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Optimal Buffer Widths for Control of Possums in the Hauhungaroa Range : 1994/95–1998/99.

Population Recovery of Possums and Wild Deer and Tb Prevalence in Possums, Wild Deer, and Cattle

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1. Summary

1.1 Project and Client

Changes in indices of possum, red deer, and feral pig densities, and in the prevalence of bovine tuberculosis (Tb) in the same species in parts of the Hauhungaroa Range controlled with 1080-loaded carrot bait in 1994/95, were monitored annually by Landcare Research for the Animal Health Board (AHB; Project No. R10480). The results were related to changes in the incidence of Tb in adjacent livestock. This report presents results from 1998/99, the last year of the study, and summarises the overall findings of the 5-year project.

1.2 Objectives

To determine the effectiveness of aerial control of possum, red deer, and feral pig populations in forest buffers 1-, 3-, and 7-km wide, and of annual and biannual maintenance control of possums on forest-pasture margins in reducing Tb in adjacent cattle herds, by:

- monitoring the recovery over 5 years of possum, deer, and pig populations in all three buffers, and possum populations on the forest-pasture margins of the 3- and 7-km buffers aerially poisoned in 1994/95,
- determining the prevalence of Tb over 5 years in possum populations in the 3- and 7-km buffers, in deer and pig populations in the 7-km buffer and in adjacent uncontrolled areas, and in possum populations on the forest-pasture margins (of the 7-km buffer) under annual and biannual maintenance control, and
- assessing trends in the incidence of Tb in cattle herds grazed alongside each buffer.

1.3 Results

The mean numbers of possum faecal pellets per line have increased from the low levels recorded in all three buffers immediately after the 1994/95 control operation. Faecal-pellet indices of possum density in the 3- and 7-km buffers in 1998/99 were 25% and 10%, respectively, of their pre-control levels, but in the 1-km buffer had reached 81% of pre-control levels and are now significantly higher than in either of the other two buffers. Presence-absence indices show the same trends in overall possum population recovery as the pellet count indices in all three buffers.

- Presence-absence indices indicated possum numbers have recovered faster in the rear of the 1-km buffer, i.e., adjacent to forest areas with uncontrolled possum populations, compared with near the front of the buffer, i.e., adjacent to pasture with maintenance control. Although less conclusive, presence-absence indices also provided evidence that possum numbers are recovering faster near the rear of the 3- and 7-km buffers.
- Trap lines within part of the 3-km buffer indicated an exponential rate of increase for the possum population of 59% per annum, and a population in 1998/99 nearing pre-control levels. This result differs sharply from trends derived from counts of possum faecal pellets. Similar surveys on the margin of the 7-km buffer suggested a statistically similar rate of recovery (41% per annum), with most of the increase recorded in 1997/98 and 1998/99.
- Residual trap-catch (RTC) estimates of possum density within the 7-km buffer indicated that the possum population is still low 5 years after control, and provided no evidence of increasing possum numbers at the rear of the buffer close to uncontrolled possum populations compared with possum populations close to the forest-pasture margin.

- Pellet-group densities (PGDs) for deer indicated that their numbers in the 3-km buffer have not changed following control, whereas those in the 1- and 7-km buffers have trended upwards. There were no differences between the buffers in the indices of deer numbers prior to the control operation, but deer numbers are now significantly lower in the 3-km buffer compared with the 7-km buffer. Faecal-pellet presence-absence indices for deer followed the same general trend as the PGD indices.
- Faecal-pellet indices of pig abundance were too low and imprecise in all three buffers to provide useful indications of either the initial reductions following control or of subsequent changes, so are excluded from this report.
- Two infected possums (2/125, 1.6%) were recovered from the 3-km buffer in 1998/99. No Tb was found in possums taken from our trap lines or from the RTC lines in the 7–km buffer in 1998/99. The prevalence of Tb in possums over all our surveys from 1993/94 to 1998/99 (including the RTC survey) was very low (7/1086, 0.64%). No infected possums have been trapped on the forest margin of the 7-km buffer in any year of our study.
- The prevalence of Tb in deer in 1993/94 exceeded 30% in both the 7-km buffer and the central uncontrolled area. Since then, Tb prevalence has declined in both areas, but the decline in the 7-km buffer has been more marked and consistent than in the uncontrolled area. In 1998/99, 6% of deer taken from controlled areas were infected, compared with 37% in adjacent uncontrolled areas. None of 39 deer born since winter 1994 and shot > 2.5 km from uncontrolled areas have been infected, compared with 26% of 57 such deer shot in the uncontrolled areas.
- For the deer shot in the uncontrolled areas, no Tb was found in any of 21 fawns (< 11 months old), but prevalence increased rapidly in subadult deer (1–2 years old) and exceeded 50% in adult deer (>3 years old).
- The prevalence of Tb in pigs in the 7-km buffer was high (80%) before the aerial control operation and has remained high, with 63% of 19 pigs shot in 1996/97, and 80% of five shot in 1997/98 or 1998/99 infected. All of the infected pigs shot in recent years were born after the control operation, and most were shot >2 km away from the uncontrolled areas.
- The incidence of Tb in cattle on farmland adjacent to all three buffers fell each year following the control operation. The decline was strongest in cattle adjacent to the 1-km buffer and to that part of the margin of the 7-km buffer under annual maintenance control for possums. Counter intuitively, the incidence of Tb in cattle declined more rapidly in areas under annual maintenance control compared with areas under biannual maintenance control.

1.4 Conclusions

- The relatively rapid recovery of the possum population in the 1-km buffer (compared to those in the 3- and 7-km buffers) indicated by our faecal-pellet surveys suggests that buffers of this size are ineffective at providing long-term relief from high within-forest possum densities close to farm margins. Possum densities in the 1-km buffer now exceed both the "40% of the assumed carrying capacity" threshold identified by modelling theory as required for Tb elimination, and the AHB's new empirical 5% RTC target.
- Faecal-pellet surveys in the 3- and 7-km buffers indicate that current possum densities are low to moderate, confirming the success of the 1994 poison operation and the potential of wider buffers to provide greater long-term "relief".
- The spatial patterns of possum population recovery evident from pellet surveys in all three buffers indicate that immigration is important in determining the overall rate of recovery. The proximity of adjoining forest areas with unpoisoned possum populations and the size of these areas in relation to the size of the control buffer appears to determine overall rates

of immigration. Although our interpretation is complicated by apparent differences in possum densities on adjacent farmland (presumably a consequence of differing intensities of maintenance control and differing possum carrying capacities), the results suggest that immigration has had relatively little effect over 5 years on the rate of recovery in areas >1 km from unpoisoned possum populations.

- Possum numbers on the forest-pasture margin of the 7-km buffer appeared to be held in check from 1994/95 to 1996/97 by maintenance control. However, the number of possums trapped in 1997/98 increased sharply, coinciding with a change in the toxin used (1080 pellets to "Feratox®"). There was no difference in the numbers of possums trapped in areas under annual and biannual maintenance control. Hence, biannual control (relative to annual control) of possums on forest-pasture margins is unlikely to further reduce the incidence of Tb in nearby cattle herds but does impose substantial extra costs.
- Our trapping surveys and recent population audits by the Department of Conservation (DOC) and Manawatu-Wanganui Regional Council indicate that possum numbers in the 3-km buffer are rapidly returning to pre-control levels. These results contrast with the slower rate of recovery indicated by our faecal-pellet results, but reasons for this difference are unclear.
- RTC estimates of possum density in the 3-km buffer are higher than the RTC estimates from the 7-km buffer, and together with the recently located infected possums, support further control in this area. RTC estimates of possum density within the 7-km buffer offer marginal support for further control of the possum population for Tb control, based on the AHB's empirical trigger level of 5% RTC.
- Data from both our population indices (standing-crop and presence-absence) suggest that the possum population in the 1-km buffer recovered most rapidly and exceeded 40% of the pre-control level within 2 years. Recovery was slower in the 3-km buffer and slowest in the 7-km buffer. It is difficult to compare the cost-effectiveness of control between the three buffers, as they were managed under different control regimes and our monitoring was insufficient to determine the time taken for populations to reach the 5% RTC trigger level. A combination of our data and common management belief supports buffers of about 3 km for ongoing Tb possum management.
- The relative merits of the three buffer widths in protecting cattle from Tb infection remains equivocal. Herd testing and slaughterhouse records of Tb infection indicate the greatest benefit from possum control has occurred adjacent to the 1-km buffer and to that part of the 7-km buffer under annual control. However, these results are counter intuitive being also affected by unquantified herd management practices, and we urge caution in their extrapolation.
- The prevalence of Tb in possums on or adjacent to the margins of the 3- and 7-km buffers occurs at very low levels and, within the limits of our sampling, appears similar to that recorded on the forest-pasture margin of the Hauhungaroa Range in 1982/83. However, possum necropsy results since the poisoning, and steadily declining prevalences of Tb in deer and Tb in cattle, suggest that the prevalence of Tb in possums on the forest-pasture margin of the 7-km buffer has declined substantially since 1994/95.
- The low prevalence of Tb in fawns compared with the high prevalence in subadult deer suggests that infection in wild deer is unlikely to arise through feeding or from hind-fawn transmission. Together with the absence of infection in deer born since the control operation and shot >2.5 km from uncontrolled areas, our evidence suggests most infection in deer result from transmission from possums. If so, infection in deer born before 1994/95 and shot >2.5 km from adjacent uncontrolled areas suggests that some deer survive for at least 5 years

after becoming infected. The low rate of new infection occurring within the 7-km buffer since 1994/95 has resulted in a marked spatial gradient in Tb prevalence in deer within that buffer, which suggests that infected deer in the central uncontrolled area seldom disperse >2 km. Therefore, the occurrence of Tb in young hinds, in particular, may provide a useful indicator of the presence of Tb in local possum populations.

- The high prevalence of Tb in feral pigs shot within the 7-km buffer throughout the study indicates a high likelihood that Tb is still present in other species in that buffer, since transmission in pigs is believed to occur largely through scavenging of infected carcasses.

1.5 Recommendations

Specific to Hauhungaroa

- Our results indicate that the 1- and 3-km buffers required further control by the end of 1998/99, with a deeper buffer of 3 km needed for the 1-km buffer area. This work was completed for the entire 3-km buffer and for about 30% of the 1-km buffer in July 1999.
- Subject to conservation requirements, the possum control proposed for the 7-km buffer in 2000/01 should be postponed, as we believe the low prevalence of Tb in deer and possums in the eastern half of this area indicates there is very little risk of a rapid increase in the number of infected possums there or of them emigrating from within the buffer to farmland. Postponement would allow the further collection of data to enhance our understanding of the rates and patterns of recovery of possum populations and the decline of Tb in possums controlled in forest buffers 7 km deep, and their relevance to the modelling theory currently underpinning the control of Tb-infected possum populations. Residual trap-catch surveys should be undertaken across the 7-km buffer annually to gather data on possum population recovery and Tb status.
- Regardless of when the 7-km buffer is next controlled, the AHB should continue to monitor Tb prevalence in wild deer and feral pigs in the easternmost 3 km of the 7-km buffer south of the Mangatu Stream for at least 3 years, to confirm that Tb prevalence in deer declines to zero as expected, and to determine whether Tb persists in pigs when the disease is absent (or nearly so) from deer and possums. We propose that this work be structured as an operational survey with the sale of carcasses used to defray survey costs.

General

- Based on the lack of evidence of any greater benefits from biannual control that might offset the lower cost of annual control, biannual control should be discontinued. The comparison should, however, be replicated elsewhere to confirm that this recommendation is appropriate.
- Where there is a high prevalence of Tb in wild deer in areas adjacent to infected livestock, the AHB should consider targeting the deer. This will reduce the reservoir of Tb in the area, and the chance (however small) that infected deer surviving for several years after control operations might eventually re-establish Tb in the recovering possum population. Alternatively, if the economic or political costs involved in targeting deer are unacceptably high, the possum population should be held below the currently accepted threshold for long-term disease persistence in possums (5% RTC) for at least a decade.
- The relationship between the persistence of Tb in possum populations within controlled areas and the size and location of gaps in bait coverage should be investigated. Control agencies should rigorously check flight-line coverage of aerial operations and ensure that untreated areas (such as those about watercourses) are adequately covered by follow-up ground-based control.

- The home-range size and dispersal distances of feral pigs should be investigated in various habitats to determine the geographic scale over which pigs can be used as sentinels of continued Tb presence.
- Based on the positive results in cattle herd testing adjacent to the 3-km buffer, the recovery of possum numbers over 3–5 years following aerial control to unacceptably high levels, the undoubtedly higher initial costs of controlling deer and possums over a 7-km buffer, and the maximum distance of 2.5 km that infected deer born after the poisoning were found away from uncontrolled areas, we recommend a buffer width of 3 km to separate infected wildlife from livestock.
- Further comparisons (replications) of the optimal buffer widths for possum control are required to substantiate our conclusions and recommendations. These should focus on comparing the effectiveness of buffers of 2-, 3-, and 4-km wide in reducing the densities of, and Tb prevalence in, possums and deer living within 1 km of forest-pasture margins.

2. Introduction

Changes in indices of possum, red deer, and feral pig densities, and in the prevalence of bovine tuberculosis (Tb) in the same species in parts of the Hauhungaroa Range controlled with 1080-loaded carrot bait in 1994/95, were monitored annually by Landcare Research for the Animal Health Board (AHB; Project No. R10480). The results were related to changes in the incidence of Tb in adjacent livestock. This report presents results from 1998/99, the last year of the study, and documents the overall findings of the 5-year project.

3. Background

The management of Tb in livestock in New Zealand in areas containing tuberculous wildlife (i.e.,Vector Risk Areas – VRAs) is based both on a herd test and slaughter programme and works surveillance, and on the control of wildlife vectors living adjacent to at-risk herds. For most VRAs, the critical wildlife maintenance (reservoir) host and vector of Tb is the possum (Coleman & Livingstone in press). Possum populations believed to harbour Tb and living alongside livestock are typically controlled by aerial poisoning followed by ground-based maintenance control to reduce their threat to livestock. Traditional aerial control of tuberculous possum populations comprises the sowing of 1080 baits over forest adjacent to the pasture margin and has typically led to poisoned strips (buffers) of forest 1–2 km wide along forest-pasture margins. On the West Coast of the South Island, possum baits are usually sown to the upper limit of the alpine scrub. This strategy is based on the documented foraging distances of possums living in forest and feeding on pasture (e.g., Green & Coleman 1986). Control of possum populations in the unbroken tracts of forest and scrub more common in the North Island, and elsewhere in the South Island, typically stopped 1–2 km from the forest-pasture margin rather than alpine scrub boundaries.

In early 1994/95, Tb-infected possum and red deer populations in the forests on both sides of the Hauhungaroa Range were controlled by aerial poisoning (Fig. 1). Routine management objectives for this operation were modified to meet a series of research objectives, which sought to compare the effectiveness of aerial control of possums across 1-, 3-, and 7-km buffers in limiting the rate at which possum populations recovered on forest-pasture margins. In 1995/96, additional control was carried out against possums and deer in the south-western part of the Hauhungaroa Range.

This research project was prompted by management concerns that possum populations on forest-pasture margins adjacent to buffers 1–2 km wide can recover to near pre-control levels within 12–24 months of initial control (P. Livingstone, AHB, pers. comm.). As the eradication of Tb from possum populations at the beginning of our study was based on the modelling premise that possum densities must be reduced to 10–20% of carrying capacity (K) and maintained below 40% of K for the disease to die out (Barlow 1991), recovery of possum populations over 1–2 years would appear to provide little opportunity for Tb in possum populations to self-eliminate, or of achieving significant reductions in the incidence of Tb in adjacent livestock. Therefore, we monitored the recovery of possum populations following control in three buffers of different width. We also monitored changes in the prevalence of Tb in possum populations within the 3- and 7-buffers and on the forest-pasture margin of the 7-km buffer, and compared the effectiveness of annual and biannual maintenance control on possum populations on forest-pasture margins. Eradication of Tb from possum populations is now based on the AHB's latest strategy of maintaining possum populations below a residual trap catch (RTC) of 5% (Animal Health Board 1997). This change did not influence the direction of our study or the relevance of our results.

The possum and deer control operation in 1994/95 also provided an opportunity to examine the role of wild deer, and to a lesser extent feral pigs, in the maintenance of Tb in wild animals and livestock. Both deer and pigs carry Tb (Morris & Pfeiffer 1995), and deer populations in the Hauhungaroa Range have a high prevalence of Tb (Nugent & Lugton 1995). However, the role of deer and particularly of pigs as maintenance hosts capable of sustaining the disease without transmission to other species is unclear. Populations of both species are affected by the aerial control of possums: deer are directly affected by their consumption of toxic baits, while pigs may be directly affected by eating baits or less directly, through scavenging of poisoned possum and deer carcasses. Therefore, a secondary objective of our study was to monitor the rate of recovery both of deer and pigs within each buffer, and to document the prevalence of Tb within each species in the 7-km buffer and adjacent uncontrolled forest areas. However, it quickly become apparent that too few pigs were present to obtain precise data on their density and Tb prevalence, and therefore the findings of this part of our study are limited.

Our final objective examined the overall effectiveness of the initial and ongoing maintenance control of possums in the three buffers on the incidence of Tb in adjacent cattle herds. Many cattle herds on farmland surrounding the Hauhungaroa Range have been heavily infected with Tb since the 1970s and, although sporadic local possum control has been undertaken to reduce Tb infection in cattle since the early 1970s, concerted and extensive possum control in forests on both sides of the Hauhungaroa Range and over the adjacent farmland began only in 1994/95.

In the first year of the study, we recorded possum kills of 78 – 92%, deer kills of up to 31%, and overall Tb prevalence rates of 0.9% for possums and 37% for deer (Fraser et al. 1995). In 1994/95, we began monitoring the anticipated recovery after control of possum and deer densities and changes in Tb prevalences in possums and deer. This monitoring has continued annually until 1998/99.

The survey of trends in Tb prevalence in deer following possum control initiated in this study have since been extended into a larger study (AHB R10479 — Epidemiology of Tb in wild deer) programmed to continue for a further 2 years. As part of the extended study, sampling of deer in the central part of the Hauhungaroa Range (where possums were not controlled) has been increased to a much higher intensity than originally planned.

4. Objectives

To determine the effectiveness of aerial control of possum, red deer, and feral pig populations in forest buffers 1-, 3-, and 7-km wide, and of annual and biannual maintenance control of possums on forest-pasture margins in reducing Tb in adjacent cattle herds, by:

- monitoring the recovery over 5 years of possum, deer, and pig populations in all three buffers, and possum populations on the forest-pasture margins of the 3- and 7-km buffers aerially poisoned in 1994/95,

- determining the prevalence of Tb over 5 years in possum populations in the 3- and 7-km buffers, in deer and pig populations in the 7-km buffer and in adjacent uncontrolled areas, and in possum populations (of the 7-km buffer) on the forest-pasture margins under annual and biannual maintenance control, and
- assessing trends in the incidence of Tb in cattle herds grazed alongside each buffer.

5. Methods

5.1 General

Possum and deer populations in the 1-, 3- and 7-km buffers were monitored prior to poison baiting in 1994/95 and thereafter each year to 1998/99 by faecal pellet surveys. Possum populations in the 3-km and 7-km buffers were monitored over the same time interval with both traditional trap-catch and the recently developed Residual trap-catch surveys. In addition, possum populations on the forest-pasture margins were monitored annually using the same trap-catch technology. The prevalence of Tb in deer and possums was determined by necropsy surveys of both species, while Tb records for cattle were obtained from AgriQuality New Zealand (formerly MAF Quality Management). These techniques are detailed below.

5.2 Recovery of possum and deer populations

Faecal pellet surveys

The rates of recovery of possum and deer populations were determined by faecal-pellet surveys in the 1-, 3-, and 7-km buffers. Each survey followed the same experimental design. Faecal-pellet densities of both species were assessed in each buffer on between 2 and 22 lines located randomly where area permitted and containing 50–400 unmarked circular plots spaced at 10-m intervals (Fig. 1).

The possum population was monitored by counting all recognisable possum pellets (i.e., standing crop) on plots 80 cm in radius. Deer populations were monitored by counting the number of intact pellet groups on plots 2.5 m in radius. Indices of abundance of each species were derived from the mean numbers of possum pellets and deer pellet groups found per line, converted to pellet and pellet-group densities (PGD) per hectare, respectively. The percentage change in the index for each species within each buffer was determined by comparing results with those from the pellet surveys conducted before control in 1994/95 with those immediately after control and in subsequent annual monitoring to 1998/99.

As pellets disappear at rates dependent on weather and habitat conditions, area-wide changes in pellet densities between years were adjusted using data from two nearby uncontrolled areas. Results from the central uncontrolled area (650 plots on thirteen 50-plot lines) were used to calibrate pellet counts in the 3-km buffer, while those from the southern uncontrolled area (400 plots on four 100-plot lines) were used to adjust data gathered in the 1- and 7-km buffers (see Fig. 1). The numbers of pellet lines monitored in both uncontrolled areas were reduced in 1995/96–1998/99, because parts of the central and southern areas were subjected to additional (and to the authors, unexpected) aerial control of possums in 1995/96.

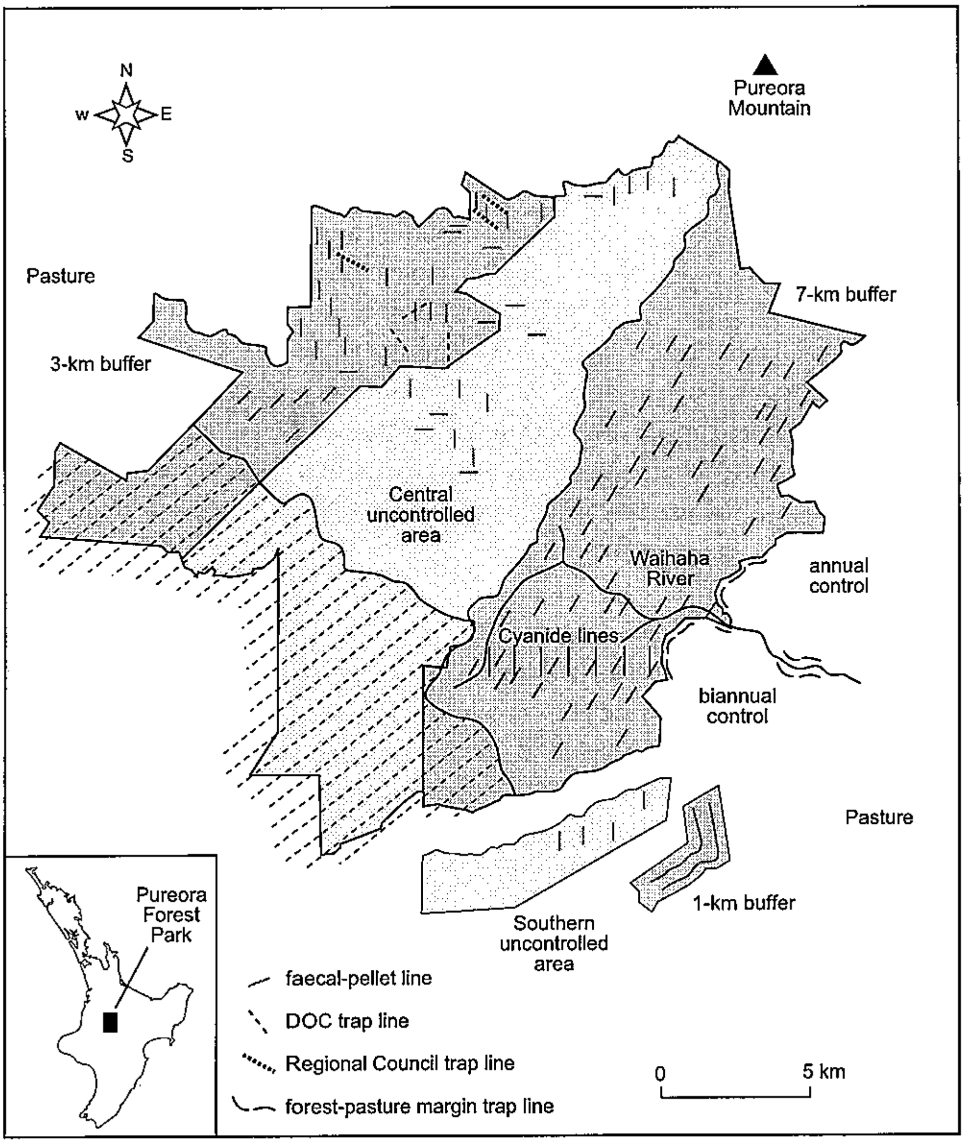

Fig. 1 Locations of the three buffer zones poisoned in 1994/95, the south-western area poisoned in 1995/96, the central and southern uncontrolled areas, and the sections of the forest-pasture margin of the 7-km buffer subjected to annual and biannual ground-based maintenance control. The locations of the faecal-pellet lines and possum trap lines are also shown.

For each of the buffer areas, we used paired t-tests (α=0.05) to determine differences in pellet density indices between consecutive years and between the 1994/95 post-control indices and those recorded in 1998/99. We used one-way ANOVA tests and pairwise LSD (α=0.05) comparisons to examine differences in possum and deer pellet densities, respectively, between the three buffers in 1994/95 prior to the control operation, and again in 1998/99. In addition, we also analysed the faecal-pellet data (using a square root transformation) with a repeated measures ANOVA to test for any time effect on the recovery rates of the residual possum populations in the three buffers.

Presence-absence indices of abundance for the original set of pellet lines (i.e., those established in 1994/95) were used to supplement our standing-crop estimates for possums and total-count estimates for deer. We graphically compared trends between the buffers and over time, with similar results from our primary indices of possum and deer abundance.

No faecal-pellet results are presented for feral pigs, because the rarity of pig faeces seen during our surveys limited any rigorous analysis.

Spatial patterns in the rates of recovery of the possum populations in the 3- and 7-km buffers in relation to distance from the forest-pasture margin and from the uncontrolled (deep) forest area were determined by surveying 91 50-plot pellet lines (29 in the 3–km buffer and 62 in the 7-km buffer). These included 39 pellet lines originally established in the 3- and 7-km buffers, plus 52 new 50-plot lines established in 1995. Most of these pellet lines were aligned parallel to the forest-pasture margin at 0.25 km, 0.75 km, 1.5 km, and at 1-km intervals thereafter, into the forest. However, some pellet lines in the 3-km buffer could not be aligned parallel to the forest-pasture margin due to the irregular shape and topography of the 3-km buffer. On each line, presence-absence data for possum pellets were collected on plots 114-cm in radius, with the percentage of plots with pellets providing an index of possum abundance. Presence-absence data for deer pellets were collected on the same plots using both 114-cm and 250-cm plot radii. In the 1-km buffer, we used the standing-crop data collected as the principal means by which to examine spatial trends in population recovery.

Trap-catch surveys

Possum recovery rates were also assessed incidentally from trapping data gathered during the collection of possums for necropsy. Initially this data was obtained solely from trapping on forest-pasture margins adjacent to the 7-km buffer. Eleven lines of from 20 to 60 leg-hold traps were established in April 1994, and re-trapped in September 1994, along the forest-pasture margin of the 7-km buffer and the Lakeside Reserves adjacent to the lower Waihaha River (Fig. 1). This trapping was done to survey possums for their Tb status, to determine the initial kill of possums frequenting the forest-pasture margin, and to evaluate the effectiveness of the subsequent annual and biannual maintenance control programme. These lines were re-trapped each year in May following trapping protocols (Fraser et al. 1995) used prior to the development of the National Trapping Protocol (B. Warburton, unpubl. report).

From 1995/96 the trapping surveys were expanded at the AHB's request to include parts of the 3-km buffer that had been surveyed in 1994/95 before and after control by management agencies. These surveys included three trap lines established within 1 km of the forest-pasture margin by the Manawatu-Wanganui Regional Council (MWRC, now called horizons.mw), and three lines established 2–3 km into the buffer in the Rātā-nu-nui Ecological Area by DOC. These lines were trapped annually from May 1995/96 to 1998/99. No trap lines were established in the 1-km buffer as additional monitoring and necropsy (see below) there was seen as having low priority. All lines associated with the 3- and 7-km buffers were trapped for 3 consecutive nights of acceptable trapping weather (fine to partly fine). The traps were set at intervals of 30–40 m and all animals captured (except for uninjured birds) were humanely euthanased.

Some further data on possum population trends in the 7-km buffer were collected from 1994/95 to1998/9 as part of an unrelated project in the headwaters of the Waihaha Catchment in the southern part of the 7-km buffer (Nugent et al. 1997). In 1993/94 and 1994/95, 10 lines of 22 traps were set at 20-m intervals across the catchment. From 1997/98 onwards, these lines were replaced by four 20-trap lines run for 3 nights every 6 months.

Excluding the trap-catch data from the Waihaha Catchment, the trap-catch estimates were analysed using a repeated measures ANOVA to test for any effect of time on trap-catch rates. The data were transformed to the natural log scale, with 0.01 added to all observations to overcome the many zero records present, and significant year effects examined using pair-wise comparisons with Bonferroni-adjusted *P* values. The exponential rate of increase (r) of the population was determined from

$$r = \log_e (N_t/N_i)/t$$

where N_t = the catch rate (index of population size) in the final year of sampling, N_i = the catch rate in the first year of sampling, and t = units of time between sampling.

In addition to the repeated surveys described above, separate once-only surveys of the possum populations in the 3- and 7-km buffers were undertaken late in the study, following the nationally approved Residual trap-catch (RTC) protocol. The primary aim of these surveys was to determine directly whether possums were above or below the 5% RTC threshold currently set by the AHB for all operations to control Tb-infected possums. In 1997/98, a survey of the 3-km buffer was conducted by the MWRC, with 4–6 trap lines located in each successive 1-km stratum across the buffer and for 1 km into the uncontrolled central part of the Hauhungaroa Range. In 1998/99, a similar survey of the 7-km buffer was conducted by Landcare Research (using contracted field staff) and comprised 10 parallel transects running from randomly located origins on the forest-pasture margin directly to the rear of the buffer. Nine transects each contained seven trap lines located 800 m apart (one trap line per kilometre of transect), while one transect contained only six trap lines due to the width of the buffer at that site. All lines comprised 10 traps set on the ground at 20-m intervals and were monitored for 3 fine nights.

The RTC results were compared with other estimates of possum density in the same buffer. Estimates of RTC from the 7-km buffer were analysed using a repeated measures ANOVA to compare values from individual transects and from lines within each 1-km forest stratum. This analysis allowed for the "systematic" location of trap lines within randomly located transects. The raw data from the RTC estimates for the 3-km buffer were not available, and differences between strata were assessed visually (from geographically presented information from MWRC) based on the overlap in confidence intervals.

5.3 Tb prevalence in wild animals and Tb incidence in livestock

Possums

The prevalence of Tb in possums collected each year from the trap lines on the forest-pasture margin and from lines in the 3-km buffer was determined by necropsy carried out by Landcare Research staff. Additional possums were collected each year from lines 2 km long of cyanide paste baits, located at 1-km intervals parallel to the forest-pasture margin of the 7-km buffer, and from RTC trap lines established in 1998/99 in the 7-km buffer. The Tb status of ferrets and feral cats trapped incidentally was also checked.

All major superficial (axillary and inguinal) and deep (axillary, mesenteric, and mediastinal) lymph nodes, and all major thoracic and abdominal organs (lungs, liver, kidneys, and spleen) were checked for macroscopic lesions indicative of Tb. All suspect lesions were excised, frozen, and forwarded to MAF Quality Management (now AgriQuality) for culture to confirm field diagnoses. Data on Tb prevalence from these possums were not analysed statistically due to the low level of infection recorded.

Some additional data on Tb prevalence in possums were obtained from separate (and ongoing) studies in the 7-km buffer and the central uncontrolled area (Fig. 1). These studies sometimes involved less rigorous necropsies than those detailed above, so data are only presented where the presence of Tb was confirmed by culture.

Deer and pigs

Changes in the prevalence of Tb in deer and feral pigs following the control in 1994/95 were determined from annual necropsy surveys of both species. The data from these surveys were combined with similar data from surveys conducted immediately before control, which covered the entire Hauhungaroa Range, and used to compare trends in Tb prevalence in deer between areas with high and low numbers of possums. The first two surveys following control(1995/96 and 1996/97) focused primarily on the 7-km buffer, but the sampling was subsequently extended in 1997/98 to include parts of the uncontrolled central area.

Most deer and pigs sampled were shot by contracted ground-based hunters or from a helicopter by Environment Waikato or EPRO Ltd staff. A few were shot by research staff involved in other work, while some were purchased from a local commercial helicopter operator. Where possible, carcasses were field dressed and transported (with intestines) to the Murupara Game Packing House for examination by meat inspectors. In the first two years of our study, however, necropsies were undertaken by I. Lugton either in the field or at Massey University, following established procedures (Lugton 1997). From 1996/97, non-saleable carcasses were inspected at the Ruakura Animal Health laboratory before their incineration or burial. Three deer were inspected in the field by project staff.

Except for some of the deer shot by Environment Waikato in 1993/94, the lymph nodes inspected included all those in the head and thoracic cavity and, typically, all mesenteric nodes. Other deep-body lymph nodes were not usually examined. Lesions that appeared potentially tuberculous, plus the tonsils and retropharyngeal lymph nodes of each deer and the mandibular lymph nodes of each pig, were excised and sent for mycobacterial culture. For deer apparently free from macroscopic lesions, the tonsils and retropharyngeal lymph nodes were pooled for culture. A mandible was taken from each carcass to assess animal age (Clarke et al. 1992; Fraser & Sweetapple 1993).

Too few pigs (< 6) were obtained in all years other than 1995/96 (19) to provide reliable data on trends in Tb prevalence. However, all our data from pigs are presented, as they provide some weak evidence of changes in pig density and Tb prevalence.

For deer, each animal was classed by sex and age, and the sample divided into deer born before the control and afterwards. The location of each animal when shot was recorded and used to calculate the distance from the kill location to the nearest uncontrolled area. All deer killed in 1993/94 were regarded as nominally being in the distance class furthest from a controlled area, as all would have been surrounded by large areas in which possums were not controlled. Log-linear analysis was used to analyse the effect of sex, age, location, year, pre- and post-control cohort, and distance class on Tb prevalence.

Cattle

The tuberculin test data for each cattle herd present immediately adjacent to the 1-, 3-, and 7-km buffers, together with the number of cattle culled from the same herds and identified as tuberculous post-mortem, were obtained from AgriQuality Management (J. Adams, pers. comm.). These data were analysed by fitting logistic regression models. Likelihood ratio tests were then used to compare models, to test the hypothesis that there was a relationship between Tb prevalence and year, and to compare these relationships before and after initial possum control, and between annual and biannual control.

6. Results

6.1 Recovery of possum and deer populations

Trends in possum faecal-pellet surveys

Temporal patterns: The standing-crop indices of possum abundance have increased steadily from the low values determined in all three buffers following the control operation (Fig. 2). Between 1997/98 and 1998/99, the average standing-crop index increased by 135% in the 1-km buffer, 54% in the 3-km buffer, and 157% in the 7-km buffer. However, none of these changes were significant, due to the high between-line variation in pellet densities particularly in the 3- and 7-km buffers, suggesting that possum population recovery is very patchy. For the 1-km buffer, the small sample size (only two 400-plot lines) also contributed to the high sample variance.

In 1998/99 (our final pellet survey), the standing-crop index of possum density in the 1-km buffer had increased by 365% from the post-control estimate, and had reached 81% of the pre-control density. The index increased by 96% and 192% from post-control lows in the 3-km and 7-km buffers, respectively, and by 1998/99, had reached 25% and 10%, respectively, of pre-control levels. Despite the trend of increases in the indices in all three buffers following post-control lows, none of these increases was statistically significant. However, given the high between-line variation in pellet indices, the *P*-values associated with our t-test results (0.06, 0.07, and 0.08 for the 1-, 3-, and 7-km buffers, respectively) confirm that the increases are real.

Although the standing-crop indices of possum density in the three buffer areas prior to control were not significantly different from one another ($F_{2,38}$ = 0.90, *P*>0.05), by 1998/99 they showed significant differences ($F_{2,38}$ = 3.47, *P* <0.05). Least Significant Difference (LSD) comparisons showed that indices of current possum densities are significantly higher in the 1-km buffer than in either the 3- or 7-km buffers, and that possum densities in the latter two buffers are similar. When we included all three buffers, repeated measures ANOVA results indicated that there was no overall treatment effect (i.e., no difference in the pellet counts between the buffers; $F_{2,44}$ = 1.84, *P* = 0.17), no year effect (i.e., no difference in the pellet counts with time; $F_{4,176}$ = 1.29, *P* = 0.28), and no treatment – year interaction effect ($F_{8,176}$ = 1.04, *P* = 0.41). However, when we excluded the 1-km buffer data, there was a significant year effect ($F_{4,148}$ = 3.46, *P* = 0.01), although there was still no overall treatment effect ($F_{1,37}$ = 3.03, *P* = 0.09) or treatment – year interaction effect ($F_{4,148}$ = 0.78, *P* = 0.54). Bonferroni-adjusted pairwise comparisons revealed the same between-year differences already identified from our previous paired t-tests, i.e., 1994/95 significantly different from 1995/96 (*P* = 0.021) and 1997/98 (*P* = 0.014), but all other year comparisons similar (*P* >0.39).

The presence-absence indices of possum abundance followed the same trends as the standing-crop indices of possum density in all three buffers, and strengthened the findings of our surveys of population recovery. With the exception of the 1-km buffer, the confidence intervals around our presence-absence indices were consistently wider than for the corresponding standing-crop indices. However, this was not unexpected given the binomial nature (i.e., less detailed) of presence-absence data.

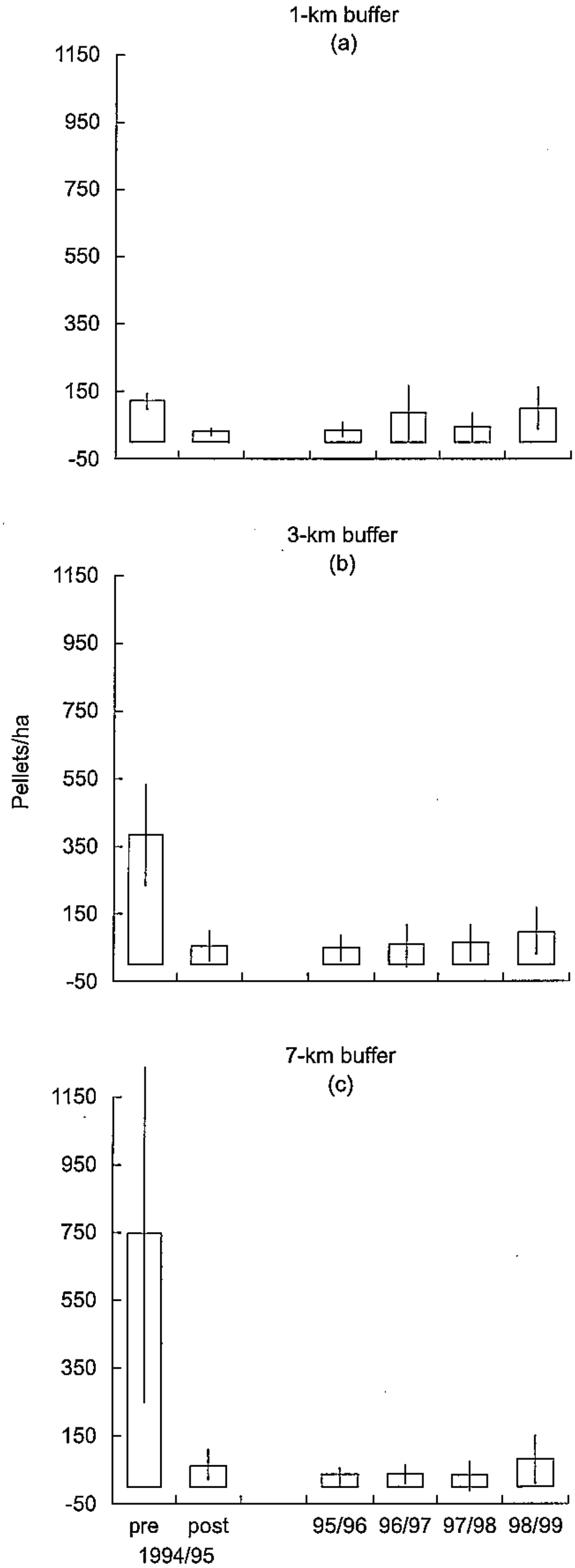

Fig. 2 Mean number of possum faecal pellets per hectare (±95% confidence intervals) between 1994/95 (pre- and post-control) and 1998/99 for the (a) 1-km, (b) 3-km, and (c) 7-km buffers.

Spatial patterns: Despite relatively similar pellet densities on lines 250 m and 750 m from the forest-pasture margin within the 1-km buffer before and immediately after control, possum numbers appear to have recovered considerably faster near the rear of this buffer (i.e., on the 750-m line, Fig. 3). Although faecal-pellet densities on the two lines were similar in 1997/98, our 1998/99 results were consistent with those recorded in 1995/96 and 1996/97, and contrast with those recorded in 1997/98. The reason for the 1997/98 anomaly is unclear. While possum pellet density on the 750-m line in 1998/99 (121.2 pellets/ha) was similar to that before control (129.9 pellets/ha), the corresponding density on the 250-m line (70.2 pellets/ha) is only about 65% of that before control (105.7 pellets/ha).

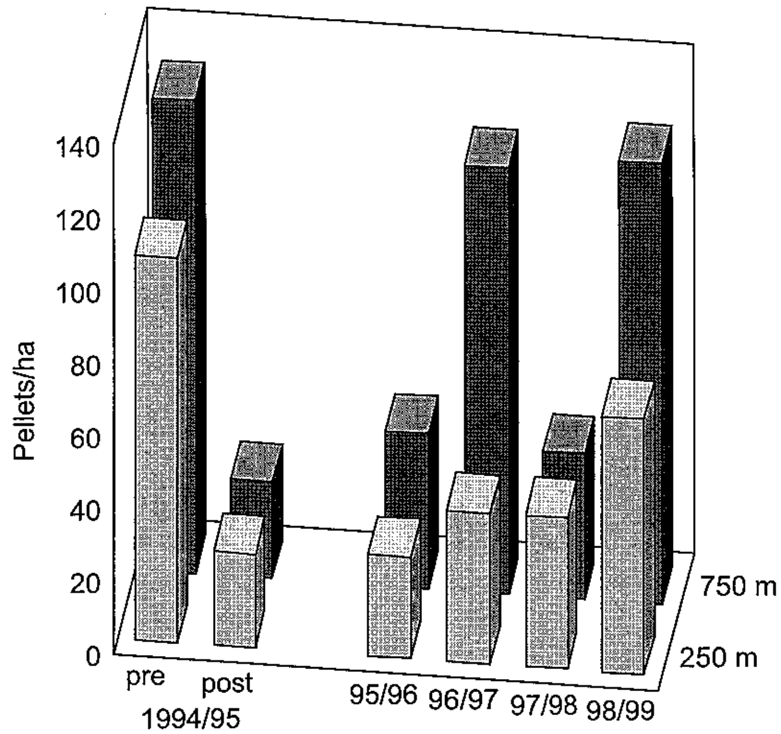

Fig. 3 Mean numbers of possum faecal pellets per hectare between 1994/95 (pre- and post-control) and 1998/99 for pellet lines 250 m and 750 m from the forest-pasture margin in the 1-km buffer.

Although the patterns are neither clear nor consistent, there is some evidence from the presence-absence indices for the 3- and 7-km blocks that indicates possum numbers are recovering faster where these buffers adjoin forest areas with uncontrolled possum populations (Fig. 4). The reason for the reversal of this pattern within the 3-km buffer in 1996/97 is unclear but the pellet data for this buffer is particularly erratic. Similarly, within the 7-km buffer, the relatively high pellet frequencies in the 1.5- and 2.5-km strata indicate "patchy" variation in possum population recovery throughout this area. Nevertheless, the overall pellet frequency of 1.4% (i.e., proportion of plots with possum faecal pellets) for pellet lines within 1 km of the farm margin compared with 5.1% for lines in the 5.5- and 6.5-km strata suggests that possum numbers near the forest-pasture margin remain substantially lower than in those parts of the buffer closer to uncontrolled possum populations.

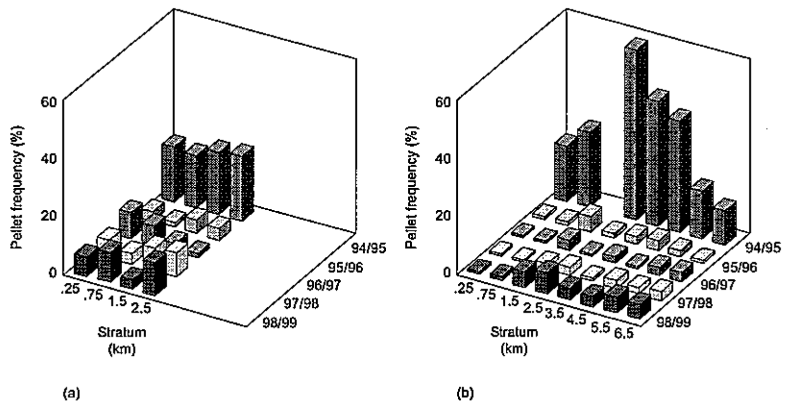

Fig. 4 Mean faecal-pellet frequency for possums in the (a) 3-km and (b) 7-km buffers with increasing distance (km) from the forest-pasture margin between 1994/95 and 1998/99.

While the number and coverage of pellet lines on which we collected standing-crop data for possums in the 3- and 7-km buffers were not as great as those for presence-absence data, the standing-crop results reflect the same general spatial trends in the recovery of the possum populations in these two areas.

Trends in trap-catch rate

The trends in possum trap-catch rates for the parts of the 3- and 7-km buffer that were repeatedly surveyed indicate a similar pattern of increasing density after control to that of the pellet counts, although the actual rates differ. For the six trap lines located in the 3-km buffer, the catch rate fell significantly ($F_{5,25}$ = 39.2, P <0.001) from 28.5% prior to aerial control to 1.2% following control (Fig. 5a) but this reduction was brief. The lines were not trapped in 1994/95, but the catch rate in 1995/96 was similar to levels prior to control (16.4%, P = 0.31; Bonferroni pair-wise comparisons). Subsequently, the trap-catch rate was significantly lower in 1996/97 (13.4%, P = 0.02) compared to the pre-control trap-catch rate, but similar again in 1997/98 (18.1%, P = 0.71) and in 1998/99 (20.8%, P = 1.0). The exponential rate of increase (r) of this population from our first post-control estimate (1994) to our final estimate (1999) was 0.59 (a finite rate of increase of 80% per year). However, the annual rate of increase for the 3 years from 1996 onward was much lower (r = 0.10), and was much closer to that observed from pellet counts.

For the 7-km buffer, trap-catch rates from the Waihaha headwaters were 18.6% in September 1993 and 24.7% in March 1994 (Nugent et al. 1997). In September 1994, immediately after the control operation, the lines trapped one year earlier were retrapped but no possums were caught. Later trapping in this area provided catch rates of 0.6% (August 1997), 5.5% (March 1998), 4.3% (August 1998), and 7.8% (March 1999). Both the August 1997 and August 1998 trapping data are believed to be biassed low, the former by adverse weather during trapping, and the latter by the effect of previous trapping on two occasions in the preceding 12 months. However, the March 1998 data are from new lines and were similar to the 8.3% catch rate recorded on the southernmost line of the RTC survey that spanned this area in 1998/99 (see below, Table 1). Averaged across these two separate surveys of the upper Waihaha, the 8% catch rate recorded in 1998/99 represents 43% of the September 1993 trap-catch rate, and 32% of the March 1994 trap-catch rate (both prior to control). Assuming that the true post-control trap-catch rate was greater than zero, the exponential rate of increase (r) for this part of the 7-km buffer is likely to have exceeded 0.57 for the 1994–1999 period. However, r for the March 1998–March 1999 period was only 0.34.

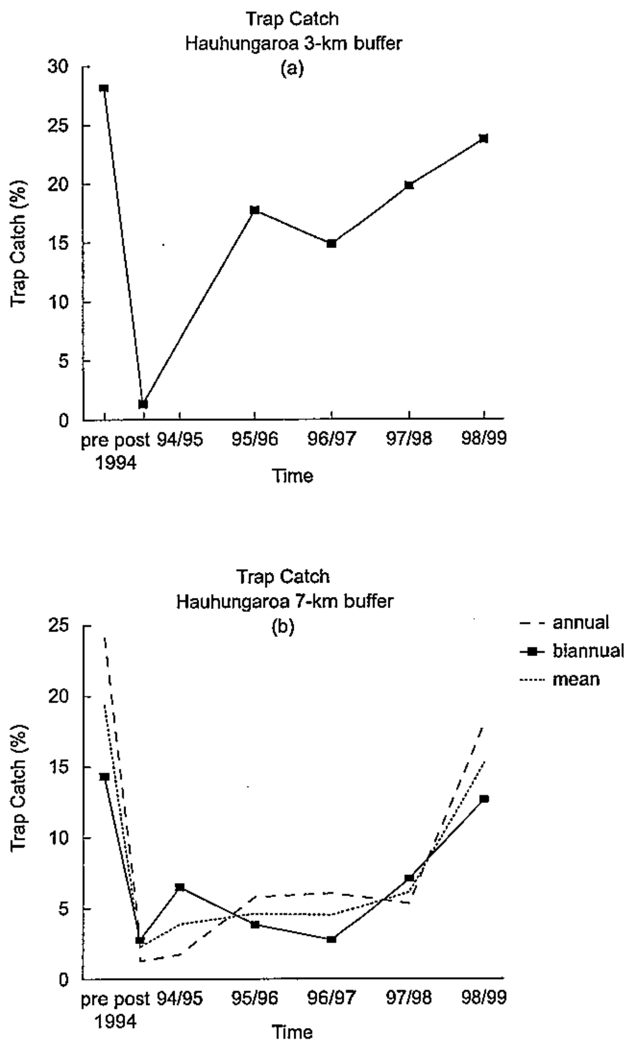

Fig. 5 The percent trap catch of possums caught on six trap lines located within the 3-km buffer (Fig. 5a; trapped before and after control in 1994/95, and 1996/97 to 1998/99), and on six lines on the margin of the 7-km buffer (Fig. 5b; three lines on margins under annual maintenance control, and three under biannual maintenance control).

The possum "catches" recorded on our cyanide lines across the 7-km buffer were heavily influenced by weather conditions (we were unable to avoid laying cyanide in showery weather), as well as by possum density, so these data have not been formally used as an index of possum density. However, we poisoned 90 possums on these lines in May prior to the control operation, but just two possums immediately after the control. The number of possums poisoned with cyanide in the following years increased to 33 in 1997/98, but then the catch declined to 17 possums in 1998/99. The average cyanide catch rate for the last 2 years represents 28% of that before control.

Along the forest-pasture margin of the 7-km buffer, trap-catch rates over the period of our study did not differ significantly between areas controlled annually and biannually ($F_{1,4} = 0.2$, $P = 0.68$, Fig. 5b), but did vary significantly over time ($F_{6,24} = 8.96$, $P < 0.0001$). Further investigation (using Bonferroni pair-wise comparisons) indicated that the trap-catch rate prior to control was greater than that recorded from 1994/95 to 1996/97 ($P < 0.007$), marginally greater than the trap-catch rate recorded in 1997/98 ($P = 0.07$), and not significantly different from that recorded in 1998/99 ($P = 1.0$). For the entire 1993/94-1998/99 period, the effective exponential rate of increase of the population following control was 0.41, and was not significantly different from that recorded within the 3-km buffer (0.59, $P = 0.64$)

The survey of possums caught across the length and breadth of the 7-km buffer in 1998/99 produced a density estimate of 6.3% (Table 1). This was not significantly different from the 5% RTC now generally targeted for the control of Tb possum populations. Although no comparable pre-control RTC data are available from the 7-km buffer, when compared with the recent (1997/98) RTC survey in the 3-km buffer and the adjacent uncontrolled area, this result indicates the population in the 7-km buffer was still low 5 years after the control. The results of our monitoring also appear to reflect the low population densities indicated by the most recent faecal-pellet count result from the 7-km buffer. The RTC for individual transects varied from 0.0% on transects 2 and 3 in the northern part of the buffer to 18.1% on transect 6 in the middle of the buffer (Table 1). Weak statistical evidence indicates RTC's were higher on the five southernmost transects than on the five northernmost transects ($F_{1,6} = 6.70$, $P = 0.041$). Individual transects were monitored by different trappers, which may partly explain the north-south pattern recorded.

Table 1 Results from the 1998/99 Residual trap-catch survey of the 7-km buffer by transect and stratum. Trap-catch transects are arranged in ascending order from north to south, and strata (which include one trap line from each transect) are arranged in order of increasing distance (km) from the eastern (i.e., forest-pasture) margin of the buffer.

Transect No.	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
Mean RTC (%)	6.2	0.0	0.0	4.4	1.4	18.1	7.7	8.2	7.2	8.3

Strata	**0–1**	**1–2**	**2–3**	**3–4**	**4–5**	**5–6**	**6–7**
Mean RTC (%)	4.5	4.8	7.2	6.1	7.2	7.5	6.4
± 95% CI	3.9	4.6	4.8	3.3	6.1	7.9	6.5

The RTC results for individual 1-km-wide forest strata within the 7-km buffer varied from 4.5% for the stratum immediately adjacent to the forest-pasture margin, to 7.5% at a distance of 6–7 km from the pasture margin and near the back of the buffer (Table 1). However, trap-catch rates varied greatly within strata (as evidenced by the wide confidence intervals about the strata means), and there was no statistical evidence of a consistent and significant trend of increasing possum density with increasing distance from the forest-pasture margin ($F_{6,36}=0.44$, $P = 0.84$). That is to say, the RTC data do not provide evidence of a faster build-up in possum numbers within 1–2 km of the rear margin of the buffer arising from the combined effects of 4 years of possum immigration from the adjacent uncontrolled population and breeding within the buffer. These results contrast with the apparent trend of more rapidly increasing possum numbers near the rear of the 7-km buffer indicated by presence-absence pellet data (see Fig. 4b).

Trends in deer faecal-pellet surveys

The faecal-pellet indices of deer density (PGDs) in 1998/99 have remained unchanged in the 3-km buffer compared with previous years, but have trended upwards in the 1- and 7-km buffers (Fig. 6). As with our earlier PGD estimates, the 95% confidence intervals around the 1998/99 indices of deer density were wide, particularly in the 3- and 7-km buffers. Although there were no differences in deer pellet indices between the three buffers prior to the control operation ($F_{2,38} = 0.72$, $P>0.05$), the most recent pellet indices (Fig. 6) were significantly different ($F_{2,38} = 7.91$, $P <0.001$). Pairwise LSD comparisons showed that pellet indices differed significantly only between the 3- and 7-km buffers.

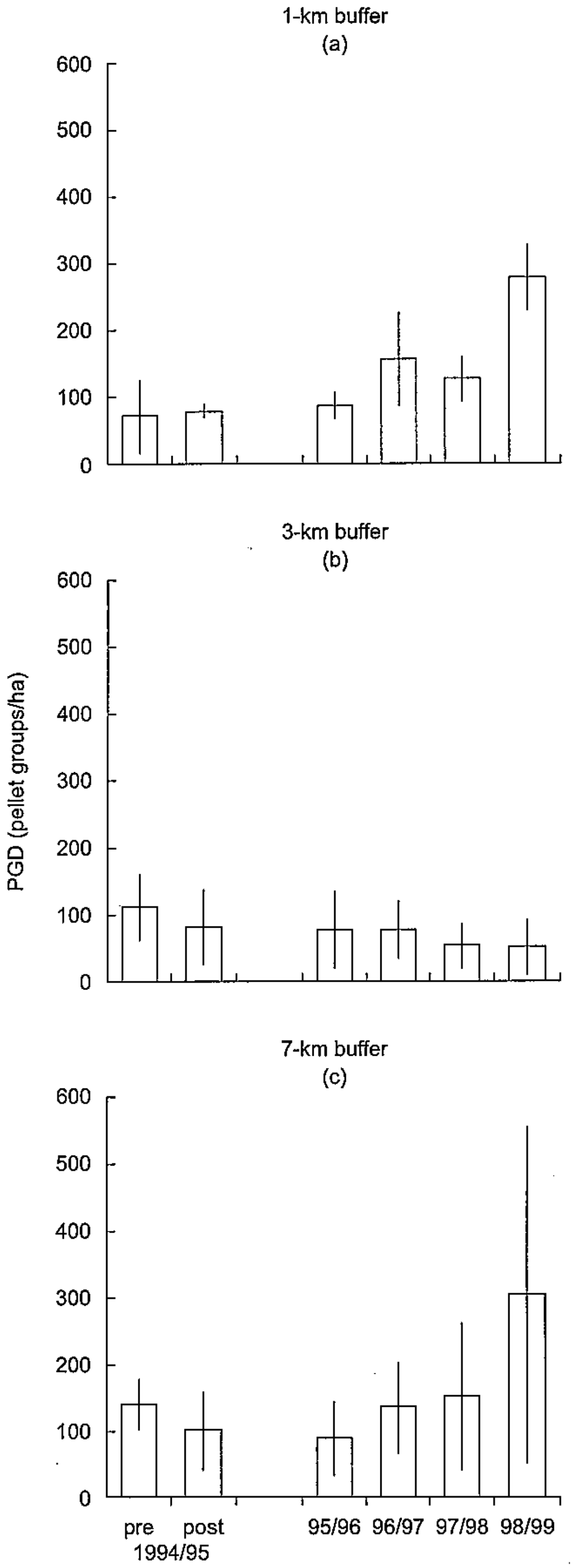

Fig. 6 Mean faecal-pellet group densities (PGDs) per hectare (±95% confidence intervals) for red deer between 1994/95 and 1998/99 for the (a) 1-km, (b) 3-km, and (c) 7-km buffers.

The presence-absence indices of deer abundance followed the same general trends as the PGD indices in all three buffers. The confidence intervals around our presence-absence indices (for both 114- and 250-cm plot radii) were similar to their corresponding PGD indices.

6.2 Tb prevalence in wild animals and Tb incidence in livestock

Possums

7–km buffer: None of 85 possums taken in 1998/99 from the forest-pasture margin of the 7-km buffer, 17 possums poisoned on cyanide lines across the same buffer, 8 possums trapped on the pasture edge of the Lakeside Reserves along the Waihaha River, or 112 possums trapped during the RTC survey conducted in 1998/99 had macroscopic lesions indicative of Tb. In fact, no Tb lesions were detected in any of the 408 possums taken in this study from the 7-km buffer after the control operation, compared with two of 205 (1.0%) possums taken immediately prior to control in the same buffer (and poisoned on successive cyanide baits 3.5 km into the buffer).

In addition, 440 further possums were necropsied during unrelated studies in the Waihaha Catchment within the 7-km buffer after the control operation. These were sampled around deer kill sites and, excluding possums known to have been within 1 km of uncontrolled possum populations, only one was infected. That possum was in its third year, so unless it was a spring birth, it would have been born (and possibly infected) prior to the control operation.

In contrast to the obviously low prevalence of Tb in possums in the 7-km buffer, nine of 202 (4.5%) possums necropsied from the central uncontrolled area in 1997/98 and 1998/99 have been confirmed as tuberculous. This figure underestimates the true prevalence in the possum population in this area, as many tissue samples were pooled prior to culture. Additional surveys in August 1999, after our study had ended, identified five (13%) of 39 possums killed as part of a demographic study in this central area had lesions indicative of Tb.

3–km buffer: Two possums of 125 taken from the 3-km buffer in 1998/99 had small caseous lesions indicative of Tb, and culture results confirmed the presence of *Mycobacterium bovis*. Furthermore, three other infected possums were taken from this buffer: two in 1995/96 and one in 1997/98. Of these five possums, two came from traps located about 150 m apart on a trap line originating on the forest-pasture margin, one from a trap line about 1 km from pasture, and two from trap lines deep (c. 3 km) into the forest. The overall prevalence for 414 possums sampled since 1995/96 in the 3-km buffer was 1.2%.

Of the non-target species trapped incidentally in 1998/99, only one feral cat taken from the Lakeside Reserve trap lines was necropsied and it appeared to be free of Tb. Non-target animals necropsied from our trap lines throughout the study included 23 ferrets and 3 feral cats, and all were free of lesions indicative of Tb.

Deer

In all, 261 deer were necropsied during the two surveys before control and four surveys after control. Field diagnoses were verified by culture for 245 of them: 17% had lesions indicative of Tb, and a further 17% had some equivocal indications of infection (Appendix 11.1). Only three (7%) of the 42 deer with typical lesions were culture negative, giving us a high level of confidence in our field diagnoses of gross lesions. In contrast, the presence of equivocal lesions or of lesions too small to allow confident diagnoses (especially tonsillar crypt lesions) appeared to provide only a slightly better indication of Tb prevalence than the absence of any macroscopic sign of Tb at all: 12% of those with equivocal lesions were culture positive, compared with 8% of those without lesions and 9% of the pooled subset of deer with either equivocal or no lesions. Overall, however, almost one-third of infected deer were free from either macroscopic lesions (23%) or had equivocal lesions (8%).

The overall prevalence of Tb in deer was 25% across all six surveys combined, but it varied with age class, location, and year of survey. Prevalence of Tb increased with age (Table 2), with only 7% (5/72) of fawns infected compared with 27% (21/79) of subadults, and 35% (38/110) of adults (χ^2_2= 16.0, $P < 0.001$; see below). Prevalence of Tb was consistently higher in the central uncontrolled area, both before and after control (χ^2_1= 8.6 , $P = 0.03$) and declined through time, in both the controlled and uncontrolled areas (χ^2_1= 4.6 , $P = 0.003$). Although the decline in the controlled areas appears to have been more marked and more consistent (Table 2), the lack of a statistically significant interaction between location and year of survey ($\chi^2_1 = 0.9$, $P = 0.33$) means we cannot yet confidently attribute the decline in overall Tb prevalence in deer in the controlled areas to the possum control operation. However, the following evidence provides strong support for that hypothesis.

Only 8% (7/86) of the deer born since the 1994/95 poison operation and shot within the 1994/95 or 1995/96 control areas had become infected. The location of the kill sites for these deer (examined in relation to the poisoned bait swaths flown by the helicopter and recorded by a Geographic Positioning System) revealed that all seven were either within 2.5 km of the control area boundary or near a greater than usual gap in bait coverage (Appendix 11.2) The four cases of definite new (i.e., since control) infection that were shot furthest away from the western boundary of the controlled area were all clustered within a relatively small area (<1000 ha) in or close to the Waihaha River headwaters. As well as streamside gaps in bait coverage deliberately left unbaited to avoid stream contamination, this area is also generally characterised by unusually variable swath widths (up to 200 m apart).

Combining the data for all of our surveys since control, and grouping deer-kill sites according to the distance to the boundary with the main uncontrolled area, there is a significant decline (χ^2_4=11.1, $P = 0.01$) in the prevalence of Tb in cohorts born since 1994/95 with increasing distance from the major uncontrolled areas (Fig.7). Excluding deer numbers A60 and 115 because they were both shot in or near much smaller uncontrolled areas resulting from gaps in poison bait coverage, there have been no definite cases of new infection recorded in any of the 39 deer born since 1994/95 and shot >2.5 km from an uncontrolled area. In contrast, 26% (15/57) of the deer born since 1994/95 and shot in the uncontrolled area have become infected (Table 3).

Table 2. Overall summary of necropsy surveys of Tb prevalence in red deer from the Hauhungaroa Range. The 1993/94 data include deer from a larger area than that surveyed in subsequent years. The main focus of the 1995/96 and 1996/97 surveys was the 7-km buffer, hence sample sizes for the uncontrolled area are low or zero.

		Percentage of deer infected (samples sizes in brackets)							
		Before control	Uncontrolled area - after control			Controlled area - after control			
Age-sex class		93/94	95/96	97/98	98/99	95/96	96/97	97/98	98/99
Fawn	Male	0 (6)	0 (1)	- (0)	0 (10)	0 (3)	20 (5)	0 (9)	12 (8)
	Female	0 (4)	- (0)	22 (9)	0 (3)	0 (2)	0 (2)	25 (4)	0 (6)
	Both sexes	0 (10)	0 (1)	22 (9)	0 (13)	0 (5)	14 (7)	8 (13)	7 (14)
Subadult	Male	41 (17)	66 (3)	0 (4)	75 (8)	0 (4)	24 (12)	0 (4)	0 (5)
	Female	33 (6)	0 (2)	0 (2)	33 (3)	- (0)	0 (2)	0 (4)	0 (3)
	Both sexes	39 (23)	40 (5)	0 (6)	64(11)	0 (4)	21 (14)	0 (8)	0 (8)
Adult	Male	46 (13)	- (0)	0 (5)	67 (6)	60 (5)	66 (3)	14 (7)	0 (3)
	Female	47 (19)	50 (2)	25 (8)	40 (10)	100 (2)	29 (7)	15 (13)	14 (7)
	Both sexes	47 (32)	50 (2)	15(13)	50 (16)	71 (7)	40 (10)	15 (20)	10 (10)
All	Male	36 (36)	50 (4)	0 (9)	42 (24)	25 (12)	30 (20)	5 (20)	6 (16)
	Female	38 (29)	25 (4)	21 (19)	31 (16)	50 (4)	18 (11)	14 (21)	6 (16)
	Both sexes	37 (65)	37 (8)	14 (28)	37 (40)	31 (16)	26 (31)	10 (41)	6 (32)

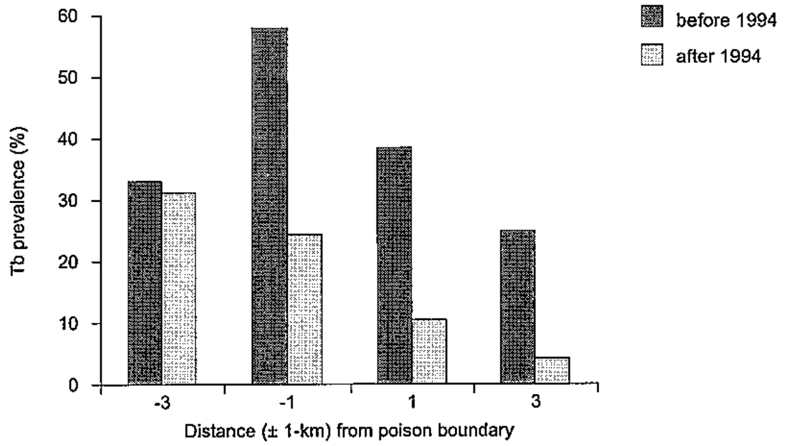

Fig. 7 Prevalence of Tb in deer born before and after the possum control, in relation to distance from poison area boundaries. The –3 and +3 distance classes include deer shot inside and outside the unpoisoned area respectively.

For those deer born before the poison operation and shot since 1994/95, overall Tb prevalence did not differ significantly between the uncontrolled and controlled areas ($\chi^2_1 = 0.5$, $P = 0.48$; Table 3). However, the prevalence in the pre-1994/95 cohort shot within the controlled areas in 1997/98 or 1998/99 (21%, N=14) was the lowest recorded for any group of adults during these surveys, but sample sizes were too small to provide sufficient statistical power to confirm that Tb prevalence in this cohort was declining.

Table 3. Percent Tb prevalence (plus sample sizes) of deer born before and after the control operations and shot since 1994/95, for the controlled and uncontrolled areas.

	Born before control	Born after control	Total
Control areas	33 (33)	7 (85)	14 (118)
Uncontrolled areas	43 (21)	26 (57)	30 (78)
Totals	37 (54)	15(142)	

The prevalence of Tb in deer increased with age in all our surveys. The relationship between age class and prevalence was examined further by grouping all deer shot in 1993/94 or in the uncontrolled areas in subsequent surveys into 6-month age-classes. The youngest infected deer in this subset was 11 months old, with no infection observed in any of 21 younger deer. For both sexes combined, prevalence increased rapidly between the 6–11 month and 12–17 month age-classes, but only gradually after that (Fig.8). This pattern appeared to be more marked for male deer than for females: 45% (13/29) of subadult males were infected compared with 46% (13/28) of older males, suggesting that Tb prevalence in males did not increase after 24 months of age. Age-specific prevalence rates for females were generally lower than for males, with only 25% (3/12) of subadult females infected compared with 42% (16/38) of older females. The equivalence in the overall infection rates of males and females (Table 2, $\chi^2_1 = 0.04$, $P = 0.88$) is probably an artefact of the younger mean age of males in these samples (typical of shot samples and most likely of the underlying population structure).

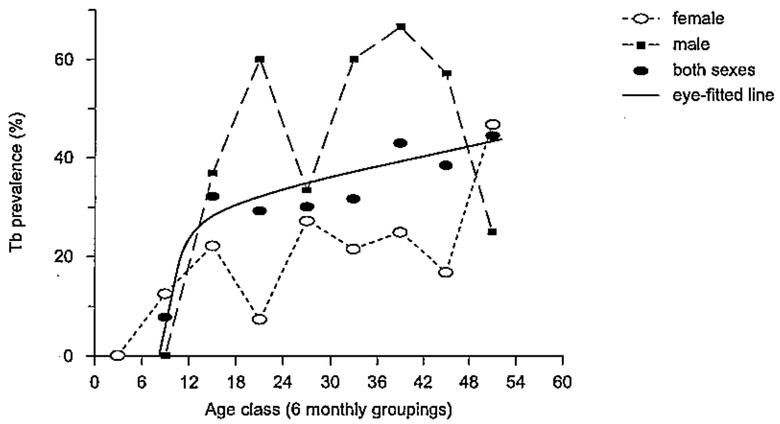

Fig. 8 Prevalence of Tb in deer shot from "unpoisoned" areas, by 6 monthly age-class, by sex (N = 142).

Pigs

Our sample sizes of pigs ranged from one in 1995/96 to 19 in 1996/97 (Table 4). All pigs shot since 1993/94 were killed within the 7-km buffer, with the variation in the numbers killed partly reflecting the varying amount of ground-based hunting undertaken each year. However, the variation in hunting effort was not sufficient to explain the much higher hunting success rate in 1996/97, which indicated that pig numbers were much higher than usual in that year (2 years after the possum control). All 19 pigs shot in 1996/97 were less than 2.2 years old and, therefore, had been born after the control. This apparent upsurge in numbers was brief as only three pigs were shot the following year (two of which were not necropsied) and only four were shot in 1998/99, despite increased ground- and helicopter-based hunting effort in those 2 years.

Table 4: Numbers of pigs necropsied each year and their Tb status.

Year	93/94	95/96	96/97	97/98	98/99	Total
No. necropsied	5	1	19	1	4	30
No. with indicative lesions	4	1	12	1	3	21
No. with equivocal lesions	0	0	1	0	0	1
% culture positive	80	100	63	100	75	70

The prevalence of Tb in the pigs necropsied was very high initially with 80% (4/5) of those shot in 1993/94 infected, and it stayed high despite the lower Tb prevalence in possums and deer in the 7-km buffer. None of the pigs judged to be free of macroscopic lesions was infected.

All (5/5) of the pigs aged 2 or more years were infected, as were 50% (5/10) of the1-year-old pigs, and 70% (7/10) of the pigs <1 year old. Three quarters (3/4) of pigs <6 months old were infected. All but six of the pigs sampled were shot >2 km east of the Hauhungaroa Range crest, with most of them obtained in the upper Waihaha Catchment.

Cattle

Between 15 706 and 25 727 cattle were tested for Tb each year on farms immediately adjacent to the 1-, 3-, and 7-km buffers. The incidence of cattle with Tb (i.e., the number of lesioned reactors and lesioned culls expressed as a percentage of the total number of cattle tested and lesioned culls examined) varied between areas and was generally highest in herds adjacent to the 3-km buffer, intermediate in herds adjacent to the 1-km buffer, and lowest in herds adjacent to the 7-km buffer (Table 5). For all buffers combined, the incidence of Tb in cattle varied between 0.92% and 1.20% in the 3 years prior to the control operation, fell to 0.67% in the year of the control operation, and then declined consistently each year thereafter to a low of 0.14% in 1997/98 (Table 5).

Table 5. The percentage of cattle with macroscopic Tb lesions (lesioned reactors and lesioned culls) in herds immediately adjacent to the 1-, 3-, and 7-km buffers (data from J. Adams, AgriQuality, Taumarunui, pers. comm.). Data from herds adjacent to the 7-km buffer are split into areas subjected to annual and biannual maintenance control of possums.

Year	Cattle tested	1-km buffer	3-km buffer	7-km buffer (annual control)	7-km buffer (biannual control)	Total for all buffers
90/91	15 706	0.33	1.25	0.19	0.78	0.92
91/92	18 922	0.26	2.14	0.38	0.38	1.20
92/93	23 276	0.93	1.36	0.54	0.66	1.03
93/94	19 665	0.87	0.88	0.17	0.29	0.67
94/95	25 727	0.42	0.53	0.52	0.18	0.43
95/96	20 949	0.20	0.47	0.06	0.15	0.29
96/97	18 212	0.0	0.25	0.18	0.15	0.19
97/98	20 307	0.05	0.20	0.07	0.11	0.14

The temporal patterns of the incidence of Tb herds adjacent to each buffer differ markedly from 1990/91 onwards (Fig. 9a–d). For herds adjacent to the 1-km buffer, there is strong evidence that the incidence of Tb in cattle varies with year, but the relationship differs between the data before (increasing incidence) and after control (decreasing incidence; $\chi^2_1 = 15.0$, $P < 0.001$). For herds adjacent to the 3-km buffer, the incidence of Tb in cattle also varies with year, and before and after control ($\chi^2_1 = 5.29$, $P = 0.021$), decreasing at a slower rate following control and as Tb-herd incidence values approach zero. For herds adjacent to the 7-km buffer under annual maintenance control, there is strong evidence that the incidence of Tb in cattle varies with year, with no clear trend prior to the control operation but a declining incidence thereafter ($\chi^2_1 = 8.05$, $P = 0.005$). For herds adjacent to the 7-km buffer under biannual maintenance control, there is evidence of a steady decline in Tb incidence over time, but no evidence of any effect of the 1994 control operation during the period monitored ($\chi^2_1 = 0.001$, $P = 0.972$). A comparison of data from herds adjacent to the areas of the 7-km buffer under annual and biannual maintenance control indicates that the incidence of Tb in cattle decreases more rapidly from 1994/95 onwards in the area under annual maintenance control, compared with that under biannual maintenance control ($\chi^2_1 = 5.47$, $P = 0.019$).

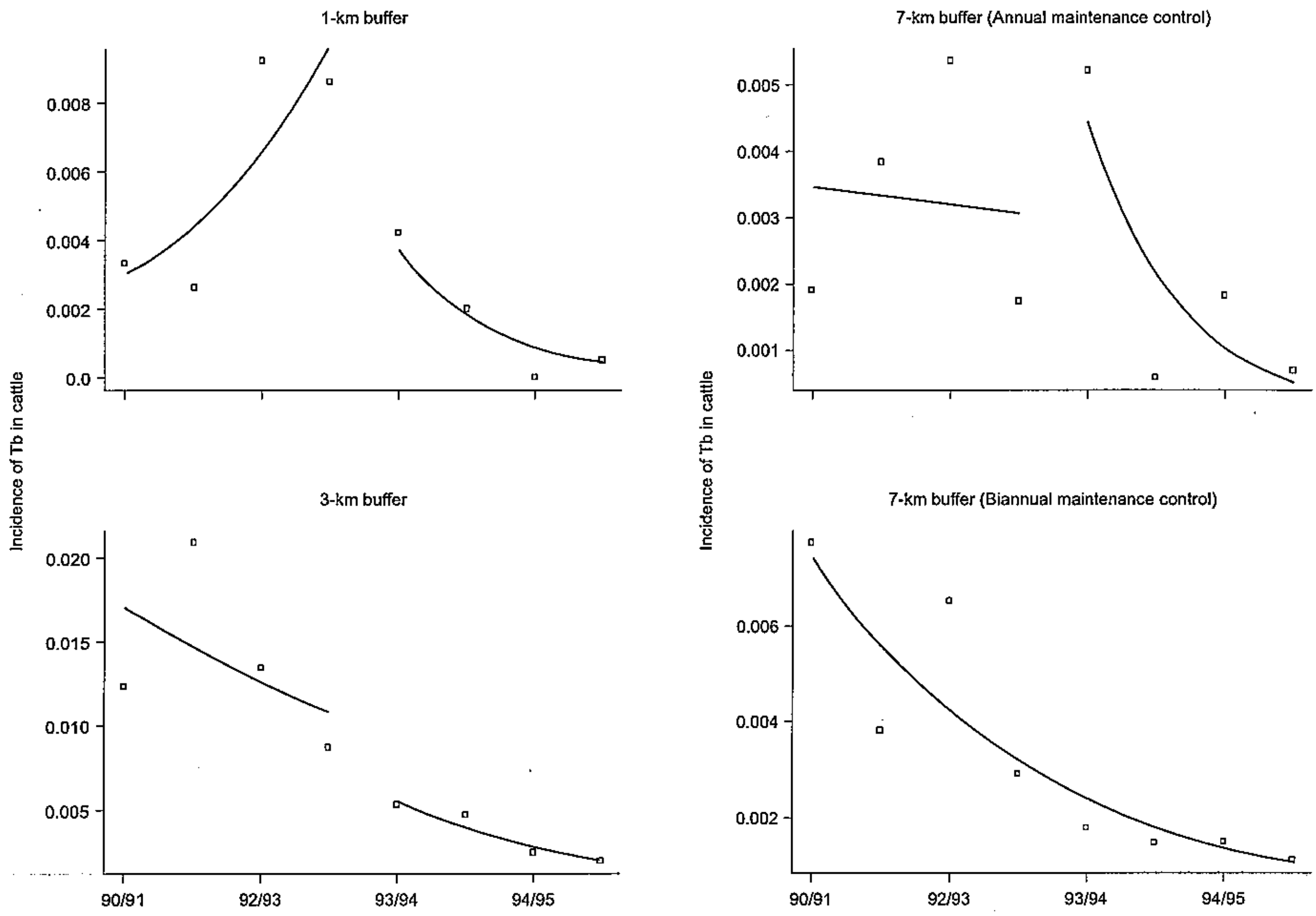

Fig. 9 The incidence of reactor and cull cattle with Tb lesions from herds adjacent to the 1-, 3-, and 7-km buffers. The equations for the fitted curves representing the probability of cattle having Tb are as follows:

1-km buffer	90/91 – 93/94	1/(1+exp(41.311– 0.394Y))
	94/95 – 97/98	1/(1+exp(– 61.272 + 0.711Y))
3-km buffer	90/91 – 93/94	1/(1+exp(–9.827 + 0.154Y))
	94/95 – 97/98	1/(1+exp(–26.675 + 0.339Y))
7-km buffer (annual control)	90/91 – 93/94	1/(1+exp(2.037 + 0.040Y))
	94/95 – 97/98	1/(1+exp(–66.269 + 0.719Y))
7-km buffer (biannual control)	90/91 – 97/98	1/(1+exp(–20.53 + 0.282Y))

7. Conclusions

7.1 Recovery of possum and deer populations

Possums

Faecal-pellet estimates: Although indices of possum density prior to control appeared to differ markedly between the three buffers, these differences were not significant because of the wide between-line variation within each buffer. Following the control operation, possum faecal-pellet densities were broadly similar in all three buffers (20.6, 49.7, and 27.0 pellets/ha in the 1-, 3-, and 7-km buffers, respectively), and our estimates confirmed that the population reduction in each of the buffers exceeded the AHB's target at that time of a 75% kill (P. Livingstone, AHB, pers. comm.). Furthermore, the lower pellet indices reported for 1995/96 (compared with those from 1994/95) in the 3- and 7-km buffers indicated that the reduction in possum numbers in these buffers may have been greater than originally reported (Fraser et al. 1995).

By 1998/99, 4 years after possum control, the relatively rapid recovery in our index of possum numbers in the 1-km buffer indicated that buffers of this size are relatively ineffective due, we believe, to the immigration of possums from adjacent uncontrolled areas. Ground-based maintenance control on the nearby farmland and along the forest-pasture margin adjacent to the 1-km buffer was carried out annually, and largely accounts for the lower pellet indices recorded closest to the forest-pasture margin within this buffer compared with pellet indices recorded near the rear of the buffer. The 3- and 7-km buffers both appear to be successful (in terms of the AHB's possum control goals of maintaining populations at <40% of carrying capacity), and assuming roughly similar levels of ground control adjacent to all three buffers, it appears that these wider buffers provide greater long-term "relief" than buffers 1 km wide.

The spatial patterns of possum population recovery evident in the three buffers indicate that immigration is important in determining the overall rate of recovery. The proximity of adjoining forest areas where possums have not been controlled, the density of possums within them, and the size of these areas in relation to the size of the controlled buffer influence the rate of recovery of controlled possum populations. For example, immature possums, particularly males, have a tendency to disperse, and immature and adult possums expand their home ranges into nearby areas where densities are lower (Green & Coleman 1984; Efford et al. 1998).

Trap-catch rates: Three trap-based indices of possum density were obtained from the 7-km buffer. In the first of these, trap-catch rates on the forest-pasture margin under either annual or biannual maintenance control remained close to the AHB's 5% "trigger level" from 1994/95 to 1996/97, but then climbed steeply in the final 2 years of our study. We believe that the population was held initially at this level by ongoing maintenance control using 1080 pellets and traps along the forest-pasture margin and on adjacent farmland, but that in the final 2 years of the study a switch to "Feratox" (cyanide) pellets was accompanied by lower kills and increased trap-catch (I. Roberts, EPRO, pers. comm.) despite a similar control effort. Reduced kills using Feratox compared with kills using hand-laid 1080 pellets and traps have been recorded elsewhere (B. Warburton, Landcare Research, pers. comm.), and indicate the need for further evaluation of this bait if it is to be used for Tb maintenance control. The rate of recovery (increase) of the possum population indicated by our trap-catch rates from 1994/95 to 1998/99 is high when compared with published estimates of the intrinsic rate of increase (r_m) of possum populations (i.e., 0.22 – 0.25; Hickling & Pekelharing 1989). The greater recovery of the possum population on the forest-pasture margin of the 7-km buffer appears to reflect the attraction of such ecotones to possums. Typically, these areas are botanically diverse, contain a high proportion of palatable plant species, are a feeding zone preferred by possums, and often contain highest densities of them (Coleman et al. 1980). Further, possums generally disperse along and build up most rapidly on forest-pasture margins during their recolonisation of an area following control (Green & Coleman 1984).

The trap-catch results from the forest-pasture margin of the 7-km buffer provided no evidence of any benefit in terms of reduced possum numbers from additional (biannual) ground control that would justify the higher cost of the extra control. However, this is counterintuitive: control along the forest-pasture margin twice a year should hold possum populations at lower levels than annual control. Our results suggest the possibility that depleted possum populations on forest-pasture margins attract immigrants from neighbouring low-density populations, but that the numbers immigrating are independent of whether the pasture-margin is controlled annually or biannually. Equally, this may have been due to subtle and undetected differences in habitat between the two maintenance control areas or to insufficient sampling.

The catch rate of possums in the forest in the southern end of the 7-km buffer was indicated by our cyanide baiting. These data, though less robust and more variable than trap-catch data, indicated a more rapid recovery to pre-control levels than did trap catch data from the forest margin of the 7-km buffer, with cyanide catches averaging 28% of pre-control levels in our final samples in 1997/98 and 1998/99. Further cyanide baiting undertaken within the Waihaha intensive research area deep within the buffer reflects similar population recovery. Our interpretation of these data is that the forest in the southern part of the buffer is generally of higher stature and more diverse and palatable than forest in the northern end of the buffer and appears to be able to support more possums.

The wide variation and low pellet densities in the 7-km buffer were consistent with in the results of our third index of possum density (RTC survey) conducted in the same buffer — the 1998/99 RTC survey. Data from this survey indicated a population close to the current AHB "trigger" level for the control of Tb possum populations 4½ years after the possums were controlled, and probably above it in the southern part of the area. Our inference arising from this result is that the frequency of "initial" control over large buffers should be about 5 years. This estimate roughly reflects the current frequency of repeat "initial" controls of many tuberculous possum populations. In contrast with the pellet data from this buffer, the RTC estimate provided no evidence of higher numbers of possums close to uncontrolled possum populations at the rear of the buffer, indicating that population recovery following poisoning over the bulk of large areas of forest must follow largely from breeding by surviving animals rather than from immigration. We have no plausible explanation for the different pattern of recovery of possum density revealed by our faecal pellet survey, except to say that the pellet data in the 3-km buffer was particularly erratic and may not reflect spatial possum population trends in the buffer as well as our RTC estimates.

Residual trap-catch estimates of possum numbers in the 3–km buffer (monitored by the MWRC but not as part of our study) are less easily reconciled with pellet data in that buffer. Trapping results from 4–6 lines each in the 1st (10.6±7.7%(CI)), 2nd (10.3±3.0%), and 3rd (9.4±5.6%) 1-km strata within this buffer indicated that the possum population in 1998/99 was evenly distributed across the buffer. Trap lines set in uncontrolled forest immediately behind the 3-km buffer and close to the centre of the Hauhungaroa Range (including one line apparently mislocated in the control zone) gave an average catch of 20.5±11.2%, but did not differ significantly from the catch in strata closer to the forest-pasture margin.

Even so, the RTC results obtained from the uncontrolled forest presumably reflected a possum population close to carrying capacity (K) as no recent management of possums had been undertaken there. If this assumption is correct, the RTC rate recorded within the 3-km buffer in 1998 suggests recovery of the possum population to about 50% of K within 4½ years.

Our trap-catch data from the 3-km buffer also showed some agreement with the RTC estimate from the same area, and again contrasted with faecal-pellet results. In addition, the rate of increase (r) determined from our trap lines was exceptionally high compared with published data (Hickling & Pekelharing 1989), and appeared to reflect a depleted possum population in prime habitat rapidly returning to K through increased breeding (i.e., adult females producing two young per year or breeding at an earlier age). Similar increases in breeding rates following population declines have been recorded elsewhere (Coleman unpubl. data).

In March 1999, the Department of Conservation established and ran five further lines of 20 traps for 3 fine nights in the Rātā-nu-nui Ecological Area within the 3-km buffer and obtained a 29% trap catch (K. Chalmers, DOC, pers. comm.). Although the form of these data does not allow rigorous comparison with data collected over the broader buffer area by MWRC or by ourselves, it does indicate a higher population in one part of this buffer than any other measured since the control operation in 1994. Along with our own high trap- catch rates in part of this buffer, these results appear to reflect the high conservation values (and hence forage) and consequent increased conservation status given to this area of forest. Rātā-nu-nui Ecological Area is a forest dominated by numerous emergent northern rātā (K. Broome, DOC, pers. comm.), a species highly favoured by possums.

All three trap-catch estimates in the 3-km buffer contrasted with estimates from the faecal-pellet results obtained from the same area that suggested a recovery in the possum population of only 25% in this time. The reasons for this were unclear, but results were undoubtedly influenced by variable rates of faecal pellet decay and the location of the annual trap lines. What was indisputable, however, was that by 1998/99, possum numbers in this buffer substantially exceeded the trigger levels set by the AHB for the further control of infected possum populations.

Our study across the Hauhungaroa Range is being partially replicated by Landcare Research near Franz Josef, central Westland (Montague 1996). There, buffers of 1- and 3-km have been established adjacent to forest-pasture margins, and the rate at which possums recolonise them is being determined by annual RTC surveys. At Franz Josef, the most recent field data, obtained 34 months after initial control, indicated that there had been no significant increase either in possum numbers or in the rates of increase in possum numbers within or between either buffer. Furthermore, there was no evidence of any build up in possum numbers in the rear of either buffer via migration from the uncontrolled forest hinterland. Results from Franz Josef therefore contrast with the differential rates of recovery recorded in the 1- and 3-km buffers about the Hauhungaroa Range, but this difference may be explained by the shorter duration of the study at Franz Josef. At this early stage of the Franz Josef work, the study does not indicate any benefit in reduced possum numbers when controlling possum populations over buffers greater than 1 km.

Deer

Faecal-pellet estimates: The faecal-pellet index (PGDs) results for deer in 1998/99 are equivocal, reflecting similar results in previous years. This is partly due to the sampling strategy, which was determined primarily by the possum population monitoring objectives: the deer monitoring was conducted using the same lines and plot centres as the possum monitoring. However, subsequent research has revealed that by using a similar number of plots, but spreading these over a greater number of survey lines improves the precision of PGD estimates significantly (Sweetapple & Fraser 1997; Fraser & Sweetapple 2000). Nevertheless, from the apparent increases in deer population densities that have occurred in both the 1- and 3-km buffers, it is clear that the control operation (which also targeted deer) had little long-lasting effect. The reductions in deer density achieved were small and the populations appear to have recovered completely. However, the result for the 3-km buffer is an exception. In this area, where the initial kill was similar to that for the 7-km buffer, the deer population appears to have remained similar to levels immediately following control or even declined further, and the reason for this is unclear. Our deer monitoring results highlight a need to tailor future control operation monitoring to each individual species. However, this would necessitate additional resources. One option for situations where both possums and deer need to be monitored is to adopt an optimal deer monitoring strategy and use this for both species. There are indications from recent work that such a strategy would not "compromise" the possum result (Sweetapple & Fraser 1997; Fraser & Sweetapple 2000).

7.2 Tb prevalence in wild animals and Tb incidence in livestock

Possums

Tuberculous possums were first officially recorded in or about the Hauhungaroa Range in 1980 (K. Patterson, MAF, unpubl. data), following breakdowns in the Tb status of local cattle herds unexplainable in terms of normal in-herd infection. A cross-sectional survey of the possum population around the perimeter of the Hauhungaroa Range in 1982/83 (Pfeiffer et al. 1995) identified low levels of infection (1.3%) in the 6083 possums necropsied, with tuberculous possums located in 27 foci (local discrete clusters of infection). Elsewhere in New Zealand, the point prevalence in possums (i.e., the proportion of the population infected at any one time) averages about 5% (Jackson 1995).

Our results, though based on a much reduced sampling of the forest-pasture margin and relatively greater sampling within the forest, showed levels of infection prior to control were similar to those identified by Pfeiffer et al. (1995). During our study and 14 years after the disease was first identified in possums in the area, Tb in possums in the 7-km buffer was identified from two individuals only and both were recovered prior to the aerial control in 1994/95. No tuberculous possums were taken from the forest-pasture margin of the 7-km buffer in any year of our study, suggesting that the control had reduced the prevalence of Tb on the edge of this buffer. However, infected possums have been taken from two sites within the buffer since 1966. Clearly our sample sizes are too small to infer the absence of Tb from large areas of the buffer and hence a successful Tb control operation — at prevalence levels of 1%, about 800 possums would need to be necropsied to provide statistically significant evidence of its presence or absence (based on sampling theory; Cannon & Roe 1982). By comparison, Tb appears to exist at higher levels in the 3-km buffer, as infected possums were taken from three trap lines there in three different years up to 1998/99. However, this apparent difference remains unproven, because our sample sizes were inadequate to test such differences statistically at such low prevalences. Nevertheless, clearly the poisoning of possums in the 3-km buffer did not eliminate the disease in possums. While the apparent differences in Tb prevalence between the two buffers is small, the greater number of infected possums taken in our surveys in the 3-km buffer may reflect the higher possum densities there from 1996/97 onwards.

Two foci of infection each involving at least two possums were located in our possum surveys, one 1 km into the 3-km buffer and the other 3½ km into the 7-km buffer, while several widely spaced infected possums were located on both sides of the Range during other studies in the area. The maintenance of Tb infection in possum populations at various densities has been documented elsewhere (Cooke et al. 1995). However, whether the infection at this site will continue to survive (and put livestock at risk) under the low possum densities achieved by the current control regime (and hence support current modelling theory underpinning the national Tb control programme) is unclear. Clearly, the need to investigate the continued survival of Tb in measured low-density possum populations is fundamental to ongoing national Tb strategies. The existing database and infected possum population within and surrounding the Hauhungaroa Range provides such an opportunity.

Deer

Prevalence of Tb in wild deer has declined steadily in the 7-km buffer since the 1994 control operation. Prevalence in deer has also declined in the uncontrolled centre of the range, but that decline has not been as consistent or as great as in the controlled areas. However, small sample sizes mean we cannot yet distinguish between these trends. However, we believe that the markedly lower rate of Tb infection observed in deer shot after control in the controlled area compared with those shot in the uncontrolled area, confirms that the overall decline in the 7-km buffer reflects reduced infection rates there, possibly coupled with a decline in prevalence in deer born before the control. Because deer densities have recovered to near pre-control levels in the 7-km buffer, our provisional inference is that the low infection rates for deer there reflects the reduction of possum populations. If so, then wild deer do not appear to be true maintenance hosts at the densities at which they now occur in the Hauhungaroa Range.
The extension and ongoing replication of this study will test that inference, but the following observations also provide strong circumstantial evidence that most of the Tb infection observed in deer within the Hauhungaroa Range is contracted from possums. Firstly, there is no evidence of any new infection within those parts of the area furthest away (>3 km) from the uncontrolled area: the only instances of Tb infection we recorded were either close to the control area boundary (i.e., within normal home-range size and dispersal distance for deer (Nugent 1994)), or close to gaps in the baited areas within the control area. Secondly, the relationship between Tb prevalence and age in the uncontrolled area indicates that most deer become infected between about 10 and 24 months of age, and that it is therefore unlikely this occurred through feeding, as there are no substantial age or sex differences in deer diet in this area (Nugent & Fraser unpubl. data). That leaves either deer-to-deer or possum-to-deer as the most likely transmission pathways. Given that the mother-fawn relationship provides the closest level of contact between deer, the apparent absence of infection in deer <11 months old, even though a high proportion of their mothers must have been infected, indicates that mother-to-fawn transmission is rare (Nugent & Lugton 1995; Lugton et al. 1998). Therefore we conclude that the observed patterns of Tb infection in deer in the Hauhungaroa Range derive from possum-to-deer transmission, with newly independent deer of both sexes being the most vulnerable to new infections.

The similarity in Tb prevalence between subadult and adult male deer suggests either that adult males acquire Tb at the rate at which infection disappears from the male population (through mortality or recovery), or that the rate of infection is lower for adult males than for subadult males. For female deer, the higher prevalence in adults, particularly those older than 4–5 years, indicates ongoing new infections of Tb in adult deer in areas inhabited by possums.

Our data indicates that few deer shot >3 km from the poisoned area became infected, and, by inference, that any infected deer shot in this area since 1994 was likely to have become infected before the control operation (1994/95). If so, the occurrence of Tb in 22% of the deer born before the control and shot in the poisoned area in 1997/98 and 1998/99 indicates that they have survived at least 4 years since becoming infected. Although sparse, these data indicate that Tb may not significantly increase deer mortality rates, and that it can persist in deer populations for at least 4 years, even where transmission rates are very low. The management implication of this premise is that deer populations may well act as medium-term reservoirs of Tb even when they are not true maintenance hosts.

In light of the apparent ability of at least some infected deer to survive several years, and of no new infection found >3 km within the controlled buffer, the strong east–west gradient in Tb prevalence in deer across the 7-km buffer and adjacent uncontrolled area is evidence that there is little mixing of the deer populations on either side of the Hauhungaroa Range. Thus, a possum-control buffer width of 3 km in forests similar to those in our study area should greatly reduce the probability that deer infected by possums in an uncontrolled area adjacent to a buffer would disperse across the buffer and reintroduce the disease to other vector species on forest-pasture margins. It is not known whether this conclusion would be valid in areas with less continuous forest cover and different vegetation.

The east–west gradient in Tb prevalence also suggests that deer occupy relatively small areas of a few hundred hectares. If this is so, the presence of any infected young deer reflects a recent and local possum-to-deer transmission event. Young female deer could therefore be used a sentinels of the presence of Tb in possums. Furthermore, surveys of the occurrence of Tb in deer may provide a more cost-effective approach to monitoring the persistence of Tb in possums in large areas of forest such as the 7-km buffer than Tb surveys of the possum population itself.

Pigs

The continued high prevalence of Tb in pigs is puzzling. In Australia, transmission between feral pigs is thought to be low, because Tb there declined naturally in a population after sympatric infected cattle and buffalo were destroyed (McInerny et al. 1995). The most plausible explanation for the high levels of Tb recorded in pigs in our study is that they become infected while scavenging carcasses of infected animals (e.g., possums, deer, or other pigs). However, we have found only one Tb-infected possum among about 400 possums killed within or near the southern half of the 7-km buffer since 1994 (the area in which all the pigs were shot). Therefore, it appears unlikely that most of the young pigs shot in 1996/97 would have scavenged enough possum carcasses during their brief lives to have eaten an infected one. In contrast to the very low availability of infected possums, deer densities in the 7-km buffer recovered to pre-control levels in 2–3 years and some of them were still infected, and therefore natural or Tb-induced mortality and hunter kills may provide pigs with an adequate supply of infective whole or part deer carcasses to maintain the levels of infection recorded. An alternative explanation is that pigs have large home ranges that, in our study, often included the uncontrolled area with higher densities of infected and uninfected possums. However, this appears unlikely for most pigs necropsied, since McIlroy (1989), in the only study of pig movements in native forest in New Zealand, reported home ranges of only a few hundred hectares near Murchison in the South Island.

If pigs are not maintenance hosts (as argued by Morris & Pfeiffer 1995), they may still be effective sentinels for detecting Tb in possums. However, if deer are present, the longer survival time of infected deer suggested by this study means that the occurrence of Tb in pigs would be a less direct and less timely signal than that provided by deer for whether Tb is present in possums. In addition, information on the movements of pigs in various habitats is sparse, and we are at present unable to delineate probable home-range sizes for pigs as precisely as we can for deer.

Cattle

Cattle herds on the periphery of the Hauhungaroa Range continue to present infected animals at herd testing and slaughter. However, levels of infection in herds adjacent to all three buffers are now lower than at any time during the last decade, and we believe much of this reduction can be attributed to the 1994 broad-scale aerial control and ongoing forest-pasture margin maintenance control of possums. Clearly, the possum control undertaken has resulted in fewer Tb-infected possums living adjacent to livestock (although tuberculous possums are not specifically targeted), and presumably fewer possible transmission events between possums and cattle. Surprisingly, levels of Tb in cattle herds fell sharply in 1993/94 (determined from herd testing undertaken in May-June), even though possum control was not undertaken till April to August of that year, and therefore cannot have had any immediate influence on rates of cattle infection. In addition, the patterns of Tb decline in cattle vary with buffer width, with highest levels occurring adjacent to the 3-km buffer where on-farm control was apparently less effective. Equally importantly, the present Tb status of herds adjacent to areas under annual and biannual maintenance control show similar levels of infection but differed prior to1994. We believe the patchwork of initial and maintenance control of possums within and around the Hauhungaroa Range from 1988 onwards, distortions in herd testing data from occasional biannual testing (J. Adams, AgriQuality, pers. comm.), variations in herd size, herd management, and farming practices, and management responses to local herd breakdowns, may account for the pre-1994 decline in Tb incidence in herds adjacent to the biannually controlled 7-km buffer. Our lack of a firm explanation also reflects the problems of the lack of replication in this study.

The relative effectiveness of the control of possums and deer in the 1-, 3-, and 7-km buffers in reducing Tb in adjacent cattle herds remains unclear. Good herd testing results were obtained from the 1-km buffer, but this area now contains few cattle and comparatively high numbers of possums, and we consider it likely that current levels of infection in cattle may rise again. Results from 1-km buffers elsewhere in New Zealand indicate that such minimalist vector control is generally insufficient to eliminate the disease from cattle. Herd testing results from the 3-km buffer are satisfactory, even though the ground-based possum control in the area was apparently the least intensive of any of the buffers. Declines in Tb in cattle herds adjacent to the annually controlled 7-km buffer appear most promising, with no appreciable advantage arising from biannual possum control. Clearly, our results have been confounded by varying intensities of ground control between the 3- and 7-km buffers. However, based strictly on the rate of recovery and current density indices of possum and deer numbers, and herd testing data following the control operation, the best option is for initial control of possums over 7-km buffers followed by annual ground control. That said, there is clearly a higher initial cost involved in controlling possums over buffers of 7 km, and we believe that with better maintenance control in the 3-km buffer, similar herd protection could have been achieved there. For this reason, we argue for buffers of 3-km for future standard Tb possum control operations.

This project has highlighted a number of difficulties associated with integrating research with "routine" management operations, particularly as it affects the within-buffer recovery of possum populations. They include the different intensity of on-farm maintenance control alongside the 3- and 7-km buffers undertaken by the two regional authorities involved in possum control, the extended period of initial control and later rebaiting, additional aerial control over part of the 3- and 7-km buffers in 1995/86, and the quality of the documentation of annual maintenance control. While these problems have compromised our interpretation of trends in possum indices, nevertheless, we believe that there are compelling reasons for conducting such research in "real world" situations in association with possum control agencies. These include the direct involvement of researchers with operators managing pest problems, and the establishment and maintenance of close linkages between pest control agencies and researchers, leading to better acceptance of research results by managers.

8. Recommendations

8.1 Recommendations specific to Hauhungaroa

- Our data indicated that both the 1- and 3-km buffers required further control by the end of 1998/99, with a deeper buffer of 3 km needed to protect the 1-km buffer area . This work was completed for the entire 3-km buffer and for about 30% of the 1-km buffer in July 1999.
- Subject to conservation requirements, the possum control proposed for the 7-km buffer in 2000/01 should be postponed, as we believe the low prevalence of Tb in deer and possums in the eastern half of this area indicates there is very little risk of a rapid increase in the number of infected possums there or of them emigrating from within the buffer to farmland. Postponement would allow the further collection of data to enhance our understanding of the rates and patterns of recovery of possum populations and the decline of Tb in possums poisoned in forest buffers 7 km deep, and their relevance to the modelling theory currently underpinning the control of Tb-infected possum populations. Residual trap-catch surveys should be undertaken across the 7-km buffer each year to gather data on possum population recovery and Tb status.
- Regardless of when the 7-km buffer is next controlled, the AHB should continue to monitor Tb prevalence in wild deer and feral pigs in the easternmost 3 km of the 7-km buffer south of the Mangatu Stream for at least 3 years, to confirm that Tb prevalence in deer declines to zero as expected, and to determine whether Tb persists in pigs when the disease is absent (or nearly so) from deer and possums. We propose that this work be structured as an operational survey with the sale of carcasses used to defray survey costs.

8.2 General recommendations

- Based on the lack of evidence of any greater benefits from biannual control that might offset the lower cost of annual control, biannual control should be discontinued. The comparison should, however, be replicated elsewhere to confirm that this recommendation is appropriate.
- Where there is a high prevalence of Tb in wild deer in areas adjacent to infected livestock, the AHB should consider targeting the deer. This will reduce the reservoir of Tb in the area, and the chance (however small) that infected deer surviving for several years after poisoning operations might eventually re-establish Tb in the recovering possum population. Alternatively, if the economic or political costs involved in targeting deer are unacceptably high, the possum population should be held below the currently accepted threshold for long-term disease persistence in possums (5% RTC) for at least a decade.
- The relationship between the persistence of Tb in possum populations within poisoned areas and the size and location of gaps in bait coverage should be investigated. Control agencies should rigorously check flight-line coverage for aerial operations and ensure that untreated areas (such as those about watercourses) are adequately covered by follow-up ground-based control.
- The home-range size and dispersal distances of feral pigs should be investigated in various habitats to determine the geographic scale over which pigs can be used as sentinels of continued Tb presence.
- Based on the positive results in cattle herd testing adjacent to the 3-km buffer, the recovery over 3–5 years of possum numbers following aerial poisoning to unacceptably high levels,

the undoubtedly higher initial costs of controlling deer and possums over a 7-km buffer, and the maximum distance of 2.5 km that infected deer born after the poisoning were found away from unpoisoned areas, we recommend a buffer width of
3 km to separate infected wildlife from livestock.

- Further comparisons (replications) of the optimal buffer widths for possum control are required to substantiate our conclusions and recommendations. These should focus on comparing the effectiveness of buffers of 2-, 3-, and 4-km wide in reducing the densities of, and Tb prevalence in, possums and deer living within 1 km of forest-pasture margins.

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11. Appendices

11.1 Comparison of diagnoses of Tb based on presence of the typical lesions, equivocal lesions, and mycobacterial culture of tissues, for the 245 deer for which mycobacterial cultures were undertaken.

Year	**93/94**	**95/96**	**96/97**	**97/98**	**98/99**	**Totals**
No. deer with tissues cultured	52	24	31	69	69	**245**
No. with typical lesions	14	5	6	7	10	**42**
No. with equivocal lesions	19	1	1	3	18	**42**
% with typical lesions culture positive	93	100	100	71	100	**93**
% with equivocal lesions culture positive	11	0	100	0	11	**12**
% culture positive with no visible lesions	12	38	13	38	25	**23**

11.2 Location details for infected deer born since 1994/95 and shot within the 7-km buffer during 1995/96–1998/99.

1. #128, a 10-month-old female shot south of Keepa Road in 1997/98 1.8 km inside the poison area boundary but within 0.5 km of a narrow (150 m) unpoisoned swath.

2. #A60, a 22-month-old male shot in 1996/97 in the south-west corner of the 7-km buffer in an unpoisoned "gap" of 82 ha.

3. #A62, a 10-month-old male shot in 1996/97 0.8 km east of the western flight line boundary in the middle of the 7-km buffer.

4. #A57 and #A58, both 22-month-old males shot at the same location on the same date in 1996/97 in the Waihora catchment about 1.7 km east of the western flight line boundary. These deer were within a 1-km radius of three gaps in bait coverage, each of at least 500 × 150 m.

5. #Z1119, a 10-month-old male shot in 1998/99 2.5 km east of the flight line boundary and 1.2 km south of #A57 and #A58. As with #128, one of the poison swaths stopped about1 km from the poison boundary leaving a narrow gap in bait coverage 1.5 km from the kill location.

6. #115, a 23-month-old female shot in 1997/98 4.9 km east of the flight boundary, and about 2.5 km northeast of #1119. This was the greatest distance at which a definite new (post-poison) case of Tb was recorded from the poison boundary, but the kill location was within 0.5 km of a water supply catchment left unpoisoned about100 m on either side of the stream. A survey of possum densities at this kill location (undertaken as part of a separate study and after the 1994 possum control) revealed possum trap-catch rates of 25% on one of four 20-trap lines, and also identified the presence of an infected possum within 0.3 km.