fig. 1). One site consisted of 3200 ha of tall indigenous forest in the Maungatautari Scenic Reserve (38°00'S, 175°05'E; ‘forest’). The forest was mixed podocarp (primarily tawa *Beilschmiedia tawa*, northern rata *Metrosideros robusta*, rimu *Dacrydium cupressinum* and kāmahi *Weinmannia racemosa*) with an understorey dominated by treeferns (*Dicksonia squarrosa*, *Cyathea dealbata*, *C. medullaris*, and *C. smithii*) and supplejack (*Ripogonum scandens*). Possums in the reserve had been controlled by aerially broadcast 1080 (0.15% in carrot) in June 1997. The control operation reduced possums from a mean  $26 \pm 8$  (SE) % RTCI to a mean  $2 \pm 2$  % RTCI ( $n = 10$  lines each; G. Cochrane, MAF Quality Management, unpublished report). Monitoring of 10 lines within the reserve in March 2000 showed that possums had increased to  $7 \pm 3$  % RTCI (G. Cochrane, AgriQuality New Zealand, unpublished report). For the 56

lines that we monitored during the course of our work the mean uncorrected RTCI was  $7.3 \pm 0.7\%$ .

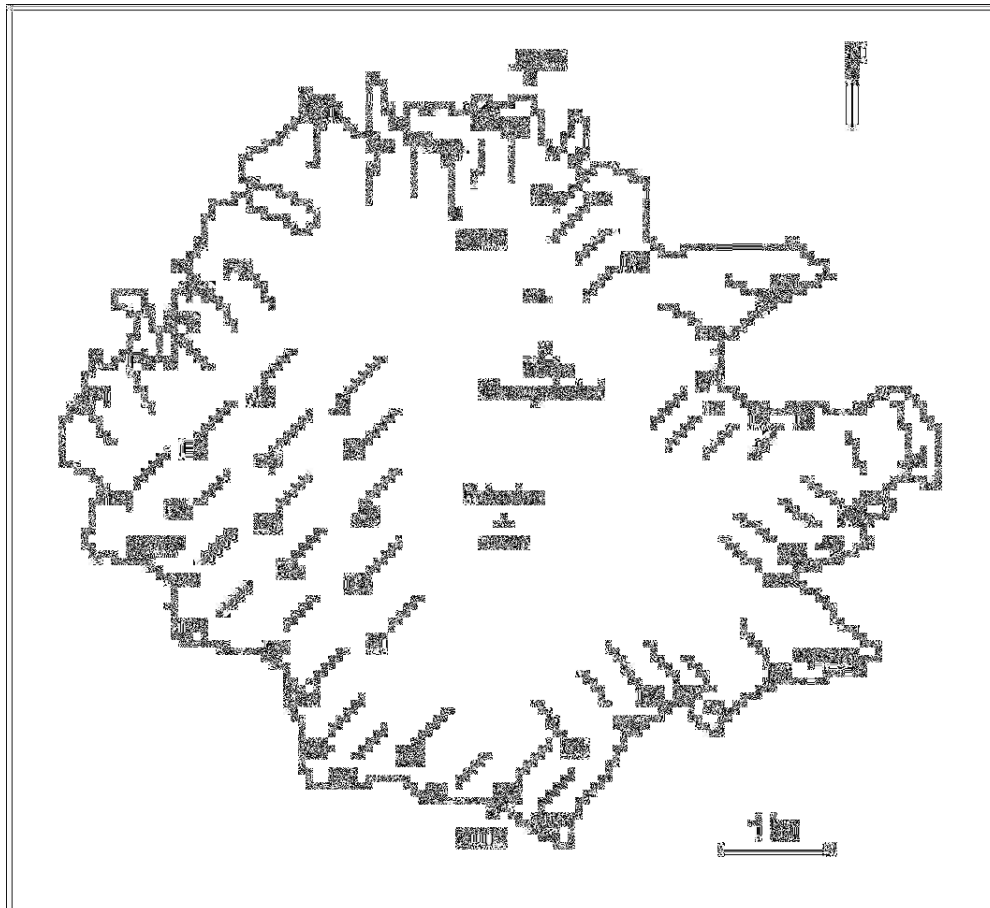
The second site was 6500 ha of farmland near Miranda ( $37^{\circ}12'S$ ,  $175^{\circ}15'E$ ; 'farmland'), c. 200 km from the forest site. The farmland was mainly rolling pasture interspersed with tall indigenous forest. Some pasture adjoined *Pinus radiata* plantations or willows (*Salix* spp.). Possums at this site had not been subject to any recent control, and for the 60 lines in this study the mean RTCI was  $22 \pm 1.3\%$ . Traplines were placed along the margins of the forest patches and exotics plantings.



**Fig. 1** The four study sites. The effect of season on RTCI was assessed at Maungatautari (indigenous forest) and Miranda (farmland). The effect of timing on RTCI was assessed at Milton (both *Pinus* forest and farmland habitats) and the Catlins (both indigenous forest and farmland habitats).

### Experimental design

Because possum abundance could be expected to vary spatially within each site, we initially delineated eight ‘blocks’ at both study sites. At Maungatautari these blocks were located in a circular fashion around the study area (Fig. 2). Six traplines 400 m long were assigned to each block, all  $\geq 250$  m from the forest edge and  $\geq 500$  m from a neighbouring line. Radio-tracking studies in tall-forest habitats (review in Cowan & Clout 2000) indicate that a distance of 250 m should ensure that possums caught on one line would not be within the ‘catchment’ of adjacent lines (i.e., lines should be independent sampling units). We randomly assigned lines within each block to one of three seasons (summer (January–March), winter (July–August), and spring (October–November)) in the 2000 and 2001 calendar years. Livestock commonly trigger leg-hold traps, making traps unavailable to possums. Because of farming practices, the random allocation of lines within blocks was impractical at the farmland site. Instead, large areas of similar habitat were delineated as blocks, and one line was located in each block (in consultation with the farm manager) at the start of each trapping session. A new trapline was always  $\geq 500$  m from a previous trapline. Following preliminary analysis of the summer and winter data in 2000, we increased the number of blocks in forest and farmland to 10 and 11, respectively.



**Fig. 2** The Maungatautari study area (tall indigenous forest) indicating the 10 blocks (A–J) and traplines located in each block (1–6). Two blocks (I, J) have only four traplines because they were established after two seasons had been completed. The order in which lines were trapped was decided randomly after the first two seasons had been completed (lines 1 and 2 for A–H). Numbers are spot heights (metres).

Each trapline consisted of 20 Victor No. 1 traps (Montague & Warburton 2000) set according to protocol (NPCA 2002). All lines within each site were trapped simultaneously, but start dates varied by up to 14 days between sites. Traps were set for between 9 and 12 fine nights, the first three of which were always consecutively fine. The end point for trapping was night 9, but if the number of possums caught on night 9 was greater than 20% of the possums caught on night 1 then we continued trapping for up to 3 more nights. Traps were checked daily and all possums humanely killed.

This work was conducted with the approval of the Landcare Research Animal Ethics Committee (AEC approval 99/3/6).

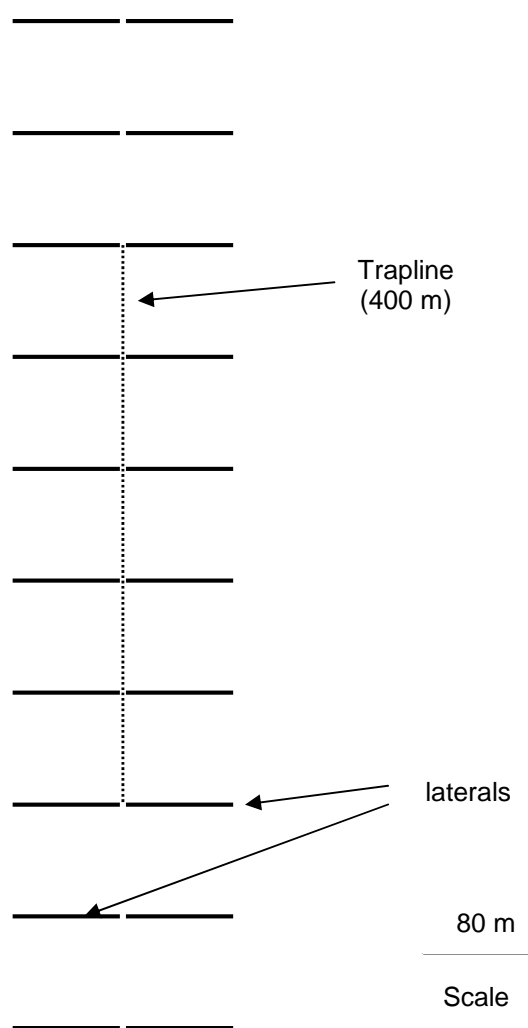
### **Alternative estimators of possum abundance**

Because the radioactive marker for possum faeces failed (see Section 5.3), we used two other methods to estimate the number of possums remaining on a line following trapping: cleared-plot faecal pellet counts, and cyanide poison. Both methods have been previously used to estimate the relative abundance of possums in New Zealand (e.g., Baddeley 1985; Hickling & Pekelharing 1989; Spurr 1995), although the form of the relationships between the indices and the actual abundance of possums is unknown.

*Cleared-plot faecal pellet counts:* Cleared-plot faecal pellet counts were made in permanently marked circular plots of 1.6-m diameter spaced at 10-m intervals along the 400-m trapline (i.e., 40 per line), and along an adjacent line that was to be trapped in the next season as a control. We recorded the total number of recognisable pellets within 80 cm of the plot centre, but removed all pellets out to 100 cm. Three counts were made along each line: (1) a pre-trapping count in the 3 days prior to the start of trapping; (2) a post-trapping count within 7 days of trapping finishing, and (3) a final count occurred between 14 and 21 days after the post-trapping count. Cleared-plot faecal pellet counts were used in the first session of the study (i.e., summer 2000) at Maungatautari, and in the first two sessions (summer and winter 2000) at Miranda. After examining these results (see Section 5.1), cleared-plot faecal pellet counts were not used again at either site.

*Cyanide poisoning:* We used cyanide poison in two ways. We first attempted to evaluate the effect of trapping on the spatial distribution of possums. We did this by poisoning possums along 10 'lateral' lines, with each lateral being 160 m long and perpendicular to the trapline, and spaced at 80 m along the trapline (Fig. 3). After traps were removed, we placed peanut-butter paste ('Ferafeed', Connovation, Auckland) every 2–3 m along the laterals. After 2 fine nights, cyanide paste (Trappers Cyanide Co., Styx Mill Road, Christchurch) was laid on the remaining prefeed (or new peanut-butter paste if the prefeed had been eaten) and topped with additional peanut-butter paste. Cyanide is a very fast-acting and humane toxin, with death occurring in 10–26 minutes (Eason et al. 2000). After 2 fine nights the number of possums dead at each bait site was recorded, and remaining baits removed. To check on the effectiveness of the poisoning operation, we placed mortality-sensing radio-collars on eight possums caught during the first three nights of trapping at Maungatautari in winter 2000. These animals were then monitored using close-approach telemetry after the completion of the poisoning. At Maungatautari, we used laterals on four and six traplines in summer 2000 and winter 2000, respectively. After examining the results from these two seasons (see Section 5.1), laterals were not used again at Maungatautari. Laterals could not be implemented at Miranda because they would have potentially exposed livestock to cyanide poison.

We also used cyanide paste to estimate the number of possums remaining after trapping. We placed c. 2 g of Ferafeed on the ground at 10-m intervals along the trapline. After 2 fine nights, cyanide paste (Trappers Cyanide Co., Styx Mill Road, Christchurch) was laid on the remaining prefeed (or new peanut-butter paste if the prefeed had been eaten) and topped with additional peanut-butter paste. After 2 fine nights the number of possums dead at each bait site was recorded, and remaining baits removed. At the forest site, consumption of both peanut butter and cyanide by rats (*Rattus* spp.) necessitated the use of a 'cyanide station' from spring 2000. A cyanide station (Appendix 1) was placed every 10 m along the trapline, and prefeed and/or cyanide paste was placed on top of the plastic tray. The bait station reduced, but did not eliminate, interference by rats (S. Hough, personal observation). At Maungatautari, we used this method of poisoning along four and two traplines in summer 2000 and winter 2000, respectively; thereafter we used it on all lines. At Miranda, we used this method of poisoning on as many lines as possible; it was not possible to use cyanide when farmers moved livestock into paddocks after trapping had finished.



**Fig. 3** Layout of the 10 lateral lines around the 400-m trapline. Each lateral was 160 m long and perpendicular to the trapline.

*Statistical analyses:* A full mathematical description of our statistical analyses is given in Appendix 2. Here we give a brief description of our approach.

We extended previous work estimating population size,  $\hat{N}$ , based on constant sampling effort with removal of individuals (Zippin 1956, 1958; Seber 1982). The RTCI can be considered a constant removal, with 20 traps per line set each night in this study. Our model estimated the number of possums along each line as a function of the number of possums caught in the previous nights. The three-night RTCI is a function of capture probability ( $p$ ) and actual population size ( $N$ ) over the first three nights. For illustration, assume that  $p$  is constant over the three nights. If  $\hat{N}$  is the estimated population size it can be shown that

$$\text{RTCI} = \frac{\bar{N}p(1 + (1-p) + (1-p)^2)}{K},$$

where  $K$  is the total number of trap nights per trapline (e.g., 60 for one trapline of 20 traps set for 3 fine nights). Thus, a model of the relationship between RTCI and  $N$  follows from that of  $p$  and  $\hat{N}$ . Our model was extended to allow capture probability to vary with many other covariates as in standard regression modelling. For the effect of habitat and season we developed a model in which  $p$  varied with  $N$  and season, but differently for the two sites (forest and farmland) according to year.

We emphasise that capture probability is the probability (i.e., a value between 0 and 1) of a possum being trapped. Variation in capture probability may be dependent on a variety of factors, including ‘shyness’ (i.e., a behavioural aversion to entering traps), general activity levels, understorey complexity, and the relative use of the canopy versus the ground. Our model assumes that there is a finite population around each trapline, and that capture probability is equal within traplines, but variable between traplines. It is the magnitude of this variation that we are modelling as a function of season and habitat in this analysis.

We used version 1.3 of the software package *BUGS* (available for free download at <http://www.mrc-bsu.cam.ac.uk/bugs/>) for our analyses. The program uses an algorithm to identify the maximum likelihood estimates (MLE) for models that are too complex to solve using traditional MLE. For a discussion of the application of *BUGS* to analyses in ecology and wildlife management see Link et al. (2002). The *BUGS* software analyses the precision, which is the inverse of the variance, as an argument. The variance is easily obtained from the estimate of precision. The importance of parameters was assessed by their 95% confidence intervals. We note that the confidence intervals calculated with this approach, in contrast to classical hypothesis testing, can be interpreted as ‘having a 95% probability that the confidence interval includes the true value’.

One way of interpreting a logistic model is by considering odds ratios. For example, if  $p_1$  is the mean capture probability in winter and  $p_2$  the corresponding summer value, the odds ratio is  $\{p_1/(1-p_1)\}/\{p_2/(1-p_2)\}$ . We used odds ratios and their 95% confidence intervals to assess the importance of the two-way seasonal comparisons at each site.

## 4.2 Effects of timing on RTCI

### Study areas

This work was conducted at four study sites in the southern South Island. Two sites were near Milton and two sites were in the Catlins area (Figs 1, 4). At Milton, one site was in *Pinus radiata* forest within Berwick Forest (‘Milton Forest’) and one site was in farmland (‘Milton Farmland’). The control operation at Milton Forest consisted of aerial application of

0.15% 1080 in cereal baits. The mean RTCI in the first session of trapping at this site (i.e., immediately after control) was 3.33% (95% CI, 0.98–5.69%;  $n = 7$  lines).

The Milton Farmland site consisted of pasture with gullies containing mixed scrub and willows (*Salix* spp.). Some paddocks were bordered by shelterbelts (primarily *Pinus* spp.). The control operation at Milton Farmland consisted of ground application of 0.15% 1080 in cereal baits; no traps were used. The mean RTCI in the first session of trapping at this site (i.e., immediately after control) was 0.95% (95% CI, 0.00–2.17%;  $n = 7$  lines).

At the Catlins, one site was in indigenous forest ('Catlins Forest') and the other was in farmland ('Catlins Farmland'; Fig. 5). The Catlins Forest site was in the Longbeach Creek catchment, north-west of Waikawa Harbour. The coastal forest was dominated by southern rata (*Metrosideros umbellata*), kāmahī, rimu and totara (*Podocarpus hallii*). The mean RTCI in the first session of trapping at this site (i.e., immediately after control) was 5.00% (95% CI, 2.33–7.67%;  $n = 7$  lines).

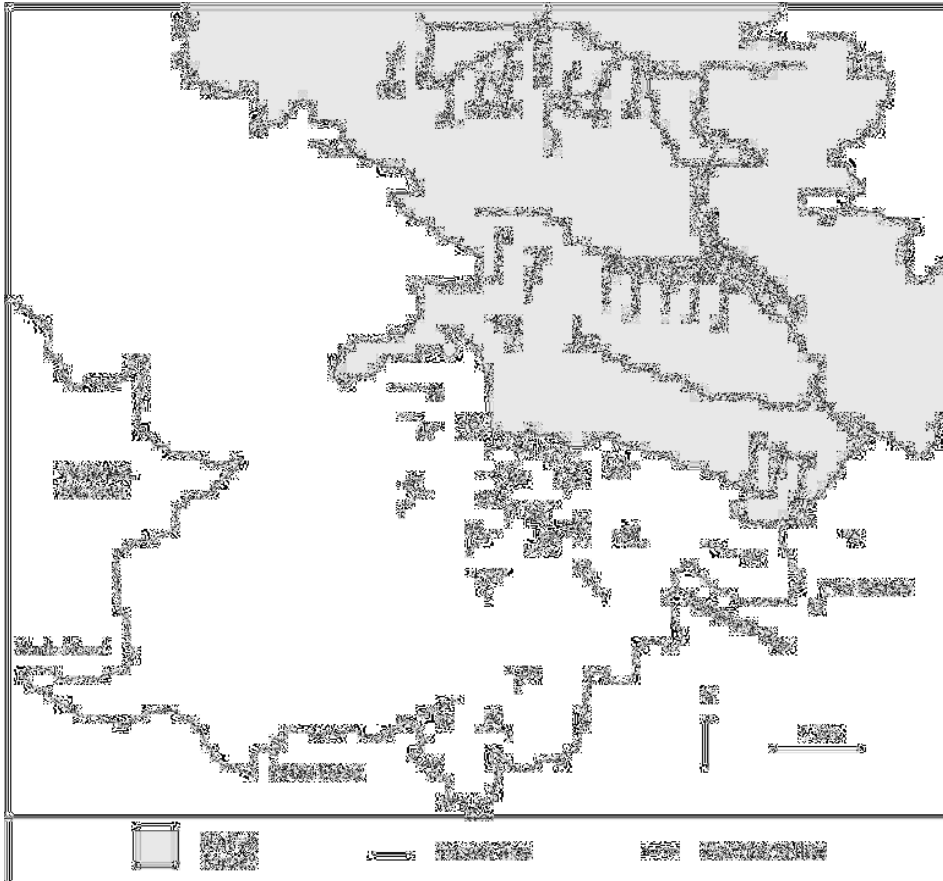
The Catlins Farmland site was in pasture adjoining gullies and steeper ridges containing remnant forest (as for Catlins Forest) between Longbeach Creek and Waikawa Harbour. The mean RTCI in the first session of trapping at this site (i.e., immediately after control) was 7.14% (95% CI, 4.52–9.77%;  $n = 7$  lines).

### **Experimental design**

At Milton Forest, the study area was divided into seven blocks (on the basis of stand age and topography), with three traplines located in each block (Fig. 4). Lines were  $\geq 500$  m apart, and the order in which the three lines within each block were used was determined randomly. The initial session started on 24 January 2000, 3 weeks after the control operation, and finished on 10 March 2000. The second and third sessions occurred during 3 June – 18 July and 9 October – 12 November, respectively. Traps were set for between 9 and 12 fine nights, with the first three nights always fine.

At Milton Farmland, contiguous areas of similar habitat were delineated into seven blocks, with three traplines located in each block. Traps were set for between 9 and 12 fine nights, with the first three nights always consecutively fine. As at Milton Forest, the initial session started on 24 January 2000, 3 weeks after the control operation, and finished on 10 March 2000. The second session occurred during 17 May – 1 June 2000. Despite informing the contractors of our work, the Milton Farmland area was controlled before we could conduct the third and final session; that session was therefore abandoned.

The two Catlins sites were both divided into seven blocks, as at the Milton sites (Fig. 4), with three traplines located in each block. Traps were set for between 9 and 12 fine nights, with the first three nights always consecutively fine. At Catlins Forest the initial session started on 28 February 2000, 4 weeks after control, and finished on 9 March 2000. The second and third sessions occurred during 5–27 June and 21–30 November 2000. At Catlins Farmland, the initial session occurred during 1–11 March 2000, the second session during 12–26 June, and the third and final session during 24 November – 2 December.



**Fig. 4** The Catlins Farmland and Forest study areas. Seven blocks of three traplines were located in each of the farmland and forest habitats.

#### **Milton Forest – Alternative estimators of possum abundance**

At Milton Forest, we used both cleared-plot faecal pellets and cyanide poisoning to estimate the number of possums remaining on all seven traplines in all three sessions. Encapsulated cyanide poison in plastic bags ('Feratox', Connovation, Auckland) was stapled to trees at c. 10-m intervals along all seven traplines after trapping had finished in the first session. In the second and third sessions we used Feratox along laterals to estimate the number of possums remaining on all traplines. The use of cyanide poison, apart from being in the form of Feratox and stapled to trees, otherwise followed the methods outlined above.

#### **Milton Farmland – Alternative estimators of possum abundance**

In the first session at Milton Farmland, cleared-area faecal pellet plots were established at 10-m intervals along counts to estimate the number of possums on 14 traplines; seven that were trapped in the first session and seven that were to be trapped in the second session. Pellets were counted and cleared on three occasions: immediately prior to trapping, immediately after trapping, and 7 days later. It was not possible to use cyanide poison at Milton Farmland because of the risk of accidentally poisoning livestock. We therefore made spotlight counts between 1 and 3 hours after dusk in the first and second sessions. One person walked 50 m parallel to the trapline searching both towards and away from the trapline with a 100-watt spotlight. Both sides of traplines along shelterbelts were walked. For a trapline along a forest edge, we walked along and back the same side. The location and time that possums were sighted were recorded on a sketch map. The counts were conducted on two consecutive fine

nights. In the first session at the Milton Forest site, cleared-area faecal pellet plots were established and conducted as at the Milton Farmland site.

No faecal pellet counts were undertaken at the two Catlins sites. Post-trapping monitoring consisted of Feratox stapled to trees along all traplines at Catlins Forest, and spotlighting at Catlins Farmland. Spotlighting at Catlins Farmland followed the method described above.

### **Statistical analyses**

Because the Milton Farmland area was controlled before we could conduct the third and final session, only data from Milton Forest, Catlins Farmland and Catlins Forest were included in these analyses.

We used the same basic model as in *Statistical analyses* above to investigate the relationship between capture probability and population size at the three sites. The model was extended to allow capture probability to vary with other covariates of interest. Of key interest was a model in which  $p$  varied with  $N$  and session, but differently for the three sites according to session. *BUGS* provides estimates of single parameters, so the model was formulated such that (1) all differences between the three sessions and three sites were fitted, (2) parameters had a practical interpretation, and (3) parameters were independent of each other. However, the unbalanced nature of the data prevented the latter from being achieved fully. For readers wishing to interpret our results in detail (see Appendix 3), the variables that we included in the model were (1) Site – the difference between Catlins and Milton; (2) Habitat – the difference between farmland and forest at Catlins (not Milton); (3) Linear session – the difference between spring and summer; and (4) Quadratic session – the difference between winter and the average of summer and spring (if there was a steady increase from summer to winter this parameter would be zero). Interactions show whether parameters have different values depending on the level of the other. To allow for block effects, a random intercept was again fitted for each block (see above). The block intercepts were similar, and there was little difference in the standard deviations of parameter estimates when block was included in the model. This was not surprising because our earlier model allowed for line variation, and block variation is a component of line variation. For simplicity we therefore do not report results for blocks.

The log odds ratio of capture probability was again used as the response variable because this avoids the limits of 0 and 1. However, for interpretation, capture probabilities are also shown.

### **4.3 A radioactive marker for possum faeces**

Fourteen adult possums were captured and acclimatised for at least 4 weeks in individual cages (350 × 200 × 200 cm) in rooms maintained at 19 ± 5°C at the Landcare Research Animal Facility, Lincoln. Possums had free access to water and specifically formulated cereal-based pellets (Western Milling Co., Rangiora) supplemented with fruit and green leafy vegetables.

Seven possums (four males and three females) were given 10 µCi (equivalent to 0.37 megabecquerels) of tritiated progesterone diluted in 1 ml of saline solution by injection into a large muscle group (hindquarter). Possums were anaesthetised with fluothane before the injection. All faecal pellets from each possum were counted and collected on days 1, 2, 3, and every 2 d thereafter, for 16 days following injection. Each pellet was frozen separately in a plastic bag until analysed. A control group of another seven adult possums (four females

and three males) were fed a diet similar to the injected possums and the number of faecal pellets voided by each possum counted each day.

The faeces were analysed for the presence of tritiated progesterone at Lincoln University. Samples were removed from the freezer, dried overnight at 70°C, weighed, and then ground into fine particles with a mortar and pestle. Scintillant (4 ml) was added to a known weight of each sample (about 0.1–0.2 g) and the level of radioactivity measured using a scintillation counter. Samples of non-radioactive faeces were treated in the same way and tested in the scintillation counter at the same time. Each sample was counted for five minutes and the counts per minute averaged.

When the marker in faeces collected on days 5 and 7 of the initial trial was found to have dropped to background levels of radiation a further trial with four possums was conducted. This was to test whether intravenous administration of the marker had a different decay rate to intramuscular injection. Two adult possums were injected intramuscularly (in the hind quarter) with 10 $\mu$ Ci of tritiated progesterone diluted in 1 ml of saline solution and two were injected intravenously (in the tail vein) with 10 $\mu$ Ci of tritiated progesterone diluted in 200  $\mu$ l of saline solution. Possums were anaesthetised with fluothane before injection. Faeces were collected and tested for marker presence in the same way as for the original trial.

This work was conducted with the approval of the Landcare Research Animal Ethics Committee (AEC approval 99/3/6).

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## 5. Results

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### 5.1 Effects of habitat and season on RTCI

#### **Alternative estimators of possum abundance**

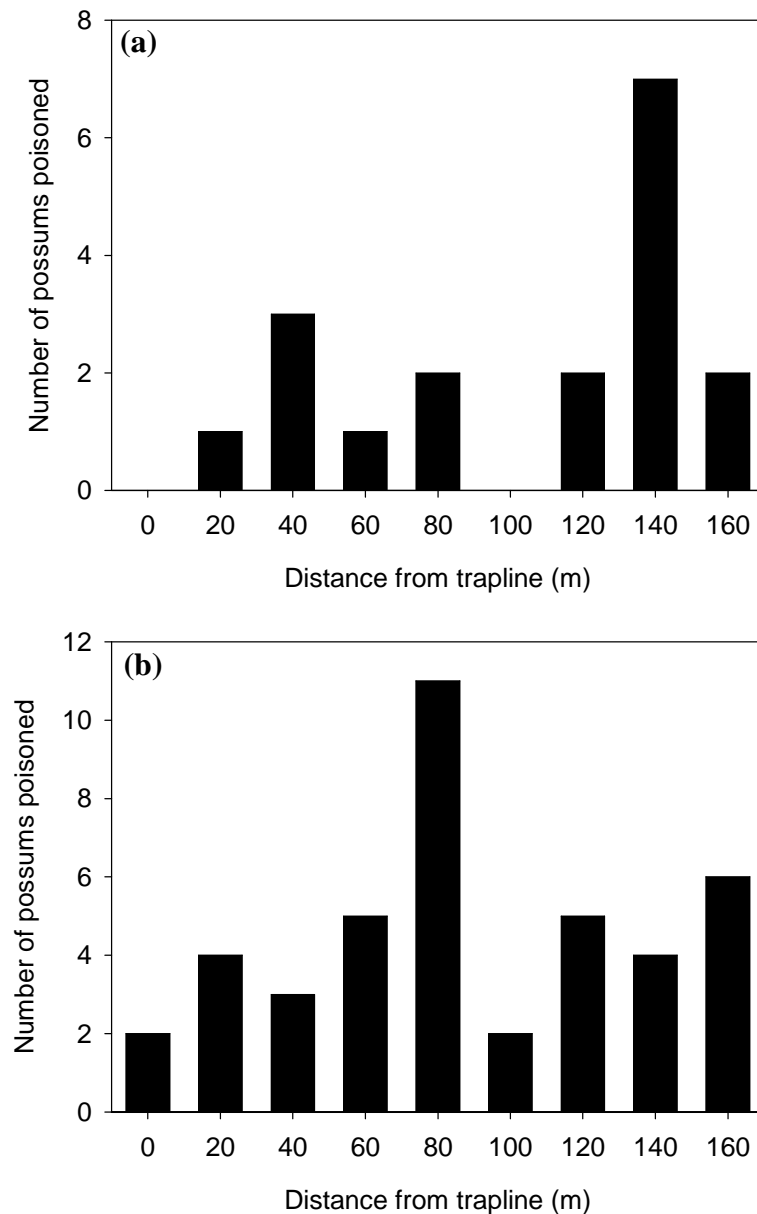
*Cleared-plot faecal pellet counts:* At Maungatautari, searches at 7 and 18 days after trapping had ceased revealed fresh faecal pellets on three plots on two of the eight traplines. Although these data suggest that few possums remained on the trapped lines, the same frequency of fresh pellets was recorded on the untrapped lines, indicating that the method was a poor basis for estimating the abundance of possums. We suspect that rats may have been eating or moving faecal pellets at this site, although an attempt to verify that (Nugent et al. 2003 unpublished) was inconclusive. We stopped faecal pellet counting at Maungatautari after the first season (summer 2000).

At Miranda, despite large numbers of possums being trapped along some traplines, faecal pellets were recorded in similarly low abundance on both trapped and adjacent untrapped lines in both summer and winter 2000. These data were too sparse for statistical analysis, and this method was abandoned.

*Cyanide poison:* Only 18 possums were poisoned along 12.8 km of laterals (four traplines) at Maungatautari in summer 2000. There was a trend in the spatial distribution of poisoned possums, with more animals killed further from the traplines (Fig. 5a). In winter 2000, 42 possums were poisoned along 19.2 km of laterals (six traplines)(Fig. 5b). Of the

eight possums released with radio-collars, five were poisoned (two at 20 m, one at 60 m and two at 80 m from the trapline); close-approach telemetry showed the remaining three were denning at 20 m, 40 m and >160 m from the traplines. The steep gullies and thick understorey (particularly supplejack) at Maungatautari meant that the use of laterals was very expensive relative to the data gained (Fig. 5).

The use of cyanide poison laid along traplines after trapping had finished is discussed in conjunction with trapping data (see below).



**Fig. 5** Spatial distribution of possums poisoned with cyanide using the lateral design at Maungatautari in (a) summer 2000, and (b) winter 2000.

### Trapping data

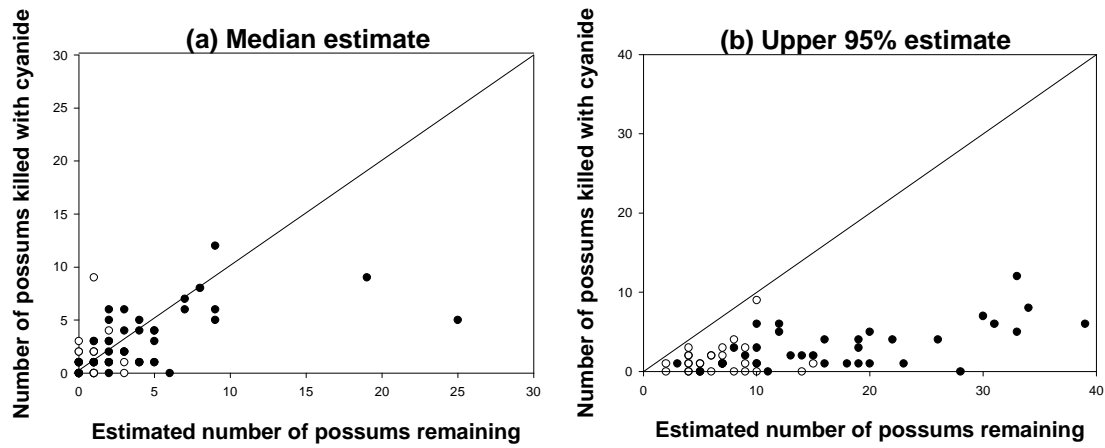
The three-night RTCI data at the forest and farmland sites in 2000 and 2001 are summarised in Table 1. However, we emphasise that our approach modelled capture probability based on more than 3 nights of trapping; we therefore present the three-night RTCI only as background information.

**Table 1** Mean three-night RTCI ( $\pm$  95% CL) for the forest (Maungatautari) and farmland (Miranda) sites in summer, winter and spring 2000 and 2001.  $N$  is the number of traplines.

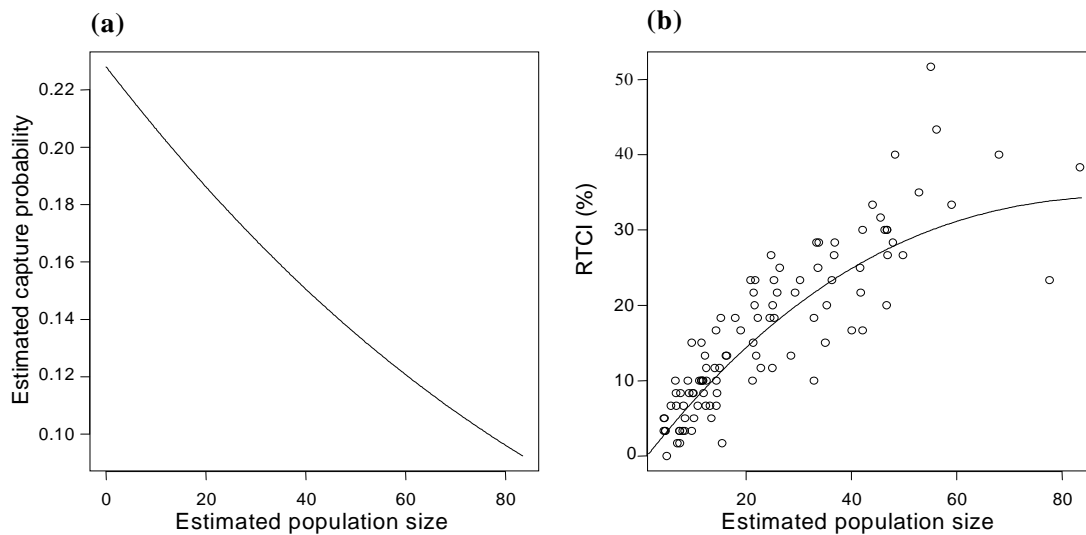
Site	Year	Season	$N$	Mean	Lower 95% CL	Upper 95% CL
Forest	2000	Summer	8	8.96	6.86	11.06
Forest	2000	Winter	8	8.96	6.73	11.19
Forest	2000	Spring	10	7.50	1.73	13.27
Forest	2001	Summer	10	8.96	2.47	15.45
Forest	2001	Winter	10	7.08	1.78	12.39
Forest	2001	Spring	10	5.00	2.32	7.69
Farmland	2000	Summer	8	17.08	11.47	22.69
Farmland	2000	Winter	8	25.42	13.60	37.23
Farmland	2000	Spring	11	29.17	22.06	36.27
Farmland	2001	Summer	11	18.13	8.81	27.44
Farmland	2001	Winter	11	23.54	16.50	30.59
Farmland	2001	Spring	11	20.21	14.32	26.09

The estimates of  $\hat{N}$  from our model were unstable for 11 lines that caught three or fewer possums. We therefore excluded those lines from further analyses, leaving a total of 105 traplines. Cyanide was laid along 66 of the 105 traplines following the completion of trapping. Using the median estimate of  $\hat{N}$  and subtracting the number of possums removed by trapping, on 15 traplines the number of possums poisoned using cyanide was equal to the estimated number remaining, on 23 lines the number poisoned was greater than the estimated number remaining, and on 28 lines the number of possums was less (Fig. 6). Using the upper 95% estimate of  $\hat{N}$ , on all 66 lines the number of possums poisoned was less than the number estimated to be remaining. These data suggest that  $N$  was likely to lie within the 95% confidence interval for  $\hat{N}$ .

Parameter estimates for the simple linear logistic model (Equation 5, Appendix 2) are shown in Appendix 3. Note that *sd.line*, *sd.pop* and *sd.rep* are standard deviations estimated from the precision values defined above and *mu.pop* is the estimated mean of the line populations (average possums per trapline). There is a 95% chance that the true slope for the relationship between capture probability  $p$  and estimated population size  $\hat{N}$  was between  $-0.0185$  and  $-0.0070$  (i.e., significantly less than zero). We interpret this result as strong evidence that capture probability declined with increasing population size. This leads to the relationship between RTCI and possum abundance being positive but non-linear (Fig. 7).

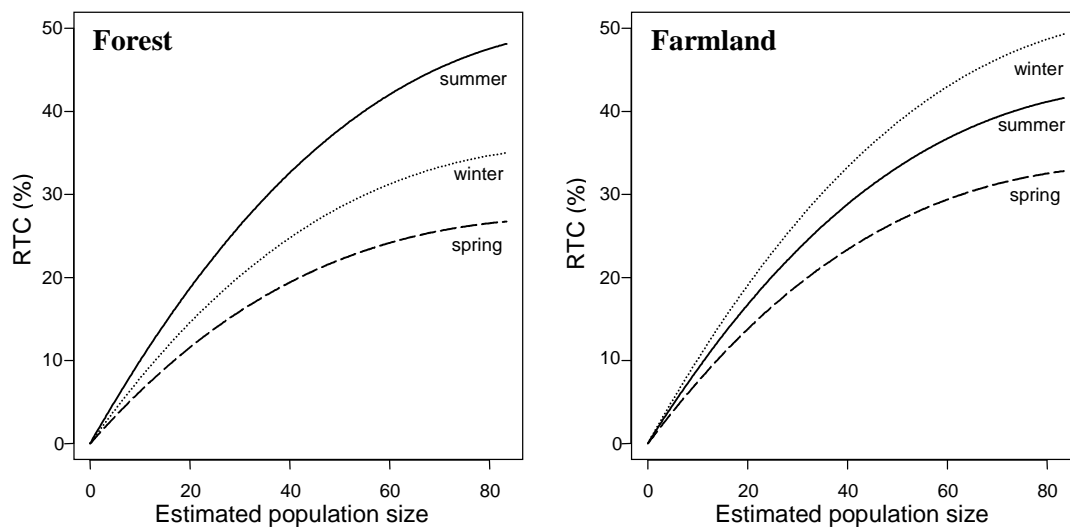


**Fig 6** Relationship between the (a) median, and (b) upper 95% estimate of the number of possums remaining after trapping, and the number of possums actually poisoned with cyanide along the trapline after trapping. The open and filled circles are traplines in forest and farmland, respectively.



**Fig. 7** The relationship between (a) estimated capture probability and population size, and (b) RTCI and population size, for 105 traplines. Note that estimated population size ( $\hat{N}$ ) must be  $>0$ .

There was little evidence that capture probability varied between the two years (Appendix 3B). The confidence interval for parameter  $a_3H \times S_{1,2}$ , a component of the site $\times$ season interaction (Equation 7, Appendix 2), excluded zero, indicating a seasonal effect that varied between the forest and farmland sites. It is easiest to interpret the relationship by considering plots of the fitted values for year 2000 in this model (Fig. 8). Estimates for 2001 were slightly lower than 2000. At the forest site, capture probability was highest in summer, followed by winter and then spring (Fig. 8). At the farmland site, capture probability was highest instead in winter, but also lowest in spring (Fig. 8). Since the distributions of the odds ratios were skewed, we quote the median, rather than the mean, values. The median odds ratios and associated 95% confidence intervals for the seasonal comparisons at each site were: forest winter/summer, 0.67 (0.39–1.09); farmland winter/summer, 1.25 (0.95–1.64); forest spring/summer, 0.50 (0.22–0.87); farmland spring/summer, 0.75 (0.56–0.99); forest winter/spring, 1.37 (0.73–2.81); farmland winter/spring, 1.68 (1.28–2.18). The odds of catching a possum were therefore lower in spring relative to summer at both sites, and higher in winter compared to spring at the farmland site. Since the remaining confidence intervals all included 1, we infer that the odds were similar in other seasonal contrasts.



**Fig. 8** RTCI as a function of population size and season (summer, winter and spring) at the forest and farmland sites. The fitted values are for 2000; values were slightly lower in 2001. Note that estimated population size ( $\hat{N}$ ) must be  $>0$ .

## 5.2 Effects of timing on RTCI

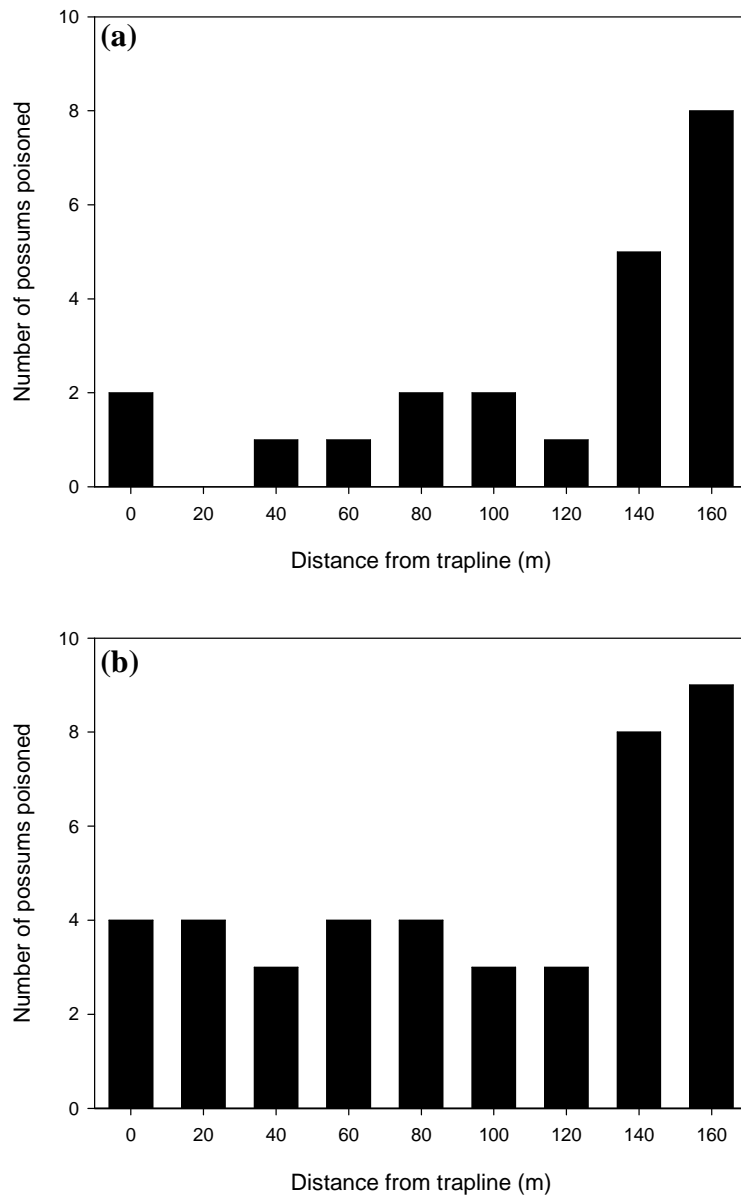
### Alternative estimators of possum abundance

*Cleared-plot faecal pellet counts:* Prior to trapping in the first session at Milton Farmland, pellets were recorded on only three lines, two of which were subject to trapping. Possums were subsequently caught on one of those lines on which pellets were counted ( $n = 2$  possums), and also on two other lines (both  $n = 1$ ). No pellets were observed on the second inspection. It was therefore concluded that cleared-plot faecal pellet counts were a poor estimator of possum abundance at this site, and no further pellet counts were undertaken there.

At the Milton Forest site, pellets were found on all but one of the 14 lines in the first inspection. The second inspection revealed pellets on only three of the untrapped lines. The third inspection revealed small numbers of pellets on four of the trapped lines and on five of the untrapped lines. There were similar inexplicable inconsistencies in the pellet counts conducted during the second and third sessions at this site. It was therefore concluded that cleared-plot faecal pellet counts were also a poor estimator of possum abundance at this site, and no further pellet counts were undertaken there.

*Cyanide poison:* In the first session at the Milton Forest site, Feratox was placed at 5-m intervals along all seven traplines. Only one possum was poisoned. That possum had a trap injury, but no escapes had been recorded on that line, suggesting that the possum had moved from another line with escapes; the nearest such line was 1 km away. In the second session at the Milton Forest site, Feratox was placed along 10 laterals on each of the seven traplines. A total of 22 possums was poisoned, and the distribution of poisoned possums (Fig. 9a) suggested that trapping had removed most of the possums present within 140 m of the traplines. In the third session at the Milton Forest site, 42 possums were poisoned along 10 laterals on seven trapped lines (Fig. 9b). In contrast to Maungatautari (Fig. 5), at Milton Farmland there appeared to be a threshold distance of about 140 m at which the number of possums poisoned increased (Fig. 9).

In the three sessions at the Catlins Forest site, Feratox was placed at 5-m intervals along all seven traplines; poisoning along laterals was not used at this site for reasons discussed below. In the first session, 66 possums were trapped and two possums were poisoned. In the second session, 70 possums were trapped and 10 possums were poisoned (two on three lines, one on three lines, and none on one line). Although 114 possums were trapped in the third session, no possums were poisoned; weather conditions were suitable and the poisoning was conducted as in the previous sessions.



**Fig. 9** Spatial distribution of possums poisoned along 10 laterals on seven traplines in the (a) second, and (b) third sessions at the Milton Forest site.

*Spotlighting:* In both the first and second sessions at the Milton Farmland site, spotlighting was conducted along the seven trapped lines for two consecutive nights immediately after trapping had finished. No possums were observed in either session.

In the first session at the Catlins Farmland site, 60 possums were trapped and one possum was seen with the spotlight on one trapline on two consecutive nights. In the second session, 80 possums were trapped and a total of five possums were seen on three lines on the first night; no possums were seen on the second night, perhaps due to some rain falling. In the third session, 109 possums were trapped and at least 17 possums were present after trapping finished.

### Trapping data

The three-night RTCI at the four Milton and Catlins sites in each of three sessions is summarised in Table 2. We again emphasise that our approach modelled capture probability based on more than 3 nights of trapping; we present the three-night RTCI as background information.

As with the North Island results, lines on which three or fewer possums were caught could not be included in the analyses. Parameter estimates for the simple linear logistic model (Equation 5, Appendix 2) are shown in Appendix 3. There is a 95% chance that the true slope for the relationship between  $p$  and  $\hat{N}$  was between  $-0.01$  and  $0.04$ . In contrast to the North Island study (Appendix 3A), capture probability did not decline with increasing population size at the three South Island sites. This difference was likely a result of the much lower range of  $\hat{N}$  at the three South Island sites. The *BUGS*-generated estimates of capture probability at the three sites in each of the three sessions are given in Table 3. Although the RTCI at the three sites was not greatly affected by  $\hat{N}$ , the model can be used to predict what the log odds would have been if all sessions and sites had the same mean number of possums (i.e.,  $\hat{N} = 12.8$ ). Adjusted log-odds are given in Table 4, and are very similar to those in Table 3. The implication is that the differences in RTCI between sessions (and sites) are largely due to changes in capture probability, rather than changes in actual possum numbers.

Parameters from a simple linear model fitted to all sessions and sites are given in Appendix 3C. The median estimate of slope was  $0.0147$  (95% CL;  $-0.010, 0.037$ ), providing little evidence that capture probability changed with population size. This is a different result from the North Island data, where the slope was  $-0.013$  and did not include 0. The difference reflects the increase in capture probability in the later sessions, which were also associated with increased  $\hat{N}$ .

Session was explicitly included in the analysis summarised in Appendix 3D, with slope now measuring the effects within a single session/site combination. Although the evidence for any effect of  $\hat{N}$  on capture probability is slight, the value is comparable with that from the North Island data ( $-0.012$ ). (Note that the latter estimate has a lower standard deviation, so was ‘significant’.) The ‘Site’ parameter shows that there was a difference between Catlins and Milton, and the ‘Site  $\times$  linear session’ parameter shows that this difference is increasing linearly with time: capture probability increased with time at Catlins, but remained constant at Milton. The ‘Quadratic session’ parameter shows that, on average, winter was lower than it would have been with a steady increase over time, and the ‘Habitat  $\times$  Quadratic session’ parameter provides some evidence that this effect differed between the forest and farmland sites in the Catlins. These results show increases in the third (spring) session, the reverse of the North Island result. This could indicate that the increase with time after control is rather larger than these results suggest.

**Table 2** Mean three-night RTCI ( $\pm$  95% CL) for the Milton Farmland, Milton Forest, Catlins Farmland and Catlins Forest sites. Session refers to 1 month, 3 months or 6 months after control occurred (1, 2 and 3, respectively), and  $N$  is the number of traplines. Milton Farmland was only trapped twice (see text).

Site	Session	Season and year	N	Mean	Lower 95% CL	Upper 95% CL
Milton Farmland	1	Summer 2000	7	0.95	0.00	2.17
Milton Farmland	2	Winter 2000	7	1.67	0.00	3.85
Milton Forest	1	Summer 2000	7	3.33	0.98	5.69
Milton Forest	2	Winter 2000	7	2.38	0.88	3.89
Milton Forest	3	Spring 2000	7	5.48	0.08	10.87
Catlins Farmland	1	Summer 2001	7	7.14	4.52	9.77
Catlins Farmland	2	Winter 2001	7	10.24	4.94	15.54
Catlins Farmland	3	Spring 2001	7	21.91	10.46	33.35
Catlins Forest	1	Summer 2001	7	5.00	2.33	7.67
Catlins Forest	2	Winter 2001	7	8.81	3.42	14.20
Catlins Forest	3	Spring 2001	7	16.67	10.76	22.57

**Table 3** BUGS-generated seasonal estimates of capture probability at the three South Island sites. The estimate is the log-odds ratio, with the probability shown in parentheses.

Site	Session			Mean
	One	Two	Three	
Milton Forest	-2.177 (0.10)	-2.257 (0.10)	-2.313 (0.09)	-2.249 (0.09)
Catlins Farmland	-1.451 (0.19)	-1.506 (0.18)	-0.951 (0.28)	-1.303 (0.21)
Catlins Forest	-2.000 (0.12)	-1.389 (0.20)	-1.052 (0.26)	-1.480 (0.18)
Mean	-1.876 (0.13)	-1.718 (0.15)	-1.439 (0.19)	-1.677 (0.16)

**Table 4** BUGS-generated seasonal estimates of capture probability at the three South Island study sites, adjusted to a mean  $\hat{N}$  of 12.8 The estimate is the log-odds ratio, with the probability shown in parentheses.

Site	Session			Mean
	One	Two	Three	
Milton Forest	-2.145 (0.11)	-2.209 (0.10)	-2.238 (0.10)	-2.197 (0.10)
Catlins Farmland	-1.523 (0.18)	-1.483 (0.18)	-0.848 (0.30)	-1.285 (0.22)
Catlins Forest	-1.955 (0.12)	-1.362 (0.20)	-0.997 (0.27)	-1.438 (0.19)
Mean	-1.874 (0.13)	-1.684(0.16)	-1.361 (0.20)	-1.640 (0.16)

To give estimates of session (time since control) effect in a more easily interpretable form the model was refitted, estimating the initial (summer) capture probability, then the difference in the subsequent winter and spring probabilities (Appendix 3E). These estimates were used to predict what the values would be if all sites had the same number of possums present at each session. The small values for the Milton Forest sessions confirm that there was very little change at that site; log odds of zero for the difference indicate that the odds of capture in the first session (summer) equalled those in the second (winter) and third (spring; Table 5). The values in Table 5 should be compared with the corresponding values for the North Island analyses listed in the text on p. 21. The odds of catching a possum were therefore higher in the third session relative to the first session (summer) at both Catlins sites. Since the remaining confidence intervals all included 1, we infer that the odds were similar in the other contrasts.

**Table 5** The median odds ratios and associated 95% confidence intervals for the seasonal comparisons at each of the three South Island sites.

Comparison	Site		
	Milton Forest	Catlins Farmland	Catlins Forest
Winter/Summer	0.94 (0.34–2.63)	1.04 (0.53–2.11)	1.82 (0.98–3.39)
Spring/Summer	0.93 (0.38–2.03)	1.96 (1.02–3.87)	2.61 (1.52–4.51)
Winter/Spring	1.03 (0.37–2.53)	0.53 (0.27–1.06)	0.70 (0.39–1.26)

### 5.3 A radioactive marker for possum faeces

For the first trial, a subsample of faecal pellets collected at 2, 3, 5, and 7 days from possums injected intramuscularly was analysed. On average, the seven possums injected with tritiated progesterone were lighter (2.9 kg compared to 3.8 kg) and voided less faecal pellets (55 compared to 81 pellets over 9 days) than the seven control possums. However, there was a large variation in the number of faecal pellets voided each day for both groups of possums, with none or <10 pellets voided some days and large numbers of pellets (up to 179 pellets) voided other days.

As all faecal pellets from all possums needed to be marked for at least 10 days, any unmarked pellets would mean that the method was unsuitable. Most pellets tested from days 5 and 7

gave readings similar to that of faecal pellets from the control group of possums (range: 21–28 scintillation counts per minute for 0.1–0.2 g of faeces). Faecal pellets from days 2 and 3 gave higher counts per minute (range 30–103 counts per minute) with some pellets from day 5 also giving higher readings. However, the majority of pellets from day 5 onwards gave readings indistinguishable from the unmarked pellets. Pellets from later days were therefore not tested.

For the second trial, a subsample of faecal pellets collected at 5 and 7 days from possums injected intramuscularly and intravenously was analysed. The four possums in the second trial weighed an average of 2.4 kg (2.3 and 2.5 kg, for intramuscular- and intravenous-injected possums respectively) and voided an average of 38 faecal pellets (13 and 63 pellets for intramuscular- and intravenous-injected possums, respectively) over the six counting days. Scintillation counts for faecal pellets from all four possums were indistinguishable from background levels at 7 days. Faeces from one intramuscularly injected possum had higher than background readings at 5 days but the other three possums had levels similar to the background readings; this could be explained by possums voiding only one pellet on day 2 and none on day 3. Since the majority of marked pellets were indistinguishable from non-marked pellets by day 5, no further analyses were conducted.

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## 6. Discussion

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### 6.1 Alternative estimators of possum abundance

Prior to discussing the key results of the study, we discuss the performance of the three alternative estimators of possum abundance.

The cleared-plot faecal pellet count methodology used here was expensive to implement because it required three inspections. The number of fresh pellets deposited by a possum per night is variable (Riney 1957; Fitzgerald 1977; Nugent et al. 1997, and see also Section 5.3), and at the low densities of possums present at the Catlins and Milton Farmland sites the number of pellets counted was simply too small to be analysed. At the sites with higher densities of possums (Miranda and Milton Forest), the number of pellets counted in the third inspection (which aimed to estimate the number of animals remaining) was small but also similar between the trapped and untrapped lines. We observed almost no fresh possum pellets at Maungatautari despite subsequently trapping moderate numbers of possums along some lines. Rats (*Rattus* spp.) were abundant throughout our study at Maungatautari, and we suspect that they may have quickly eaten or disturbed and buried fresh possum pellets. For the above reasons we decided to stop counting faecal pellets at the Maungatautari and Miranda sites, and did not use the method at either of the Catlins sites. We conclude that although cleared-plot faecal pellet counts indicated the *presence* of possums, it was not a suitable estimator of the *relative abundance* of possums.

Although tritiated progesterone injected directly into the bloodstream has previously been used to mark possums for 5 days, pellets from injected animals were indistinguishable from control animals by day 5. We do not believe that this method warrants further investigation. Rather, alternative methods for identifying individual possums from faecal pellets need to be

developed. Landcare Research has recently shown that DNA profiling is a viable method for estimating the abundance of possums (Nugent et al. 2003 unpublished).

Spotlighting can only be used in open habitats, and we used this method at the Milton and Catlins Farmland sites. There were very low densities of possums at the Milton Farmland site, and no possums were observed after trapping in either of the two sessions. Possums were counted by spotlighting after trapping at the Catlins Farmland site, but the results were extremely variable. Vegetation or topography will obscure some possums, and others may actively avoid the spotlight. There may also be variation in how the observer operates the spotlight. Finally, as noted earlier, interpreting counts of animals on both nights is problematic because previously sighted animals are not marked. We conclude that although spotlighting indicated the *presence* of possums and gave a minimum number of possums alive (MNA), it was not a suitable estimator of the *relative abundance* of possums, especially at low abundance.

Our attempts to define the spatial distributions of possums poisoned after trapping achieved mixed results. At Maungatautari, the number of poisoned possums did not increase with increasing distance from the trapline in either summer or winter 2000 (Fig. 5). The rugged topography and thick understorey at Maungatautari meant that these data were very expensive to collect, and thus the technique was not used further at that site. In contrast, the number of possums poisoned after trapping greatly increased at a distance of 140 m from the trapline at the Milton Forest site (Fig. 9). However, there were insufficient data to make inferences at the level of individual traplines. That three of eight radio-collared possums released during the first 3 days of trapping subsequently survived the poisoning operation also suggests that cyanide poison is a relatively ineffective method for estimating the abundance of possums. One possible reason why these patterns differed between Maungatautari and Milton Forest was the much greater abundance of rats at the former. Rats apparently removed much of the peanut butter and cyanide paste at Maungatautari. A cyanide station greatly reduced consumption by rats in later seasons.

In contrast to the methods outlined above, the use of cyanide poison along the trapline after trapping did provide a useful alternative estimate of the abundance of remaining possums (Fig. 6). We believe that those data confirm that our estimates of population size (and hence capture probability) based on trapping data (see below) were sensible. Although our use of cyanide laid along the trapline provided a valuable alternative estimator of possum abundance in this study, we believe that it is unlikely to be a good estimator of possum abundance in many situations. First, it is a deadly toxin that cannot be used where the general public or livestock may access it. Second, its legal use requires the approval of the local Medical Officer of Health, and this may not always be forthcoming. Third, as noted above, cyanide can be eaten by rats such that it is unavailable to possums. Fourth, cyanide may become less effective when used in an area where cyanide has been used as the control tool.

## 6.2 RTCI, abundance, and capture probability

The RTCI is calculated as the number of possums caught (including escapes) in the first two or three nights of trapping (NPCA 2002). Variation in RTCI may therefore reflect changes in the abundance of possums along the trapline, or changes in the probability of possums being trapped ('capture probability'), or some combination of the two. Previous work has largely assumed that changes in RTCI reflect changes in possum abundance, but some recent evidence suggests season (Nugent et al. 2001 unpublished; Fraser et al. 2002 unpublished)

and time since control (Coleman & Coleman 2000 unpublished; Nugent et al. 2001 unpublished) affect RTCI.

We originally aimed to quantify the abundance of possums remaining after trapping finished with a variety of estimators, but none of the tools used provided useful and completely reliable estimates of this (see above). We instead used the pattern of captures to model capture probability and abundance (the two are dependent; Fig. 7) along each trapline, and then modelled the capture probability as a function of the variables of interest (habitat and season or timing). We therefore emphasise that capture probability is the probability (i.e., a value between 0 and 1) of a possum being trapped, and is not ‘trap shyness’, which is a behavioural aversion to entering traps. Behavioural studies would be required to determine how trap shyness affects the RTCI.

### 6.3 Effects of habitat and season on RTCI

Our results demonstrate that the RTCI is a positive and non-linear index of possum abundance that varies seasonally (Fig. 8). Although the potential for non-linearity has long been recognised in indices of abundance (Caughley 1977), to our knowledge this is the first study to explicitly test for seasonal biases in an index of possum abundance. The non-linearity in RTCI is inevitable, in that once RTCI exceeds 50%, the index cannot double in response to a doubling of the population. However, we demonstrate empirically, for the first time, how capture probability declines with increasing population size (Fig. 7). Note, though, that the fitted curve in Fig. 7 is thought to overstate this decline, because it suggests that RTCI is likely to reach an asymptote below 50%, yet mean RTCIs in excess of 50% are recorded (e.g.; 61% at Motatau, Northland, 1997; Nugent et al. 2002). Additionally, the relationship between RTCI and population size is poorly defined at high RTCs because of the paucity of data points. The non-linearity in the index results in a reduction in the ability of the index to discriminate abundances as abundance increases. This limitation of trap-catch removal can be addressed by increasing the number of nights trapped. Other constant removal techniques in which the number of individuals that can be ‘captured’ per unit of effort is small relative to the absolute population size can also be expected to have a non-linear relationship with absolute abundance (see also Gibbs 2000).

Interestingly, although capture probability for a given population size was lowest during spring at both sites, the pattern for summer and winter differed. At the forest site, capture probability was highest in summer, followed by winter and then spring. Two recent studies support this finding: (1) Nugent et al.’s (2001 unpublished) observation that two-night RTCI increased from winter to summer in two uncontrolled blocks in indigenous forest in the Matemateaonga Range, North Island and (2) in an analysis of c. 1600 RTCIs from throughout New Zealand, Fraser et al. (2002 unpublished) observed that, when other variables were held constant, RTCI increased from June to January. (Fraser et al.’s analysis was based largely on results from indigenous forest.) At the farmland site, capture probability was highest instead in winter, but also lowest in spring. Unfortunately, there are no other studies of the influence of season on RTCI in farmland. Further work at farmland sites is required to determine the consistency of seasonal bias in that habitat. On the basis of this and other studies (Nugent et al. 2001 unpublished; Fraser et al. 2002 unpublished), we suggest that repeated RTCI sampling of an area be restricted to as similar a time period as possible.

Seasonal changes in the capture probability of possums might be a consequence of seasonal changes in the behaviour of possums. For example, male possums move about most during

summer and autumn (Cowan & Clout 2000), which could increase their probability of encountering a trap. The difference in the pattern of seasonal variation between farmland and forest indicates that environmental influences also play some role. Seasonal variation in distribution of food sources is one obvious possibility, and is consistent with the suggestion by Nugent et al. (2001 unpublished) that the pattern of seasonal variation in RTCI was more marked at high possum density than at low possum density.

Our model extends earlier work on constant sampling with removal of individuals (Zippin 1956, 1958; Seber 1980) by allowing for sampling error in both local population size and nightly capture probability. By specifying uniform priors (i.e. equal model weighting), the *BUGS* software calculated MLEs for our models. However, the Bayesian approach can incorporate weighted prior knowledge into subsequent parameter estimates (see Link et al. 2002), usually resulting in parameter estimates with greater precision. The posterior parameter estimates generated in this study (Appendix 3B, 3D) could therefore be used as priors in further work evaluating bias in the RTCI.

The removal method of estimating population abundance relies on several key assumptions being met (Seber 1982). First, the sampled population is assumed to be closed. Since trapping occurred over a maximum of only 21 nights in a season (i.e., 12 fine nights interrupted by 9 wet nights, when traps were closed), any recruitment or natural mortality would have been negligible. Efford et al. (2000) observed that shifts and extensions in the home ranges of possums neighbouring experimentally culled animals on a forest–farmland margin occurred ‘in a matter of weeks’. Such movements may have violated the assumption of a closed population, but we had no means of assessing their importance in our study. Second, it is assumed that all animals in the population are available to be sampled. This assumption would be violated if some possums exhibited a behavioural aversion to entering traps. Although such behaviour has not been documented, it would be difficult to quantify, although recent use of DNA could provide a method. Third, capture efficiency is assumed to remain constant during sampling. Since traps were checked daily, and reset or replaced if necessary, capture efficiency was unlikely to have changed.

An index of abundance that is to be used by many people in different agencies, as is required for the management of possums in New Zealand, needs to be simple to implement but yield information relevant to the management objective. Until recently, the RTCI was primarily used for estimating kill rates in control operations aimed at ‘knocking down’ populations at high abundance (i.e., >20% TCI). Veltman & Pinder (2001) assessed how operational and environmental factors affected kill rates in 48 aerial 1080 operations throughout New Zealand. The kill rates were estimated using pre- and post-control RTCI estimates, and were found to increase with decreasing air temperature, a result that was consistent with the role of temperature in clinical trials of 1080 toxicity in possums (Veltman & Pinder 2001). The majority of possum control in New Zealand has changed from knocking down populations to one of ‘maintenance control’. Maintenance control generally aims to maintain populations at RTCIs of 5%, or lower, because empirical data indicate that this strategy can dramatically reduce the annual Tb reactor incidence in associated livestock herds (Coleman & Livingstone 2000). A target RTCI is stipulated in the control operation contract, and the contractor is paid only when that RTCI (or lower) is attained. Given that the index is approximately linear at such low possum abundance, and that the seasonal bias is small, the RTCI appears adequate for such monitoring. However, at very low density (i.e. <2% RTCI) the number of possums captured can be too small to be statistically useful. The number of lines required to estimate a RTCI with a desired level of precision can be calculated using several methods (review in

Thompson et al. 1998). Webster & Caley (2001 unpublished) illustrate how such methods can be applied to the RTCI.

We also note that the advantages and disadvantages of the RTCI must be weighed against competing methods for estimating the abundance of possums. Capture-mark-recapture techniques can generate precise estimates of absolute possum abundance, but are considered far too expensive and impractical to implement at the management scale in New Zealand. Faecal pellet counting has been used to index the abundance of possums (e.g., Hickling & Pekelharing 1989), but we found it to yield little useable data at low possum densities. Although cyanide poison may be useful in some situations, its potential for use is restricted compared to the TCI. Provided its limitations are recognised, the RTCI appears adequate for the purposes of the majority of possum management in New Zealand.

#### **6.4 Effects of timing on RTCI**

Capture probability increased with time at the Catlins Farmland and Catlins Forest sites, but there was no change in capture probability at the third (Milton Forest) site. However, the increase in capture probability at both of the Catlins sites was relatively small, with only the difference between the third session and the first session being 'significant' (Table 3). The effects of timing were also confounded by season. However, the three trapping sessions were coincidentally aligned with the summer, winter and spring trapping sessions at Maungatautari and Miranda. Capture probabilities were highest in spring at the Catlins sites, but were lowest in that season at Maungatautari and Miranda, suggesting that the effects of timing may in fact be greater than our analyses revealed.

It is unfortunate that the Milton Farmland site was controlled before the third session, because results from a fourth site would have added greatly to the robustness of the result. Nonetheless, the patterns at the Catlins sites do suggest that capture probability does increase with time, with the mean for all sites increasing by about 50% within 6 months of control (Table 4). The tripling of RTCI over 6 months after control at the Catlins sites (Table 2) is consistent with the quadrupling of RTCI within 2 years of control in large treatment areas in native forest reported by Nugent et al. (2001 unpublished). Coleman & Coleman (2000 unpublished) also report rapid increases in RTCI after control, but some of those increases may have reflected immigration. Overall, these results together provide strong evidence that a substantial post-control bias in RTCI exists, and this study suggests the effect is a result of some temporary difference in average possum behaviour before and after control that largely disappears over 6 months (this issue is being investigated under AHB contract R-10580). One way of avoiding that bias would be to have post-control monitoring done at least 6 months after control; but adopting such a change has implications for the payment of contractors based upon performance standards.

It would be desirable to replicate this study at many more sites. However, the data collected from working with possum populations at very low densities are statistically difficult to analyse. There will be, by definition, many traplines with no or very few captures. Statistically, such data provide estimates with very large confidence intervals, and one limitation of this study was that we had to discard data from traplines with three or fewer captures because their estimates of population size were nonsensical.

The statistical techniques used in our analyses represent an important advance in the analysis of trapping data, and should be used in future studies. One way to evaluate the effect of

timing on RTCI over larger parts of New Zealand would be to use the statistical methods developed here to analyse data collected in monitoring operations conducted at different timings after control. The major advantages of such an approach are that a large amount of data could be collected such that more covariates (e.g., season, habitat and control methods) could be included in the analyses, and that inferences from the study would apply to monitoring conducted at large spatial scales. Fraser et al. (2002 unpublished) applied Generalised Regression Analysis and Spatial Prediction (GRASP) techniques to RTCI data collected in monitoring surveys throughout New Zealand. Whereas they modelled patterns in RTC, we explicitly model both trappability and  $N$  for each line. Hence, we do not make assumptions about the number of possums available to be trapped (cf. Fraser et al. 2002 unpublished). However, our approach requires trapping for more than the current 2 or 3 nights. An alternative approach would be to study the behaviour of possums before, during and after control operations; such experiments would identify the mechanisms underlying any change in RTCI with time after control, information that would be useful in developing control techniques for targeting those individuals; such an experiment is being undertaken by Landcare Research for the Animal Health Board.

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## 7. Conclusions

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- RTCI does not provide an accurate year-round index of possum abundance when possum densities are high (e.g., > 30% RTCI) due to the combined effects of saturation and seasonal bias. When possum abundance is low (i.e. <10%), the effects of both saturation and season are much reduced. Therefore the RTCI is a useful index in the context in which most possum monitoring is now conducted in New Zealand.
- The variation in capture probability between seasons (and the difference in this variation between habitats) indicates that monitoring of RTCI trends through time are likely to be valid only for assessments made in the same season and habitat, especially for populations at moderate to high density.
- Capture probability increased with time since control at the two Catlins sites (farmland and forest), but not at the Milton forest site, consistent with other evidence of a downward bias in immediate post-control RTCI (i.e. an over-estimation of % kill or under-estimate of 'true' residual RTCI). One implication is that post-control monitoring should be delayed for at least 6 months, but that is not likely to be a practical option for management of possum control contracts. The alternative is to accept that the bias exists and manage populations accordingly (i.e., assume that the apparent rate of increase indicated by changing RTCI will often be higher than is biologically possible in terms of actual possum numbers).
- A statistical technique was developed for estimating the abundance of possums from RTCI monitoring lines trapped for 9–12 days. The technique could be used in other studies of the 'trappability' of possums (and other pests).
- Faecal pellet sampling and spotlighting were poor alternative estimators of the abundance of possums at low densities. The number of possums killed with cyanide poison was a useful alternative estimator of abundance for the purposes of our study.
- Possums injected either intramuscularly or intravenously with 10  $\mu$ Ci of tritiated progesterone in saline solution will not consistently void marked faecal pellets after 3 days.

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## 8. Recommendations

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- Managers should continue to use the RTCI to monitor control operations that are expected to maintain populations at low abundance.
- Whenever possible, seasonal biases in the RTCI should be minimised by conducting repeat sampling in the same season.
- Further work is required to better define the extent to which time following control affects the RTCI. We do not recommend any changes to current timing of post-control monitoring.
- Further work, possibly including recently developed methods for identifying individual possums from faecal pellets using DNA, is also needed to substantiate the extent of variable trappability within possum populations.

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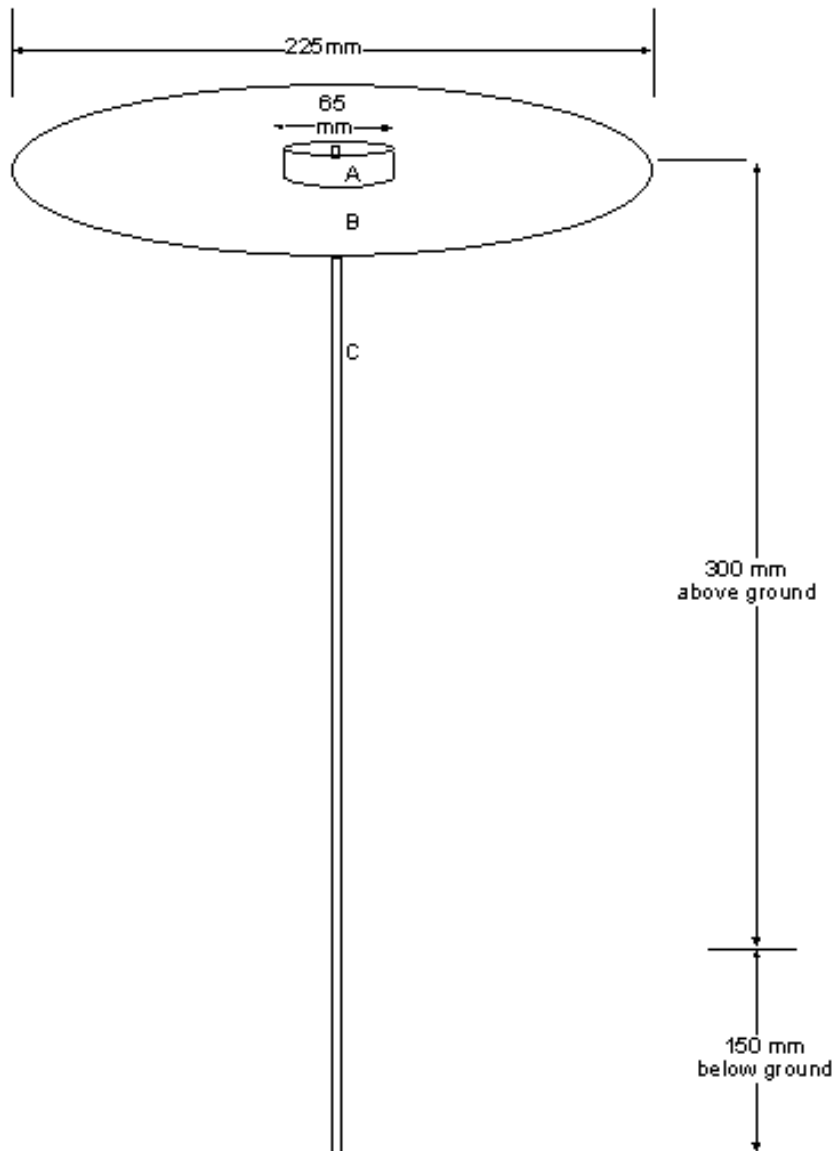
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## 11. Appendices

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### Appendix 1 Cyanide station designed by S. Hough, Landcare Research

Consumption by rats was reduced because the plastic tray ('B') prevented rats that climb 'C' from accessing the peanut butter and cyanide pastes, which were placed in 'A'.



## Appendix 2 Statistical analyses

We extended earlier work estimating population size,  $\hat{N}$ , based on constant sampling effort with removal of individuals (Zippin 1956, 1958; Seber 1982). We modelled the catches on each night as:

$$X_{ij} \sim \text{Binomial}(p_{ij}, N_{ij}), \quad (1)$$

where  $\hat{N}_{ij}$  is the estimated population remaining on the  $j$ th night for the  $i$ th line prior to trapping. This is calculated as the difference between those already caught on previous nights and the initial population,

$$N_{ij} = N_i - \sum_{k < j} X_{ik}. \quad (2)$$

The parameter model for the capture probabilities we used was:

$$\text{logit}(p_{ij}) \sim \text{Normal}(\mu_i, \tau_{rep}), \quad (3)$$

where

$$\mu_i \sim \text{Normal}(E[\mu_i], \tau_{line}).$$

The  $\hat{N}_i$  were modelled as:

$$N_i \sim \text{Poisson}(E[N_i]) \Big| \sum_j X_{ij}, \quad (4)$$

where

$$E[N_i] \sim \text{Gamma}(p_{pop}, \lambda_{pop}),$$

and  $\sum_j X_{ij}$  is the sum of the numbers killed on each line on each night (summed over all nights within a session). This is effectively the minimum possible population size prior to trapping, and making  $\hat{N}_i$  conditional on this ensured that we did not obtain estimates below that value. The second equation defines the distribution of the expected line population means. Finally, we defined the relationship between the mean (on the logit scale) capture probability on a line and the line's initial possum population as a simple regression equation:

$$E[\mu_i] = a_0 + b_1 N_i, \quad (5)$$

where  $a_0$  is the intercept and  $b_1$  is the slope. The model therefore allows for sampling error in both local population  $\hat{N}_i$  and the capture probability on a line on the particular night,  $p_{ij}$ ,

where  $i$  indexes the trapping lines and  $j$  the trap night (from 1 to 9–12, depending on the trapline).

The RTCI is thus a function of capture probability and population size over the first three nights. For illustration, assume that  $p$  is constant over the three nights. If  $\hat{N}$  is the estimated population size it can be shown that

$$\text{RTCI} = \bar{N}p(1 + (1 - p) + (1 - p)^2) / K, \quad (6)$$

where  $K$  is the total number of trap nights per trapline (e.g., 60 for one trapline of 20 traps set for 3 fine nights). Thus, a model of the relationship between RTCI and  $N$  follows from that of  $p$  and  $\hat{N}$ .

The model (Equation 5) can be extended to allow capture probability to vary with many other covariates as in standard regression modelling (see Cam et al. 2002; Link et al. 2002). For the effect of habitat and season, we were interested in a model in which  $p$  varies with  $N$  and season, but differently for the two sites according to year:

$$E[\mu_i] = a_0 + a_1H_i + a_2Y_i + a_3S_i + a_{13}SY_i + b_1\bar{N}_i, \quad (7)$$

where  $H_i$  is the site factor (two levels, forest and farmland),  $Y_i$  is the year factor (two levels, 2000 and 2001),  $S_i$  is the season factor (three levels, summer, winter and spring),  $SY_i$  is the site  $\times$  season interaction, and  $\hat{N}$  is the estimated population size. To allow for block effects, a random intercept was fitted for each block in equation (7). These intercepts,  $a_{0,k}$  ( $k=1, \dots, 21$ ) were specified as coming from a normal distribution with mean  $E[a_0]$  and precision  $\tau_{\text{block}}$ . The block intercepts were similar, and there was little difference in the standard deviations of parameter estimates when block was included in the model. This was not surprising because our earlier model allowed for line variation, and block variation is a component of line variation. For simplicity we therefore do not report results for blocks.

We used version 1.3 of the software package *BUGS* (Spiegelhalter et al. 1995; available for free download at <http://www.mrc-bsu.cam.ac.uk/bugs/>) for our analyses. The program uses the Gibbs sampler (Casella & George 1992) to generate Markov chain Monte Carlo (MCMC) solutions to evaluate Bayesian posterior distributions (Gelman et al. 1998). If a flat prior is specified, as we did, then the method finds maximum likelihood estimates (MLE) for models too complex to solve using traditional MLE methods. For a discussion of the application of *BUGS* to analyses in ecology and wildlife management see Link et al. (2002). The *BUGS* software analyses the precision, which is the inverse of the variance, as an argument. The variance is easily obtained from the estimate of precision. The importance of parameters was assessed by their 95% confidence intervals. We note that the confidence intervals calculated with this approach, in contrast to frequentist methods, can be interpreted as ‘having a 95% probability that the confidence interval includes the true value’. The MCMC can be highly transient when the starting value lies outside the range of the stationary distribution. Our parameters were estimated using 100 000 iterations thinned by 10, and then by 30, with a burn-in of 20 000 (see Link et al. 2002).

### Appendix 3 BUGS-generated results

The following tables are edited output from the *BUGS* software. Readers interested in understanding this output should consult the *BUGS* website (<http://www.mrc-bsu.cam.ac.uk/bugs/>) and the references cited there. Link et al. (2002) also provides a readable account of BUGS-generated results.

**Table 3A** *BUGS*-generated estimates of slope and intercept for the relationship between RTCI,  $p$  and  $\hat{N}$  (equation 5) at the farmland and forest sites.

Node	Mean	SD	MC error	2.5%	Median	97.5%
Mean	-1.22	0.1047	0.00456	-1.432	-1.22	-1.018
Slope	-0.01277	0.00303	0.00015	-0.0185	-0.01275	-0.006961
mu.pop	23.95	1.802	0.056	20.66	23.9	27.69
sd.line	0.2952	0.0746	0.0046	0.1401	0.2976	0.4422
sd.pop	16.51	1.853	0.05567	13.33	16.33	20.6
sd.rep	0.1567	0.07585	0.006496	0.03404	0.1537	0.31

**Table 3B** *BUGS*-generated posterior distributions of parameters for the model specified in equation 7.  $a_3S_{0,1}$  is the summer–winter contrast for the forest site ( $H_0$ ).  $a_3S_{0,2}$  is the spring–summer contrast for the forest site.

Node	Mean	SD	MC error	2.5%	Median	97.5%
Mean	-0.9224	0.1882	0.004767	-1.307	-0.9177	-0.5678
$a_0$						
$a_1H_0$	-0.19	0.2137	0.00582	-0.5976	-0.1942	0.2528
$a_2Y_0$	-0.131	0.1027	0.002211	-0.3417	-0.1295	0.06212
$a_3S_{0,1}$	-0.4048	0.2541	0.008118	-0.9245	-0.3978	0.0809
$a_3S_{0,2}$	-0.7242	0.3487	0.01541	-1.486	-0.691	-0.1282
$a_3H \times S_{0,1}$	0.6271	0.2896	0.008852	0.06743	0.6232	1.214
$a_1a_3S_{0,1}$	0.4311	0.3834	0.0162	-0.2378	0.4039	1.248
$a_1a_3S_{0,2}$	0.2252	0.3655	0.02653	-0.5711	0.248	0.8908
$b_1\hat{N}$	-0.01151	0.004044	1.319E-4	-0.01992	-0.01147	-0.003813
sd.line	0.2135	0.08899	0.00361	0.0482	0.211	0.3949
sd.pop	16.43	1.937	0.03809	13.14	16.26	20.75
sd.rep	0.1484	0.07578	0.002927	0.02974	0.1451	0.2997

**Table 3C** BUGS-generated estimates of slope and intercept for the relationship between RTCI,  $p$  and  $\hat{N}$  (equation 5) at the Milton Forest, Catlins Forest and the Catlins Farmland sites.

Node	Mean	SD	MC error	2.5%	Median	97.5%
Mean	-1.79	0.21	0.006	-2.21	-1.79	-1.37
Slope	0.0139	0.0128	4.283E-4	-0.01	0.015	0.04
mu.pop	14.78	1.08	0.038	12.93	14.73	17.04
sd.line	0.38	0.13	0.007	0.09	0.38	0.64
sd.pop	5.42	1.03	0.032	3.53	5.30	7.67
sd.rep	0.15	0.10	0.004	0.03	0.13	0.39

**Table 3D** BUGS-generated posterior distributions of parameters for the model in which session was explicitly included (see text). Rows in bold highlight parameters where the estimate was larger than its SD. Parameters were estimated using 100 000 iterations thinned by 10, and then by 30, with a burn-in of 20 000.

Node	Mean	SD	MC error	2.5%	Median	97.5%
<b>Mean</b>	<b>-1.556</b>	<b>0.18</b>	<b>0.015</b>	<b>-1.90</b>	<b>-1.56</b>	<b>-1.21</b>
<b>Site (Catlins-Milton)</b>	<b>0.90</b>	<b>0.22</b>	<b>0.021</b>	<b>0.48</b>	<b>0.90</b>	<b>1.31</b>
Habitat (farmland-forest)	0.16	0.16	0.011	-0.15	0.16	0.47
Linear Session	-0.09	0.18	0.011	-0.45	-0.09	0.27
<b>Quadratic session</b>	<b>0.25</b>	<b>0.10</b>	<b>0.009</b>	<b>0.04</b>	<b>0.25</b>	<b>0.45</b>
<b>Site <math>\times</math> linear session</b>	<b>0.85</b>	<b>0.47</b>	<b>0.046</b>	<b>-0.10</b>	<b>0.86</b>	<b>1.77</b>
Site $\times$ quadratic session	0.42	0.57	0.045	-0.69	0.40	1.56
Habitat $\times$ linear session	-0.15	0.20	0.016	-0.54	-0.14	0.25
<b>Habitat <math>\times</math> quadratic session</b>	<b>-0.45</b>	<b>0.36</b>	<b>0.024</b>	<b>-1.12</b>	<b>-0.45</b>	<b>0.23</b>
Slope	-0.0084	0.0094	6.85E-04	-0.0275	-0.0081	0.0109
mu.pop	15.23	1.10	0.054	13.11	15.21	17.50
sd.line	0.13	0.09	0.008	0.03	0.12	0.34
sd.pop	5.77	1.09	0.038	3.84	5.68	8.20
sd.rep	0.14	0.08	0.007	0.03	0.12	0.33

**Table 3E** BUGS-generated posterior distributions of parameters for the refitted model (see text). Rows in bold highlight parameters where the estimate was larger than its SD. These data were generated from 40 000 iterations, a burn-in of 11 000, and then thinned by 2000.

<b>Node</b>	<b>Mean</b>	<b>SD</b>	<b>MC error</b>	<b>2.5%</b>	<b>Median</b>	<b>97.5%</b>
Milton Forest, summer	-2.14	0.37	0.019	-2.86	-2.14	-1.41
Milton Forest, winter-summer	-0.06	0.53	0.024	-1.07	-0.06	0.97
Milton Forest, spring-summer	-0.09	0.42	0.022	-0.96	-0.07	0.71
Catlins Farmland, summer	-1.52	0.27	0.010	-2.10	-1.51	-1.03
Catlins Farmland, winter-summer	0.04	0.34	0.013	-0.63	0.04	0.75
<b>Catlins Farmland, spring-summer</b>	<b>0.67</b>	<b>0.33</b>	<b>0.013</b>	<b>0.02</b>	<b>0.68</b>	<b>1.35</b>
Catlins Forest, summer	-1.96	0.24	0.011	-2.48	-1.94	-1.50
<b>Catlins Forest, winter-summer</b>	<b>0.59</b>	<b>0.32</b>	<b>0.013</b>	<b>-0.02</b>	<b>0.60</b>	<b>1.22</b>
<b>Catlins Forest, spring-summer</b>	<b>0.96</b>	<b>0.28</b>	<b>0.012</b>	<b>0.42</b>	<b>0.96</b>	<b>1.51</b>
Slope	-0.0084	0.0088	2.92E-04	-0.0263	-0.0084	0.0095
mu.pop	15.08	1.09	0.035	13.14	15.02	17.31
sd.line	0.13	0.09	0.004	0.03	0.12	0.36
sd.pop	5.70	1.08	0.026	3.84	5.60	8.16
sd.rep	0.15	0.09	0.004	0.03	0.13	0.36