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R. R. Kao

M. G. Roberts

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A comparison of wildlife control and cattle vaccination as methods for the control of bovine tuberculosis

R. R. KAO* AND M. G. ROBERTS

AgResearch, Wallaceville Animal Research Centre, P.O. Box 40-063, Upper Hutt, New Zealand

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SUMMARY

The Australian brushtail possum is the major source of infection for new cases of bovine tuberculosis in cattle in New Zealand. Using hypothetical values for the cost of putative cattle and possum Tb vaccines, the relative efforts required to eradicate Tb in cattle using possum culling, possum vaccination or cattle vaccination are compared. For realistic assumed costs for 1080 poison bait, possum culling is found to be a cost-effective strategy compared to cattle vaccination if the required control area is below 13 ha per cattle herd, while possum vaccination is cost-effective for control areas of less than 3 ha per herd. Examination of other considerations such as the possible roles of possum migration and heterogeneities in possum population density suggest that each control strategy may be superior under different field conditions. Finally, the roles of the possum in New Zealand, and the Eurasian badger in Great Britain and Ireland in the transmission of bovine tuberculosis to cattle are compared.

INTRODUCTION

Bovine tuberculosis or Tb (*Mycobacterium bovis*) infection in cattle is a world-wide zoonotic health concern (see for example [1]); in the absence of control, it is also the cause of a significant loss of production [2]. As a result, rigorous test and slaughter in conjunction with quarantine has been adopted and ultimately has led to the successful eradication of Tb in many countries [3]. In New Zealand, the disease persists in cattle at levels above international community standards for freedom from Tb (Office Internationale des Epizooties or 'OIE' standards require more than 99·8% herds accredited Tb free [4]), resulting in a risk of significant impact on dairy and beef export revenues if these standards are not met.

The testing procedure in New Zealand is similar to that used in other developed countries; all cattle are regularly tested for Tb using a tuberculin skin test (the caudal fold test), and herds containing infected cattle are placed under quarantine or on 'movement control' status. Tb in movement control herds is strictly regulated via test and slaughter until the herd is accredited as Tb free. To supplement caudal fold testing, a variety of other tests are available, most importantly the comparative cervical test.

The Australian Brushtail Possum (*Trichosurus vulpecula*) was imported into New Zealand in the last century, but is now the target of costly control effort, both because of the environmental damage it causes and because it is a wildlife Tb reservoir and the major source of new cases of Tb in domesticated cattle [5]. Field studies of bovine Tb have concentrated on estimates of Tb prevalence in possums, possum behaviour, and comparisons of possum Tb prevalence and cattle Tb (e.g. [6]). Less attention has been paid to quantitative estimates of possum population parameters such as density, or determining the force of infection on cattle, possibly due to the difficulty in

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* Author for correspondence. Current address: Institute for Animal Health, Compton Laboratory, Compton, Newbury, Berkshire RG20 7NN, UK.

measuring these parameters. Modelling efforts have looked at the dynamics of Tb transmission in possums [7–9] and more recently, within cattle herds [10, 11]. Based on the previous work by this group on possum and cattle Tb, we now examine the relative effort required to eradicate Tb using different control and eradication strategies, where the effort is expressed in terms of the cost of the control operation. Throughout this paper, cost is expressed in New Zealand dollars. At the time of writing, the New Zealand dollar was valued at approximately US$0.55 and UK£0.33.

Because the Eurasian badger (*Meles meles*) in the United Kingdom has a similar role to the possum in New Zealand as a wildlife reservoir for Tb [12], the two situations are often compared. Hence the relevance of this study to the badger Tb situation is discussed.

Possum density and Tb incidence

Estimates of absolute possum densities are difficult to obtain. Catch percentage on trap lines, estimates from bait consumption, spotting and faecal pellet abundance are typically used as markers to monitor population changes; these should correlate with absolute possum population densities but the exact nature of the correlation is subject to speculation. Different methods have been used to estimate wildlife population densities from trap catches [13–15]. Pfeiffer [8] used a variety of techniques to infer possum density from trap catch data, but in all cases an estimate of the probability of capture was required. The results from this study showed significant variation in estimated relative densities depending on the approach used; absolute densities could not be estimated without further knowledge of possum home ranges.

Field control operations are typically monitored by trap catch percentage, in which trap lines are set to monitor changes in density – the higher the density, the higher the catch percentage (Meenken, personal communication). In large areas comprehensive trap coverage would be prohibitively expensive, and local variations in possum density would be difficult to measure. This could lead to problems with understanding the epidemiology of the disease. For example a stubbornly persistent incidence of infection may be a result of a locally high possum density. Dispersal of poison bait is based on achieving a fixed coverage of the control area rather than being possum density dependent. Therefore the cost of the control operation is directly related to ease of access and dispersal and is typically quoted as a cost per unit area.

Using the *SI* model of Tb in possums (see appendix A), and based on the parameters of Table 3, the expected possum Tb prevalence is 3·1%. Estimates from the Hauhungaroa Ranges data [16] show prevalences of about 1–3%.

Transmission from possums to cattle

The correlation between possum and cattle Tb has been well established, even though the role of possum behaviour in transmission is unknown. For example, the number of available denning sites may impose an upper limit on transmissibility; the fewer the number of sites in close proximity to cattle pasture, then the lower the transmission to cattle. However, the existence of a small number of favoured dens in a high density area may also increase possum-to-possum transmission, due to increased direct and indirect contact through den sharing. With no knowledge of the number and quality of den sites in the study area, it is assumed that both possum-to-possum and possum-to-cattle transmission are dependent on possum density.

Correlated possum and cattle Tb data are scarce. Data from the Hauhungaroa Ranges [8, 17] have been used as an example. These ranges lie on the central plateau of the North Island of New Zealand. The studied area consists of pastoral land with adjacent patches of forest and scrub. This is an excellent possum habitat in close contact to cattle, representing an area where the force of infection is relatively high.

Assuming a linear dependence of 'force of infection' on possum Tb prevalence, the data shown in Figure 1 are used to determine an average force of infection over the entire region. The high degree of scatter implies that general characteristics at best will be recoverable from the analysis. Averaging over all regions with non-zero possum Tb prevalence, the possum-to-cattle transmission parameter was found to be

$$\beta_{\mathrm{pc}} = 4{\cdot}60 \times 10^{-3}\ \text{contact}^{-1}\ \text{yr}^{-1},$$

resulting in a force of infection of

$$\beta_{\mathrm{pc}} Z = 1{\cdot}41 \times 10^{-4}\ \text{contact}^{-1}\ \text{yr}^{-1},$$

where Z is the local prevalence of Tb in possums.

Using the herd control model of appendix B, the force of infection can be used to infer required possum Tb prevalence and therefore culling effort. Given a

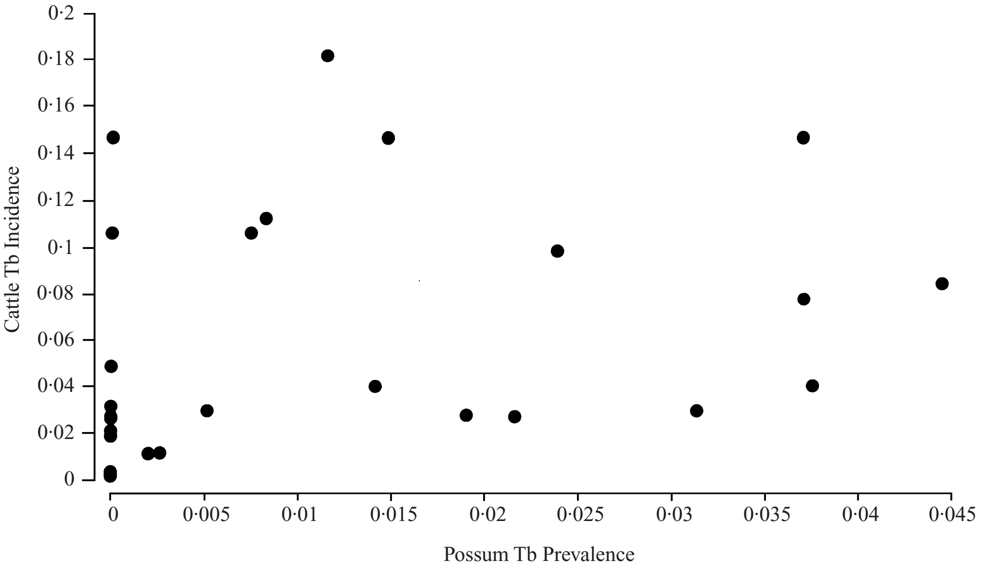

Fig. 1. Plot of possum Tb prevalence *vs.* cattle Tb incidence in the Hauhungaroa Region study [16].

mean time on movement control of just under 10 months (typical in non-wildlife vector areas), then approximately 0·47 % cattle reacting to the caudal fold test would correspond to 0·2 % movement control herds. Working backwards, this would require a force of infection of $4{\cdot}08 \times 10^{-6}\ \text{yr}^{-1}$, or a possum Tb prevalence of 0·89 %. Reduction in possum Tb prevalence to this level would require a culling effort of just over 9 % of the assumed possum carrying capacity per year (just under 1 possum per ha), essentially that required to cull to Tb free levels (9·2 % of carrying capacity or about 21 % of actual density per year, to a level of 4·3 possums per ha [9]).

Eradication of bovine Tb in cattle, in the absence of possums

Evidence from countries which have implemented rigorous test and slaughter procedures in the absence of wildlife Tb vectors indicates that current control procedures are sufficient to eradicate the disease in most circumstances [3]. This is supported by model results (see appendix B). While parameter estimates are extremely rough, only drastic changes in the estimated values of the intra-herd transmission parameter β_{cc} (sensitive, for example, to increases in stocking densities) and the probability per Tb test of failing to detect the disease f (through a serious breakdown in management practice) would result in self-sustaining Tb, and these are the most significant parameters.

Barlow and colleagues [11] indicate that cattle-to-cattle Tb transmission is a significant cause of herd breakdowns, even though the proportion of movement control herds is not likely to persist above 0·2 % without the existence of the possum wildlife reservoir. The cattle-to-cattle transmission parameter β_{cc} is found by fitting it to experimental data using numerous computer simulations. This results in a lower value of the possum-to-cattle transmission parameter than that quoted in [10]. In the earlier work the required cattle vaccine efficacy for $\beta_{pc} = 4{\cdot}42 \times 10^{-4}\ \text{yr}^{-1}$, $\beta_{cc} = 7{\cdot}19 \times 10^{-5}\ \text{yr}^{-1}$ was found to be about 96 % [10]. With $\beta_{pc} = 1{\cdot}63 \times 10^{-4}\ \text{yr}^{-1}$, $\beta_{cc} = 9{\cdot}85 \times 10^{-3}\ \text{yr}^{-1}$, as dictated by the Barlow and colleagues estimate [11], required vaccine efficacy would be 89·9 %. For the remainder of this paper, the latter value of β_{cc} is used. In all cases, the required incidence of Tb reactors in cattle herds is 0·47 %, assuming movement control parameters similar to non-wildlife vector areas.

Comparing control strategies

Three control strategies are considered; possum culling, possum vaccination, and cattle vaccination. Roberts [9] examined possum control, while Woolhouse and colleagues [18] reviewed the general problem of vaccination of domestic and wild animals against various diseases. In bovine Tb modelling, Kao and colleagues [10] consider efficacy requirements for a cattle Tb vaccine under existing management schemes. We consider relative control effort *vs.* cattle Tb incidence, with the following assumptions:

(1) Distribution of tuberculous cattle is typified by many herds with a single case of infection, and a few with larger clusters. The data can be effectively described by a negative binomial distribution; it is assumed that the index of dispersion of the distribution is described by an average over all indices of dispersion in vector areas prior to control, and by an average in non-vector areas after control [10].

(2) The delivery of a cattle vaccine is no more expensive than the costs associated with cattle testing.

(3) A possum that consumes a poisoned bait dies and all bait consumption contributes to the control effort. However, vaccinated possums will continue to consume vaccine doses.

(4) A quarantine system will remain in place to handle cattle Tb outbreaks.

(5) Culling operations are based on the use of compound 1080 (Sodium monofluoroacetate) poison. While delivery methods include aerial dispersal and ground-delivery (bait stations), maintenance control operations would use ground-delivery and thus aerial dispersal will not be considered.

(6) A cattle vaccine is deliverable to all herd members, with no significant vaccine side effects.

(7) A possum vaccine offers complete protection against Tb, with no significant vaccine side effects. While it is unlikely this efficacy will be achieved, all possible efficacy/delivery scenarios cannot be covered. The consequences of lower efficacies are discussed in Roberts [9].

Approximate costs for control efforts are given in Table 1. The cost of a putative possum vaccine is assumed to be the same as the cost for a cattle vaccine; research and development costs are not considered, nor is the cost of development of a new field test. The cost of the poison in culling operations is assumed to be a negligible part of the total operational cost.

As the probability that a possum will consume a given bait is not known, it is difficult to estimate the total number of poison or vaccine doses which would be required to achieve Tb eradication. *Ad hoc*, we assume a 10% probability that bait will be consumed.

We now examine the relative costs of wildlife vector culling and vaccination and cattle vaccination.

Comparing wildlife culling with wildlife vaccination

The value of the basic reproduction ratio for Tb in possums, based on a combination of generic parameters and estimated parameters from the Hauhungaroa study is $R_0 = 1{\cdot}63$ (appendix A). The aim of possum culling and/or vaccination strategies is to reduce this below the threshold value of one. Currently, possum culling operations rely on spreading bait evenly over the required control area and are only incidentally correlated to the density of the possums in the habitat (Meenken, personal communication). Measures of cost are related to cost per unit area, as opposed to cost per possum killed. The efficiency of operations will vary widely from region to region, and a survey of operations in New Zealand [20] reflects this, with costs ranging from approximately NZ$60 per ha down to NZ$2 per ha (Fig. 2).

Table 1. *Approximate annual costs of different Tb control measures – sources are* [20] *for possum control measures, and* [19] *for hypothetical cattle vaccination parameters. CFT, caudal fold testing; CCT, comparative cervical testing*

Programme	Per unit cost
Possum culling	$8–$60/ha +$2.50/cow (CFT) +$7.50/cow requiring CCT testing
Possum vaccination	$1/dose +$8–$60/ha +$2.50/cow (CFT) +$7.50/cow requiring CCT testing
Cattle vaccination	$5.50/cow +$40/cow requiring *in vitro* testing

While the cost of 1080 poison bait is only a small part of the overall cost of culling operations (at NZ$0.05 per bait), the cost of a vaccine dose may be significant. For most comparison purposes we assume *ad hoc* a cost of NZ$1 per dose, but also compare this with NZ$2 and NZ$5 vaccines. The minimum required rate of possum vaccination is 173 vaccine doses/ha/year, maintaining 43% of the population in a vaccinated state.

Since it has been assumed for the model that the possum population is isolated, the additional effort required to completely eliminate the possum population is negligible compared to the culling effort required to make the population disease-free. Using these parameters, Roberts [9] found that a culling effort of 9·2% of possum carrying capacity per year would be sufficient to eradicate Tb. A culling effort of

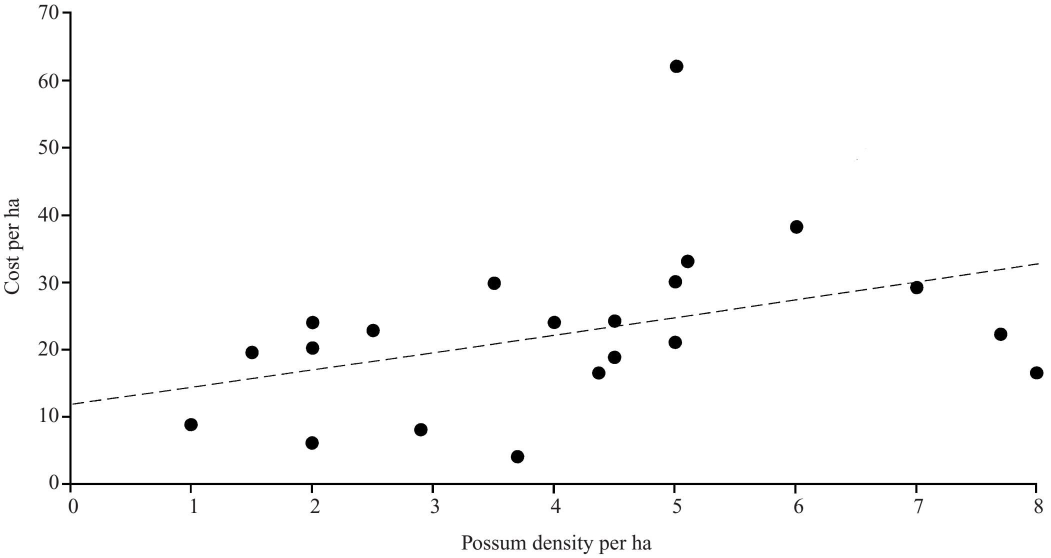

Fig. 2. Plot of estimated possum density *vs.* cost of culling operations per ha. Best fit line is show for comparison purposes with cost per ha = NZ\$13.28 + NZ\$2.28 × (possums per ha) [20].

10 % of carrying capacity per year however, is all that is required to increase the minimum death rate above the maximum birth rate and eventually force the local population to extinction. As existing field operations should have been sufficient to achieve these objectives other factors must be considered. For example, migration may quickly repopulate a possum-free area. Thus it is likely that any control procedure must be combined with effective possum containment programmes.

Further, while it has been assumed at times that pseudo-vertical transmission almost always occurs in possums [8], the typical life-span of an infected possum is probably less than 4 months. A possum joey stays with its mother for about 6 months. Within the context of the model, a joey is only a new population member once it is acting on its own, so a lower effective birth rate for infected possums should be considered, resulting in lowered requirements for possum Tb eradication. To determine the lower limit of control under this scenario, if we assume no age structured differences in Tb infected possums, then without pseudo-vertical transmission, $R_0 = 1{\cdot}55$. The required control effort via vaccination is 157 vaccine doses/ha/year to keep just under 39 % of the population vaccinated.

If we assume that possum-to-possum transmission parameters are constant, then change in R_0 is interpreted as a change in the local geography, as reflected in the contact function and the density dependence of disease transmission (see appendix A). Increasing R_0 implies a superior possum habitat, resulting in increased disease-free carrying capacity and higher endemic infection prevalence. A comparison of operations is shown in Figure 3, showing dependence of required culling and vaccination effort as R_0 increases from 1 to 1·66 (in the model, $R_0 = 1{\cdot}66$ corresponds to density-independence). As the vaccine has a significant add-on cost compared to culling, this simple analysis would imply that it is never cost-efficient to employ vaccination.

While reduction of the possum population is attractive for reasons other than Tb eradication, a possum vaccine has the advantage over possum culling that it is less likely to have a negative impact on humans, domestic animals or other wildlife than poison bait or traps. Further, successful vaccination will result in a persistent immune population, which would help to prevent immigration of susceptible and infected possums into the area, making migration and spatial effects less significant than under a culling programme. Delivery of a possum vaccine could also involve delivery of other population control agents such as sterility drugs, however this is not considered here.

Comparing wildlife control strategies with cattle vaccination

The choice of a strategy is dependent on the final goal of the programme. Meeting international OIE standards for Tb eradication, and choosing a strategy which minimizes or eliminates Tb are two different goals which may coincide. Clearly a cattle vaccination

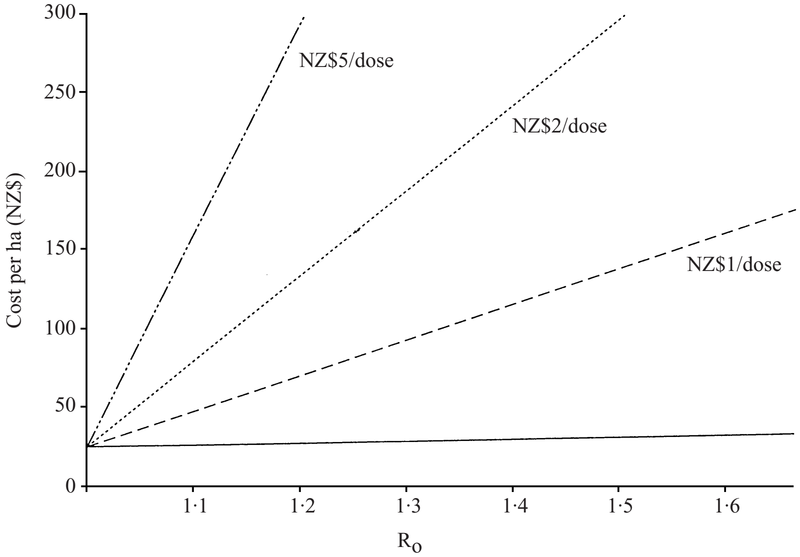

Fig. 3. Comparison of control operations for increasing R_0. Possum culling (solid line) *vs.* possum vaccination at NZ$1, NZ$2 and NZ$3. Displayed range of R_0 from 1·0 (poor possum habitat) to 1·66 (excellent possum habitat).

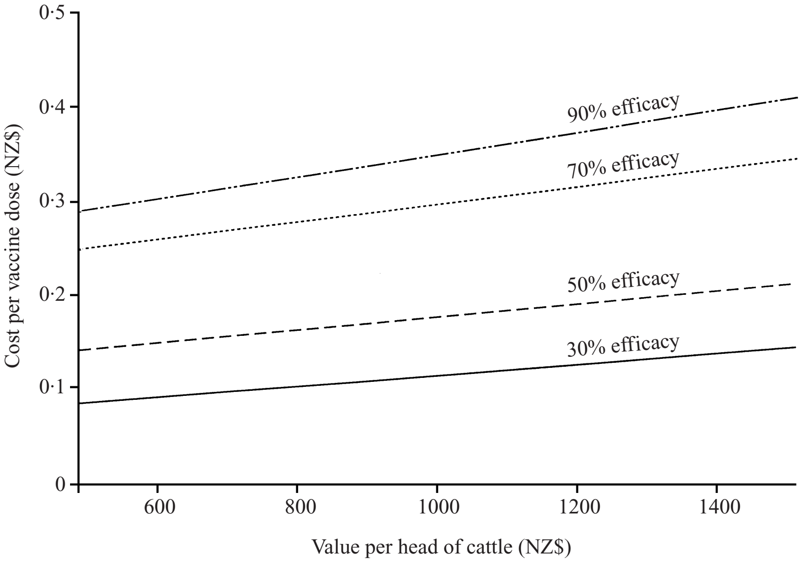

Fig. 4. Breakeven cost for cattle vaccination at various efficacies. Assumed 100% coverage and lifelong immunity.

programme or improvement in Tb testing procedures will have no effect on wildlife Tb prevalence. In contrast, even in the absence of the Tb problem, the possum would still be regarded as a pest in New Zealand and control of the possum population would remain desirable, especially if potential problems such as the risk of poisoning other local inhabitants (both human and animal) could be reduced.

Problems specific to the development of cattle Tb vaccines were reviewed in Newell and Hewinson [21]. A disadvantage of a hypothetical cattle vaccine is that it could compromise the existing caudal fold test, which is simple to use in the field and inexpensive. A new test that is effective under a vaccination programme is likely to be more costly or complicated. While currently not cost effective, such a testing procedure may become useful if required only for the small number of herds under strong suspicion of Tb infection.

If a cattle vaccine could be developed which did not compromise the caudal fold test, or alternatively if an inexpensive replacement test were discovered, the reduction in losses to production due to Tb may be important, even if the vaccine alone does not lead to

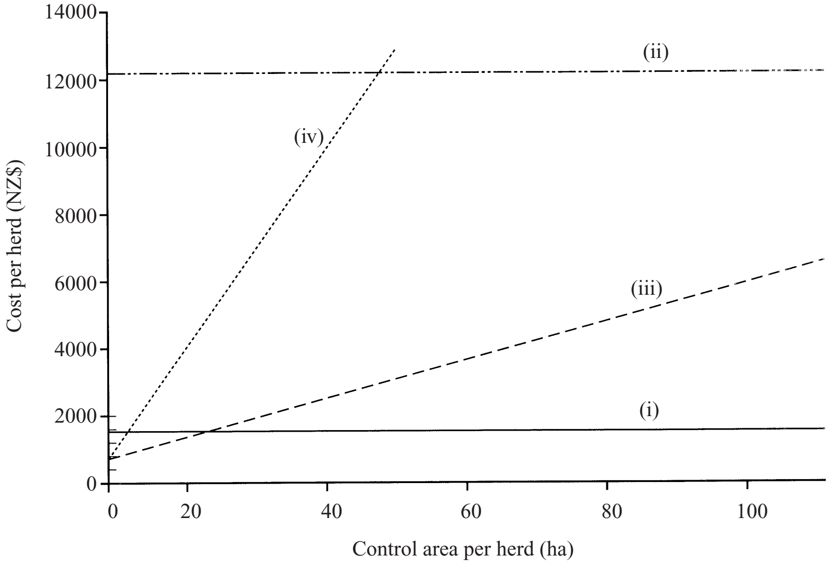

Fig. 5. Comparison of control operations for increasing control area. (i) Cattle vaccination plus whole herd caudal fold testing (ii) Cattle vaccination plus whole herd *in vitro* testing (iii) Possum culling (iv) Possum vaccination.

national Tb-free accreditation. Figure 4 shows the levels at which vaccine cost would be defrayed by reduced losses for Tb infected cattle, and for reduced ancillary testing. Value of a head of cattle varies from NZ$500 to NZ$1500, and various vaccine efficacies are assumed, together with 100% vaccine coverage.

In order to make this comparison, the additional costs associated with testing of movement control herds must be considered as well, as the number and length of time on movement control can be expected to vary, depending on the efficacy scenario. From Kao and colleagues [10] we assume that current movement control data for herds in vector areas are valid for the situation with no control, while the data for herds in non-vector areas are valid for the situation with a 90% effective vaccine. The clustering of infection (expressed in the parameter b_{disp}) and the average time on movement control are linearly interpolated with respect to vaccine efficacy, based on these values. Movement control herds are tested for infection every 2–6 months, depending on the situation [22]; it is assumed here that on average, a movement control herd will be tested every 4 months or part thereof. Finally, we assume the mean stated values for the force of infection (*vide supra*), implying a Tb endemic population density of 4·3 possums per ha, and disease prevalence of 3·04%.

It is apparent from Figure 4 that even for a vaccine of high efficacy, the breakeven cost of a cattle vaccine is quite low, and unless other control measures help reduce Tb levels below OIE standards, it is unlikely that a cattle vaccine will prove cost effective in this scenario.

Using the model parameters, the cost of a 89·9% effective vaccine with 100% coverage would be NZ$1540 per herd, if the caudal fold test is not compromised. This cost would be reasonably constant for any wildlife vector situation; the only changing parameter would be the efficacy of the vaccine, which would be a consideration for feasibility and development costs (Table 2).

Another possible strategy relies on vaccination plus abattoir testing to identify Tb-infectious cattle. Edwards [23] give a general summary of meat inspection, together with guidelines for risk analysis and potential benefits/hazards. Though some infected cattle lacking gross lesions have been shown to be infectious [24], these animals can be neglected as a small proportion of the population for modelling purposes. As a worst case scenario, all animals with lesions are considered to be infectious. Corner [25] suggested that 95% of cattle with a single lesion (representing over 66% of all lesioned cattle) can be identified through careful inspection of six lymph node pairs; a variety of testing methods are then available to determine if they are tuberculous. In the absence of test and slaughter there is an enhanced probability that disease-related mortality will occur. However only perhaps 10–20% of infected cattle would eventually die of the disease [26]. This is probably not relevant considering the abbreviated life-span of a domestic animal; it is assumed here that

Table 2. *Herd infection levels for various cattle vaccine efficacies. Approximate time on movement control* (*MC*) *based on linear interpolation of MC data for herds in vector and non-vector areas from the New Zealand national livestock database* (*see* [*10*])

Vaccine efficacy (%)	Test reactors/herd (%)	Infected/herd (%)	MC herds (%)	Time on MC (months)
90	0·47	0·51	0·20	10
70	1·06	1·17	0·60	12
50	1·76	1·95	1·19	13
30	2·47	2·74	2·00	14
No vaccine	3·54	3·92	3·26	21

increased death due to Tb is negligible, as is consistent with model assumptions disregarding the anergic disease stage. In this case Tb-infected cattle in non-movement control herds will only be found through the abattoir inspection; a 95 % sensitivity and 100 % specificity is assumed, with all infectious cattle being detectable.

Because abattoir testing detects Tb at a later stage than the caudal fold test, meeting the required 0·2 % herds on movement control requires less than 0·47 % incidence of infected and infectious cattle in non-movement control herds, and a vaccine efficacy of only 70 %, compared to an efficacy of 89·9 % which is required to achieve 0·47 % incidence of reactor cattle when the caudal fold test can be used. To achieve 0·13 % infected and infectious cattle, or the same level as with 0·47 % reactor cattle, vaccine efficacy of 90 % is required, only marginally greater than in the previous case, and a negligible difference considering the approximations used in this evaluation. The form of this model is given in appendix B.

Considering only the cost of the vaccine a comparison is made to the cost of equivalent possum control programmes in Figure 5; the value of the basic reproduction ratio is assumed to be $R_0 = 1{\cdot}63$, which implies a cost per hectare of possum culling of just under NZ$60 per ha, and a cost of possum vaccination of about NZ$240 per ha. It is assumed that 0·2 % of herds will be quarantined, with these herds requiring the higher cost of *in vitro* testing. From [10], the mean cattle herd size in New Zealand is 276 head. If operating costs are the principal consideration, then the size of the required possum control area will be indicative of the preferred strategy. A possum vaccination programme becomes preferable to cattle vaccination if the possum control area is below about 3 ha per herd, while possum culling is preferable to cattle vaccination if the control area is below 13 ha per herd. If successful use of a cattle vaccine requires *in vitro* testing for all cattle in all herds, then culling in a control area of less than about 200 ha per herd will have costs competitive with cattle vaccination, while possum vaccination will be competitive for control areas of less than 50 ha per herd.

Time course of control strategies

Roberts [9] examined the progress of the possum population to disease eradication under culling and vaccination options, assuming minimum required control levels were maintained. Kao and colleagues [10] examined progress of the cattle population to Tb-free status under cattle vaccination, assuming minimum required vaccine efficacy, and an exponential implementation of a vaccine programme, with half the population covered in 3 months. In both cases, the time frame of programme success was on the order of 5 years. Further examination of time course of events will depend on choices of management strategies which lie outside the scope of this paper.

Relevance to badgers as wildlife vectors

The bovine Tb situation in the United Kingdom is complicated by the presence of badgers (*Meles meles*) as a wildlife disease reservoir. This interaction is a subject of much scientific and political interest [27], and has resulted in the recent government publication of a report on 'Bovine tuberculosis in cattle and badgers' [28]. Commonly referred to as the 'Krebs report', it is a summary of all aspects of the bovine Tb problem in the United Kingdom. The consensus of the report is that scientific research at all levels must continue in a coordinated fashion, and it further suggests that the most appealing long term strategy is the development of an effective cattle vaccine and complementary diagnostic test. As a fall back strategy, badger vaccination should also be considered.

Because they play a similar role to the possum in New Zealand, comparisons are often made between the two situations. Despite some similarities, there are several key differences which make it difficult to compare studies between the two. Direct possum-to-cattle transmission has been implicated, however this appears to have little relevance to badgers, where pasture contamination with urine and faecal matter is a more likely source of infection [29]. Little direct contact between badgers and cattle has been observed. The location of fence lines and thus crossing points for multiple badger runs has been implicated in transmission, while the proximity of possum dens to pastures is a concern in New Zealand. This is emphasized by evidence that tuberculous possums have reduced ranges as clinical disease symptoms become more prevalent [30]. The dens may be shared sequentially; possums move nightly within the home range and do not cohabit. In contrast the description by a well known authority of the 'solitary grey badger, who lived his own life by himself, in his hole in the middle of the Wild Wood' [31, p. 44] and 'cared little for Society' [31, p. 240], is a misrepresentation. The Eurasian badger is a gregarious animal living in communal setts, often populated by several generations at once. From a modelling perspective, the difference in modes of infection would change the contact function between badgers and cattle; while we expect possum-cattle interaction to be essentially random, the relatively static badger population implies a less density-dependent contact function than for the possums. Further, the dependence of the force of infection on spatial distribution and climatic changes would be different, although neither of these are considered in this model.

As badgers are a protected species in the United Kingdom (the Protection of Badgers Act of 1992 exacts severe penalties for unauthorised killing of badgers) control strategies for badgers must be substantially different from the wholesale culling approach used with the possum population. Current efforts target culling of selected regions proximate to cattle pasture; this approach has the problem that depopulated areas are then quickly repopulated [12], and under certain conditions may result in a smaller population with higher absolute numbers of infected badgers [33]. Tb control of this sort is likely to be amenable to a modelling approach similar to that used here to examine Tb control in cattle, as there are analogies between the fixed communities of badgers (the setts) being isolated and intensively tested for Tb, and the quarantine and testing done in movement control cattle herds.

Vaccination is an attractive option considering that it potentially benefits both the cattle and the badger population. The method of badger vaccination may differ from possum vaccination, and thus a new analysis of cost would have to be made based on those methods.

An additional problem is the difficulty associated with vaccinating young animals before infection, especially since pseudo-vertical transmission may be important. Badgers do not leave the sett until approximately 2 months of age [12], by which time the offspring of a tuberculous badger would have likely already been infected. It can be shown (see for example, [32, p. 32]) that vertical transmission alone is insufficient to maintain an endemic Tb level, however consideration of diagonal (between infected adults and the young of other badgers in the sett) transmission or age structure in the Tb epidemiology may complicate matters further.

While all these factors complicate understanding the epidemiology of wildlife disease transmission, from a mathematical perspective the epidemiology of Tb can be described in both possums [9] and badgers [33] via an *SI* model with pseudo-vertical transmission. Thus while specific parameters will have different values, the qualitative results for the models should be valid for both.

DISCUSSION

If Tb eradication is the goal, a single control procedure that will eliminate Tb in possums would be superior to a combination of strategies or a cattle Tb strategy which will only serve to reduce Tb levels. As this may not be possible, other options must be considered.

A programme targeted at possums (either vaccination or culling) does not affect cattle testing; further, possum control operations are desirable even in Tb free areas. Culling has the advantage of reducing possum numbers, however there are serious reservations regarding the use of poisons in the environment. Further, experience with culling operations to date have shown that, despite culling rates that are theoretically adequate to eliminate possum Tb, the disease persists. It is speculated that possum migration or the effects of the spatial structure of the disease may be involved; in this case, the required culling effort may be significantly greater than that previously suggested. This may be especially relevant for aerial dispersal of poison, which in theory can completely depopulate a region of possums, but has often not been effective in Tb eradication. A further complication is that while ground operations may be reasonably approximated as continuous events, aerial dispersal is more reasonably represented by a single event, or periodic events, and might be more amenable to a pulsatile model such as found in Roberts and Kao [34]. The drastic variation in possum density may also make spatial considerations more important.

Similar to culling, a possum vaccine would be required to hold a sufficient proportion of the population in a disease-free and non-susceptible state, reducing the number of potentially infectious contacts below the point where the disease can persist. The population density in this case would of course be higher than under a culling programme. While an effective possum vaccine has yet to be developed, it would have the advantage of having minimal environmental impact compared to culling. Further, the persistent presence of vaccinated possums in target areas would help to prevent the immigration of susceptible or infected possums, and thus vaccination is less likely to be sensitive to spatial structure or migration than culling strategies would be.

Cattle vaccination relies on preventing the transmission of Tb from possums to cattle. As with a possum vaccine, a cattle vaccine has yet to be developed. There are also concerns that a vaccine would be likely to compromise the inexpensive caudal fold test currently used to detect cattle Tb; in this case the costs of a new testing regime would also have to be considered. Implementation would require acceptance by the international community of the revised testing regime based on either a new cost effective and generally applied Tb test or alternatively, a histological examination of abattoir-collected material combined with a more expensive but highly sensitive and specific ancillary test. Especially in the latter case, difficulties with acceptance by international bodies could be considerable, as they would require evaluation *vis à vis* the well-established and successful Tb control procedures used in other countries. In either case, a vaccination programme has the advantage of ease of delivery to the target group, and relatively low ecological impact. It would also be much easier to target costs at the user level, as cost to the individual would be dependent on herd size, not on proximity, size and density of possum habitat.

The choice of strategy is clearly dependent on the are of control required. In a large area, or one where delivery to possums is difficult, a cattle vaccine might prove preferable. However, in easily isolated areas possum culling may be preferable, whereas in small control areas and where migration may be a problem, a possum vaccine may prove the best option. Also important is consideration of the overall goal – to eradicate Tb, or reduce cattle Tb incidence below OIE standards of freedom. While these goals are related they are not the same, and without possum control or a fully effective vaccine, eradication of cattle Tb is unlikely.

Due to the uncertainty in epidemiological parameters, it is important to consider the effect that changing parameter estimates would have on these results. For example, variations in stocking density will change levels of cattle-to-cattle transmission, while local variations in possum density may complicate possum control operations. To properly evaluate these effects, better establishment of the quantitative relationship between possum and cattle Tb in New Zealand is required. This implies further work in providing epidemiological and demographic parameters from the field, as well as analysis of models involving spatial dispersal and possible age structure effects. Also to be considered are environmental impact, public perception and research and development costs, which are not usually explicit in modelling efforts. While not directly relevant to eradicating Tb, these are considerations which are nonetheless important to the overall picture. These recommendations are largely mirrored in the ‘Krebs report’ [28] on Tb in badgers and cattle in the United Kingdom, where it is suggested that continued research in mathematical modelling with emphases on spatial dispersal, coordination with experimental research and inclusion of economic considerations is a key component to developing an effective Tb control strategy.

In this paper, a simple model of possum-to-cattle Tb transmission is used to evaluate various Tb control strategies. Examination of the underlying parameters and the model results show that it is too soon to rule out any of the three control strategies considered here. It is intended that the results presented here be guidelines for the further experimental and theoretical work required to properly understand this complicated problem.

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APPENDIX

A Model Possum Equations

The SI model

These equations are first discussed earlier. The population of possums is assumed to consist of two distinct classes, those susceptible to the disease, and those infected and infectious. Let the number of possums per unit area be N, and the number of infected and infectious possums per unit area be I. Then the number of susceptible possums per unit area is $S = N - I$. The model is of SI form, and

$$\left.\begin{aligned}\frac{\mathrm{d}N}{\mathrm{d}t} &= (B(N) - D(N))N - \alpha I\\ \frac{\mathrm{d}I}{\mathrm{d}t} &= pB(N)I + \beta_{\mathrm{pp}}\frac{C(N)}{N}SI - (\alpha + D(N))I,\end{aligned}\right\} \qquad (1)$$

where $B(N)$ and $D(N)$ are the density dependent birth and death rates respectively, α is the increase in death rate due to disease, p is the probability of pseudo-vertical transmission, and β_{pp} is the possum-to-possum mass action transfer rate for the disease in fully susceptible animals. The non-decreasing density dependent contact function $C(N)$ is correlated to possum behaviour. For $C(N) = N$, contact between possums is strictly random, while $C(N) = 1$ implies a fixed contact rate, such as would be the case with territorial animals with a fixed number of neighbours, or if solitary pair bonds are the dominant interaction.

The basic reproduction ratio of the disease is the expected number of new cases of the disease caused by a single diseased animal in a totally susceptible population. It is expressed by the ratio of the rate of occurrence of all new cases of the disease (both through pseudo-vertical transmission at birth and general infectious contact) divided by the death rate due to the disease plus death due to all other causes, and is given by

$$R_0 = \frac{pB(K) + \beta_{\mathrm{pp}}C(K)}{\alpha + D(K)},$$

where K is the disease-free carrying capacity. In this paper, calculations assume the forms

$$\begin{aligned}B(N) &= b - \delta r N^{\theta}\\ D(N) &= d + (1-\delta) r N^{\theta}\\ C(N) &= \frac{N}{1 - \epsilon + \epsilon N},\end{aligned}$$

where δ measures the relative importance of density dependence in the birth and death rates, and θ and ϵ are shape parameters which reflect the form of the density dependence in population dynamics and inter-host contact respectively. All parameters are shown in Table 3. In this paper, δ is fitted to the data to allow for varying geography.

Equations (1) together with measured and estimated demographic and epidemiological parameters (Table 3) can be used to obtain a rough estimate of possum population density. Local variation in sustainable populations are accounted for by allowing the density dependence of the birth and death rates to vary; a richer environment is assumed to result in less density dependence, allowing for larger local disease-free carrying capacities. While the carrying capacity is important for determining the required efficacy of control procedures, for 100 % pseudo-vertical transmission the size of the disease endemic population is the same, regardless of the carrying capacity.

In Swinton's [33] model of badger Tb, the SI model is also used, but the birth term is replaced by an annual resetting of the population. For reasonable parameter values for the possum model, this birth resetting results in only small differences in critical parameters from the continuous model [34].

Modelling control and monitoring procedures

Vaccination in the SI model. Possum vaccination is discussed above, and is based on Roberts [9]. In order to compare the relative effort for the control strategies, it is necessary to extend equations (1) to consider the vaccination process in more detail. Let F be number of available vaccine doses. Assume that the movements of individual possums are not correlated with each other. The vaccine is randomly dispersed at rate k; λ is the decay/decomposition rate constant for the vaccinated bait.

Table 3. *Possum Tb parameter values from Roberts* [9]

Possum Tb parameters	Symbol	Value
Maximum birth rate (yr^{-1})	b	2·7
Minimum death rate (yr^{-1})	d	1·7
Maximum population growth rate (yr^{-1})	r	1·0
Logistic shape parameter	θ	3
Density dependence parameter	δ	0·5
Mortality rate due to disease (yr^{-1})	α	3
Pseudovertical transmission probability	p	1
Contact rate shape parameter	ϵ	0·5
Disease transmission parameter (yr^{-1})	β_{pp}	5
Disease-free carrying capacity (ha^{-1})	K	10

Table 4. *Cattle Tb parameter values from Kao and colleagues* [10]*; *taken from Barlow and colleagues* [11]

Cattle Tb parameters	Symbol	Value
Rate of secondary infection (yr^{-1})*	β_{cc}	$9{\cdot}86 \times 10^{-3}$
Rate of development of reactor stage (yr^{-1})	η	0·347
Cattle per herd	n	276
Rate of development of infectious stage (yr^{-1})	ω	8·32
Probability of Tb test failure	f	0·2
Mean time on movement control (wildlife vector areas) (yr)	—	1·548
Mean time on movement control (non-wildlife vector areas) (yr)	—	0·808
Overdispersion parameter	b_{disp}	1·23

Often we are more interested in the proportion of the population which must be in a vaccinated state, rather than the total number. In order to facilitate this, the transformation $Z = I/N$ is made, where Z is the proportion of infected and infectious animals. A proportion of the population W is vaccinated and is partially susceptible. The mass action transfer rates for the disease in vaccinated animals is denoted by γ. Vaccine doses are consumed with rate constant c, and a fraction ψ of consumed doses successfully provide protection against Tb. The equations become

$$\left.\begin{aligned}\frac{dN}{dt} &= (B(N) - D(N) - \alpha Z)N \\ \frac{dZ}{dt} &= -(1-p)\,B(N)Z + (\beta_{pp}\,C(N) - \alpha) \\ &\quad \times (1-Z)\,Z - (\beta_{pp} - \gamma)\,C(N)\,WZ \\ \frac{dW}{dt} &= c\psi(1 - W - Z)\,F - (\rho + B(N) \\ &\quad + (\gamma C(N) - \alpha)Z)\,W \\ \frac{dF}{dt} &= k - cNF - \lambda F.\end{aligned}\right\} \qquad (2)$$

This determines the effort required to achieve disease-free status. With $Z = 0$, and assuming a unique equilibrium can be reached, the vaccination effort is given by

$$k = D(K)\left(\frac{cK+\lambda}{c\psi}\right)\left(\frac{W_T}{1-W_T}\right)$$

$$W_T = \frac{pB(K) + \beta_{pp}\,C(K)}{(\beta_{pp} - \gamma)\,C(K)}\left(1 - \frac{1}{R_0}\right).$$

W_T represents the proportion of the population that must be kept vaccinated.

Model herd control equations

Unlike the possum, once cattle are exposed to Tb there is a significant period typically lasting from several months to a few years, where the animal is exposed and infected, but not infectious. The total population is assumed to be fixed and there are additional terms to account for the external source of infection (the wildlife vector) plus herd testing (see above). To avoid confusion with the possum parameters, a number of variable and parameter symbols have been changed from [10] and the common susceptible/exposed/infectious or *SEI* model notation is not used (Table 4). The parameter for possum-to-cattle transmission parameter is β_{pc}, resulting in a force of infection of $\beta_{\mathrm{pc}} Z$. The number of animals per herd is n, of which l are in the exposed, latent Tb stage, x react to the caudal fold test, and i (a subset of x) are infectious. Infection parameters are $\beta_{\mathrm{cc}}\, i$ for the force of infection for cattle-to-cattle transmission, and η and ω for the rate of change to the reactor and infectious disease stages respectively. The caudal fold test sensitivity is $1-f$. Test specificity is assumed to be 100% since supplementary testing is conducted to eliminate false positive test results.

Disease is removed from the population on a herd by herd basis. To handle this in the model, the distribution of the disease amongst the herds is assumed to be negative binomial with index of dispersion b_{disp}, where $0 \leqslant b_{\mathrm{disp}} < \infty$. The lower limit corresponds to a Poisson distribution with increasing b_{disp} indicating increased clustering of infection. The probability that disease will be detected in a herd with X reactor cattle in it is $1-f^X$. If we assume that b_{disp} is constant, then the rate of removal of herds to quarantine can be approximated by

$$g(t) = (1-K_1^{-\frac{x(t)+b_{\mathrm{disp}}}{b_{\mathrm{disp}}}}),$$

where $K_1 = 1+b_{\mathrm{disp}}(1-f)$. If $\sigma(x)$ is the rate of removal for a reactor animal, then the rate of removal of reactor animals per herd is similarly expressed by

$$\begin{aligned} h(t) &= x(1-fK_1^{-\frac{x(t)+b_{\mathrm{disp}}}{b_{\mathrm{disp}}}}),\\ &= x\sigma(x) \end{aligned}$$

(see [10] for details of the derivation). This expected time until a reactor animal is put on movement control is thus $1/\sigma(x)$. Then if I_H and H are quarantine herds and the constant number of total herds respectively, and $\phi(\tau)$ is the fraction of herds which remain on quarantine a time τ after the disease is first detected, model equations are given by

$$\left.\begin{aligned} \frac{\mathrm{d}l}{\mathrm{d}t} &= (\beta_{\mathrm{pc}} Z+\beta_{\mathrm{cc}}\, i)\,(n-l-x)-\eta l-l\sigma(x)\\ \frac{\mathrm{d}x}{\mathrm{d}t} &= \eta l-x\sigma(x)\\ \frac{\mathrm{d}i}{\mathrm{d}t} &= \omega(x-i)-i\sigma(x)\\ I_H(t) &= \int_0^\infty \phi(\tau)\,(H-I_H(t-\tau))\,(1-\mathrm{K}_1^{-\frac{x(t-\tau)+b_{\mathrm{disp}}}{b_{\mathrm{disp}}}})\,\mathrm{d}\tau. \end{aligned}\right\} \quad (3)$$

Herd equations with vaccination and abattoir testing

In a system where herd testing consists of histological inspection for gross lesions, the equations become somewhat simplified. A reactor stage need not be considered, and detection is dependent on the number of infected and infectious animals; while there is evidence that some animals have no detection lesions but are infectious, it is assumed that detectable lesions are common at this disease stage. The system of equations would then be written

$$\left.\begin{aligned} \frac{\mathrm{d}l}{\mathrm{d}t} &= (\beta_{\mathrm{pc}} Z+\beta_{\mathrm{cc}}\, i)\,(n-l-i)-\nu l-l\sigma(i)\\ \frac{\mathrm{d}i}{\mathrm{d}t} &= \nu l-i\sigma(i)\\ I(t) &= \int_0^\infty \phi(\tau)\,(H-I_H(t-\tau))\,(1-\mathrm{K}_1^{-\frac{i(t-\tau)+b_{\mathrm{disp}}}{b_{\mathrm{disp}}}})\,\mathrm{d}\tau \end{aligned}\right\} \quad (4)$$

where ν is the rate at which infected animals become infectious. Inclusion of the cattle vaccination programme is as in [10].

Cattle Tb model without wildlife vectors

In the absence of possums, it is necessary to determine if cattle Tb can be eliminated by current or alternative control or eradication procedures. A cursory examination of the system of equations (3) shows that the disease-free solution always exists; a more detailed analysis establishes conditions for the existence of a steady state endemic solution. The steady state is given by the solution of the system

$$\beta_{\mathrm{cc}}\, \eta\omega\,(n-x) = (\beta_{\mathrm{cc}}\, \eta x+(\eta+\sigma(x))\,(\omega+\sigma(x))\,\sigma(x), \quad (5a)$$

$$i = \frac{\omega x}{\omega+\sigma(x)} \quad \text{and} \quad (5b)$$

$$l = x\sigma(x)/\omega. \quad (5c)$$

Equations (5*b*) and (5*c*) show that i and l are specified once x is known. The left hand side of equation (5*a*) is decreasing in x, while the right hand side is increasing in x, so a unique equilibrium solution for x exists if

$$\frac{\beta_{\mathrm{cc}}\, n}{\sigma(0)} \times \frac{\eta}{(\eta+\sigma(0))} \times \frac{\omega}{(\omega+\sigma(0))} \geqslant 1. \quad (6)$$

We can see that this expression is R_0 for this system by examining it term by term. The first term is the expected number of new exposed cases created by a single infectious animal introduced into a totally susceptible herd. The second term is the expected number of reactor class animals arising from a single exposed case, and the third term is the expected number of infectious animals arising from a single reactor animal which is not infectious, in both cases in otherwise totally susceptible herds. Thus the product of these terms is the expected number of infected and infectious animals arising from a single infectious animal, or by definition, R_0. The disease-free solution always exists; if the condition (6) holds true, a unique endemic steady state exists as well. Substituting in parameter values from Table 2 the value of the left hand side of relation (6) is $5{\cdot}55 \times 10^{-3}$. Thus existing procedures should be more than adequate to eradicate Tb in cattle.

Results for the stability of the steady state with an external infection are valid for this case, with $\beta_{pc} = \mu = 0$ [10].

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