Rodent density indices from tracking tunnels, snap-traps and Fenn traps: do they tell the same story?

Grant L. Blackwell, Murray A. Potter[1] and John A. McLennan[2]
Institute of Wildlife Research, School of Biological Sciences, Heydon-Laurence Building AO8, University of Sydney, New South Wales 2006, Australia (E-mail: gblack@bio.usyd.edu.au)
[1]Ecology Group, Institute of Natural Resources, Massey University, Private Bag 11 222, Palmerston North, New Zealand
[2]Manaaki Whenua - Landcare Research, 33 Simla Ave, Havelock North, New Zealand

Abstract: Comparisons were made of density indices of free-living populations of ship rats (*Rattus rattus*) in mixed forest in New Zealand by using footprint tracking tunnels and two kill-trapping methods. Tracking tunnels and snap-trap removal indices of rat densities showed similar trends when run on a 9 ha trapping grid, although immigration onto the grid occurred, thus violating one of the assumptions of the analysis. Tracking rates and snap-trap capture rates were not significantly correlated when run along a trapping line for a 12 month period, although tracking rates and the total number of rats caught in a trapping session were significantly correlated. Time series analysis showed that rat density indices from tracking tunnels and Fenn traps were significantly correlated when run for 27 consecutive months in a rat population with moderate density, but were not correlated in a low density rat population. The findings highlight the importance of habitat, sample size and target species behaviour in influencing relative density indices obtained from tracking tunnels, snap-traps and Fenn traps. Given the widespread use of rodent tracking tunnels in New Zealand, we suggest that tracking tunnels should only be used to compare relative abundance within similar habitat types, and should always be complemented with a second density index. The relationship between the commonly used density indices and true rodent population density requires urgent attention.

Keywords: calibration; density indices; Fenn trap; *Rattus rattus*; snap-trap; tracking tunnel.

Introduction

In the majority of studies of small mammal populations, difficulty in measuring absolute abundance necessitates the use of relative density measures. Obtaining a measure of absolute abundance requires that the study area can be checked completely, that all individuals can be recognised and counted, and that contagion effects do not bias the estimate of population size (Caughley, 1977; Pollock *et al*., 1990). In comparison, relative density indices are less costly and time consuming to measure, do not rely on exhaustive enumeration of all individuals in a population and, in many situations, can provide similar amounts of information to direct counting methods (Caughley, 1977).

Despite their widespread and frequent use in all areas of ecology and population biology, relative density indices are susceptible to a number of biases. Problems include saturation of the indexing technique which allows non-linear relationships to develop (Tanaka, 1960; Caughley, 1977), and modification of responses of the target species to the indexing method by competitors or predators (Brown *et al*., 1996). There is also a tendency for relative indices to measure activity as well as abundance (Sheppe, 1965; Sarrazin and Bider, 1973; King and Edgar, 1977). This can increase variability in the index, and may reduce the wide-scale applicability of any conclusions. In the worst case, this tendency may mean the index has no validity beyond a particular study.

In New Zealand, footprint tracking tunnels (King and Edgar, 1977) are used widely to gain an index of the density of introduced small mammals. Tracking tunnels rely on ink-pads and paper to record target species' tracks, and by extrapolation, their abundance. In recent years, use of such tunnels has largely replaced the use of kill-trapping as the primary rodent density index (Innes *et al*., 1995). Brown *et al.* (1996) are the only authors we know of who have tested indices of ship rat and mouse relative density in New Zealand. They compared density estimates of ship rat (*Rattus rattus*) and house mouse (*Mus musculus*) populations using footprint tracking tunnels and removal trapping from a trapping grid. They found a tight relationship between the two indices for their brief, intensive experiment, but noted that the relationship may not be as tight under different experimental protocols, or if the experiment was run at a different time or location.

Clearly, further investigation of the relationship between relative indices and measures of absolute abundance of rodents in New Zealand is needed. In recognition of this, we compared ship rat density indices obtained from tracking tunnels and trapping, under four experimental situations:

1. Density estimates obtained from a removal trapping grid similar to that of Brown *et al.* (1996);
2. Density indices obtained along a trap-line (rather than a grid) run through the same habitat as 1;
3. Density indices obtained from the tracking tunnel run from January 1996 to March 1998 and indices from two established Fenn trap predator-trapping lines that were run continuously over the same period. Although the Fenn traps targeted stoats, rats were a common by-catch in these traps. This period included a rodent population eruption that occurred following synchronous southern beech (*Nothofagus* spp.) seeding in autumn 1995 (Dr C. Ward, Department of Conservation, Gisborne, New Zealand *pers. comm.*);
4. We also compared the indicated magnitude, and rates of change, in the rat populations obtained from tracking tunnels and Fenn traps run in beech forest from January 1996 to March 1998.

Thus we had four tests of the tracking tunnel indexing technique, using two trap types and two trap arrangements.

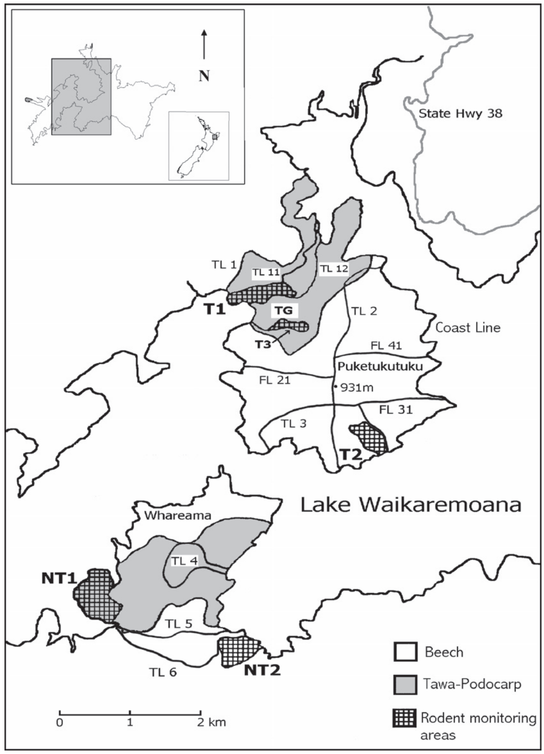

Figure 1. Map of the study area at Lake Waikaremoana, North Island, New Zealand. Predator trap lines (TL) were established on the Puketukutuku peninsula in September 1995. Fenn traps were run on the TLs and three Fenn Lines (FLs) from May 1995 to March 1998. The snap-trapping and tracking tunnel line was established in Area T1, and was run from January to December 1996. The trapping grid (TG) was established and run in June 1998. Density indices from tracking tunnels in Area T2 and Fenn traps on lines FL 31 and TL 3 were also compared.

Methods

Study area

The study was conducted at Lake Waikaremoana (177° 05' E, 38° 47' S), situated at the south-eastern corner of Te Urewera National Park (212 000 ha), in the North Island of New Zealand. This study was part of a larger project investigating the dynamics of the rodent/ mustelid predator/prey system, and the implications of this system for threatened northern brown kiwi (*Apteryx australis mantelli*).

Trapping grid monitoring

We followed the methods of Brown *et al.* (1996), and used the Zippin removal method of density estimation (Zippin, 1958). In June 1998, a 300 x 300 m grid was established in an area of tawa-podocarp forest on the 750 ha Puketukutuku peninsula, which juts into Lake Waikaremoana (Area TG; Fig. 1). Single Ezeset Supreme™ rat traps baited with peanut butter were placed at 25 m intervals across the grid, giving 169 traps on thirteen transect lines. Plastic covers, secured by a pin at each end, were placed over all traps to prevent non-target animal capture. At the same site, a total of 28 tracking tunnels were placed at 50 m intervals along four transect lines that were 100 m apart, giving seven tracking tunnels on each of the four transect lines. Each tracking tunnel was within 1-2 m of a snap-trap. Tracking tunnels were baited with peanut butter, set in the evening, and checked the following morning. Tracking rates are expressed as the percentage of tunnels tracked by a given species.

Traps and tracking tunnels were placed on the lines on 21 June 1998 and run for five consecutive nights, from 23-28 June 1998 with daily checks. The location, species, colour morph (for *Rattus rattus*) and sex of any animals caught were recorded. Any sprung traps were recorded, re-baited with peanut butter if required, and reset.

All carcasses were kept for necropsy in the laboratory. Each animal was weighed and measured as per Cunningham and Moors (1983). The age of each individual was determined using reproductive indices (Daniel, 1972) and tooth wear criteria developed for *R. rattus* (Karnoukhova, 1971; Innes, 1990) and for *M. musculus* (Lidicker, 1966). The effective trapping area was calculated by adding a boundary strip (Brown *et al.*, 1996), equal to an average home-range radius for ship rats (56 m; Hooker and Innes, 1995). This gave an effective trapping area of 17 ha.

Snap-trapping line monitoring

In December 1996, a calibration experiment was conducted by placing 40 Ezeset Supreme™ rodent snap-traps at 50 m intervals along an established Fenn trap-line (25 m spacing) in tawa-podocarp forest on Puketukutuku peninsula. The traps ran along Fenn trap-line TL 11 for approximately 700 m, before cutting 400 m through the bush to intersect with a second trap-line (Fenn trap spacing 150 m; TL 12) running across the neck of the peninsula. The trap-line ran for a further 700m, back down to the lake edge, and thus encompassed an area of approximately 18 ha (Area T1; Fig. 1). Each trap had a plastic cover similar to that used on the trapping grid to exclude non-target animals. Traps were baited with peanut butter, and run for three consecutive nights every six weeks between January and December 1997. The details of any captures were recorded as for the trapping grid. Sprung traps were recorded, re-baited if required, and reset. At the end of the trapping session all traps were sprung, and left in place until the next trapping session. Captures per hundred trap nights (C100/TN) were corrected for sprung traps by subtracting half a trap night for every sprung trap recorded (Nelson and Clark, 1973).

A total of 18 tracking tunnels (King and Edgar, 1977) were placed at 100 m intervals along the trap-line to establish a calibration experiment. Tunnels were run for a single night, usually 1-3 nights prior to the snap-traps, although on one occasion the tracking tunnels were run two weeks before the snap-trap indexing. Tracking tunnels were used in the same way as on the trapping grid. Tracking rates were expressed as the proportion of tunnels tracked, and gave a one-night tracking index.

Fenn-trapping lines

As part of a large-scale predator control programme, six predator-monitoring trap-lines (TLs) were established in September 1994 through the bush and around the coastline on Puketukutuku peninsula (TLs 1, 2, 3, 11, 12, and Coast Line; Fig.1). In May 1995, Mk 4 and Mk 6 Fenn kill traps (FHT Works, Redditch, England) were placed at 150 m intervals along each of the trap-lines on the peninsula (TLs 1, 2 and 3), and on three additional ridges between transects (Fenn-lines; FL 21, 31, and 41). Trap-lines ranged in length from 900 m (6 traps) to 3100 m (21 traps). Traps were placed at 25 m intervals on two more trap-lines across the neck of the peninsula (TL 1, length 1425 m; TL 11, 1600 m) in an attempt to intercept any predators moving into the trapped area. Fenn traps were also placed at each of 47 coastline stations on Puketukutuku peninsula (Coast Line, Fig.1). The total number of traps set at any one time ranged from 244 to 426. All traps were placed under wooden covers to prevent capture of non-target animals, and were baited with either a hen egg or rabbit meat. Traps were run continuously from May 1995 until March 1998 and were checked every 7-10 days. Species, sex, capture date and location were recorded for each animal caught. Captures per 100 trap nights were calculated as described previously.

Correlation between indexing methods

Capture rates on the Fenn trap-lines in tawa-podocarp forest (TL 1, TL 11, TL 12) were compared with those from the tracking tunnels on the trapping line (100 m spacings) used in the snap-trapping trap-line calibration experiment.

The tracking tunnels were run each month from January 1996 to March 1998, using the one-night index described previously, and were compared with two density indices calculated from the Fenn trap-lines. A trapping rate was calculated for only those Fenn traps on the sections of trap-lines that had tracking tunnels on them (‘Halfline’). The tracking tunnel rate was also compared with the average capture rates for all Fenn traps in the tawa-podocarp forest on the peninsula (Fig. 1).

Density indices were also compared from tracking tunnels and Fenn traps placed in beech forest on Puketukutuku peninsula. A line of tracking tunnels with 100 m spacing was established in December 1995 in beech forest at the far end of the peninsula (Area T2, Fig. 1). The tracking tunnels ran along a Fenn trap-line (FL 31, 150 m spacing) for 500 m (5 stations), before looping back down to the lake edge (900 m, 9 stations), enclosing an area of approximately 15 ha. The tracking tunnels were run monthly using the one-night tracking protocol. These tracking rates were compared with average Fenn capture rates from Fenn-line 31 (900 m, 6 stations) and TL 3 (3150 m, 21 stations), which ran across the peninsula and enclosed both Fenn-line 31 and the tracking tunnel line.

Statistical analysis

Differences in capture rates between sexes and ages of rats caught in the trapping grid experiment were compared using contingency table analysis, with significance levels determined from the chi-square (χ^2) distribution with the appropriate degrees of freedom.

Due to the short time frame and small sample size of the snap-trapping grid and trap-line experiments, the relationship between tracking rates and snap-trap capture rates was analysed using linear regression in the SYSTAT 8.0 computer program (SPSS Inc., 1998). Tracking rates were classed as the independent variable in the analysis, and snap-trap captures as the dependent.

Broad-scale differences in the density estimate between years on individual indexing lines were analysed using the Genmod procedure in the SAS (SAS Institute, 1990) computer program. An individual tunnel could be tracked or untracked, so a binomial distribution was used. The Genmod analysis produces a χ^2 statistic that can be compared with the critical value from the χ^2 distribution with the appropriate degrees of freedom. A first-order auto-regressive correlation matrix was used in the model, which correlated the data for each trapping period with the previous period only.

The relationship between tracking tunnel and Fenn trap density indices was compared using a time-series analysis to allow for possible trends and auto-correlation in the data. The tracking and trapping data for each habitat were first tested for stationarity (i.e., that there was no long-term trend in the average value of the data series) using the Dickey-Fuller test (Hendry and Doornick, 1999). Any paired tracking and trapping series that were stationary were compared using an auto-regressive least squares regression that controlled for auto-correlation between the residuals (Engle and Granger, 1987). The regression was forced through zero under the assumption that both indices will record no rats when none are present. The occurrence of auto-correlation between residuals in time-series analysis means that R^2 values are not good indicators of the variation explained by the model; rather, the auto-correlation coefficient gives a measure of the significance of the regression (Engle and Granger, 1987). Any paired series that were non-stationary, and thus showed long-term trends, were compared using co-integration analysis (Hendry and Doornick, 1999), which looks for agreement in long-term trends between data series.

Trends in density estimates from the different indices were compared using the Wilcoxon Signed Ranks Test (Zar, 1974). For each year (1996 and 1997) the number of months that each index scored rat density higher in either tawa-podocarp or beech forest was calculated, and agreement in overall population trends among tracking tunnels, numbers of rats caught, and captures per 100 trap-nights (C/100TN) was assessed.

Results

Trapping grid

Over the five-night trapping period 121 ship rats were caught on the grid. No house mice were caught. The overall male:female sex ratio was 1:1.03, and the capture rate did not differ significantly either between sexes ($\chi^2 = 0.01$, df = 1, $P > 0.05$), or between nights ($\chi^2 = 2.381$, df = 4, $P = 0.67$). The vast majority of rats caught were immature, both on the basis of reproductive classification (83% juvenile) and from tooth wear indices [Age class III or less (*sensu* Innes, 1990); 70% juvenile]. The proportion of juvenile rats caught each night did not differ over the five trapping nights ($\chi^2 = 3.44$, df = 4, $P = 0.49$). The number of rats caught on the edge of the grid increased through the trapping period, so that by the final night, 89% of captures were on the edge of the grid.

The minimum density of rats on the grid was calculated to be 7.1 rats ha^{-1} (121 rats in 17 ha), while

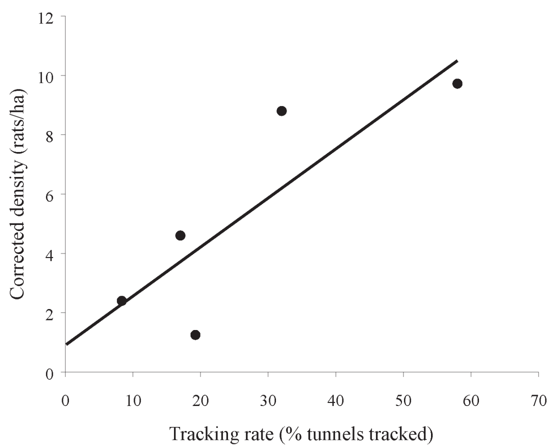

Figure 2. Nightly tracking rate (% of tunnels tracked) plotted against the corrected density of rats remaining on the trapping grid, during the removal trapping experiment in June 1998. The corrected density of rats remaining was calculated as the average of the rat density at the end of the previous night's trapping, and the density of rats at the end of the current trapping night (after Brown *et al.*, 1996).

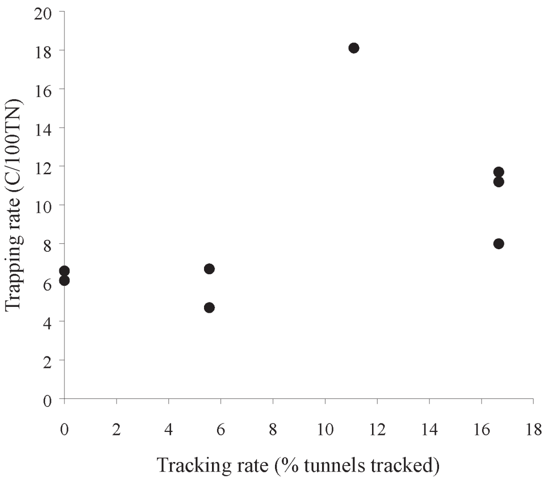

Figure 3. Tracking rate (% of tunnels tracked) plotted against rat captures per hundred trap nights (C100/TN), for rats caught on the snap-trapping line between January and December 1997.

the regression of nightly catch against cumulative catch generated the equation: cumulative catch = 139.8 - 2.043 (nightly catch) (R^2 = 0.87, n = 5, P < 0.05). This gives an estimated density of 8.2 rats ha^{-1} (95% CI = 5.9 to 10.53 rats ha^{-1}). The regression of percentage tracking rate against the estimated density of rats remaining on the grid is shown in Fig. 2; the relationship density = 0.153 (% tracking rate) + 1.199, explained 72% of the variation (P = 0.07). The relationship was heavily influenced by the last night of trapping, when density was calculated at 1.25 rats/ha and the tracking rate was 19.8% (Fig. 2). One tracking tunnel (line 5, 150 m station) recorded mouse prints on the last night of trapping.

Snap-trapping line

From January to December 1997, 75 ship rats and 7 house mice were caught on the trap-line. The overall rat male:female sex ratio was 1.28:1, which was not significantly different from unity (χ^2 = 1.08, df = 1, P > 0.05), and this did not differ significantly over the trapping period (χ^2 = 1.213, df = 4, P > 0.05). More juvenile rats were caught in autumn and winter (28% and 45% respectively) than in spring and summer (23% and 0%), but these differences were not significant (χ^2 = 6.31, df = 3, P > 0.05). There was a significant relationship between the number of rats caught and the tracking rate (R^2 = 0.57, n = 8, P = 0.03), but not between tracking rate and C/100 TN (R^2 = 0.31, n = 8, P = 0.15; Fig. 3).

Relationship between tracking tunnels and Fenn traps

The monthly tracking rates and monthly rat captures per 100 trap-nights in Fenn traps on the Halfline and all tawa-podocarp forest Fenn trap-lines are shown in Figure 4a. The two density indices obtained from the Fenn traps were very similar, and only differed in their estimation of relative population trends in October 1997.

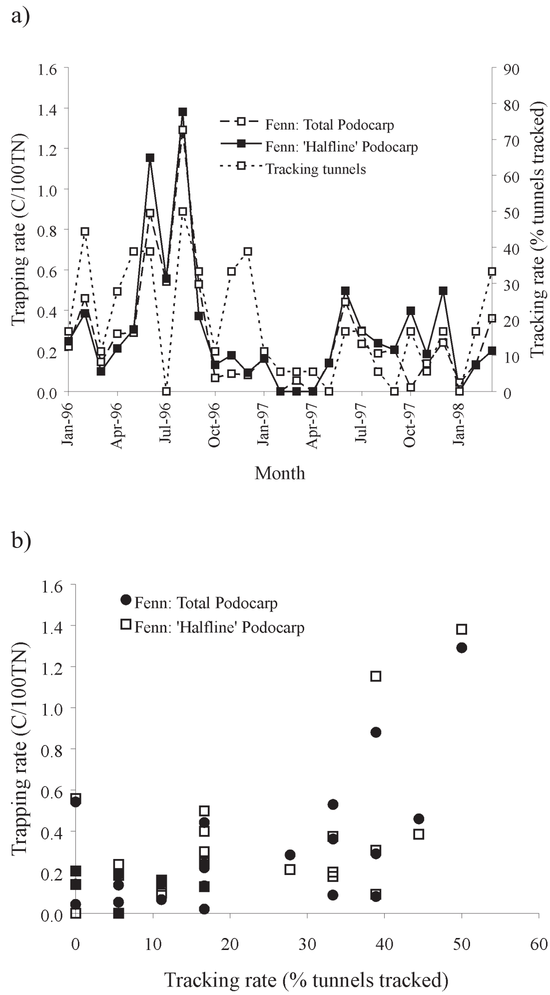

Figure 4. a) Monthly density indices obtained from tracking tunnels and Fenn traps run from January 1996 to March 1998 at Lake Waikaremoana in tawa-podocarp forest. b) The relationship between density indices obtained from tracking tunnels and Fenn traps on all lines and on the 'Halfline' in tawa-podocarp forest.

The relationship between the tracking tunnels and the Fenn traps was not as tight as that between the two Fenn trap density estimates. The tracking tunnels showed greater amplitude in fluctuations over the study period and a relatively smaller increase in population size between Jan 1996 and Aug 1996 than the Fenn traps. The tracking tunnel index also stayed high for longer in 1996, relative to the Fenn trap density indices. The difference in average use between 1996 and 1997 was significant for both the tracking tunnel indices ($\chi^2 = 28.67$, df = 1, $P < 0.01$), and the Fenn trap capture rates ($\chi^2 = 77.63$, df = 1, $P < 0.01$).

The co-integration analysis showed that the time-series from the tawa-podocarp forest were stationary for the tracking tunnels (Unit-root *t*-test, $t = -3.69$, n = 23, $P < 0.001$), all podocarp Fenn traps ($t = -2.26$, n = 23, $P < 0.05$), and the Halfline Fenn traps ($t = -4.83$, n = 23, $P < 0.01$). The relationship between the tracking tunnel and Fenn trap indices is shown in Fig. 4b. The regression of tawa-podocarp forest tracking tunnel tracking rates on Fenn trap C/100TN was significant for all Fenn traps [regression equation: tracking rate = 63.45 (Fenn C/100TN), n = 26, SE of regression coefficient = 11.94, auto-correlation coefficient = 0.43, $P < 0.001$] and for the Halfline traps [regression equation: tracking rate = 27.24 (Fenn C/100TN), n = 26, SE of regression coefficient = 7.46, auto-correlation coefficient = 0.53, $P < 0.01$].

The monthly density indices for rats in beech forest obtained from tracking tunnels and Fenn traps, and the relationship between the two indices, are shown in Figure 5. The tracking tunnels showed a peak in rat density in March-May 1996, followed by a gradual decline over 1996 to a low level in March-April 1997. This was followed by a gradual increase in tracking rate over 1997, to a peak level in March 1998 that was comparable to the March-May 1996 peak. Rat captures per 100 trap-nights from the Fenn traps showed a different trend; there was no large peak in captures in March-May 1996, and numbers remained low throughout 1996 and early 1997. Capture rates increased from June 1997, but the capture rates varied from month to month. There was no significant difference in mean density between 1996 and 1997 from either the tracking tunnels ($\chi^2 = 2.69$, df = 1, $P > 0.05$) or the Fenn traps ($\chi^2 = 1.86$, df = 1, $P > 0.05$).

The co-integration analysis for the beech forest area suggested that the tracking tunnel time-series was non-stationary ($t = -1.72$, n = 23, $P > 0.05$), while the Fenn trap data series was stationary ($t = -3.22$, n = 23, $P < 0.01$). There was no evidence of co-integration between the two series ($t = -1.35$, $P > 0.05$), and no long-term agreement between the density indices obtained from the two techniques.

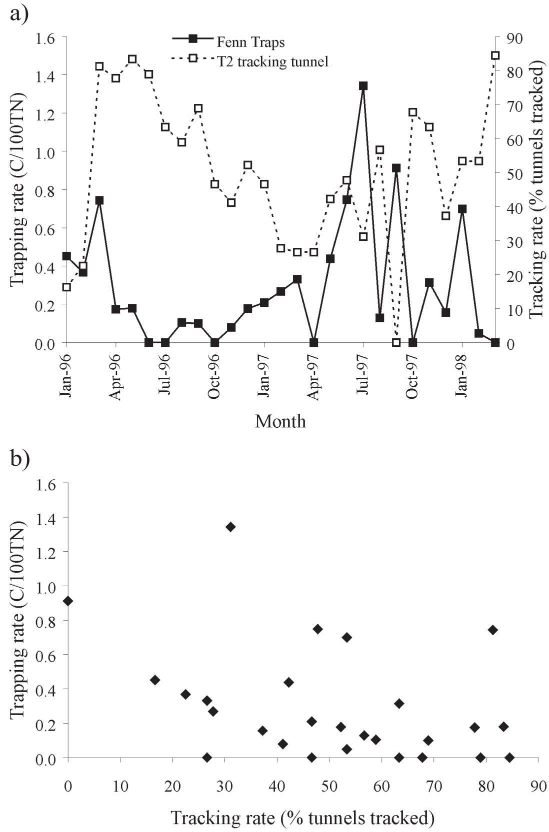

Figure 5. a) Monthly density indices obtained from tracking tunnels and Fenn traps run from January 1996 to March 1998 at Lake Waikaremoana in beech forest. b) The relationship between density indices obtained from tracking tunnels and Fenn traps run in beech forest.

Relationship between indices and forest types

Comparisons of relative density between the tawa-podocarp and beech forest sites show that the estimation of rat density is greatly influenced by the density index used. Tracking tunnels indicated significantly higher rat numbers in beech forest than in tawa-podocarp forest in 1997 (Fig. 4a, 5a; T = 0, $T_{crit} = 13$, n = 12, $P < 0.05$). In comparison, numbers of rats caught per month were significantly higher in tawa-podocarp forest than in beech forest in both 1996 (T = 9, $T_{crit} = 12$, n = 12, $P < 0.05$) and 1997 (T = 4.5, $T_{crit} = 5$, n = 12, $P < 0.05$). Rat captures per 100 trap-nights were higher in tawa-podocarp forest than in beech forest in 1996, but were significantly higher in beech forest than in tawa-podocarp forest in 1997 (T = 3, $T_{crit} = 10$, n = 12, $P < 0.05$).

Discussion

The ship rat density indices obtained by the different methods varied considerably with index type, and with experimental protocol. This variation clearly warrants further investigation if research and management decisions are to be based upon information gained from such indices. Specifically, the reliability, repeatability and applicability of density indices obtained from tracking tunnels require further examination, given their widespread and frequent use in rodent ecology in New Zealand.

Tunnels and snap-trap captures

Density indices from tracking tunnels and snap-traps showed similar trends in population size over the course of the trapping grid experiment, although the relationship was not significant at the 0.05 level. The relationship was influenced by immigrant rats on the last night of the experiment, thus violating one of the assumptions of Zippin (1958) that there is no immigration during the experiment. Given the short time frame of the trapping, it is unlikely that births, deaths or emigration affected the results. Both sexes and all age classes appeared to be equally trappable, although this assumption should be tested further, as should the effect of immigration on removal trapping density indices.

No mice were caught during the experiment, although mouse prints were recorded in one of the tracking tunnels in the centre of the grid on the last night of trapping. It is probable that mice were present in the area at very low density, but avoided or were excluded from the tracking tunnels while rats were present. Very little is known about the relationship between ship rats and house mice in New Zealand forests (King *et al.,* 1996; Blackwell *et al.*, 2001).

The lack of a significant correlation between footprint tracking rates and snap-trap indices along the same trapping line is interesting. If two indices sampling the same population fail to show the same trend, the validity of both needs to be investigated. Both tracking tunnels and snap-traps record activity as well as abundance (Sheppe, 1965; Sarrazin and Bider, 1973; King and Edgar, 1977), however, the ability of a single rat to track multiple tracking tunnels (cf. only being caught once in a kill-trap) may make tracking tunnels particularly susceptible to variation in activity levels.

With small numbers of traps, C/100 TN becomes sensitive to the numbers of sprung traps recorded (Caughley, 1977), which can be influenced by the condition of the traps, the experience of the trapper, and the densities of other non-target animals.

Tunnels and Fenn trap captures

Tracking tunnel and Fenn trap density indices were strongly correlated in tawa-podocarp forest areas, where the underlying rat population size was high. In these areas, the rat by-catch in the predator traps showed similar timing and amplitude of population peaks and declines as those shown in the tracking rates on the tracking tunnel line. With medium to high rat population density, changes in tracking rate appear to follow changes in population density.

The weak relationship between the tracking tunnel and Fenn trap rat density estimates in the beech forest site highlights the influence of animal behaviour on tracking tunnel density indices. Rats in low-density populations may be more active, and may cover larger areas. This could lead to individual rats tracking a greater proportion of tunnels, and this relationship should be tested. We could find no published information on ship rat territory size and activity in beech forest. However, home range size and use in this species is know to be variable and adaptive (Ewer, 1971; Daniel, 1972; Innes and Skipworth, 1983; Hooker and Innes, 1995; Innes *et al*., 1995). The effect of rodent behaviour must therefore be explicitly considered when tracking tunnels are used as an indexing method.

Applicability of the indices

The problems with the various rodent density indices highlighted above suggest that caution must be used when choosing an appropriate indexing technique, and the research or management questions posed should be considered when choosing an index. While there are a number of advantages in using tracking tunnels (King and Edgar, 1977), they are particularly susceptible to changes in activity and rodent abundance. Greater consideration of these limitations on tracking tunnel use may help to increase the accuracy and reliability of this index. Given the widespread and continued use of tracking tunnels in New Zealand for studies of small-mammal ecology, we recommend the following steps are always taken to maximize the reliability of the index:

1. Tracking tunnels should be used to compare populations directly, in the same habitat type only. The density index will more closely reflect abundance, rather than activity, if tracking tunnels are run with a consistent protocol, run in treatment and non-treatment areas on the same night(s) to account for activity, and only compared within the same habitat types.
2. Sufficient numbers of tunnels should be run to enable detection of treatment effects. If individual animals are not marked, tracking tunnels can only be scored as tracked or untracked. Ideally, a power analysis of the number of tracking tunnels required

to detect biologically significant differences should be conducted before any study commences.

3. The underlying behaviour of the study animals should be considered. The various tracking tunnel protocols that have been proposed use different trap layouts and spacing (King and Edgar, 1977; Innes *et al*., 1995; Brown *et al*., 1996). Studies of ship rat home range use in broadleaf-podocarp forest in New Zealand have revealed average home ranges of around 1 ha for males, and less than this for females (Hooker and Innes, 1995). The commonly used tracking tunnel spacing of 50 m is therefore susceptible to contagion of the index through multiple tracking of tunnels by the same individual. A tracking tunnel spacing of 100 m would mean a lower number of tunnels overall, but it may increase the reliability of the index.
4. The tracking tunnel index should always be correlated with a second density measure. Use of more than one index allows the correlation of the density index and increases the confidence in observed population trends, as well as increasing the quality and quantity of information gained.

Confidence in the accuracy and applicability of the density indices used in this study can only be increased by calibration against true density estimates. Specifically, the influence of index type, activity, target animal catchability, trap (or tunnel) placement and sampling effort on the density index need to be determined.

Acknowledgements

The authors thank S. Bassett, P. Blackwell, L. Dew, J. Miles, R. Stevenson, and R. Waiwai and the Lake Waikaremoana Conservation Corps, who assisted with the collection of the Fenn and snap-trapping data. Thanks also G. Jones and D. Hedderley for statistical advice, and to E. Minot and three anonymous referees for comments on the manuscript. G. L. Blackwell was funded by a Massey University Doctoral Scholarship.

References

Blackwell, G.L.; Potter, M.A.; Minot, E.O. 2001. A computer simulation of rodent and predator population dynamics in an eruptive system. *Ecological Modelling 142(3)*: 227-245

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

Caughley, G. 1977. *Analysis of vertebrate populations*. John Wiley and Sons, London, U.K.

Cunningham, D.M.; Moors, P.J. 1983. *A guide to the identification and collection of New Zealand rodents*. New Zealand Wildlife Service, Wellington, New Zealand.

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

Engle, R.F.; Granger, C.W.J. 1987. Cointegration and error correction representation, estimation and testing. *Econometrica 55:* 251-276.

Ewer, R.F. 1971. The biology and behaviour of a free-living population of black rats (*Rattus rattus*). *Animal Behaviour Monographs 4:* 127-174.

Hendry, D.F.; Doornick, J.A. 1999. *Empirical econometric modelling using PcGive*. Timberlake Consultants Press, London, U.K.

Hooker, S.; Innes, J.G. 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, J.G. 1990. Ship rat. *In:* C. M. King (Editor), *The handbook of New Zealand mammals*, pp. 206-225. Oxford University Press, Auckland, N.Z.

Innes, J.G.; Skipworth, J.P. 1983. Home ranges of ship rats in a small New Zealand forest as revealed by trapping and tracking. *New Zealand Journal of Zoology 10:* 99-110.

Innes, J.G.; Warburton, B.; Williams, D.; Speed, H.; Bradfield, P. 1995. Large-scale poisoning of ship rats (*Rattus rattus*) in indigenous forests of the North Island, New Zealand. *New Zealand Journal of Zoology 19:* 5-17.

Karnoukhova, N.G. 1971. Age determination of brown and black rats. *Ekologiya 2:* 71-76.

King, C.M.; Edgar, R.L. 1977. Techniques for trapping and tracking stoats (*Mustela erminea*); a review and a new system. *New Zealand Journal of Zoology 4:* 193-212.

King, C.M.; Innes, J.G.; Flux, M.; Kimberley, M.O.; Leathwick, J.R.; Williams, D.S. 1996. Distribution and abundance of small mammals in relation to habitat in Pureora Forest Park. *New Zealand Journal of Ecology 20:* 215-240.

Lidicker, W.Z. 1966. Ecological observations on a feral house mouse population declining to extinction. *Ecological Monographs 36:* 27-50.

Nelson, L., Jr.; Clark, F.W. 1973. Correction for sprung traps in catch/effort calculations of trapping results. *Journal of Mammalogy 54:* 295-298.

Pollock, K.H.; Nicholls, J.D.; Brownie, C.; Hines, J.E. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs 107:* 1-97.

Sarrazin, J.P.R.; Bider, J.R. 1973. Activity, a neglected parameter in population estimates - the development of a new technique. *Ecology 54:* 369-382.

SAS Institute. 1990. *SAS/STAT users guide, version 6, 4th Edition.* SAS Institute Inc., Cary, U.S.A.

Sheppe, W. 1965. Characteristics and uses of *Peromyscus* tracking data. *Ecology 46:* 630-634.

SPSS Inc. 1998. *SYSTAT 8.0 for windows: statistics.* SPSS Inc., Chicago, U.S.A.

Tanaka, R. 1960. Evidence against the reliability of the trap-night index as a relative measure of population in small mammals. *Japanese Journal of Ecology 10:* 102-105.

Zar, J.H. 1974. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey, U.S.A.

Zippin, C. 1958. The removal method of population estimation. *Journal of Wildlife Management 22:* 82-90.