Animal Health Board Project R-10619

Eliminating Tb – results from a spatially explicit, stochastic model

Dave Ramsey & Murray Efford

Animal Health Board Project R-10619

Eliminating Tb – results from a spatially explicit, stochastic model

Dave Ramsey[1] & Murray Efford[2]

[1]Landcare Research
Private Bag 11052, Palmerston North
New Zealand

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

Prepared for:
Animal Health Board
PO Box 3412
Wellington

DATE: December 2005

Reviewed by:

Dan Tompkins

Dan Tompkins
Scientist
Landcare Research NZ Ltd

Approved for release by:

PCowan

Phil Cowan
Science Manager
Biosecurity &Pest Management

Landcare Research Contract Report: LC0405/118
DOI: https://doi.org/ 10.7931/acmj-fa31

Contents

Summary

Project and Client

Research to model the cost-effectiveness of various residual trap-catch index (RTCI) targets, and the efficacy of Tb vaccination, for the control of bovine tuberculosis (*Mycobacterium bovis*; Tb) in brushtail possums was undertaken using a new spatially-explicit, stochastic model of the dynamics of possums and Tb by Landcare Research for the Animal Health Board (Project R-10619), between July 2003 and May 2005.

Objectives

- To predict the probability of eliminating Tb from possum populations within any given time (duration) and intensity (level) of control by refining and using a new spatially explicit, stochastic model to simulate disease dynamics and control.
- To predict the likely cost effectiveness of RTCI for monitoring these levels by linking a spatially explicit model of the RTCI monitoring process with the model of disease dynamics and combining this with empirical data on the costs of achieving various levels of control. The implications of patchy control for elimination of disease will also be explored.
- To predict the rate at which disease is 'exported' from the site by possums dispersing under the various control regimes.
- To compare the likely efficacy and cost effectiveness of culling (lethal control) and possum vaccination in eliminating Tb from possum populations within any given time.

Methods

A spatially explicit, stochastic possum/Tb model has been developed during this project. The model simulates events (i.e. birth, death, infection, dispersal) for individual possums located uniquely in a two-dimensional landscape. We combined the possum-Tb model with a spatially explicit model of possum trap-catch to simulate possum monitoring. We used the combined model to predict how well current RTCI targets eradicate disease in a given time and also explored the implications of patchy control on disease eradication probabilities by simulating an area of possum habitat that had been "missed" by control.

Empirical data on the cost of aerial and ground-based possum control were collated from the literature, as were data on the efficacy of control (% reduction in possum density). These data were then used to estimate the per hectare cost of achieving a certain control efficacy for both aerial and ground based control for the purposes of simulating the accumulated present cost of achieving Tb eradication under various RTCI target thresholds.

We added Tb vaccination to the model in order to compare the effectiveness of lethal control with vaccination for eradicating Tb from possum populations within any given time. Vaccination efficacy was incorporated into the model via parameters for the probability of non-response, the duration of complete protective immunity (the "guarantee time"), and the rate of decay in immunity once the guarantee time had elapsed. This flexibility allowed predictions about the minimal specifications for a useful Tb vaccine.

Results

The probability of eradicating Tb within a given time did not differ substantially between aerial and ground based control. In general, populations reduced and held to a 5% RTCI had a 95% probability of Tb extinction within 5–7 years, while populations reduced to either 2% or 1% RTCI had a 95% probability of Tb extinction within 3–5 years and 3–4 years respectively. If possums were controlled uniformly over the area, then control only had to be undertaken between 2 and 4 times to

achieve eradication, even taking monitoring errors into consideration. However, when a high density patch of possums was missed by control, Tb could not reliably be eradicated within 10 years. Setting a threshold on the number of possums caught per trapping line (line thresholds) to detect patchy control was only partially successful at reducing times to Tb eradication.

Very few Tb-infected possums were predicted to disperse beyond the control area over the 10-year period following possum control for all control scenarios. In stark contrast, with no control infected dispersers were numerous.

Overall, reducing the RTCI target threshold from 5% to 2% increased the accumulated cost of achieving a 95% probability of eradication by 15% on average (including monitoring costs). Reducing the RTCI threshold from 2% to 1% resulted in a further increase in the cost of eradication by 16% on average.

Vaccination combined with a single ground control operation was more efficient at eradicating Tb than vaccination alone. Vaccination applied each year following an initial control operation can be expected to eradicate Tb within 7 years and is little affected by variation in the response rate or decay in immunity assuming vaccination is effective for a period of at least 1 year. If vaccination is applied every 3 years following an initial reduction in possum density, then a 95% probability of Tb extinction could be achieved within 10 years if the vaccine had a 95% response rate and a guarantee time of 1 year with a 2-year half-life, or a 95% response rate and a guarantee time of 3 years with a half-life of at least 1 year. To achieve the same benefit, the cost of a single vaccine application (cost/ha treated) would have to be less than the cost of a single application of maintenance control. This was because vaccination needed to be applied more frequently than lethal control.

Conclusions

- Adopting RTCI targets lower than 5% incurs an opportunity cost because the accumulated cost of control for RTCI targets of 2% and 1% exceeds that for 5% RTCI for the same benefits. However, this conclusion is sensitive to the modelled relationship between RTCI and cost. If control is more cost effective than assumed in the model, then achieving a specified RTCI is less cost sensitive and this opportunity cost would be reduced or disappear entirely.
- This opportunity cost appears greater when controlling high density populations than low density populations, as greater control intensity (percent reduction) is required to reduce high density populations down to a specified RTCI target, compared with low density populations. Hence, the cost of achieving that RTCI is also greater than for low density populations.
- The benefits of adopting RTCI targets lower than 5% appear to be related entirely to the time taken to eradicate Tb. Lower RTCI targets result in Tb being eradicated sooner; however, the accumulated cost will be higher. The time taken to eradicate Tb applies to larger control areas (2500 ha and larger). Times to eradication would be progressively shorter on smaller control areas due to the greater influence of stochastic events on small populations.
- Areas of habitat missed by control can significantly increase the time taken to eradicate Tb. For the case where a 30-ha high-density area containing infected possums within an 859-ha area of farmland/scrub habitat was missed by control, Tb could not be eradicated within 10 years. Using line thresholds in conjunction with RTCI targets can detect patches of this size, especially using double the number of lines and half the number of traps per line. However, even when using these monitoring strategies, the time to eradicate Tb is increased compared with that when no patches are missed.
- There appears to be a finite, albeit very small risk that Tb is exported by possums from control areas compared with areas where no control occurs. This suggests that the probability of Tb being spread by possums from within the control area is also small.

- Vaccination can potentially be used to eradicate Tb from possum populations, and hence is a viable, alternative Tb control technique in situations where lethal control is undesirable. However, vaccination will cost substantially more than lethal control, with its most efficient use likely to be where lethal control is used to obtain an initial population reduction.
- Vaccination applied each year after an initial control operation should eradicate Tb within 7 years and is little affected by variation in the response rate or decay in immunity provided vaccination is effective for at least 1 year. Vaccination every 3 years following an initial control operation should eradicate Tb within 10 years. However the vaccine must have a response rate of at least 95% and a guarantee time of at least a year with a half life of no less than 2 years, or a 95% response rate and a guarantee time of 3 years with a half life of at least 1 year. If repeat vaccinations "reset" the guarantee time, then decay in vaccine immunity can be largely ignored.

Recommendations

- Control applied to high density possum populations should adopt a RTCI target of 5% while low density and most farmland/scrub populations should adopt a RTCI target of 2%. The use of RTCI targets lower than 2% incur more of an opportunity cost and do not significantly reduce the time taken to eradicate Tb.
- To achieve Tb eradication, monitoring (each year) and control should be undertaken for at least 7 years, using a 5% RTCI target, and 5 years, using a 2% RTCI target, when controlling possum populations in continuous forest. On farmland/scrub habitats the minimum time for conducting control operations can be reduced to 6 and 4 years for RTCI targets of 5% and 2% respectively. Controlling an area every year is not necessary to achieve Tb eradication as long as control is uniformly applied and monitoring undertaken each year to "trigger" control.
- Vaccination could be developed as a complementary disease control tool to lethal control. To eradicate Tb, vaccination will need to be applied each year for 7 years following an initial reduction in possum density. To be more cost-effective, vaccination could be applied every 3 years. However, to achieve eradication the vaccine will need to have response rate of at least 95% and an effective immune period of between 1–3 years. Additional studies should compare the efficacy of vaccination and culling when used as 'buffer' areas to prevent disease spread.

1. Introduction

Research to model the cost-effectiveness of various residual trap-catch index (RTCI) targets, and the efficacy of Tb vaccination, for the control of bovine tuberculosis (*Mycobacterium bovis*; Tb) in brushtail possums was undertaken using a new spatially-explicit, stochastic model of the dynamics of possums and Tb by Landcare Research for the Animal Health Board (Project R-10619), between July 2003 and May 2005.

2. Background

The current approach used by the Animal Health Board for eliminating Tb from possum populations is based on predictions from deterministic epidemiological models developed by Nigel Barlow (Barlow 1991a; Barlow 1991b; Barlow 2000). There is some empirical support for these predictions (Caley et al. 1999), and the rapid decline in reactor rates in recent years suggests that in many areas the average density of possums has been controlled below the threshold for maintenance of Tb. However, there is still substantial need for improvement, with Tb persisting in some areas despite possum control, and in others, the very low residual trap catch index (RTCI) targets that have been widely adopted as a means of 'purging' Tb from possum populations may carry a large price tag and opportunity cost.

Tb in possums is usually clustered in space (Barlow 1991a; Pfeiffer et al. 1995; Hickling 1995), indicating local dynamics plays a role in persistence of the disease. As Tb in possums requires close contact for transmission, the spatial relationship between infected and susceptible possums on a local scale will largely govern disease transmission. Barlow (2000) modelled clustering with a heterogeneous mixing term for disease transmission that subsumed any local disease dynamics. We propose a spatially explicit model that represents directly the processes that give rise to clustering. Spatially explicit models have the potential to highlight properties of disease dynamics that are difficult or impossible to replicate with non-spatial models.

Both control and monitoring are also spatial processes. A spatial modelling approach may therefore provide insights into failures of possum control (e.g. incomplete bait coverage). In addition our research addresses a concern that adherence to very tight residual trap-catch index (RTCI) thresholds may be extremely wasteful of resources; resources freed up by less stringent control needs, particularly once reactor levels in sympatric livestock have fallen to near zero, would deliver benefits (i.e. faster achievement of Tb goals) if applied to control elsewhere.

Vaccination of possums using bacille Calmette-Guérin (BCG) has been shown to afford some protection to possums from Tb infection, with an efficacy of 70% being demonstrated in wild individuals whether vaccinated by intranasal aerosol or conjunctival instillation (Corner et al. 2002). Hence BCG is being considered for wide-scale use to help control the disease as a possible alternative or complement to lethal control techniques. Little information exists on the duration of protection afforded by BCG in possums and how decay in vaccine immunity might affect vaccination strategies.

The research presented here uses a spatially explicit, stochastic model of possums and Tb, in combination with a spatial model of the monitoring process, to explore the efficacy and cost effectiveness of RTCI thresholds to eliminate Tb from possum populations. In addition, we also explore the potential for possum vaccination to complement or replace existing lethal control strategies.

3. Objectives

- To predict the probability of eliminating Tb from possum populations within any given time (duration) and intensity (level) of control by refining and using a new spatially explicit, stochastic model to simulate disease dynamics and control.
- To predict the likely cost effectiveness of RTCI for monitoring these levels by linking a spatially explicit model of the RTCI monitoring process with the model of disease dynamics and combing this with empirical data on the costs of achieving various levels of control. The implications of patchy control for elimination of disease will also be explored.
- To predict the rate at which disease is being 'exported' from the site by dispersing possums under the various control regimes.
- To compare the likely efficacy and cost effectiveness of culling (lethal control) and possum vaccination in eliminating Tb from possum populations within any given time.

4. Methods

4.1 The spatial possum/Tb model

A spatially explicit, stochastic possum/Tb model was developed. The model simulates events (i.e. birth, death, infection, dispersal) for individual possums located uniquely in a two-dimensional landscape. The model is partly based on the deterministic, non-spatial, Anderson/May type SI (susceptible/infected) compartment model of Barlow (2000) and uses many of the same parameters (Appendix 1). As in the Barlow (2000) model, possum population dynamics are assumed to be regulated by theta-logistic population growth (Barlow & Clout 1983; Barlow 2000). However, the spatial model differs from that model in other several important respects. The model is stochastic and individual-based, allowing spatial structure to be modelled explicitly. Disease transmission occurs at a local scale and is based on the probability of contact between infected and susceptible individuals, which is dependent on the degree of home range overlap. The model includes both sexes and two age classes to account for sex-specific dispersal behaviour.

An important feature of the possum/Tb spatial model is the ability to represent real landscapes through the importation of habitat maps created from remotely sensed imagery. Using data derived from satellite imagery (EcoSat; Dymond & Shepherd 2004, http://www.landcareresearch.co.nz/services/ecosat/), we classified possum habitat using a 50 m pixel size. Based on the classified vegetation type for each pixel derived from EcoSat, a possum carrying capacity (K) was assigned to each pixel based on estimates of equilibrium possum densities estimated for different vegetation classes given in Efford (2000). In this way, possum carrying capacity was allowed to vary spatially according to the spatial distribution of different vegetation classes in the landscape. We used this feature to create one of the modelling scenarios outlined below.

4.2 Model sensitivity and habitat effects on Tb persistence

We used the spatial possum/Tb model to explore the probability of disease extinction within a given time under varying levels of possum control (reduction in possum density). Using the three modelling scenarios outlined below, we simulated various levels of possum maintenance control (percent reduction) over a 10-year period to determine the effect of habitat type on the probability of Tb eradication. The scenarios were: (1) uniform (forest) habitat with a carrying capacity (K) of 10 possums/ha; (2) uniform (forest) habitat with a carrying capacity (K) of 3 possums/ha; and (3) an actual farmland scrub habitat in the Wairarapa containing highly dissected patches of possum habitat interspersed with farmland (Figure 1). Thus for scenario 3, carrying capacity varied across the landscape according to habitat type with the highest carrying capacities found in the predominantly willow riparian habitat (unspecified woody = 16.7 possums/ha) and the lowest in pine forest (2 possums/ha). Pasture habitat was assumed to have a carrying capacity of 0 possums/ha and the overall area of possum habitat was 859 ha with an average carrying capacity of 6.1 possums/ha. For each scenario, the total area of habitat simulated was 2500 ha (5 x 5 km) with possums distributed randomly within each 50 m habitat cell (Poisson distribution) with an expected density equal to the carrying capacity of that cell. The starting prevalence of Tb in the population varied stochastically around an expected value of 5% at equilibrium density with Tb individuals initially located randomly within the population. Before simulated possum control was applied to the population the model population was first subjected to a "burn-in" period to eliminate any artefacts due to the specified initial starting conditions. Burn-ins were undertaken by specifying the initial starting conditions and then running the model for 20 years, in the case of scenarios 1 and 2 and 40 years, in the case of scenario 3, before any simulated control was applied. Population density and Tb prevalence were checked and were within expectations after the burn-in periods. Simulated possum control intensities consisted of 50%, 70% or 90% reduction from pre-control equilibrium densities, maintained over a 10-year period. Five hundred replicate simulations were undertaken for each habitat scenario and possum control intensity with the probability of Tb eradication within any given time expressed as the proportion of the 500 replicates where Tb became extinct. We defined 'eradication' as the time taken to achieve a 95% probability of Tb extinction.

Default parameters in the model (Appendix 1) were systematically varied to determine their effect on the model predictions (sensitivity analysis). In particular we explored the effect of (1) linear vs. non-linear contact rates, (2) an increase in the intrinsic rate of population increase from 0.2/year to 0.3/year and (3) variation in the rate of pseudo-vertical transmission between 0.25 (default) and 0.75. For each set of parameters, the transmission rate was adjusted to produce an expected 5% prevalence at equilibrium density (rationale given in Appendix 1).

4.3 Sensitivity of RTCI targets for eradicating Tb

We combined the possum-Tb model with a model of possum trap-catch (Ramsey et al. 2005). The possum trap-catch model is also a spatially explicit, individual-based model, and can be overlaid directly on the disease model. This model simulated the actual RTCI monitoring process by placing lines of 10 leg-hold traps within possum habitat at 20m spacing with no line within 200m of any other line as per the NPCA protocol and simulating "captures" of possums in traps over 3 nights (see Ramsey et al. (2005) for a description of the trapping algorithm). The most common RTCI targets used in AHB possum control operations are between 1% and 5% RTCI. Thus, the combined model was used to predict how well RTCI targets of 5% 2% or 1% resulted in eradication of disease in a given time.

We also explored the implications of patchy control on disease eradication probabilities by simulating an area of possum habitat that had been "missed" by control. This used scenario 3 by simulating a 30 ha area of riparian habitat (high possum density, K=16.9/ha) within the 859 ha total area of possum habitat to be the area "missed" by control efforts. We initially assumed a worst-case scenario where the area of habitat missed is never subject to control. We then explored how efficient monitoring data were at detecting the area of uncontrolled habitat. Two sampling strategies were evaluated that set limits on the maximum number of possums that could be caught on an individual trap line (line thresholds). These were

1. Mean RTCI of either 5%, 2% or 1% and including line thresholds of 16.7%, 10% or 6.7% respectively (i.e., 5, 3 or 2 possums per line over 3 nights),

2. Mean RTCI and line thresholds as for 1 but reducing the number of traps per line to 5 and doubling the number of lines. Line thresholds apply to trapping over 6 consecutive nights with the mean RTCI calculated over the first 3 nights.

Line thresholds and monitoring strategy (2) above were suggested by Ramsey & Ball (2004) as the most efficient for patch detection within the constraints of line based monitoring.

Following initial control down to the specified target RTCI, monitoring was undertaken each and every year. If the mean RTCI or individual line RTCI was above the threshold, control was undertaken until post-control monitoring indicated the mean RTCI and all individual line RTCI were below the threshold. For sampling strategies 1 and 2 above, the missed area was judged to have been detected when a line intersected the area of habitat that missed control and that particular line RTCI was above the line threshold. Once detected, the missed area was then subject to any follow up control required to achieve the specified monitoring targets. This behaviour mimics the current practice used by contractors who have failed a line RTCI threshold, with follow up control being undertaken within the vicinity of that line. For each scenario and target RTCI threshold, 500 simulations were undertaken with the probability of eradication each year after control calculated as the proportion of the 500 simulations where Tb became extinct in that year. Logistic linear regressions were fitted to these probabilities with time since start of control fitted as the independent variable. By inverting the regression, the time to achieve a 95% probability of Tb eradication could be predicted with 95% confidence intervals (Collett 1991).

The possum-Tb model included both juvenile and adult dispersal (Appendix 1); therefore, we were able to obtain model-based predictions of the rate at which disease is "exported" from the site under the various control regimes. This will provide some indication of the implications for disease spread.

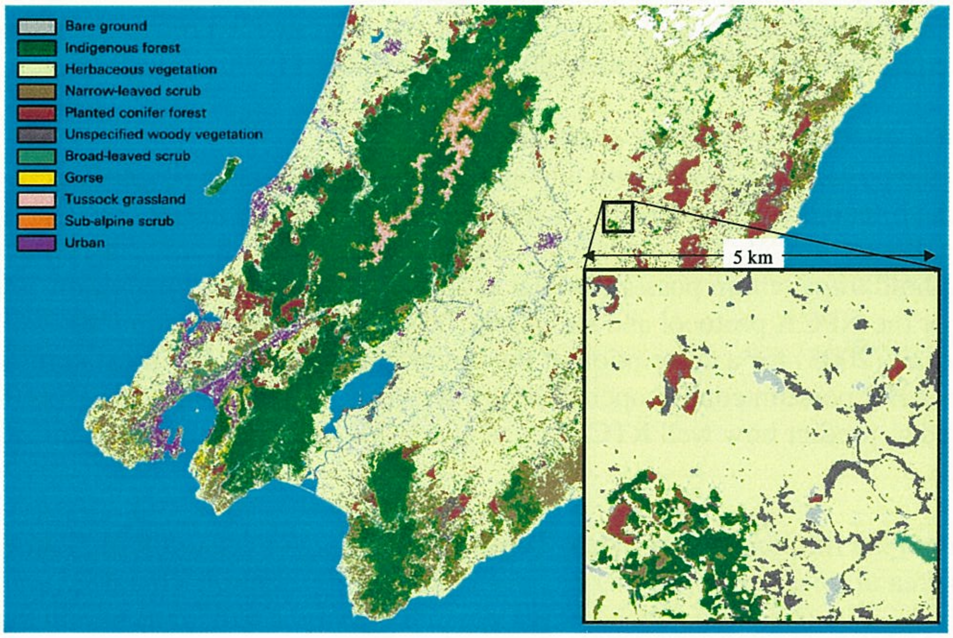

Fig. 1 Farmland/scrub habitat area (inset) used in simulations for scenario 3. The area of habitat within the 2500 ha total area was 859 ha.

4.4 Cost effectiveness of RTCI targets for eradicating Tb

Empirical data on the cost of aerial and ground based possum control were collated from the literature. The main sources were AHB and DOC contract reports in which the author had attempted to estimate both the true cost of applying control and the actual areas over which control had been applied (Table 1). These data included estimates of the efficacy of the control operation (% reduction in RTCI). The data were used to estimate the per hectare cost of achieving a certain control efficacy for both aerial and ground based control. As the control operations occurred over a 12-year period, between 1991 and 2003, all costs were inflation adjusted against the annual consumer price index (CPI) to 2004 dollars to facilitate comparisons.

The data on costs were inadequate for estimating the likely variability in the efficacy of possum control by different methods. Therefore, we also collated data on the efficacy of aerial and ground-based possum control undertaken between 1996 and 2004 on 131 Department of Conservation operational areas with both pre- and post-control trap-catch monitoring (Table 2). These data were used to estimate the likely variability in the efficacy of aerial and ground-based possum control.

Table 1 The per hectare cost ($) and control efficacy (% reduction in RTCI) of aerial and ground-based possum control operations carried out between 1991 and 2003 for populations initially at high (≥ 15% RTCI) or low (< 15% RTCI) population densities. Data were collated from Warburton and Cullen (1993), Montague (1997), Corson (1999), Warburton and Thompson (2002), and Speedy (2003). Areas ranged from 144 ha to 18 000 ha.

Control	Population	Cost ($/ha 2004)	Efficacy (%)	N
Aerial	H	$23.6	85	10
	L	$26.8	74	2
Ground	H	$39.6	87	16
	L	$27.4	89	5

Table 2 Control efficacy (mean and standard deviation (SD) of % reduction in RTCI) in 131 DOC possum control operations carried out between 1996 and 2004 for aerial and ground based control operations on populations initially at high (≥ 15% RTCI) or low (< 15% RTCI) population densities. Data obtained from Department of Conservation records (C. Veltman pers. comm.)

Control	Population	Efficacy (%)	SD	n
Aerial	H	90	7.1	12
	L	69	16.8	15
Ground	H	84	14.9	47
	L	73	21.2	57

Based on data in Tables 1 and 2, we determined the approximate cost of achieving a certain RTCI by simulating either aerial or ground based possum control until a target RTCI was achieved. The expected mean control efficacy (and its variation) (Table 2) was used to simulate the outcome of a particular control operation. If the control operation did not reduce the population below the specified RTCI level, then control was repeated until it did. Cost was calculated as the accumulated per ha cost (from Table 1) over the number of control operations required to achieve that RTCI. This assumed that if the initial control did not meet the specified target, then control was repeated over the entire area. This is somewhat unrealistic as contractors (especially for ground-based control) usually only undertake repeat control near monitoring lines where the catch was high. Nevertheless, this simulation procedure should adequately approximate the relationship between cost of control ($) and achievement of a target RTCI.

Efficacies for aerial and ground-based control were treated as random variables by drawing random deviates from a Beta distribution. The probability density distributions for each control type are given in Figure 2. For each of 9 different target RTCI values between 15% and 1%, 100 simulated control operations for both aerial and ground control were undertaken. For each target RTCI, the resulting accumulated cost of achieving that target RTCI was calculated as the mean of the 100 simulated control operations. The relationship between the target RTCI values and cost was described by fitting the following model by non-linear least squares.

$$\text{cost (\$/ha)} = a - b\left(1 - e^{(-cI)}\right) \text{ (Equation 1)}$$

Where a, b and c are fitted constants, I is the target RTCI value and cost ($/ha) was the mean (over 100 simulations) accumulated cost of control.

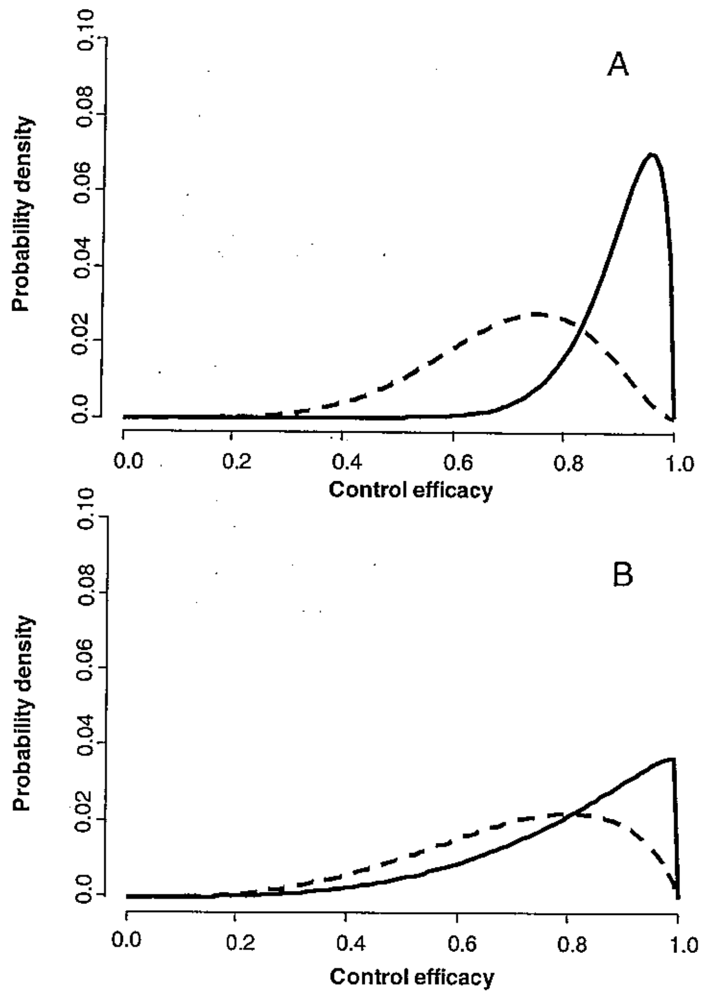

Fig. 2 Beta probability densities describing the variation in control efficacy achieved by (A) aerial and (B) ground based possum control operations. Solid line – efficacy of control operations on high (initial ≥ 15% RTCI) possum densities; Dashed line – efficacy of control operations on low (maintenance < 15% RTCI) possum densities. Probability distributions were derived using data given in Table 2.

To determine the cost-effectiveness of RTCI targets for eradicating Tb, we calculated the accumulated cost of reducing possum populations to RTCI targets of 5%, 2% and 1% using either aerial and ground based control over a 10-year period for each of scenarios 1–3 using the methods detailed in section 4.3. Control efficacy was specified as a random variable using the distributions in Figure 2 and costs of each type of control were specified from data in Table 1. Logistic linear regressions were fitted to the probability of Tb eradication with the accumulated cost fitted as an independent variable. Cost effectiveness of different RTCI targets was then expressed as the accumulated cost of achieving a 95% probability of Tb eradication, predicted from the inverted logistic regressions. All accumulated costs were also discounted to determine their present value by applying an annual discount rate of 10%. A discount rate of 10% has been used previously for calculating the present value of possum control operations, e.g., (Barlow 1991b).

Monitoring costs were also calculated separately based on a cost of $300 per line. The accumulated cost of monitoring was similarly discounted to calculate the present value.

4.5 The effectiveness of possum vaccination

We added Tb vaccination to the model to compare the effectiveness of lethal control with vaccination for eradicating Tb from possum populations within any given time. Vaccination efficacy was incorporated into the model by allowing for the probability of non-response, the minimal duration of complete protective immunity (the "guarantee time"), and the rate of decay in immunity once the guarantee time had elapsed. Under this model each individual vaccinated possum has only a single guarantee time. Hence, repeat vaccination of the same individual does not 'reset' the guarantee time. The extended model with vaccination allowed us to predict the minimum specifications for a successful Tb vaccine.

We used the model to examine disease control strategies involving the use of either vaccination or lethal control as well as the integration of vaccination with lethal control strategies in different temporal sequences to determine how vaccination could replace or complement existing disease control strategies. All vaccination simulations used scenario 2 (uniform low density possum populations). Vaccination was assumed to have been applied in bait stations using "best practice" developed for application of poison baits, which has been shown to give at least a 90% rate of encounter with baits (e.g., Thomas & Fitzgerald 1994). Hence, we assumed the coverage of the vaccine was 90% (i.e. 90% of the target population had eaten a vaccine bait). However, we examined how changing the response rate, guarantee time and half-life of the vaccine affected the success of vaccination strategies. Finally, we attempted to determine the cost effectiveness of vaccination relative to culling by determining the substitution costs if vaccination was to give the same benefits as culling alone.

5. Results

5.1 Model sensitivity and habitat effects on Tb persistence

Eradication of Tb could only be achieved within 10 years for all 3 scenarios when populations were maintained below 10% of their equilibrium density (i.e. a 90% cull) (Figure 3). Tb was hardest to eradicate for populations at high uniform carrying capacity (scenario 1) and easiest for populations on the dissected farmland/scrub habitat (scenario 3). This is due to the dissected nature of habitat in scenario 3 where the relative abundance of neighbours for individuals occupying discrete patches is reduced compared with populations occupying uniform habitat. A reduced abundance of neighbours results in more limited opportunities for transmission and hence, persistence of disease.

We specifically examined the sensitivity of the model predictions to changes in some of the key parameters for scenario 3. One parameter was varied at a time, while keeping others at their standard values. Tb extinction probabilities were most affected by assuming a non-linear instead of linear relationship between contact rates and population density (Figure 4) (see Appendix 1 for a spatial treatment of non-linear contact rates). Predictions were relatively insensitive to changes in either the intrinsic rate of increase (from 0.2/year to 0.3/year) or the rate of pseudo vertical transmission (0.25 to 0.75) (Figure 4). In general, the sensitivity of predictions to changes in model parameters decreased as the level of population reduction increased.

These results predicted that Tb would be more difficult to eradicate if a non-linear contact rate structure was assumed. As it seemed prudent to use conservative assumptions, we incorporated non-linear contact rates into the model as the default condition. Non-linear contact rates were also assumed by the Barlow (2000) non-spatial model. Henceforth, all model predictions assumed non-linear contact rates with the default parameter set.

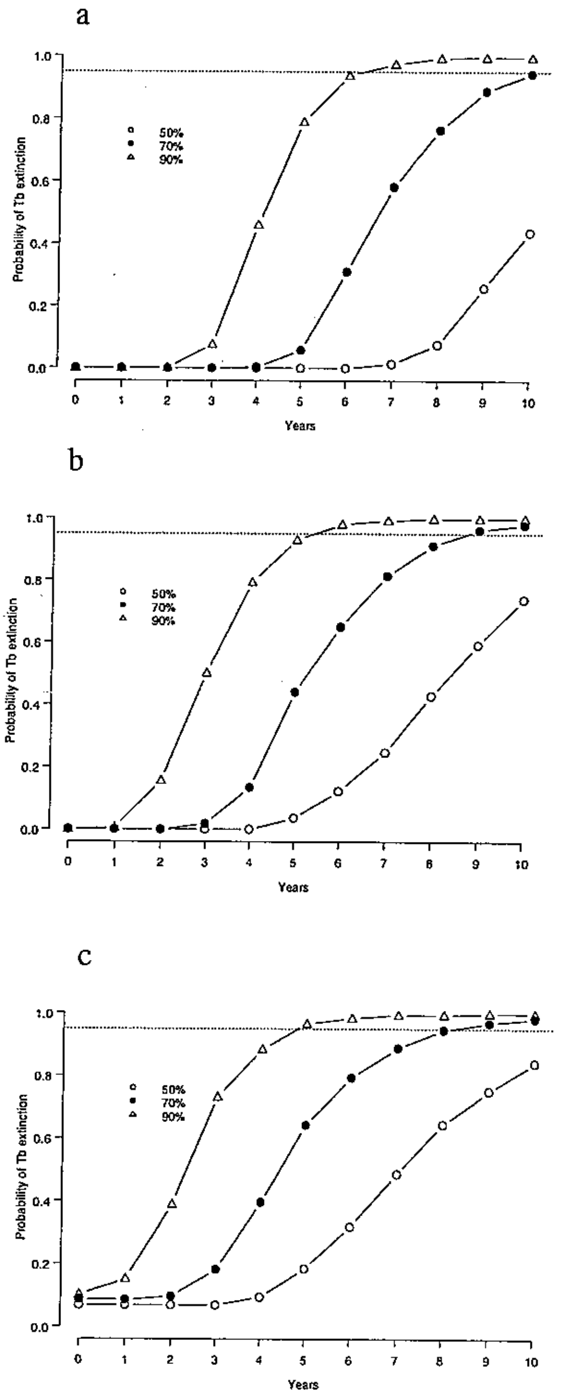

Fig. 3 The probability of Tb extinction vs. time since start of maintenance control for populations reduced by 50%, 70% or 90% of equilibrium density. (a) Uniform habitat at high K (scenario 1), (b) Uniform habitat at low K (scenario 2) and (c) farmland/scrub habitat (scenario 3).

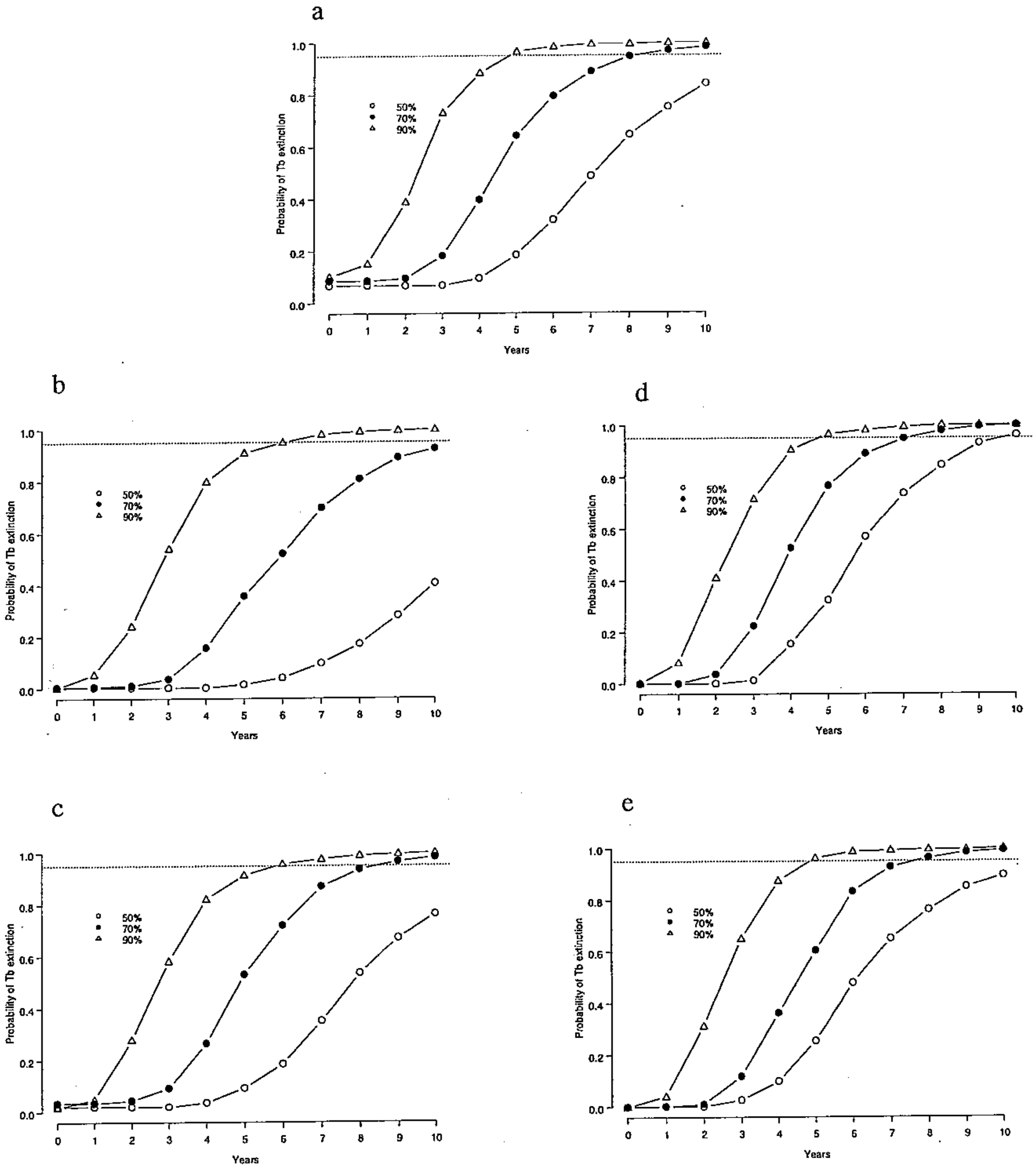

Fig. 4 The sensitivity of predictions of the probability of Tb extinction vs. time since start of maintenance control for populations reduced by 50%, 70% or 90% of equilibrium density in farmland scrub habitat (scenario 3). (a) default parameter set, (b) non-linear contact rates, (c) pseudo vertical transmission rate (p) = 0.75, (d) intrinsic rate of increase (r) = 0.3/year and (e) r=0.3/year and p=0.75. (All parameters at their initial default values except as indicated).

5.2 Sensitivity of RTCI targets for eradicating Tb

The probability of Tb extinction within a given time did not vary substantially between simulated aerial or ground-based control. Tb was eradicated sooner under the three RTCI targets on the farmland/scrub habitat (scenario 3) compared with populations under the other scenarios and took longest to eradicate on the uniform low density habitat (scenario 2) (Tables 3–5). In general populations reduced and held to a 5% RTCI had a 95% probability of Tb extinction within 5–7 years, while populations reduced to either 2% or 1% RTCI had a 95% probability of Tb extinction within 3–5 years and 3–4 years, respectively. The number of times control was "triggered" up to the time to achieve eradication ranged between 2 and 4. Generally, RTCI targets of 5% and 2% required the area to be controlled at least twice to achieve eradication with the exception of a 2% RTCI target used on uniform high density populations where 3 control events were required.

When a 30 ha patch of habitat in scenario 3 was missed by control, Tb could not be eradicated within 10 years (Table 6). Time to eradication was improved by using line thresholds on standard monitoring lines (monitoring strategy 1) to trigger 'mopping up' of missed patches (Table 6). However, the rate of Tb extinction was still slower than that predicted when no patches are missed, with the time taken to achieve Tb eradication for mean RTCI targets of 5%, 2% and 1% pushed out to 9, 7 and 6 years respectively. Eradication times were further improved by adopting monitoring strategy 2, with the time taken to achieve eradication for mean RTCI targets of 5%, 2% and 1% decreasing to 7, 5 and 4 years respectively (Table 6). However, these are still greater than those predicted when no patches are missed.

Table 3. The time in years to achieve a 95% probability of Tb extinction (eradication) for RTCI targets of 5%, 2% or 1% for aerial and ground-based possum control on a uniform high density possum population (scenario 1). Values in parentheses are upper and lower 95% confidence intervals. n – mean number of times control occurred to achieve eradication.

	RTCI target					
Control type	5%	n	2%	n	1%	n
Aerial	5.8 (5.3, 6.4)	2	4.7 (4.2, 5.1)	3	3.8 (3.4, 4.2)	3
Ground	6.0 (5.5, 6.6)	3	4.6 (4.2, 5.1)	3	3.8 (3.4, 4.2)	4

Table 4. The time in years to achieve a 95% probability of Tb extinction (eradication) for RTCI targets of 5%, 2% or 1% for aerial and ground-based possum control on a uniform low density possum population (scenario 2). Values in parentheses are upper and lower 95% confidence intervals. n – mean number of times control occurred to achieve eradication.

	RTCI target					
Control type	5%	n	2%	n	1%	n
Aerial	7.1 (6.6, 7.7)	2	5.1 (4.6, 5.5)	2	4.1 (3.7, 4.5)	2
Ground	7.3 (6.7, 7.9)	2	5.0 (4.6, 5,5)	2	3.8 (3.4, 4.1)	3

Table 5. The time in years to achieve a 95% probability of Tb extinction (eradication) for RTCI targets of 5%, 2% or 1% for aerial and ground-based possum control on a farmland/scrub habitat (scenario 3). Values in parentheses are upper and lower 95% confidence intervals. n – mean number of times control occurred to achieve eradication.

	RTCI target					
Control type	5%	n	2%	n	1%	n
Aerial	5.0 (4.6, 5.5)	2	3.8 (3.5, 4.2)	2	2.9 (2.6, 3.3)	3
Ground	5.2 (4.8, 5.7)	2	3.4 (3.1, 3.8)	2	3.0 (2.7, 3.4)	3

Table 6. The time in years to achieve a 95% probability of Tb extinction (eradication) for RTCI targets of 5%, 2% or 1% for possum populations on farmland/scrub habitat (scenario 3) when a 30 ha patch of habitat was 'missed' by control. 'Monitor 1' and 'Monitor 2' refer to monitoring strategies 1 and 2 in section 4.3 used to trigger patch detection. Values in parentheses are upper and lower 95% confidence intervals.

	RTCI target		
Patch detection	5%	2%	1%
No patch	5.2 (4.8, 5.7)	3.4 (3.1, 3.8)	3.0 (2.7, 3.4)
Missed patch	10.7 (9.9, 11.5)	10.8 (9.9, 11.7)	10.6 (9.8, 11.4)
Monitor 1	9.1 (8.5, 9.9)	7.2 (6.6, 7.8)	5.9 (5.4, 6.5)
Monitor 2	7.4 (6.8, 8.0)	5.1 (4.6, 5.6)	3.5 (3.1, 3.9)

Rate of dispersal out of the control area by Tb infected possums

The cumulative number of Tb infected possums predicted to have dispersed beyond the control area over the 10 year period following the start of possum control was low for all control scenarios (Table 7). Dispersal of Tb infected possums was unlikely to occur under a target mean RTCI of 1%, unless part of the habitat was missed by control. However, even under mean RTCI targets of 5% and 2% the expected number of dispersing infected possums was only 2 or 1 over the 10-year control period, with a predicted upper 95% limit of 9 possums. This contrasts dramatically with the numbers expected to disperse from areas without control (Table 7).

Table 7. Predictions of the rate of dispersal of infected possums out of the control area for each RTCI target threshold for each scenario vs. the number dispersing when no control was applied. Values are the median (50th percentile) and upper 95th percentile (U95) number of infected possums dispersing outside the control area over the 10 year control period.

	RTCI							
	5%		2%		1%		No control	
Scenario	median	U95	median	U95	median	U95	median	U95
1	2	9	1	4	0	2	851	955
2	1	9	1	4	0	2	238	301
3	0	3	0	1	0	1	127	165
3 + missed 30 ha patch	2	7	1	6	1	5	127	165
3 + monitor strategy 1	1	6	0	4	0	3	127	165
3 + monitor strategy 2	0	5	0	2	0	1	127	165

5.3 Cost effectiveness of RTCI targets for eradicating Tb

Based on the expected variation in control efficacy (Table 2 and Figure 2), and the costs of applying aerial or ground based possum control (Table 1), the costs of achieving a particular target RTCI are given in Figure 5. In general, the cost of control was greatest in the uniform high density habitat and least in the uniform low density habitat. The cost of achieving a 5% RTCI was predicted to be between $27/ha and $38/ha for aerial control and $50/ha and $61/ha for ground based control. The cost of achieving a 2% RTCI was predicted to be between $36/ha and $53/ha for aerial control and $63/ha and $80/ha for ground based control.

The cost effectiveness of different RTCI targets for each scenario and control type is given in Table 8. Overall, reducing the RTCI target threshold from 5% to 2% increased the accumulated cost of achieving a 95% probability of Tb extinction by 15% on average (including monitoring costs).

Further reducing the RTCI threshold from 2% to 1% resulted in a further increase in the cost of eradication by 16% on average.

Considering each scenario, the uniform low density possum population (scenario 2) had the lowest percent increase in the cost of achieving eradication when moving from a 5% to a 2% threshold (11%) (Table 8). The corresponding highest increase in the cost when moving from a 5% to a 2% RTCI threshold occurred in the uniform high density population (scenario 1) (19%) (Table 8). The scenarios that had the lowest and highest percent increases in cost when moving from a 2% to a 1% RTCI threshold were the uniform high density possum population (scenario 1) (12%) and the uniform low density possum population (22%), respectively.

It should be noted that these conclusions are sensitive to the modelled relationship between RTCI and cost. If control is more cost effective than assumed in the model, then achieving a specified RTCI is less cost sensitive and this opportunity cost would be reduced or disappear entirely.

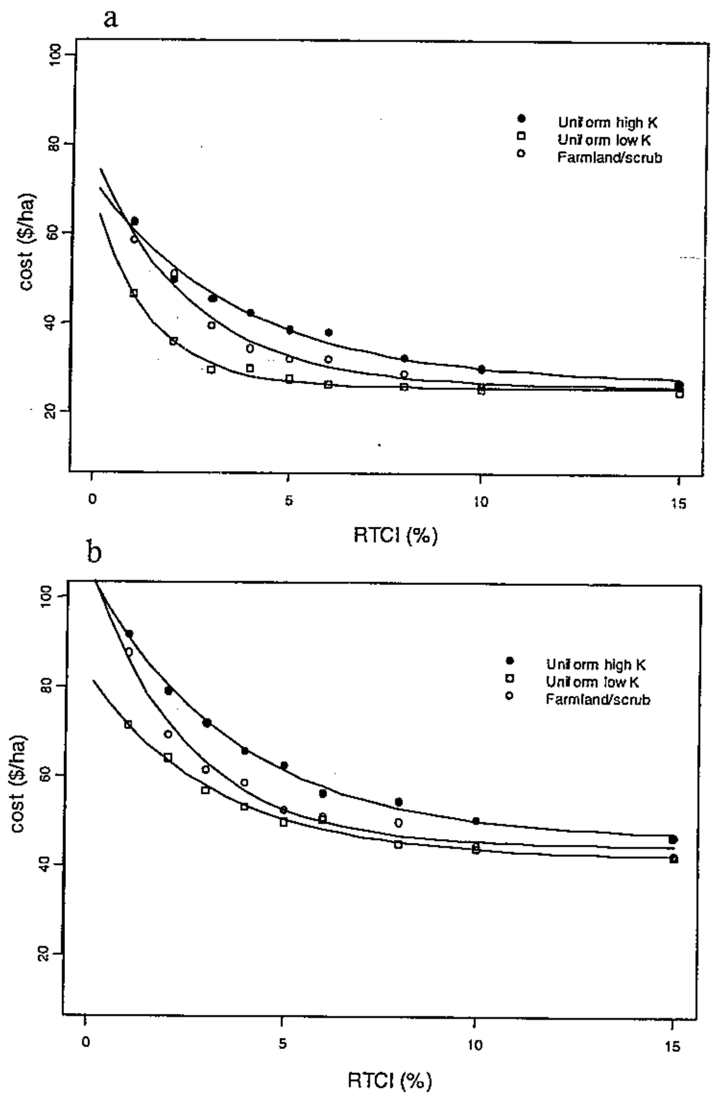

Fig. 5 The cost ($/ha) of achieving a certain RTCI for (a) aerial and (b) ground based possum control for different habitat types. Each point is the mean of 100 simulated control operations. Line is the least-squares regression fit of equation 1.

Table 8. The predicted accumulated cost ($/ha) of achieving a 95% probability of Tb extinction (eradication) for RTCI target thresholds of 5%, 2% or 1% for each of the three scenario types. Costs are discounted to present value (2004 dollars). Values in parentheses are upper and lower 95% confidence intervals.

		RTCI target		
Scenario type	Control type	5%	2%	1%
Uniform high density populations (Scenario 1)	Aerial	$ 51 (46, 56)	$ 66 (58, 74)	$ 77 (68, 87)
	(with monitoring)	$ 69 (62, 76)	$ 84 (74, 93)	$ 94 (83, 106)
	Ground	$ 76 (68, 84)	$ 92 (81, 103)	$ 104 (92, 117)
	(with monitoring)	$ 95 (85, 105)	$ 110 (98, 123)	$ 122 (108, 137)
Uniform low density populations (Scenario 2)	Aerial	$ 36 (33, 39)	$ 44 (39, 48)	$ 56 (50, 63)
	(with monitoring)	$ 54 (49, 59)	$ 60 (54, 66)	$ 72 (64, 80)
	Ground	$ 58 (53, 63)	$ 69 (61, 76	$ 88 (78, 99)
	(with monitoring)	$ 77 (70, 84)	$ 85 (76, 94)	$ 105 (92, 117)
Mixed farmland/scrub habitat (Scenario 3)	Aerial	$ 37 (33, 41)	$ 50 (44, 55)	$ 62 (54, 70)
	(with monitoring)	$ 59 (53, 65)	$ 71 (63, 79)	$ 82 (72, 93)
	Ground	$ 62 (55, 68)	$ 75 (66, 83)	$ 85 (74, 96)
	(with monitoring)	$ 84 (76, 93)	$ 95 (84, 107)	$ 110 (96, 125)

5.4 The effectiveness of possum vaccination

When used as the sole disease control method, vaccination was predicted to be not as effective as lethal control for achieving Tb eradication. Vaccination applied every year (assuming a 90% coverage) achieved Tb eradication within 9 years assuming a 95% vaccine response rate or 10 years assuming a 70% vaccine response rate (Figure 6a). However, if vaccination is applied only every 3 years then Tb could not be eradicated within 10 years, even assuming no decay in immunity (Figure 6b).

If immunity does decay, then the efficacy of vaccination depends on the response rate, the guarantee time and the vaccine half-life following the guarantee time. When vaccination was applied each year assuming 90% coverage, then the effect of decay in vaccine immunity diminished if the guarantee time was 3 years as opposed to one year (Figure 7). However, Tb could only be eradicated within 10 years if the vaccine had at least a 95% response rate and a one year guarantee time with a half life of 2 years, or a 3-year guarantee time with a half life of 2 or 1 years (Figure 7).

Vaccination combined with a single ground control operation was more efficient than vaccination alone (Figure 8). In addition, variation in the vaccine response rate had a minor effect on the probability of Tb extinction within a given time, especially if vaccination was applied each year following a single ground control operation.

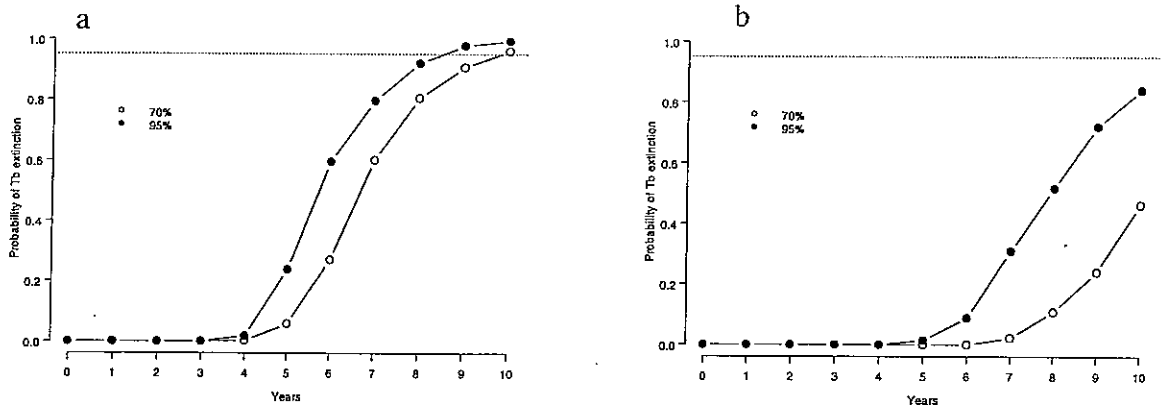

Fig. 6 The probability of Tb extinction vs. time since start of vaccine application assuming 90% coverage and a vaccine responder rate of 70% or 95% with no decay in immunity. (a) vaccination application every year and (b) vaccine application every 3 years.

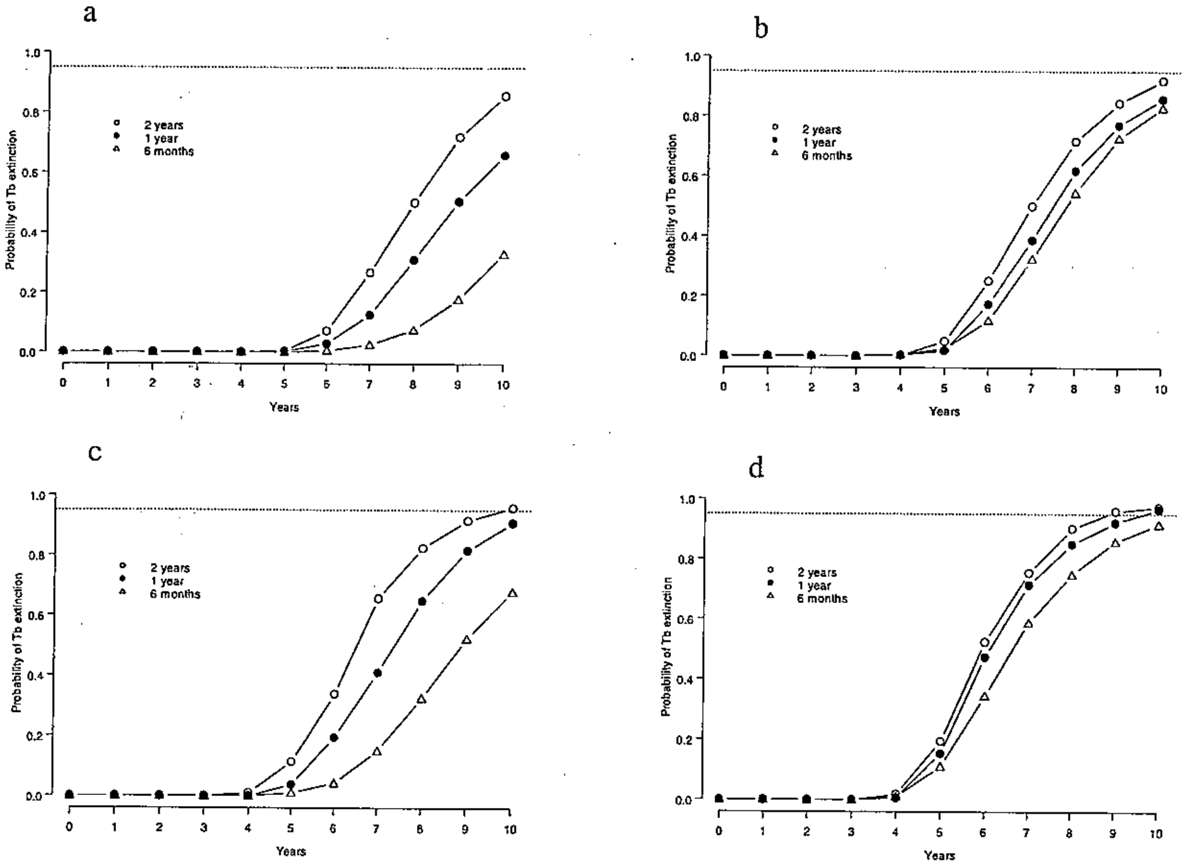

Fig. 7 The probability of Tb extinction vs. time since start of vaccine application assuming 90% coverage and vaccine application every year with a vaccine half life of either 2 years, 1 year or 6 months. (a) vaccine efficacy of 70% with a 1 year guarantee time (b) vaccine efficacy of 70% with a 3 year guarantee time, (c) vaccine efficacy of 95% with a 1 year guarantee time and (d) vaccine efficacy of 95% with a 3 year guarantee time.

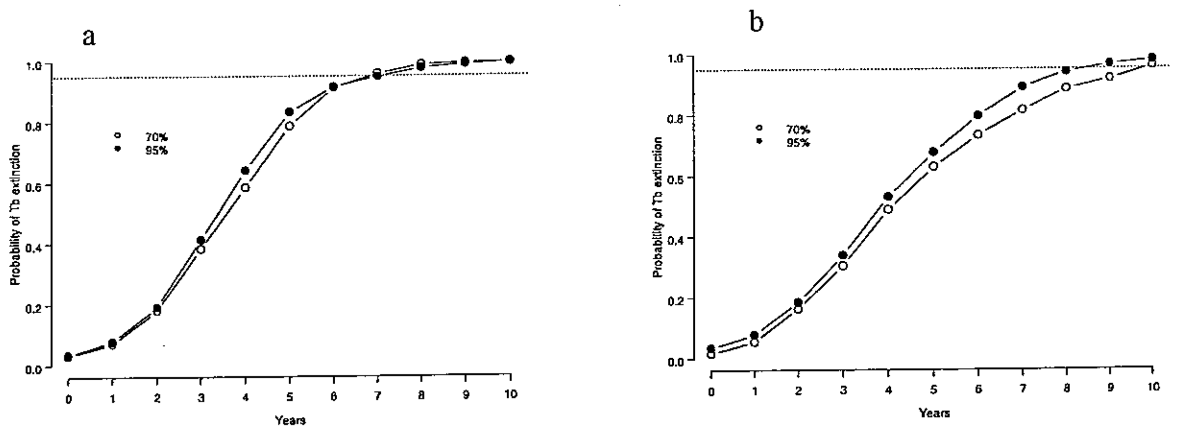

Fig. 8 The probability of Tb extinction vs. time since start of combined ground control and vaccination for vaccine response rates of 70% or 95% with no decay in immunity and a vaccine coverage of 90%. (a) single ground control operation followed by vaccination application every year and (b) single control operation followed by vaccine application every 3 years.

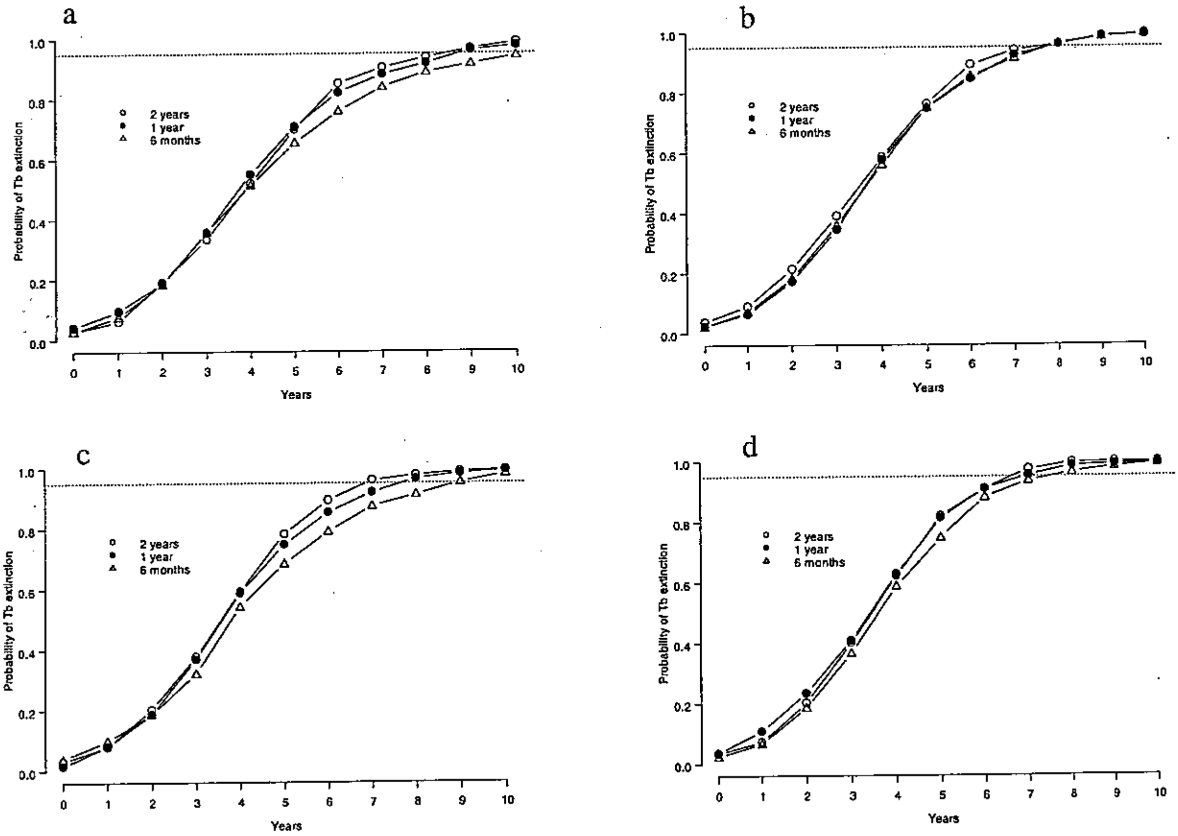

Fig. 9 The probability of Tb extinction vs. time since start of combined ground control and vaccination assuming 90% coverage and vaccine application every year with a vaccine half life of either 2 years, 1 year or 6 months. (a) vaccine efficacy of 70% with a 1 year guarantee time (b) vaccine efficacy of 70% with a 3 year guarantee time, (c) vaccine efficacy of 95% with a 1 year guarantee time and (d) vaccine efficacy of 95% with a 3 year guarantee time.

If immunity decays, then the predictions are similar to those for vaccination used alone; that is, the efficacy of vaccination following a single control operation depends on the response rate, the guarantee time and the vaccine half-life following the guarantee time. If vaccination is applied each year following control, then the time taken to achieve Tb eradication was not affected greatly by the vaccine response rate, the guarantee time and the decay rate, taking 7–10 years to achieve a 95% probability of Tb extinction unless the vaccine had only a 70% response rate, 1 year guarantee time and a half life of 6 months (Figure 9).

If vaccination is applied only every 3 years following control, then the specifications of the vaccine become more important. Here, a 95% probability of Tb extinction could only be achieved within 10 years if the vaccine had a 95% response rate, a guarantee time of 1 year with a 2-year half life or a 95% response rate and a guarantee time of 3 years with a half life of at least 1 year (Figure 10).

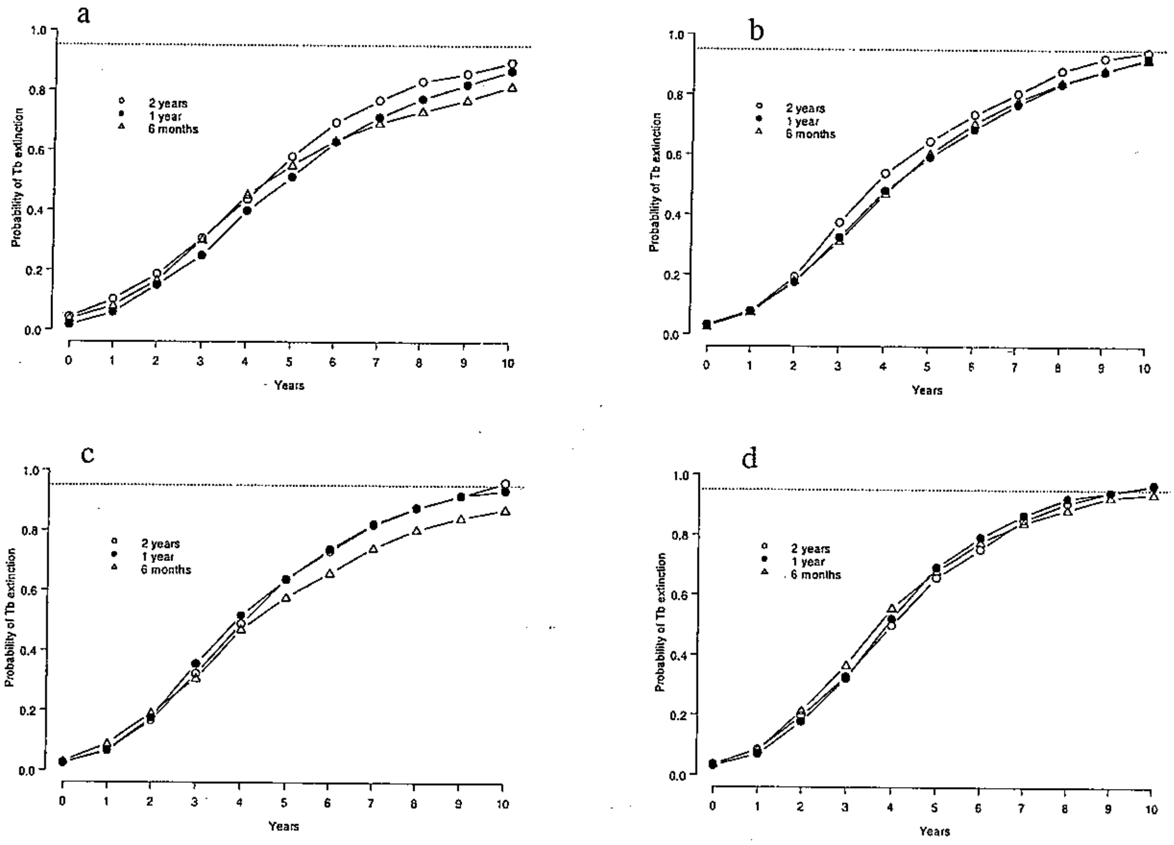

Fig. 10 The probability of Tb extinction vs. time since start of combined ground control and vaccination assuming a 90% coverage and vaccine application every 3 years with a vaccine half life of either 2 years, 1 year or 6 months. (a) vaccine efficacy of 70% with a 1 year guarantee time (b) vaccine efficacy of 70% with a 3 year guarantee time, (c) vaccine efficacy of 95% with a 1 year guarantee time and (d) vaccine efficacy of 95% with a 3 year guarantee time.

5.5 Substitution costs of vaccination

Based on the accumulated cost of achieving Tb eradication for ground based possum control for uniform low density possum populations (scenario 2) (Table 8), we can determine the substitution cost of vaccination that will achieve the same benefits as lethal control using RTCI targets. We calculated this for the strategy using vaccination after a single ground control operation and determined the substitution cost for vaccination applied every year and every 3 years. Using the accumulated total cost of control (including monitoring costs) for ground control given in Table 8 and subtracting the cost of initial control used ($40/ha), we obtained the discounted accumulated cost of maintenance control and monitoring required to achieve Tb eradication (Table 9). To achieve the same benefits as current RTCI targets, vaccination applied each year requires 7 years to achieve eradication (assuming no decay in immunity). This requires 8 annual vaccination applications (i.e. 1 in year 0 and 1 in each of 7 years following the initial control). Therefore, we calculated the substitution cost of each vaccine application that gave the same total discounted cost as maintenance control for each RTCI target. For example, the total cost of maintenance control required to achieve Tb eradication using an RTCI of 5% was $37/ha (Table 9). Therefore the substitution cost of each vaccination application needed to be no more than $6.30/ha, for each of 8 vaccine applications, to give the same benefits as maintenance control (Table 9).

These calculations indicated that the substitution costs for a single vaccine application had to be less than the cost of a single application of maintenance control ($27/ha; Table 1). For example, vaccination applied every 3 years would need a cost per application that was 48% less than ground based maintenance control to achieve the same benefits and costs as an RTCI target of 5%. This is entirely because vaccination needed to be applied more frequently, on average, than lethal control, to achieve the same benefits. Typically, bait costs represent between 10% and 30% of the cost of applying ground control (e.g., Speedy 2003). Therefore, if the cost per application for vaccination needs to be 48% less to achieve similar costs and benefits to lethal control, then this is likely to be unachievable, even if the cost of vaccine baits was negligible.

Table 9. The substitution cost of each vaccine application applied following a single control operation required to achieve the same benefits (95% probability of Tb extinction) and costs as lethal control alone using RTCI targets of 5%, 2% or 1%.

		Vaccination substitution costs per application ($/ha)	
RTCI	Total cost of maintenance control ($/ha)	Annual vaccination ($/ha)	3 yearly application ($/ha)
5	37	$ 6	$ 14
2	45	$ 8	$ 16
1	65	$ 11	$ 24

6. Conclusions

- Adopting RTCI targets lower than 5% incurs an opportunity cost because the accumulated cost of control for RTCI targets of 2% and 1% exceeds that for 5% RTCI for the same benefits. However, this conclusion is sensitive to the modelled relationship between RTCI and cost. If control is more cost effective than assumed in the model, then achieving a specified RTCI is less cost sensitive and this opportunity cost would be reduced or disappear entirely.
- This opportunity cost appears greater when controlling high density populations than low density populations, as greater control intensity (percent reduction) is required to reduce high density populations down to a specified RTCI target, compared with low density populations. Hence, the cost of achieving that RTCI is also greater than for low density populations.
- The benefits of adopting RTCI targets lower than 5% appear to be related entirely to the time taken to eradicate Tb. Lower RTCI targets result in Tb being eradicated sooner; however, the accumulated cost will be higher. The time taken to eradicate Tb is specific to the area simulated (2500 ha). Times to eradication would be shorter on smaller control areas and longer on larger ones.
- Areas of habitat missed by control can significantly increase the time taken to eradicate Tb. For the case where a 30-ha high-density area containing infected possums within an 859-ha area of farmland/scrub habitat was missed by control, Tb could not be eradicated within 10 years. Using line thresholds in conjunction with RTCI targets can detect patches of this size, especially using double the number of lines and half the number of traps per line. However, even when using these monitoring strategies, the time to eradicate Tb is increased compared with that when no patches are missed.
- There appears to be a finite, albeit very small risk that Tb is exported by possums from control areas compared with areas where no control occurs. This suggests that the probability of Tb being spread by possums from within the control area is also small.
- Vaccination can potentially be used to eradicate Tb from possum populations, and hence is a viable, alternative Tb control technique in situations where lethal control is undesirable. However, vaccination will cost substantially more than lethal control, with its most efficient use likely to be where lethal control is used to obtain an initial population reduction.
- Vaccination applied each year after an initial control operation should eradicate Tb within 7 years and is little affected by variation in the response rate or decay in immunity provided vaccination is effective for at least 1 year. Vaccination every 3 years following an initial control operation should eradicate Tb within 10 years. However the vaccine must have a response rate of at least 95% and a guarantee time of at least a year with a half life of no less than 2 years, or a 95% response rate and a guarantee time of 3 years with a half life of at least 1 year. If repeat vaccinations "reset" the guarantee time, then decay in vaccine immunity can be largely ignored.

7. Recommendations

- Control applied to high density possum populations should adopt a RTCI target of 5% while low density and most farmland/scrub populations should adopt a RTCI target of 2%. The use of RTCI targets lower than 2% incur more of an opportunity cost and do not significantly reduce the time taken to eradicate Tb.

- To achieve Tb eradication, monitoring (each year) and control should be undertaken for at least 7 years, using a 5% RTCI target, and 5 years, using a 2% RTCI target, when controlling possum populations in continuous forest. On farmland/scrub habitats the minimum time for conducting control operations can be reduced to 6 and 4 years for RTCI targets of 5% and 2% respectively. Controlling an area every year is not necessary to achieve Tb eradication as long as control is uniformly applied and monitoring undertaken each year to "trigger" control.
- Vaccination could be developed as a complementary disease control tool to lethal control. To eradicate Tb, vaccination will need to be applied each year for 7 years following an initial reduction in possum density. To be more cost-effective, vaccination could be applied every 3 years. However, to achieve eradication the vaccine will need to have response rate of at least 95% and an effective immune period of between 1–3 years. Additional studies should compare the efficacy of vaccination and culling when used as 'buffer' areas to prevent disease spread.

---

8. Acknowledgements

We thank Clare Veltman for data used to calculate the efficacy of possum control operations on the DOC estate.

9. References

Barlow, N.D. 1991a: A spatially aggregated disease / host model for bovine Tb in New Zealand possum populations. *Journal of Applied Ecology* 28: 777-793.

Barlow, N.D. 1991b: Control of endemic bovine Tb in New Zealand possum populations: results from a simple model. *Journal of Applied Ecology* 28: 794-809.

Barlow, N.D.; Clout, M.N. 1983: A comparison of 3-parameter, single-species population models, in relation to the management of brushtail possums in New Zealand. *Oecologia* 60: 250-258.

Barlow, N.D. 2000: Non-linear transmission and simple models for bovine tuberculosis. *Journal of Animal Ecology* 69: 703-713.

Caley, P.; Hickling, G.J.; Cowan, P.E.; Pfeiffer, D.U. 1999: Effects of sustained control of brushtail possums on levels of *Mycobacterium bovis* infection in cattle and brushtail possum populations from Hohotaka, New Zealand. *New Zealand Veterinary Journal* 47: 133-142.

Coleman, J.; Caley, P. 2000: Possums as a reservoir of Bovine Tb. *In* Montague T.L. *ed.* The brushtail possum; Biology, impact and management of an introduced marsupial. Manaaki Whenua Press, Lincoln, New Zealand. Pp. 92-104.

Collett, D. 1991: Modelling binary data. London, UK., Chapman & Hall.

Corner, L.A.L.; Norton, S.; Buddle, B.M.; Morris, R.S. 2002: The efficacy of bacille Calmette-Guerin vaccine in wild brushtail possums (*Trichosurus vulpecula*). *Research in Veterinary Science* 73: 145-152.

Corson, P. 1999: Pirongia possum control operation 1996-1998. Department of Conservation Report (unpublished), 44 p.

Dymond, J.R.; Shepherd, J.D. 2004: The spatial distribution of indigenous forest and its composition in the Wellington region, New Zealand, from ETM+ satellite imagery. *Remote Sensing of Environment* 90: 116-125.

Efford, M. 2000: Possum density, population structure, and dynamics. *In* Montague T.L. *ed.* The brushtail possum: Biology, impact and management of an introduced marsupial. Manaaki Whenua Press, Lincoln, New Zealand. Pp. 47-61.

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

Efford, M.G. 1996: Simulating spatially distributed populations. *In* Floyd R.B., Sheppard A.W., and De Barro P.J. *eds.* Frontiers of population ecology. CSIRO publishing, Melbourne, Australia. Pp. 409-418.

Hickling, G.J. 1995: Clustering of tuberculosis infection in brushtail possum populations: implications for epidemiological simulation models. *In* Griffin F. and de Lisle G.W. *eds.* Tuberculosis in wildlife and domestic animals. University of Otago Press, Dunedin. Pp. 174-177.

Montague, T.L. 1997: The relative cost and effectiveness of hunting and aerial 1080 poisoning for reducing possum populations in native forest. Landcare Research Contract Report LC9697/82, 23 p.

Pfeiffer, D.U.; Hickling, G.J.; Morris, R.S.; Patterson, K.P.; Ryan, T.J.; Crews, K.B. 1995: The epidemiology of *Mycobacterium bovis* infection in brushtail possums (*Trichosurus vulpecula* Kerr) in the Hauhungaroa ranges, New Zealand. *New Zealand Veterinary Journal* 43: 272-280.

Ramsey, D.; Ball, S. 2004: The statistical limits of RTCI monitoring. Landcare Research Contract Report LC0304/068, 37 p.

Ramsey, D.; Efford, M.; Ball, S.; Nugent, G. 2005: The evaluation of indices of animal abundance using spatial simulation of animal trapping. *Wildlife Research* 32: 229-237.

Roberts, M.G. 1996: The dynamics of bovine tuberculosis in possum populations, and its eradication or control by culling or vaccination. *Journal of Animal Ecology* 65: 451-464.

Speedy, C. 2003: Hatepe trial - comparison of ground and aerial Tb vector control methods. Epro research report to the Animal Health Board, 35 p.

Thomas, M.; Fitzgerald, H. 1994: Bait-station spacing for possum control in forest. Landcare Research Contract Report LC9394/118, 9 p.

Warburton, B.; Cullen, R. 1993: Cost-effectiveness of different possum control methods. Landcare Research Contract Report LC9293/101, 16 p.

Warburton, B.; Thomson, C. 2002: Comparison of three methods for maintaining possums at low density. Science for Conservation 189, 20 p.

---

10. Appendix

The spatial possum/Tb model

Births in the model occur as a single 'pulse' at the beginning of each year with the overall (population) birth rate given in Barlow (2000: Table 1) adjusted by the adult sex ratio to give the number of weaned offspring per female. The model simulates other events for each individual (i.e. deaths, infection, dispersal) in continuous time by treating them as stochastic, Poisson processes. Hence, the time-to-the-next-event is modelled as an stochastic exponential process with the rates for each event based on the parameter estimates given in Table 1. Exponential pseudo-random numbers are used to draw a random time-to-the-next-event with event times occurring before the end of the next time horizon queued for processing. The advantage of this procedure is that 'events' occur in random order for each individual; hence, no arbitrary time sequence is imposed on event processing.

Dispersal, population regulation and disease transmission

Adult possums were assumed to occupy a fixed home range, unless a "decision" was made to disperse. Adult dispersal rates were assumed to be low (males – 10%; females – 5%). All offspring were assumed to disperse from the natal range (hard-wired dispersal) with males dispersing twice as far, on average, as females (2 km cf. 1 km). However, the distribution of dispersal distances had long 'tails' and effectively, females tended to settle close to the natal range.

Population size was defined locally, for any point on the landscape, as the sum of the intensity of home range use of each home range overlapping that point. Conceptually, this can be thought of as the 'intensity' of competition at that point; hence, it integrates all the pair-wise interactions between a notional animal residing at that point, and the existing members of the population (Efford 1996). Thus, local population size, $N_{x,y}$, was defined for a point, x_0 ($=x_{x,y}$) as

$$N_{x,y} = \sum_i g(|x_0 - x_i|) \qquad \text{Equation A1.}$$

where the function g() describes the degree of overlap between the ranges of two individuals. We assumed that each individual had a circular bivariate-normal home range utilisation distribution. Hence $g()$ was equal to

$$g(d) = e^{\frac{-d^2}{2\sigma^2}} \qquad \text{Equation A2.}$$

where d is equal to the distance between the home range centres of individuals x_0 and x_i and σ indexes home range size. For convenience, we have scaled local population size so that the total population size N is equal to

$$N = \int_{\text{all space}} N_{x,y} \qquad \text{Equation A3.}$$

achieved by representing the contribution of each individual as a bivariate probability density distribution (Efford 1996). Hence the sum of a single home range utilisation distribution is equivalent to 1 individual.

Similarly, the Tb transmission risk at any point on the landscape $I_{x,y}$ was defined as the sum of the intensity of home range use of each home range for each infected individual overlapping that point. Conceptually, I_{xy} is equivalent to the local contact rate between a susceptible individual located at (x,y) and all the infected individuals in the population with home ranges overlapping that point. However, unlike local population size, individual contributions are not scaled to unit density. This has the characteristic that the contact rate between two individuals whose home range centres coincide is equal to 1 per unit time (i.e. they are certain to contact over the next time interval). Hence, the transmission rate parameter (β) can be defined as the probability that an infectious contact results in transmission. Thus, the force of infection (λ) can also be defined locally as

$$\lambda_{x,y} = \beta I_{x,y} \qquad \text{Equation A4}$$

where β is the transmission rate parameter. No independent estimates of β exist for Tb in possums. The large-scale Tb prevalence in possum populations from cross sectional surveys averages 5% and is typically between 1% and 10% (Coleman & Caley 2000). Therefore, values of β were found numerically that gave a steady-state 5% prevalence of infection at equilibrium density. This follows the same procedure as Barlow (1991a) for estimating the value of β.

Birth and death rates were density-dependent and varied spatially as a function of $N_{x,y}$ and the local carrying capacity $K_{x,y}$. These functions followed the continuous time form for theta-logistic population growth used by Barlow (2000) e.g.,

$$B(N_{x,y}) = b - \delta r \left(\frac{N_{x,y}}{K_{x,y}} \right)^{\Theta} \qquad \text{Equation A5}$$

$$D(N_{x,y}) = d + (1-\delta)r\left(\frac{N_{x,y}}{K_{x,y}}\right)^{\Theta} \qquad \text{Equation A6}$$

where $B(N_{x,y})$ is the density-dependent birth rate and $D(N_{x,y})$ is the density-dependent death rate for an individual located at (x, y). Other parameters are as in Table 1.

Non-linear contact rates

Barlow (2000) and Roberts (1996) relaxed the assumption that the contact rate between individuals scales linearly with population density. Roberts (1996) implemented a saturating function that has the characteristic of being equal to 1 when population density and carrying capacity are equal (i.e. relative density N/K = 1) for any value of the shape parameter.

A spatial implementation for non-linear contact rates should allow the local infectious contact rate ($I_{x,y}$) to be a function of local population size ($N_{x,y}$). The contact rate between a susceptible individual located at a point (x,y) and its infectious neighbours is a function of the number of infectious neighbours whose home ranges overlap that point. If home range size, indexed by the parameter σ (equation A2), is not a function of local population size, then $I_{x,y}$ will scale linearly with $N_{x,y}$. However, if σ is a function of local population size, for example, if home range size is inversely related to local population size, then $I_{x,y}$ will not scale linearly with $N_{x,y}$. To elucidate this relationship, we determined the empirical relationship between σ and population density from field data using routine mark-recapture trapping of possums. As a byproduct of the estimation of population density (Efford 2004), the parameter σ was also estimated using information of distance between recaptures. Using the same dataset given in Ramsey et al. (2005), a non-linear relationship between σ and (local) population density was determined (Figure 11). Using this relationship, individual home range size σ was made dependent on local population size $N_{x,y}$, effectively resulting in a non-linear relationship between the local infectious contact rate $I_{x,y}$ and local population size $N_{x,y}$ (Figure 12). Thus, possums enlarge their range as (local) population density reduces; in effect, this goes some way to maintaining their contact rate with their neighbours.

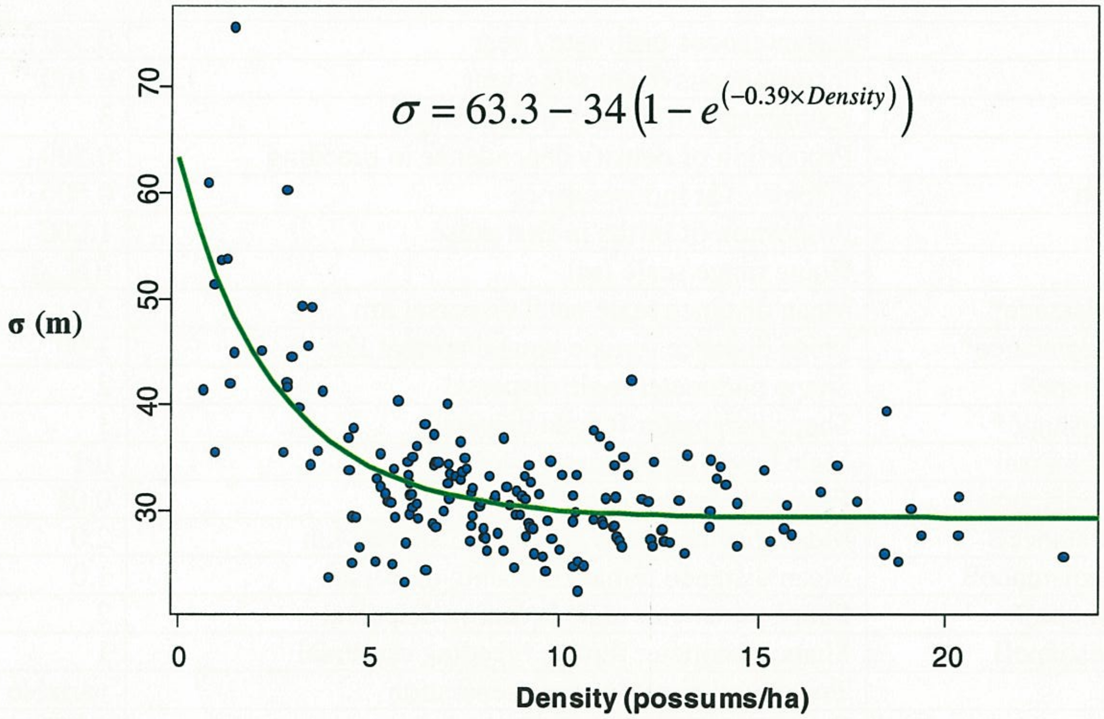

Fig. 11 The relationship between an index of home range size (σ) and population density derived from mark-recapture trapping.

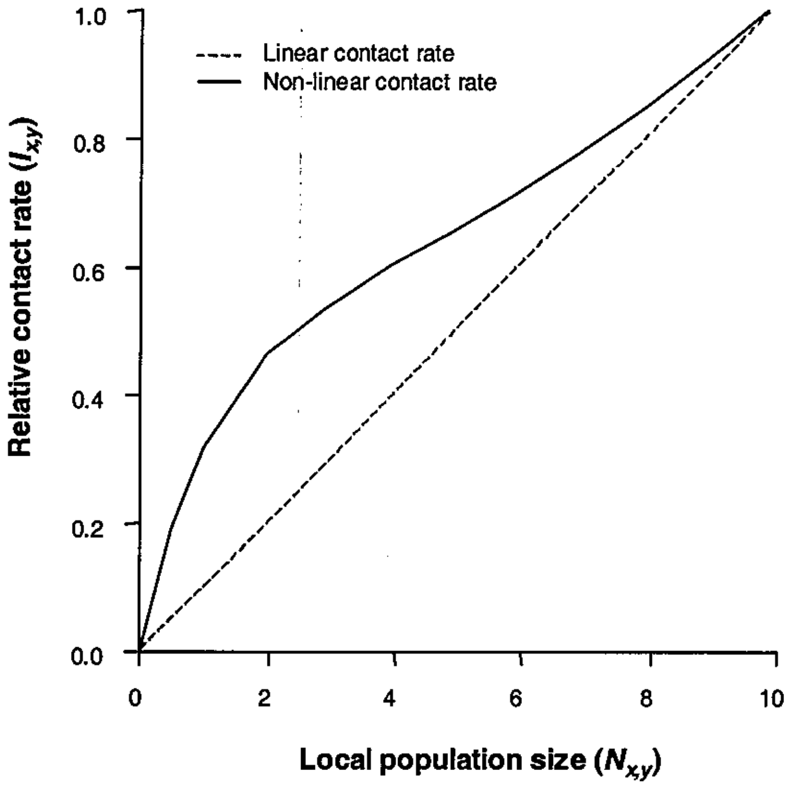

Fig. 12 Non-linear contact rate function (solid line) used in the model based on data in Figure 5 and predicted from the home range model of contact structure compared with the linear contact rate of the default model (dashed line).

Table 11. Default parameters for the possum Tb model

b	Instantaneous birth rate / year	0.300
d	Instantaneous death rate / year	0.100
θ	Asymmetry of density dependence	3
δ	Proportion of density dependence in breeding	0.500
sexratio	P(female) at independence	0.500
γ	Proportion of births in first pulse	1.000
σ	Home range scale (m)	$f(N_{x,y})$
Maledistance*	Mean distance male natal dispersal km	2.0
Femaledistance*	Mean distance female natal dispersal km	1.0
Maleshape*	Shape parameter male dispersal	2
Femaleshape*	Shape parameter female dispersal	1
Maledispersal	Male breeding dispersal rate/year	0.1
Femaledispersal	Female breeding dispersal rate/year	0.05
maledistanceB	Mean distance male breeding dispersal km	2.0
femaledistanceB	Mean distance female breeding dispersal	1.0
MaleshapeB	Shape parameter male breeding dispersal	2
femaleshapeB	Shape parameter female breeding dispersal	1
β_0	Transmission rate at zero separation	variable
p	Pseudovertical transmission	0.250
α	Extra mortality if infected	1.000