Cost–benefit analysis of deer control within a TB eradication programme

Animal Health Board

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Landcare Research
Manaaki Whenua

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Mandy C Barron, Graham Nugent

Landcare Research

Prepared for:

Animal Health Board

PO Box 3412
Wellington

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Landcare Research, Gerald Street, PO Box 40, Lincoln 7640, New Zealand, Ph +64 3 321 9999,
Fax +64 3 321 9998, www.landcareresearch.co.nz

Reviewed by:	*Approved for release by:*
Andrew Gormley Quantitative Wildlife Ecologist Landcare Research	Andrea Byrom Science Team Leader Wildlife Ecology & Epidemiology

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Summary

Project and Client

- As part of the TB Eradication – Effectiveness and cost of alternative operational strategies research programme (R-10731), Landcare Research was contracted by the Animal Health Board from November 2010 to April 2011 to assess the likely consequences of deer control on the time taken to achieve TB freedom in wild deer and possum populations, and in reducing the risk of TB spillback and re-establishment from infected deer to TB-free possum populations.

Objectives

- To predict the duration and magnitude of the risk of TB spillback from deer to possums without any deer control and estimate the cost and impact of various deer control regimes on reducing that risk.

Methods

- A non-spatial, discrete-time, age- and sex-structured, deer-TB population model was constructed to explore the consequences of deer control on deer demography and TB prevalence. It was assumed that wild deer were primarily spillover hosts of TB, thus any TB infection in deer was assumed to result from transmission from infected possums. Possum-TB dynamics were modelled using a discrete-time version of Barlow's (2000) model.
- Spillback or transmission of TB from deer to possum populations was modelled in two stages comprising (a) the probability of an individual possum becoming infected by a TB-infected deer carcass, and (b) the probability that a single TB-infected possum could re-establish TB within the possum population. The latter probability was derived from the spatial possum-TB model of Ramsey & Efford (2010), using a map of carrying capacity derived from the Hauhungaroa Range Vector Control Zones and across a range of possum densities.
- Three deer-control strategies were modelled: one-off foliage baiting, 5 years' targeted hunting of female deer pre-eradication of TB from possums, and 5 years' targeted hunting of female deer post-eradication of TB from possum. Deer control was modelled as an annual proportional cull of the specified age and sex classes of the deer population.

Results

- With no deer control, the spillback risk period following eradication of TB from possums was about 7 years duration and the probability of TB spillback and re-establishment occurring over that period was 0.06.
- Simulated deer control by foliage baiting resulting in an 80% kill reduced the risk period by 2 years and the probability of spillback and re-establishment by a quarter and was the most cost effective of the control options simulated.

- Model predictions were sensitive to the parameter defining the probability of an individual possum becoming infected given encounter with a TB-infected deer carcass, a parameter for which we have only quantitative circumstantial evidence.

Conclusions

- None of the deer control methods tested were very cost effective at reducing the spillback risk period or the probability of TB spillback and re-establishment occurring. Given the overall low probability of spillback and our assumption that TB will eventually drop out of wild deer populations once interspecies transmission is curbed by effective possum control, spending additional money on deer control does not appear to be warranted.

Recommendations

- We do not recommend either broad-scale 'whole population' deer control or selective control of adult female deer as specific tools for reducing the risk of TB spillback from deer resulting in re-establishment of TB in possums. Instead, we recommend that the AHB maintain low possum numbers for a period of at least 15 years after possum control was initiated in all of the areas occupied by the deer population.
- However, we consider that where surveillance of TB infection levels in deer is planned (to contribute toward assessment of TB levels in possums), the twin incidental benefits of assessing the potential size of the spillback and providing a small reduction in the duration of spillback risk should be taken into account.

1 Introduction

As part of the TB Eradication – Effectiveness and cost of alternative operational strategies research programme (R-10731) Landcare Research was contracted by the Animal Health Board from November 2010 to April 2011 to assess the likely consequences of deer control on the time taken to achieve TB freedom in wild deer and possum populations, and in reducing the risk of TB spillback and re-establishment from the deer to TB-free possum populations.

2 Background

Eradication of bovine tuberculosis (TB) has not yet been confirmed for any large Vector Risk Area (VRA) that includes an extensive forest tract in which TB was previously well established in multiple species of wildlife including deer (AHB 2009). Although wild deer are not considered to be maintenance hosts of TB in New Zealand at their current population density, TB-infected deer, particularly females, can live for many years, so they can potentially vector or carry the disease through long periods of time before becoming infectious close to, or after, death (Nugent 2005). Further, such historically infected deer could potentially 'spillback' or reinfect possum populations with TB (Nugent 2011) long after it had been eradicated from the possum population, particularly if possum control had ceased and possum density had subsequently recovered to above a threshold for TB persistence. That would subvert efforts to achieve TB freedom in possum populations. To avoid this risk, the current management solution is to maintain possum numbers below that threshold density for a period of 15 years based on the premise that any infected deer present at the start of the possum control programme should have died out by then. For large areas of native forest, the main context in which deer densities are high enough to be of concern, this is likely to involve 3–4 aerial poisoning operations at approximately 5-year intervals (AHB 2009).

The key question addressed here is whether control of an infected deer population could substantially reduce the long-run total cost of the possum monitoring and control needed to eradicate TB from wildlife. If such deer control was able to remove all infected deer within 10 years, for example, then one less poisoning operation would be needed – a 25–33% saving in possum control costs. The cost-effectiveness of controlling a TB-infected deer population was therefore investigated as part of a wider project looking at the feasibility and cost-effectiveness of different operational strategies for confirming that TB has been eradicated from wildlife hosts in vector control zones (VCZs) across the central North Island VRA (R-10731: TB Eradication – Effectiveness and cost of alternative operational strategies).

In the absence of empirical data on the spillback risk deer pose, we have taken a three-stage modelling approach. Firstly, we constructed a non-spatial age- and sex-structured population model for deer and used that to model both a range of deer control scenarios (and their cost) and the effect of that control on TB levels in deer, specifically the continued 'availability' of TB-infected deer capable of transmitting TB back to possums. Secondly, we used a spatial possum-TB model (Ramsey & Efford 2010) to predict the probability that a single TB-infected possum could re-establish TB within the possum population over a range of possum densities. These two models were linked using Barlow's (2000) non-spatial model of possum population dynamics, control, and TB persistence.

This suite of interlinked models was then used to assess the epidemiological consequences of conducting deer control in addition to the current standard possum control regime designed to eradicate TB from the possum population. Using a simple cost–benefit calculation we estimate the reduction in duration of the spillback risk period and the overall probability of TB spillback from deer to possums per dollar spent on deer control.

3 Objectives

- To predict the duration and magnitude of the risk of TB spillback from deer to possums without any deer control and estimate the cost and impact of various deer control regimes on reducing that risk.

4 Methods

4.1 Overall modelling approach

The risk of interspecies transmission of TB from deer to possums (‘spillback’; Nugent 2011) was a parameter of primary interest in this study and was assumed to occur via possums scavenging or investigating infected deer carcasses (Nugent 2005). A complete two-species model for TB in deer and possum populations would require four host pairs: deer to deer, possums to possums, possums to deer and deer to possums. However, intraspecies transmission in deer is considered to occur only rarely in the low-density wild deer populations in New Zealand, with most TB infection in deer attributed to transmission from sympatric infected possum populations (Nugent 2005). Deer-to-deer transmission was therefore not modelled.

TB incidence rates in deer appear to vary with age and be highest in young independent deer aged 1–3 years and there is some evidence that rates are higher for young males compared with young females (Nugent 2005). In addition, effectiveness of deer control can vary according to age and sex (especially if control is targeted at specific age–sex classes), and even without control females tend to live longer than males. An age- and sex-structured population modelling approach was therefore chosen to simulate both the epidemiology of TB in deer and the population dynamics of deer in response to a range of control scenarios. A non-spatial approach was adopted as the complexity and high cost of developing an explicitly spatial deer population was considered to be not warranted for our purposes.

Options for deer control include private (recreational and commercial) hunting, contract hunting, or poisoning. We considered that it would be difficult to achieve increased deer control via some form of enhanced recreational hunting (Nugent & Choquenot 2004) but nonetheless we assumed that some form of recreational and commercial hunting combined would provide a ‘background’ control that happened regardless of which deer control strategy disease managers temporarily imposed to speed the eradication of TB. Two contrasting approaches to control were modelled. The first was non-selective ‘whole population’ reductions via foliage bait 1080 poisoning in which toxic gel is applied to the leaves of deer-palatable plants. This method has delivered high percentage kills (>80%) of whitetail (Nugent 1990) and red deer (Sweetapple 1997) populations in field trials. The second deer control approach modelled was contract ground hunting that enabled simulation of scenarios involving targeting of specific age–sex classes within the deer population (specifically adult female deer, the age class most likely to carry TB for the longest periods of time).

A complementary non-spatial model developed by Barlow (2000) was used to simulate the effect of a range of possum control scenarios on possum density and TB prevalence in possums. As the control scenarios typically resulted in the rapid eradication of TB from possums, the re-establishment of TB in possums was modelled as spontaneous regeneration, with the probability of that occurring based on the number of infected deer still present. The spatial possum-TB model (Ramsey & Efford 2010) was then used to predict the probability that a single TB-infected possum could re-establish TB within the possum population over a range of possum densities.

The Hauhungaroa Ranges were nominally used as the case study we were attempting to model, both because the main investigations of TB epidemiology in wild deer were conducted there (Nugent 2005) and because that area is designated as one of two areas in which the AHB aims to prove TB can be eradicated from wildlife in large forest areas (AHB 2009).

4.2 Deer–TB–possum model

4.2.1 Deer population dynamics

Red deer populations were divided into two infection-status (TB^-, TB^+), two sex (females, males) and 16 age (years 0–15) classes and modelled in discrete time using an annual time-step. Both fecundity and survival were assumed to be density-dependent, with deer density having the greatest impact on the fawn and yearling (0 &1 year) age classes (Table 1) as has been observed in red deer populations overseas (Guinness et al. 1978; Coulson et al. 2004). The maximum proportion of females producing offspring per annum was assumed to be 0.7 for yearlings, 0.95 for 2–9 year olds then declining to 0.9 for females aged 15 years or older (Table1; Nugent & Fraser 2005). Twin fawns are rare in the wild (Nugent & Fraser 2005) so only single offspring were modelled and an even sex ratio at birth was assumed. The realised proportion of females producing offspring per annum was the maximum proportion multiplied by a 'Ricker'-type density-dependent function (Ricker 1954). Likewise, proportional survival for each sex/age class was the maximum possible survival modified by Ricker-type density dependence. Survival was assumed to be relatively low in fawns and yearlings, very high for 2–5 year olds then declining with age for 6–15 year olds (Table1; Nugent & Fraser 2005). Stags in the 0–2-year-old age classes were assumed to have lower survival relative to hinds (Table 1) producing an adult sex ratio biased towards females, similar to that observed in unhunted populations (Nugent & Fraser 2005). This combination of vital rates produces a maximum instantaneous rate of increase of r_m=0.29 from very low deer densities, which is similar to maximum population rates of increase measured in overseas studies (Table 1 in Forsyth et al. 2010).

Table 1 Description and default values of deer population model parameters

Parameter description	Symbol*	Value	Unit	Parameter values for those that vary with age (in years):															
				0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15+
Deer carrying capacity	K	20	km^{-2}																
Proportion births female	x	0.5	-																
Strength of density dependence	d_a	var	-	0.45	0.45	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10
Maximum proportion females producing offspring	f_a	var	yr^{-1}	0.00	0.70	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.92	0.92	0.92	0.92	0.92	0.92
Maximum proportional survival	$S_{F,a}$	var	yr^{-1}	0.80	0.95	0.99	0.99	0.99	0.99	0.97	0.96	0.95	0.94	0.90	0.60	0.60	0.50	0.50	0.50
	$S_{M,a}$	var	yr^{-1}	0.80	0.85	0.89	0.99	0.99	0.99	0.97	0.96	0.95	0.94	0.90	0.60	0.60	0.50	0.50	0.50
Proportional survival from TB	S_{inf}	0.96	yr^{-1}																
Proportional resolution of TB	v	0.12	yr^{-1}																
Instantaneous possum to deer TB transmission rate	$i_{F,a}$	var	yr^{-1}	0.005	0.010	0.010	0.010	0.007	0.003	0.003	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002
	$i_{M.a}$	var	yr^{-1}	0.005	0.011	0.015	0.016	0.011	0.006	0.003	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002	0.002

*F = female deer, M = male deer, a = age class

The proportion of deer infected per annum was modelled as an exponential function of the infected possum density and the instantaneous incidence rates listed in Table 1. Incidence rates were assumed to be highest for 1–4-year-old deer and higher in stags than hinds as was found by Nugent (2005). Mortality due to TB infection was assumed to be minimal with annual proportional survival of TB-infected deer set to 0.96. A small proportion of the infected deer population (0.12) resolved the disease per annum, as was suggested by Nugent (2005).

The change in deer abundance D in infection class TB^{-} or TB^{+}, in sex class F and in age class a from year t to year t+1 is represented by the following equations (symbols as in Table 1).

For females (sex = F) in the yearling age class (a = 1):

$$D_{TB-,F,1\,\boldsymbol{t+1}} = \sum_{a=1}^{15} \left(D_{TB-,F,a\,\boldsymbol{t}} + D_{TB+,F,a\,\boldsymbol{t}}\right) \cdot f_a \cdot e^{-d_a \cdot D/K} \cdot x \cdot S_{F,0} \cdot e^{-d_0 \cdot D/K} \cdot e^{-i_{F,0} \cdot P_{i\,t}}$$

$$D_{TB+,F,1\,\boldsymbol{t+1}} = \sum_{a=1}^{15} \left(D_{TB-,F,a\,\boldsymbol{t}} + D_{TB+,F,a\,\boldsymbol{t}}\right) \cdot f_a \cdot e^{-d_a \cdot D/K} \cdot x \cdot S_{F,0} \cdot e^{-d_0 \cdot D/K} \cdot \left(1 - e^{-i_{F,0} \cdot P_{i\,t}}\right)$$

For females (sex = F) in adult age class ($a \geq 2$):

$$D_{TB-,F,a+1\,\boldsymbol{t+1}} = \left(D_{TB-,F,a\,\boldsymbol{t}} \cdot S_{F,a} \cdot e^{-d_a \cdot D/K} \cdot e^{-i_{F,a} \cdot P_{i\,t}}\right) + \left(D_{TB+,F,a\,\boldsymbol{t}} \cdot S_{F,a} \cdot e^{-d_a \cdot D/K} \cdot S_{inf} \cdot v\right)$$

$$\begin{aligned} D_{TB+,F,a+1\,\boldsymbol{t+1}} = &\left(D_{TB+,F,a\,\boldsymbol{t}} \cdot S_{F,a} \cdot e^{-d_a \cdot D/K} \cdot S_{inf} \cdot (1 - v)\right) \\ &+ \left(D_{TB-,F,a\,\boldsymbol{t}} \cdot S_{F,a} \cdot e^{-d_a \cdot D/K} \cdot \left(1 - e^{-i_{F,a} \cdot P_{i\,t}}\right)\right) \end{aligned}$$

where $P_{i\,\mathbf{t}}$ is the density of infected possums (km^{-2}) at time t and all other parameters are as described in Table 1. The equations for males (sex = M) are the same except, x, the proportion of births female, is replaced with (1−x). Demographic stochasticity was included in the model by drawing the number of deer dying or moving between infection and/or age classes at each time step from a binomial distribution.

4.2.2 Possum population dynamics

Possum populations were modelled using a discrete-time derivation of Barlow's (2000) model, which includes heterogeneous mixing and a non-linear transmission function to describe the transmission of TB within possum populations. The same parameter values were used here as given by Barlow (2000) except the disease transmission coefficient and the disease aggregation parameters were changed to $\beta = 1.2$ and $\kappa = 0.03$, respectively, to produce a 2.5% TB prevalence within possum populations at an equilibrium density of about 650 possums/km^2. Pfieffer et al. (1995) report a 2.5% prevalence of TB from a 1982–83 survey of the Hauhungaroa Range, and Fraser et al. (1995) report a 2.2% prevalence of TB in a sample of possums from the south-eastern part of the Hauhungaroa Range before possum control in 1994.

4.2.3 Deer to possum TB spillback

The hypothesised mechanism of 'spillback' or re-infection of possum populations with TB from infected deer was via possums investigating or scavenging infected deer carcasses. While there is clear evidence that TB transmission from deer to possums has occurred (Mackereth 1993; de Lisle et al. 1995), the rate at which this occurs is unknown. It has been suggested that the risk of spillback transmission is highest when hunters cut off the head of infected deer and leave it at the kill site, thereby increasing the likelihood that possums would come into contact with the retropharyngeal lymph nodes that are the most common site of lesions in infected deer (Nugent 2005). This practice was commonplace in the first three decades of the commercial deer hunting era.

Here we assumed that the probability of an individual possum acquiring TB from a deer carcass was:

$$P(Inf) = 1 - e^{-\alpha \cdot IDC \cdot b} \ ;$$

where α is the possum encounter rate of deer carcasses, *IDC i*s the density of TB-infected deer carcasses in the environment, and *b* is the probability a possum becomes infected given encounter with an infected deer carcass. The rate that an individual possum would encounter a deer carcass was approximated by dividing the area of a typical possum home range by that of a deer's home range, i.e. α = 0.02 km^2/2.5 km^2 = 0.01. The density of TB-infected deer carcasses was estimated by tallying within the model the number of TB-infected deer that died each year. The model includes an option to include in the tally those TB-infected deer that died due to control, to simulate hunters leaving deer carcasses or the most infectious part of the carcass, the head, in the field. The probability that a possum becomes infected with TB given encounter with an infectious deer carcass is unknown and was assumed to be relatively high for the simulations presented here, at *b* = 0.25 (i.e. one in four possums encountering an infected deer carcass becomes infected). However, as this is the parameter value we know least about, we investigated how the simulated number of spillback events changed over a range of probabilities. Nugent and Whitford (2004) used simulated carcass remnants of deer containing lymph nodes injected with a marker dye to show that wild possums sometimes ingested the dye, and inferred that TB in lymph nodes would also sometimes be eaten. In that study, at least 7% of possums known to have encountered the dyed tissue were marked at each of two sites, but none at a third.

Once a single possum has become infected with TB through contact with an infected deer carcass there is some probability that it would subsequently infect other in-contact possums and establish a disease focus within the possum population. To estimate this risk for the Hauhungaroa Range case study we used the possum-TB spatial model (Ramsey & Efford 2010) to model the possum population, adding a single infected individual to an otherwise uninfected population and determining if TB subsequently established in that population. We used the 'Hauhungaroa Stage 1 & 2' and the 'Tihoi' AHB vector control zones (VCZs) and derived a map of predicted possum carrying capacity (*K*) for that area (=916 km^2: Fig. 1) from the habitat classifications of the LCDB2 and Ecosat GIS layers as has been previously described (Warburton et al. 2009). Possum populations within the simulated VCZs were initialised at a range of densities (*N*) relative to the carrying capacity (*N/K* = 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1). The average predicted possum carrying capacity for the two VCZs was 6.7 possums per hectare, thus initial possum densities ranged from 0.67 to 6.7 possums per hectare.

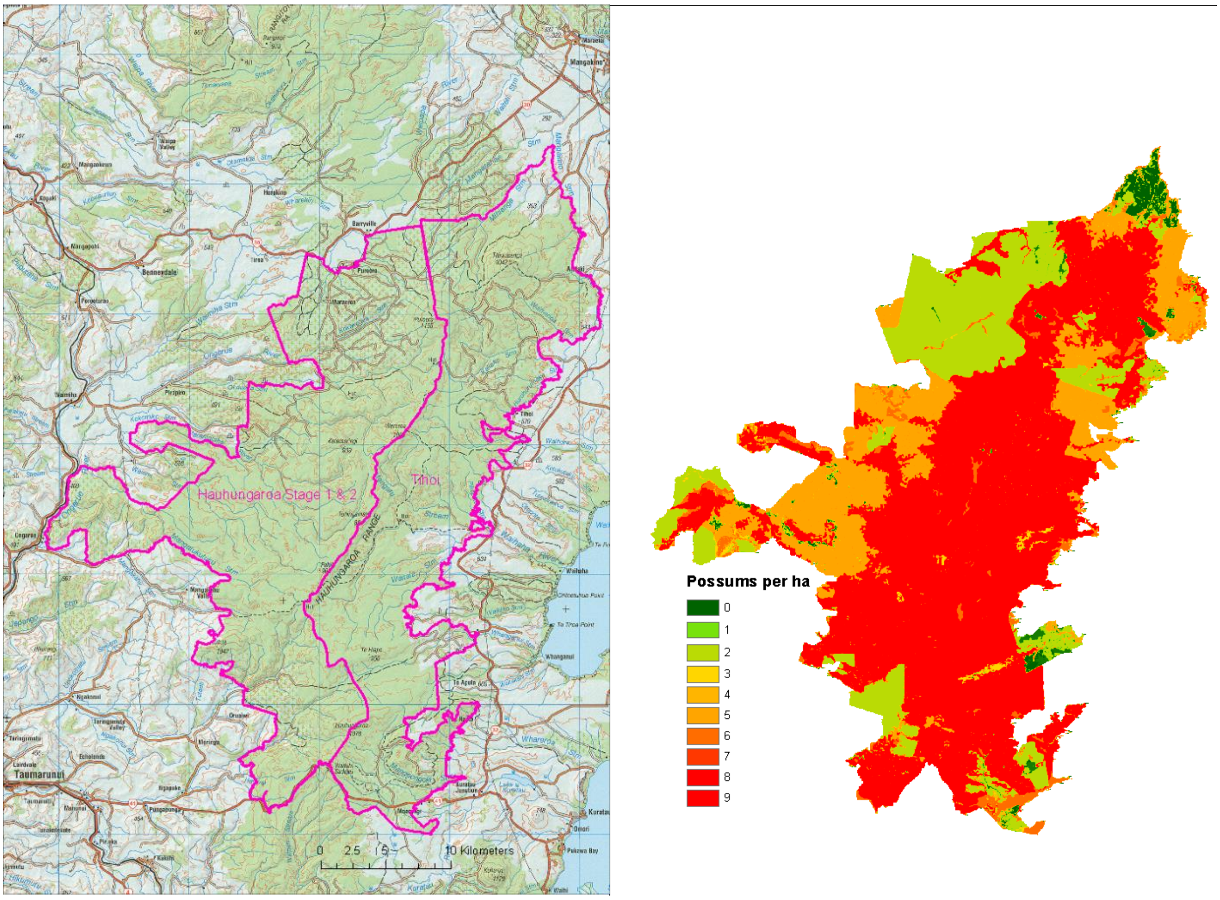

Figure 1 Left panel shows the vector control zones used in the spillback simulations, the right panel shows the possum carrying capacity (K, possums/ha) assumed for the simulation area.

In year 1 of the simulation a single infected individual was randomly located within the simulated population and the model was run for a further 5 years to assess whether TB was still present in the population. Five years was considered a good benchmark to assess TB establishment since there was less than a 0.01 probability that the original infected individual would survive for 5 years or more (based on an annual instantaneous mortality rate of 1.1) so any infected individuals present at that time are most likely due to the disease establishing and persisting in the population. The transmission coefficient used in the spatial model simulations ($\beta = 0.32$) was one that generated an average 2.5% TB prevalence when the possum population was at equilibrium. For each initial relative density the model was run 200 times and the proportion of simulations where TB was still present in the population 5 years after TB 'regeneration' was used as the probability of a single infected possum re-establishing TB in the Hauhungaroa possum population. As expected, given our assumptions, this predicts a positive relationship between relative possum density and the probability of TB establishment (Fig. 2). The predictions show an enhanced probability at N/K = 0.5–0.6 (~3.5–4.0 possums/ha). This is because contacts between possums in the spatial model are a function of their home range overlap and home ranges are assumed to contract non-linearly with increasing density and have an inflection point and thus a local maxima in contacts at these densities (Fig. 12 in Ramsey & Efford 2005).

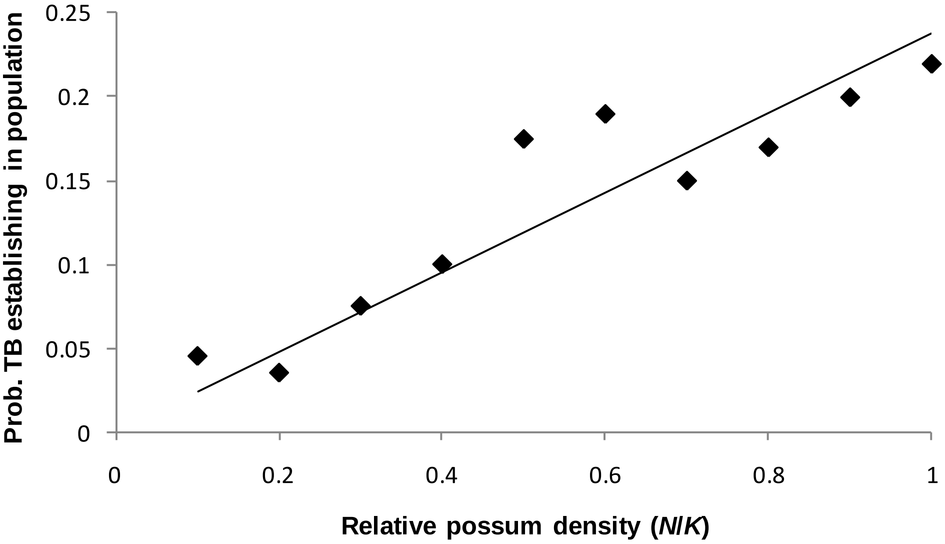

Figure 2 Probability of a single infected possum establishing TB in the possum population over a range of relative possum density (*N*/*K*). For these simulations possum carrying capacity (*K*) averaged 6.7 possums/ha.

4.3 Simulations

Five deer-and-possum control scenarios were modelled:

1. No possum control plus annual 'background' control of deer by private hunting. This is the scenario that would have prevailed in the Hauhungaroa Ranges before 1994.
2. Possum control at a 5-year frequency with an initial control efficacy of 95% (and a 30% by-kill of deer) and thereafter possum control efficacy of 85% with no deer by-kill (simulating use of deer-repellent bait) plus background control of deer by private hunting.
3. Possum control plus background control of deer as in (2) plus a one-off foliage baiting operation with an 80% kill in the year following initial possum control.
4. Possum control plus background control of deer as in (2) plus annual 'targeted' deer control (culling of adult females) over 5 years following the initial possum control.
5. Possum control plus background control of deer as in (2) plus annual 'targeted' deer control (culling of adult females only) over 5 years following the eradication of TB from possums.

All controls were implemented as a simple proportional removal from the population. Private hunting was assumed to have a bias towards removing male deer (Fraser 1995) whereas the targeted deer control was deliberately aimed at removing most adult female deer (Table 2). It was assumed that private hunting left part or all of the deer carcasses in the bush thus potentially providing a source of TB infection for possums. All carcasses were assumed to be removed from the field in the targeted deer control. Percentage by-kill of deer from aerially-broadcast 1080 poison targeted at possums varies widely from near zero to 93% (Nugent et al. 2001). Coleman et al. (1996) estimated a percentage by-kill of deer of 30% from the first aerial 1080 poisoning of the Hauhungaroa Range in 1994, which is the value we have assumed here for scenarios 2–5. Foliage baiting was assumed to have an efficacy of 80%, as was estimated by Sweetapple (1997) from a trial conducted in deep forest in the southern Hauhungaroa Range. The estimated cost per hectare of baiting from that trial was $11; to account for inflation we have assumed a higher cost of $15 for these simulations. The per hectare cost of possum control was assumed to be $36 for the initial 95% control, representing aerial broadcast of 1080 poison with two prefeeds. Subsequent control operations for possums were assumed to cost $20 per hectare, conservatively representing less intensive aerial control (e.g. reduced sowing rates). Targeted deer control by contract hunters was assumed to cost $7 per hectare, while deer control by private hunting was assumed to incur no cost to TB managers.

The model was run over an area of 900 km^2 approximating the combined area of the 'Hauhungaroa Stage 1 & 2' and the 'Tihoi' AHB VCZs (Fig.1). The simulations were run for 20 years with the initial possum control operation occurring in year 1 and background deer controlling occurring every year. Managers were assumed to have imperfect knowledge of the TB status of the possum population so that three possum control operations were always done despite eradication of TB from the possum population occurring on average in year 8 of the simulation, which was 7 years after the initial possum control and 2 years after the second control.

To account for demographic stochasticity five thousand replicate simulations were run for each combination of control scenario (scenarios 1–5) and probability of deer-to-possum infection (b = 0.1, 0.25, 0.5, 0.75). The outcomes calculated from these simulations were the mean time until TB eradication in both possums and deer, the mean number and cost of the possum control operations conducted, and the probability of spillback and TB re-establishment occurring after TB had been eradicated from the possum population. Cost–benefit ratios of deer control were assessed relative to scenario 2, which is the current operational practice of three possum control operations and no additional deer control. Cost–benefit ratios were expressed as (a) the reduction in eradication time in years for each dollar/km^2 spent on deer control and (b) the proportional reduction in spillback and re-establishment risk for each dollar/km^2 spent on deer control.

Table 2 Proportional kills of deer population under different deer control regimes with deer sex and age

Deer control regime	Sex	Deer age (in years):															
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15+
'Background' control by private hunters	Female	0.08	0.14	0.07	0.06	0.06	0.05	0.04	0.03	0.02	0.02	0.02	0.02	0.02	0.02	0.02	0.02
	Male	0.08	0.22	0.18	0.13	0.11	0.07	0.05	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04
'Targeted' control by contract hunters	Female	0	0.3	0.70	0.75	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80	0.80
	Male	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

5 Results

With no possum control and background deer control, equilibrium deer densities were 11.4 deer/km^2 with a TB prevalence of 0.33 and possum densities were 652 possums/km^2 with a TB prevalence of 2.5% (Figures 3 and 4.1). The sex ratio was 61 males for every 100 female deer (Fig. 3). TB prevalence was highest in male deer aged 4–5 years, at around 58%, and in the females aged 5–6 years, at around 50%, declining with age thereafter for both sexes (Fig. 3). These predictions are broadly consistent with empirical evidence from the Hauhungaroa Ranges before intensive possum control was initiated in 1994, but we note that predicted possum and deer densities are somewhat higher than probably prevailed at that time (see Nugent et al. 1997) and the proportion of male deer surviving beyond 10 years is likewise high (Nugent & Fraser 2005). The deer and possum control scenarios simulated are therefore likely to be conservative in estimating how quickly TB could be eradicated.

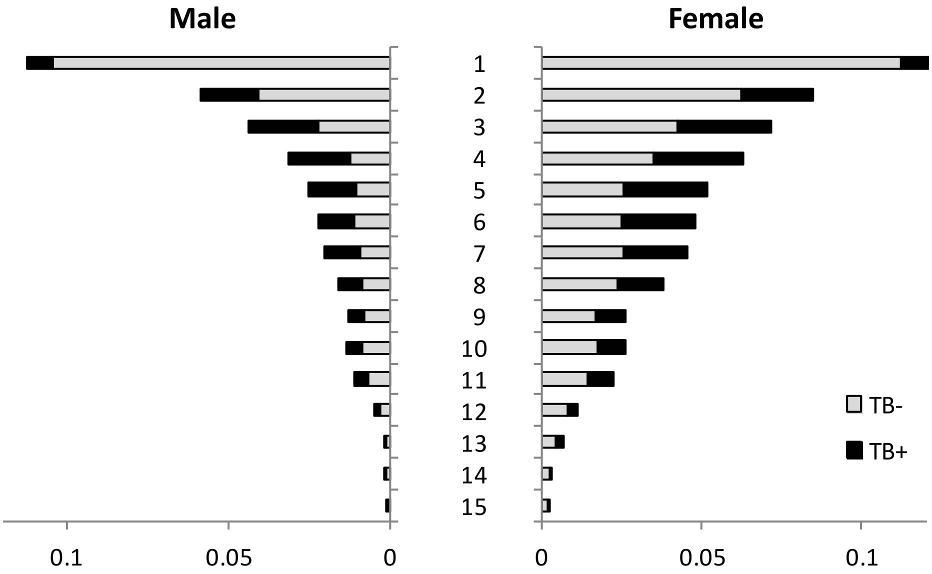

Figure 3 Proportion of deer population in different age, sex and TB infection classes when the possum population is uncontrolled and deer populations are subject to background private hunting (scenario 1). Length of bar for each age/sex/TB-status class represents proportion of total population.

Under standard possum control and background deer control (scenario 2), TB disappeared from the deer population on average 14.1 years after the first possum control operation with lower deer densities averaging 10.3 km^{-2} due to by-kill from the initial possum control (Table 3, Fig. 4.1). The deer control scenarios reduced average deer abundance with foliage baiting resulting in the greatest reductions (Fig. 4.3), followed by initial targeted control (Fig. 4.4), and lastly delayed targeted control (Fig 5.5) because it allowed some recovery of deer populations between initial possum control and the start of culling. However reduction in deer densities did little to lessen the time to TB eradication, with the best being the foliage baiting (scenario 3) which had uniform proportional kills across all age and sex classes and achieved TB eradication in deer at 12.3 years (Table 3). TB in the possum population declined rapidly to extinction following two simulated aerial controls which reduced possums to very low densities of less than 35 km^{-2} (Table 3, Fig. 4.2-4.5).

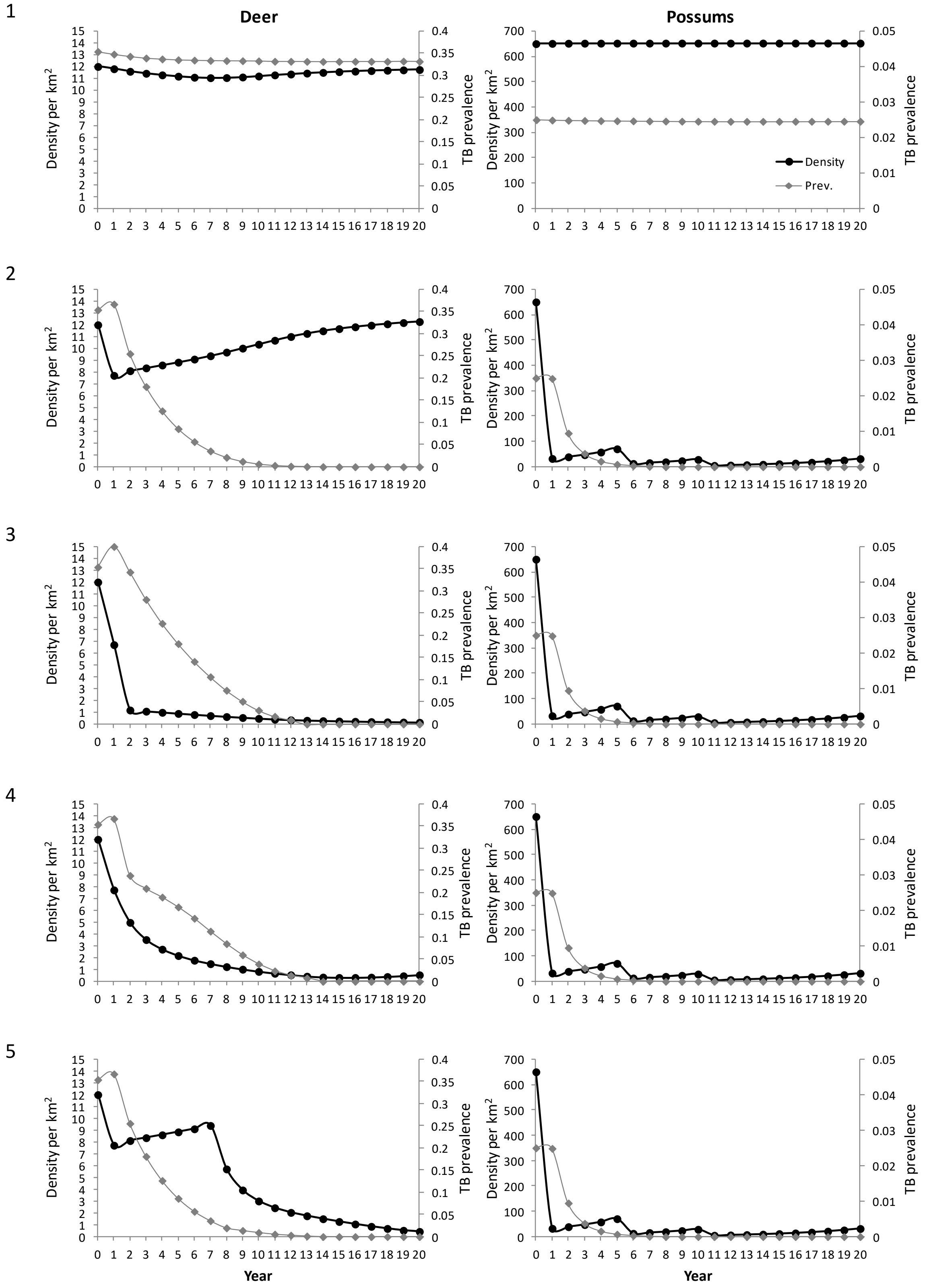

Figure 4 Changes in mean deer and possum density and TB prevalence under control scenarios 1–5.

Table 3 Results from deer–possum–TB simulation model under five control scenarios. Results are means of 5000 replicate simulations

Control scenario	Possums					Deer			
	Years to eradicate TB[a]	No. control operations	Cost of control operations ($/km^2)	Population density (km^{-2})[a]	No. deer to possum spillback and re-establishment events[b]	Years to eradicate TB[a]	No. control operations	Cost of control operations ($/km^2)	Population density (km^{-2})[c]
1	na	0	0	652	na	na	0	0	11.4
2	7	3	7600	25	0.057	14.1	0	0	10.3
3	7	3	7600	25	0.015	12.3	1	1500	0.8
4	7	3	7600	25	0.034	13.2	5	3500	1.6
5	7	3	7600	25	0.031	13.2	5	3500	4.3

[a] Assessed over years since initial possum control, [b]number of events from time TB eradicated from possums to time TB eradicated from deer, [c]assessed over 20 years of simulation.

Under scenario 2 (standard possum control alone), the probability of TB spillback and re-establishment occurring at least once after TB was eradicated from the possum population varied from 0.01 to 0.17 depending on the parameter value of *b* (Table 4). Deer control reduced that risk by 37–75% with scenario 3 providing the greatest reduction in risk.

Table 4 The estimated cost–benefit ratios of deer control under scenarios 3–5 relative to possum control alone (scenario 2) and the sensitivity of model simulations to the probability of a possum becoming infected with TB given encounter with an infected deer carcass (*b*)

Probability of possum becoming infected with TB given encounter with infected deer carcass (*b*)	Control scenario	Cost of deer control operations ($/km^2)	Mean spillback[a] risk period (yrs)	Probability of spillback[a] occurring	Reduction in spillback[a] risk period for each $/km^2 spent on deer control	Proportional reduction in probability of spillback[a] occurring for each $/km^2 spent on deer control
0.05	2	0	7.1	0.0132	-	-
0.05	3	1500	5.3	0.0024	0.0012	0.0005
0.05	4	3500	6.2	0.0068	0.0003	0.0001
0.05	5	3500	6.2	0.0074	0.0003	0.0001
0.1	2	0	7.1	0.0292	-	-
0.1	3	1500	5.3	0.0040	0.0012	0.0006
0.1	4	3500	6.2	0.0090	0.0003	0.0002
0.1	5	3500	6.1	0.0114	0.0003	0.0002
0.25	2	0	7.1	0.0566	-	-
0.25	3	1500	5.3	0.0154	0.0012	0.0005
0.25	4	3500	6.2	0.0334	0.0003	0.0001
0.25	5	3500	6.2	0.0298	0.0003	0.0001
0.50	2	0	7.2	0.1108	-	-
0.50	3	1500	5.3	0.0218	0.0012	0.0005
0.50	4	3500	6.2	0.0602	0.0003	0.0001
0.50	5	3500	6.2	0.0592	0.0003	0.0001

[a] Spillback and re-establishment of TB in the possum population

Foliage baiting (control scenario 3) was the most cost effective method out of the three deer control options investigated for reducing time until eradication and spillback and re-establishment risk. However, the absolute reduction in the spillback risk period was less than 2 years (Table 4), so there was little reduction in cost through avoiding a further repeat of aerial poisoning of possums.

6 Conclusions

6.1 Model predictions

Under the assumptions and scenarios modelled, there was a predicted lag time of around 7 years for TB to be cleared from the deer population once it had been eradicated from the possum population, due to the greater longevity of infected deer compared with possums. Because we modelled TB in deer as being maintained only by transmission from possums, once TB was eradicated from possums, the rate of decline of TB in deer was solely a function of the combined ('natural', diseased, hunting) deer mortality rates.

Overall, TB was predicted to persist in deer for about 14 years after initial possum control. Consistent with that, TB prevalence in the eastern Hauhungaroa Ranges had declined within 10 years of the initiation of possum control (Nugent 2005) but there have been credible reports of TB-infected deer being shot by hunters since then. The most recent, from 2010, was shot by a professional hunter who had previously been involved in surveys of TB prevalence in this area (D. Wilson pers. comm.). As the reduction of possum populations to very low density was not achieved in all parts of the Hauhungaroa Range until 2005 (Nugent & Whitford 2008)), these results suggest that some small spillback risk will persist in the Hauhungaroa Range until 2020, with the greatest risk being in the western central part of the range which was the last area in which possums were successfully controlled.

Increasing deer mortality rates through control measures did not greatly reduce the duration of the spillback risk period, at least for the control scenarios modelled. Even an 80% reduction in deer numbers (by foliage bait poisoning) produced only a small decrease in the risk period. That is because although the reduction decreases the number of infected deer, it has little effect on the survival probabilities of the infected deer that remain. In extremis, of course, removal of all deer would remove the risk, but the financial and (perhaps more importantly) the social cost of that would likely be prohibitive.

Moderately intensive control targeted at the adult female deer population (scenarios 4 and 5) resulted in only small reductions in the spillback risk period, of less than one year, despite females making up 60% of the deer population overall and having double the number of TB-infected deer in the older (>10 years) age classes. Demographic stochasticity in mortality rates means that small populations are more likely to go extinct than larger ones so if the initial infected deer population was much smaller than the c. 10 000 deer assumed here, then the spillback risk period would be shorter than the 7 years identified here. It is important to note that our inferences relate to a large population of deer, and that the risks diminish greatly if the affected population is only a few hundred deer, and/or the prevalence of TB in them (and the local possum population) was lower than in the Hauhungaroa Range.

Under the default parameter values, and with no deer control, the predicted probability of spillback with re-establishment occurring in an area the size of the Hauhungaroa Range was 6%. The 6% re-establishment probability implies that most of the time we can be fairly (94%) confident that spillback and re-establishment of TB would not occur in the Hauhungaroa Range even without deer control, given our assumptions are accurate.

However, the predictions are highly sensitive to the parameter (*b*), the rate of infection per encounter with a TB deer carcass. As already noted, that parameter has never been measured, and probably never will be. Instead, we rely on circumstantial evidence that spillback from deer to possums occurs, with the most compelling evidence being the detection of 'Otago' strain *Mycobacterium bovis* being detected in wild possums at Waipawa after farmed deer infected with that strain were moved into the area (Mackereth 1993). In addition, we know that possums readily visit deer carcasses and that about one-third of these visits result in contact with the carcass (Nugent 2005), and Barron et al. (2011) showed that most possum contacts with possum carcasses placed in the field occurred within the period that viable *Mycobacterium bovis* were shown to survive in a carcass. Further, Nugent and Whitford (2007) recorded uptake of dye by at least 7% of possums in two areas where the possum population was exposed to 30 deer-meat 'baits' containing dyed lymph nodes. We therefore conservatively chose a fairly high default value of $b = 0.25$ here. However, this parameter is likely to be highly variable over space and time, depending on the probability of contact with lesioned deer tissue given encounter, the duration and nature of the infectious contact, longevity and amount of the *M. bovis* bacilli in the deer carcass, the infective dose received, and the dose required to initiate infection.

While it cannot be proved, Nugent (2005) speculates that TB originally established in possums as spillover from deer in the 1960s, at the time commercial hunting of deer emerged and resulted in decapitation of deer as standard practice in deer carcass recovery. That hypothesis gains plausibility from the emergence of TB in possums at multiple locations nationally at about that time, rather than at any other time in the preceding century when possums and TB-infected cattle had had ample opportunity to interact. The key premise underpinning the hypothesis is that decapitation of deer, and the leaving of the head at the kill site (or at some other field processing site), massively increased the accessibility to possums of the retropharyngeal lymph nodes that are the most commonly lesioned tissue in TB-infected wild deer. If valid, then the risk of spillback from commercially killed deer is likely to have virtually ceased in about 1994, when new regulations required that deer be recovered for sale with the head on. For deer killed by recreational hunters, the risk is also likely to be low as carcasses are frequently butchered in the field with much larger amounts of meat and tissue being left at the kill site, so that any lesioned tissue is both physically and proportionately far less available than when just a head and gut pile is left at a kill site.

The frequency, duration and nature of the infectious contact is also likely to be lower than historically. Obviously the frequency of encounter is much reduced for an intensively controlled possum population at low density. In addition, it is likely that individuals in such a population are well fed and arguably therefore could be less likely to consume carrion, as it appears that it is not a highly preferred food given that only some possums actually exhibit this behaviour.

The amount of infectious material in a deer carcass (and number of bacilli within that) is also likely to be low in deer that have been infected for most of their lives, particularly where they are killed by hunters rather than dying as a result of TB.

Overall, for the three reasons above, we consider that the default value ($b = 0.25$) should be viewed as leading to highly precautionary estimates of the spillback risk. Likewise the relatively high values assumed for the habitat carrying capacity and deer survival will produce overestimates of the number of infected animals and duration of the risk period. Given this and our confidence that the important dynamics of deer-possum TB interactions have been captured by the model we consider the spillback risk predicted by the default model values to be a worst-case scenario.

6.2 Management implications

The modelling suggests that the 'standard' AHB approach to possum control in large forested areas (at least three aerial operations at about 5-yearly intervals) is already well suited to minimising the TB spillback risk from deer, as it keeps possum numbers low for about 14–15 years. This strategy is based on keeping possum numbers below the threshold for maintenance of TB as indicated by the positive relationship between TB establishment and possum density shown in Figure 2. In fact, for most of the Hauhungaroa Range, the current operations in winter 2010 will be the fourth operation, so the period of low possum numbers will extend to >20 years, obviating any potential for deer control to reduce the duration of possum control required. In other words, the very few remaining TB-infected deer in those areas are likely to have died out before possum numbers increase to the TB-re-establishment threshold. The main area of concern is the western central area (the eastern parts of the VCZs designated as AS2, AS3, AS4, and AS6), some parts of which had had aerial 1080 baiting applied only twice before 2011 (with some indications that the first operation in 2001 was ineffective; Nugent & Whitford 2008). As TB-infected possums were still present in 2005 (Coleman & de Lisle 2006), TB-infected deer could potentially be present until 2020, with the possibility of some of these having dispersed to other parts of the area.

Given that the modelling predicts that even moderately intensive deer control will not reduce the duration of spillback-and-re-establishment risk by more than 2 years, an aerial possum poisoning operation would still be required around the 2015-2016, so there would be no great saving in possum control. In addition, the third operation might be a low-cost operation (based on recent evidence that new approaches to aerial baiting with very low sowing rates can deliver adequate control of low-density possum populations: Nugent & Morris, 2010), so the potential saving is reduced further still.

Also, the costs of deer control as modelled are likely to be conservative. We modelled control as a simple proportional kill/removal from that cohort. In reality, proportional kill rates would be expected to decline with population density, resulting in increased effort expended or dollars spent to remove an individual deer at low compared with high deer densities, (Nugent & Choquenot 2004), which means we may have underestimated costs here. Further, costs only tallied monetary costs associated with the control. The large reductions in deer density required to have any major effect in reducing the spillback risk would be controversial, especially if poisoning were involved. The AHB already uses EDR deer-repellent bait to reduce rather than increase deer kill, for this reason. There would therefore be substantial 'social' planning and consent costs as well as the direct costs of deer control.

We therefore conclude that deer control to reduce spillback risk is rarely likely to be warranted in its own right. We assume TB will eventually drop out of wild deer populations once interspecies transmission is curbed by effective possum control. While additional money spent on deer control will do little to hasten that decline (unless very high percentage kills are achieved), selective culling and necropsy of deer as TB sentinels will help confirm that a decline is occurring, and provide data for calculating both the likelihood that TB has been eradicated from possums and for assessing the risk of spillback. Deer 'control' may therefore be warranted on surveillance grounds, with the reduction in spillback risk being an incidental benefit.

7 Recommendations

- We do not recommend either broad-scale ‘whole population’ deer control or selective control of adult female deer as specific tools for reducing the risk of TB spillback from deer resulting in re-establishment of TB in possums. Instead, we recommend that the AHB maintain low possum numbers for a period of at least 15 years after possum control was initiated in all of the areas occupied by the deer population.
- However, we consider that where surveillance of TB infection levels in deer is planned (to contribute toward assessment of TB levels in possums), the twin incidental benefits of assessing the potential size of the spillback and providing a small reduction in the duration of spillback risk should be taken into account.

8 Acknowledgements

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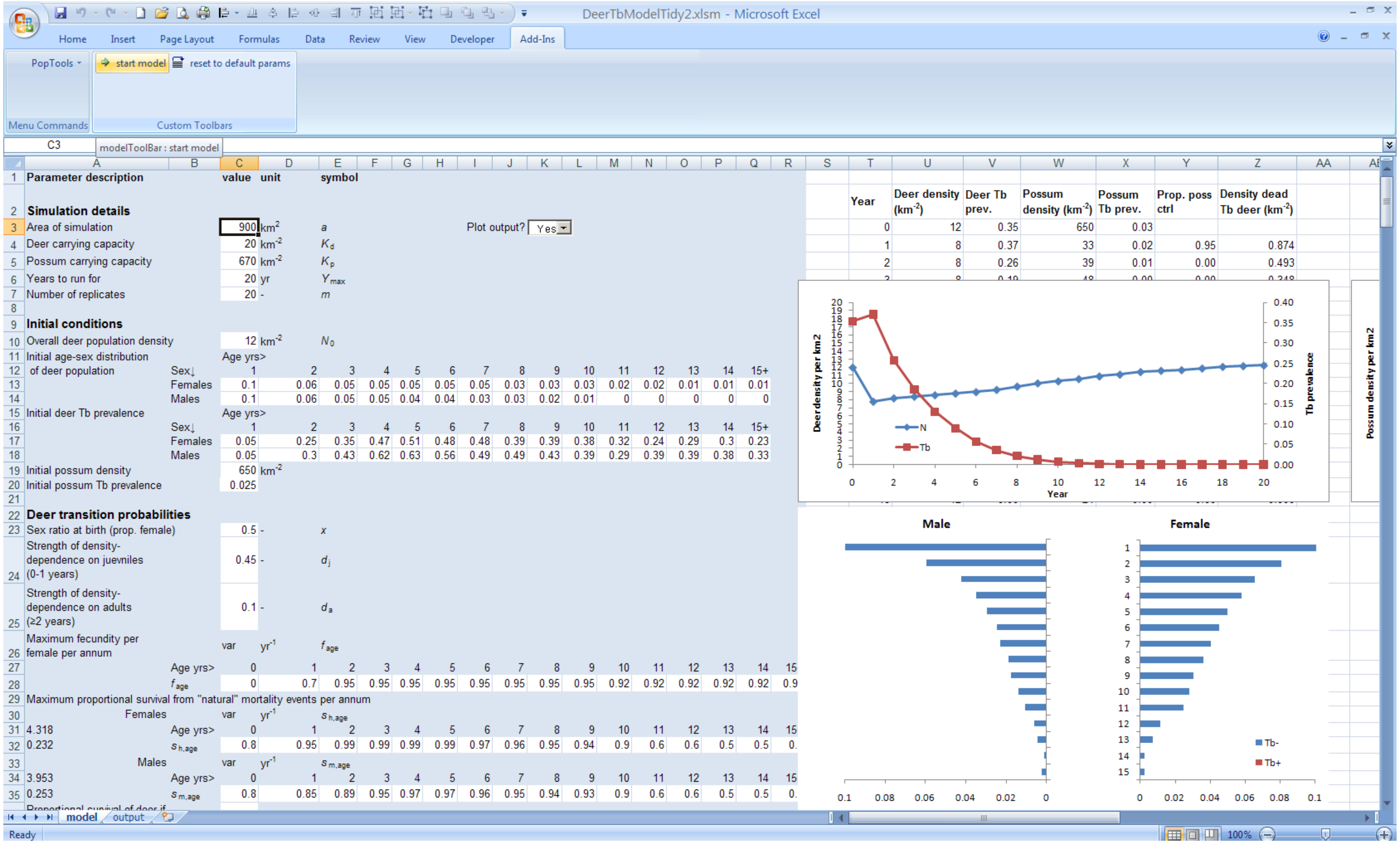
Appendix 1 – Spreadsheet Deer-TB-possum model

The model developed for this report can be requested from the author (barronm@landcareresearch.co.nz) or downloaded from the Landcare Research ftp site: ftp://ftp.landcareresearch.co.nz/Deer%20Model/DeerTbModelTidy3.xlsm.

Because the model is a macro you run from within Microsoft Excel, you may get a security warning pop-up when you try to open the file or there may be a warning below the ribbon saying ‘Some active content has been disabled’; you must enable this content for the model to run. Once enabled, under the ‘Add-Ins’ tab there will be a custom toolbar which has two buttons: one to start the model running and another to reset to the default parameter values.

To run the model, go to the ‘model’ worksheet, alter the parameter values as necessary, and then hit the ‘Start model’ button on the ribbon (Fig. A1). The parameters are described in the methods section of this report. The spreadsheet is protected and you can only alter parameter values in the white boxes on the spreadsheet. There is no option to alter the possum-TB model parameters. Note that there is no error checking enabled so if you enter a nonsensical parameter value you will either get a nonsensical result or the program will crash. If this happens, hit the ‘Esc’ button on your keyboard, then hit the ‘reset to default params’ button on the ribbon and try again.

The output on the ‘model’ worksheet consists of time series charts of deer and possum density and prevalence from year 0 to year max and a histogram of the age/sex/infection status of the deer population at year max. Because updating of these charts takes time, if you are running more than 20 replicates, turn off the updating by selecting ‘no’ in the ‘Plot output?’ combo box. The ‘output’ worksheet has a more detailed summary of the results of each replicate simulation and calculates the means of these results and the proportion of times an event (TB eradication, spillback) occurred over all the replicates.



	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R
1	**Parameter description**		**value**	**unit**	**symbol**													
2	**Simulation details**																	
3	Area of simulation		900	km^{2}	a					Plot output?	Yes							
4	Deer carrying capacity		20	km^{-2}	K_d													
5	Possum carrying capacity		670	km^{-2}	K_p													
6	Years to run for		20	yr	Y_{max}													
7	Number of replicates		20	-	m													
8																		
9	**Initial conditions**																	
10	Overall deer population density		12	km^{-2}	N_0													
11	Initial age-sex distribution		Age yrs>															
12	of deer population	Sex↓	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15+	
13		Females	0.1	0.06	0.05	0.05	0.05	0.05	0.05	0.03	0.03	0.03	0.02	0.02	0.01	0.01	0.01	
14		Males	0.1	0.06	0.05	0.05	0.04	0.04	0.03	0.03	0.02	0.01	0	0	0	0	0	
15	Initial deer Tb prevalence		Age yrs>															
16		Sex↓	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15+	
17		Females	0.05	0.25	0.35	0.47	0.51	0.48	0.48	0.39	0.39	0.38	0.32	0.24	0.29	0.3	0.23	
18		Males	0.05	0.3	0.43	0.62	0.63	0.56	0.49	0.49	0.43	0.39	0.29	0.39	0.39	0.38	0.33	
19	Initial possum density		650	km^{-2}														
20	Initial possum Tb prevalence		0.025															
21																		
22	**Deer transition probabilities**																	
23	Sex ratio at birth (prop. female)		0.5	-	x													
24	Strength of density-dependence on juevniles (0-1 years)		0.45	-	d_j													
25	Strength of density-dependence on adults (≥2 years)		0.1	-	d_a													
26	Maximum fecundity per female per annum		var	yr^{-1}	f_{age}													
27		Age yrs>	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
28		f_{age}	0	0.7	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.92	0.92	0.92	0.92	0.92	0.9
29	Maximum proportional survival from "natural" mortality events per annum																	
30		Females	var	yr^{-1}	$s_{h,age}$													
31	4.318	Age yrs>	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
32	0.232	$s_{h,age}$	0.8	0.95	0.99	0.99	0.99	0.99	0.97	0.96	0.95	0.94	0.9	0.6	0.6	0.5	0.5	0.
33		Males	var	yr^{-1}	$s_{m,age}$													
34	3.953	Age yrs>	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
35	0.253	$s_{m,age}$	0.8	0.85	0.89	0.95	0.97	0.97	0.96	0.95	0.94	0.93	0.9	0.6	0.6	0.5	0.5	0.
	Proportional survival of deer if																	

Year	Deer density (km^{-2})	Deer Tb prev.	Possum density (km^{-2})	Possum Tb prev.	Prop. poss ctrl	Density dead Tb deer (km^{-2})
0	12	0.35	650	0.03		
1	8	0.37	33	0.02	0.95	0.874
2	8	0.26	39	0.01	0.00	0.493

Figure A1 Screenshot of deer-TB-possum model showing the ‘model’ worksheet and the custom toolbar (top left, on ribbon) to start and reset the model.