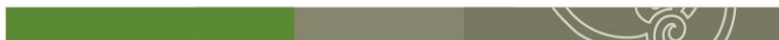




Identifying habitat patches with low risk for TB persistence

Animal Health Board R-10721 (Module 3)



Landcare Research
Manaaki Whenua

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Summary

Project and Client

- Ground-based control of possums for TB management has a high cost per habitat hectare. The control coverage achieved by contractors is primarily governed by their individual experience (i.e. personal decisions on whether certain habitat requires control or not), and a management paradigm of needing to target all habitat that could potentially harbor possums. This management paradigm does not take into account that for TB to persist there must be sufficient contact between individual possums. Consequently, it is possible, where possum numbers are low, that control effort is not required. Landcare Research was contracted by the Animal Health Board from Nov 2009 to June 2010 to assess this hypothesis by determining if there might be a minimum density of possums or, alternatively, number of possums per patch below which TB is unlikely to persist.

Objectives

- To determine the number or density of possums necessary in a given patch for TB to persist.
- To explore how the risk of disease introduction influences the relationship in (a).
- To determine the probability of persistence in realistic, patchy landscapes under no control, area-wide control, and targeted control using the information obtained in (a) to identify patches targeted for control.

Methods

- Possum populations were simulated using a spatial possum-TB model in which two modes of TB transmission were modelled: density-dependent and frequency-dependent. The range of patch sizes simulated was 1, 4, 9 or 25 ha, and patch carrying capacity (K) ranged from 1 to 10 possums per hectare. For each mode of transmission, patch size, and patch density combination 1000 replicates of the model were run. A further set of simulations that assumed frequency-dependent transmission was run where each year there was either a 0.1, 0.05, or 0.01 probability of an infected possum arriving at a patch. For each simulation a patch was populated with the specified number of possums (= patch size x patch density), then in year 1 season 3 a single resident possum was converted to an infected, and the model was run for a further 5 years to assess whether TB persisted in that patch over that period. The probability of persistence was calculated as the number of replicates where infected possums were still present after 5 years divided by the total number of replicates (1000). The probability of persistence was assessed in relation to both the density of possums per patch and the total number of possums per patch.
- TB persistence simulations were also run using realistic landscapes. Two selected areas from the Hawke's Bay were modelled using national maps of possum carrying capacity (K) at 50-m resolution. Spatially-referenced trapping data from these two areas were used to represent the abundance and home range locations of the possum population in

the areas and as a starting point for the model simulations. Three control scenarios were simulated: no control, area-wide control, and targeted control. The expected number of possums per patch at carrying capacity was used to generate sites (i.e. control masks) for the targeted control scenario. Patches with an expected number of possums greater than a threshold number (identified from the first set of simulations) were part of the targeted control area whereas patches with less than the threshold number per patch were not controlled. A habitat patch was defined as a collection of adjacent cells with positive possum habitat carrying capacity values. The minimum patch size was 50 x 50 m (0.25 ha), and a moving window algorithm was used to assess whether the focal cell had a positive carrying capacity ($K > 0$) and if any of the eight adjacent 50 x 50-m cells also had positive carrying capacity. If so, then these adjacent cells were lumped together as the same 'patch'.

Results

Patches in isolation, density-dependent transmission

- Under the assumption of density-dependence, TB persistence after 5 years showed a non-linear relationship with possum *density*. Fitting a curve to this relationship for the 5% TB prevalence simulations predicted that a threshold density of approximately 4 possums per ha would result in a 0.05 probability of persistence, and 1.6 possums per ha a 0.01 probability of persistence. The fitted relationship for the 2% TB prevalence simulations predicted only slightly higher density thresholds, namely that 4.3 and 1.7 possums per ha would result in 0.05 and 0.01 probabilities of persistence, respectively.
- At lower possum population sizes TB persistence was sensitive not to possum density but to the *number* of possums in the patch, and more than 8 possums per patch (a patch of 1 ha with a density of 8 per ha or a patch of 8 ha with a density of 1 per ha) would result in a greater than 0.01 probability of TB persistence, assuming 5% prevalence at carry capacity. There was no clear relationship between TB persistence and the number of possums for the 2% prevalence simulations.

Patches in isolation, frequency-dependent transmission

- Under the assumption of frequency-dependence, persistence was related to possum *numbers* rather than density. Fitting a curve to the relationship between TB persistence and the number of possums in a patch seemed to produce illogical thresholds with less than one possum required to give a greater than 0.01 probability of persistence assuming 5% TB prevalence at equilibrium. Contour plots of the actual probabilities showed more than three possums per patch resulted in a 0.01 probability of persistence and more than nine possums a 0.05 probability of persistence, under the assumption of 5% prevalence at equilibrium. The threshold numbers were similar under the assumption of 2% prevalence at approximately 3 possums and 10 possums per patch to result in a 0.01 and 0.05 probability of persistence, respectively. Including a constant probability of immigration to the simulated patches did not change the shape of the relationship between the probability of TB persistence and possum numbers; it simply increased the probability of persistence by the level of immigration assumed.

Patches in context

- For both real landscapes simulated, more than 90% of possum habitat was part of one large patch, an outcome of the way we classified habitat patches as contiguous areas where possum carrying capacity was predicted to be greater than zero. Under a no control scenario (i.e. starting at 2% RTC and the population then left to recover), 97.3% and 99.6% of infected possums were located in the main patch at both sites. With area-wide control and targeted control that excluded patches with less than 8 possums, the average number of infected possums was reduced by 95% compare to no control.
- Targeted control resulted in a similar reduction in overall possum density to area-wide control, but the probability of TB persisting for 5 years and the average number of infected possums at the end of 5 years was slightly higher under targeted control. Under targeted control there were potential savings in control costs for the two areas simulated of 10 and 6% relative to area-wide control.

Conclusions

- The probabilities of TB persistence for the various patch configurations need to be interpreted relative to each other rather than as absolute probabilities because they are sensitive to the disease transmission coefficient (β), which has never been empirically measured.
- Assuming 5% TB prevalence at equilibrium and density-dependent transmission, simulations indicated that patches of possums should have no more than 8 possums per patch (8 possums in one hectare or 8 possums over 8 hectares) to have less than a 1% chance of TB persisting in an isolated patch over 5 years. Above this threshold number there is sufficient home-range overlap and contacts between infected and susceptible possums to enable TB persistence with a greater than 1% probability.
- Assuming 2% TB prevalence at equilibrium and density-dependent transmission then the threshold for persistence was related more to possum density than possum numbers, so that a patch should have a density of no more than 4 possums per hectare to have less than a 1% chance of TB persistence regardless of patch size. At a low patch density of 1 possum per hectare (with possums assumed to be uniformly distributed) a patch should have no more than 21 individuals to have less than a 1% probability of TB persistence.
- For the frequency-dependent simulations, TB persistence was related to the number of possums per patch and about three possums were required in a patch to give a 1% chance of persistence, indicating an infected possum needs at least 2 other susceptible possums to infect for TB to persist in the patch for at least 5 years (assuming 5% prevalence at equilibrium). These probabilities were for patches in isolation, but TB can also be ‘imported’ by infected possums dispersing from other patches to the focal patch which increases the probabilities of persistence by the importation rate.
- Simulations of actual landscapes showed that most of the landscape can be described as one large patch in terms of possum habitat, and most infected possums are located in this large patch whether the area is controlled or not. Because most of the landscape was part of one large patch, excluding those patches that could not support more than 8 possums resulted in a less than 4 % reduction in the total area requiring control.

However, the percentage reductions in possible control exclusion will depend on the patchiness of the habitat and the isolation of any patches from neighbouring patches.

- Infected possums occasionally appeared in the small (<8 possum) patches indicating these patches were sufficiently connected to other patches to receive immigrants. There was a greater than 5% chance that TB would persist in trapped areas if there was no control to prevent the possum population recovering, but with either area-wide or targeted control this probability dropped below 1%.
- For the simulated landscapes, patches were highly connected on the basis of habitat alone and less than 4% could be missed from control operations using a critical patch size rule. The scale of possum dispersal and home range movements are large relative to our isolation distance, so programme managers and control contractors should not assume some habitat patches can be missed or eliminated from control coverage.
- In the trapped areas with a low proportion of possum habitat (<55%) and an initial density of possums below 2% RTC, simulations suggested control could be postponed for 2-3 years with the probability of TB persistence remaining below 0.06.

Recommendations

- If habitat type and patch size suggest that no more than 8 possums can inhabit that patch then such areas should be considered as low risk.
- Further research is required to understand how possum movement and home range behaviour is affected by landscape structure so we can better define the functional connectivity of the landscape and the probabilities that possums in different patches interact with each other in ways conducive to TB transmission, or disperse between patches .
- Empirical estimates of the disease transmission coefficient (β) are required to give more accurate probabilities of TB persistence.
- Control costs could be reduced by spelling areas from control if there is robust trap-catch data indicating RTCIs are at or below 2% and possum habitat is sparse (<55% of the total area).

1 Introduction

Ground-based control of possums for TB management has a high cost per habitat hectare. The control coverage achieved by contractors is primarily governed by their individual experience (i.e. personal decisions on whether certain habitat requires control or not), and a management paradigm of needing to target all habitat that could potentially harbor possums. This management paradigm does not take into account that for TB to persist there must be sufficient contact between individual possums. Consequently, it is possible, where possum numbers are low, that control effort is not required. Landcare Research was contracted by the Animal Health Board from Nov 2009 to June 2010 to assess this hypothesis by determining if there might be a minimum density of possums or, alternatively, number of possums per patch below which TB is unlikely to persist.

2 Background

Possum populations are not distributed uniformly across landscapes due to the underlying patchiness in habitat resources that determine the carrying capacity or potential size of populations within each habitat patch. Because TB is understood to be transmitted directly from possum to possum, the potential for disease transmission depends on how and how often possums interact in space and time. Without a certain level of interaction between possums, TB is likely to die out. The transmission function or mode that relates the TB transmission rates to the densities of susceptible and infected possums affects how disease persistence is related to possum density or possum number. Density-dependent transmission is where the possum to possum contact rate is proportional to possum density and frequency-dependent transmission where the contact rate is independent of host density and instead depends on the proportion of infected possums (=prevalence) in the population. In disease-host models density-dependent transmission is usually expressed as βSI and frequency-dependent transmission as $\beta SI/N$ where β is the disease transmission coefficient and S, I and N are the densities of susceptible, infected, and total possums in the population respectively. We would expect persistence under density-dependent transmission to depend primarily on possum density in the patch since this is explicit in the transmission function. Under frequency-dependent transmission we would expect persistence to depend on the number of possums since the initial prevalence in the frequency-dependent simulations was one infected possum divided by the total number of possums per patch. Regardless of the assumed mode of transmission, when possum numbers are very low we would expect stochastic or chance effects to have a significant influence on the probability of persistence whereby TB is expected to fade out more frequently in patches with low numbers of individual possums.

The first stage of this project was to consider habitat patches in isolation and identify abundance thresholds below which TB would not persist. We were interested in two measures of population abundance affecting TB persistence in patches: possum *density* per patch and the total *number* of possums per patch. Persistence was assessed theoretically using the individual-based spatial possum-TB model (Ramsey and Efford 2010) to simulate a range of patch sizes (in ha), within patch densities (in possums per ha) and thus number of possums per patch (= patch size x patch density).

The second stage of this project considered TB persistence in patches within a landscape where the number of, distance to, size of, and density within adjacent patches affected the

probability of a patch being infected with TB. Again this was assessed theoretically using the possum-TB model, but two real landscapes were used to describe the patch geometries and configurations used in the simulations. In these realistic landscapes three control strategies were compared: no possum control, area-wide control where all habitat patches were controlled, and targeted control where only those habitat patches above the threshold patch size identified in the first part of the project were controlled.

3 Objectives

- To determine the number or density of possums necessary in a given patch for TB to persist.
- To explore how the risk of disease introduction influences the relationship in (a).
- To determine the probability of persistence in realistic, patchy landscapes under no control, area-wide control, and targeted control using the information obtained in (a) to identify patches targeted for control.

4 Methods

4.1 Patches in isolation

Possum populations were simulated using the spatial possum-TB model and default parameter values except for the disease transmission coefficient (β) which was adjusted to produce either 2% or 5% TB prevalence in a large homogeneous possum population (area = 2500 ha) at carrying capacity ($K = 10$ possums per hectare). Two modes of TB transmission were modelled: density-dependent transmission where the possum to possum contact rate is proportional to possum density (βSI = model default) and frequency-dependent transmission where the contact rate is independent of host density and instead depends on the proportion of infected possums in the population ($\beta SI/N$). The transmission coefficients assumed for each of these four transmission scenarios are listed in Table 1. In the model there is no latent disease stage so all infected possums (I) are also infectious (capable of causing infection). Possum home ranges were assumed to be a function of local possum density with home ranges expanding at low density and contracting at high density. This assumption tends to maintain contact rates at low densities (Ramsey & Efford 2005).

Table 1 Transmission coefficient (β) values used in model to generate specified prevalence in large homogeneous possum populations under two different transmission modes.

	2% TB prevalence	5% TB prevalence
Density-dependent transmission	0.258	0.279
Frequency-dependent transmission	0.695	0.707

The range of patch sizes simulated was 1, 4, 9 or 25 ha (patches were square in shape). Patch carrying capacity (K) ranged from 1 to 10 possums per hectare. The average number of possums in a simulated patch was thus patch size multiplied by the patch density. Patches

were considered in isolation i.e. there was no immigration or emigration of possums to or from the habitat patch. For each patch size and density combination, we ran 1000 replicates of the model. Under the assumption of frequency-dependent transmission and 5% prevalence at equilibrium, a further set of simulations was run where each year there was a 0.1, 0.05 or 0.01 probability of an infected possum migrating into the patch. For each simulation the patch was populated with the specified number of possums, then in year 1 season 3 one of the resident possums was converted to an infected, and the model was run for a further 5 years to assess whether TB persisted in that patch over that period. Five years was considered a good benchmark to assess persistence since there was less than a 0.01 probability that an infected individual would survive for 5 years or more (based on an annual instantaneous mortality rate of 1.1 which is equivalent to an average longevity of 11 months) so any infected individuals present at that time are most likely due to the disease establishing and persisting in the population.

The probability of persistence was calculated as the number of replicates where one or more infected possums were still present after 5 years divided by the total number of replicates (1000). Threshold densities or numbers of possums resulting in a 0.01 or 0.05 probability of TB persistence were determined by fitting the generalised function $y = ax^b / 1 + cx^b$ to the data where y was the probability of persistence, x was the number or density of possums in the patch and a , b and c were constants describing the shape of the function. Curves were fitted using the non-linear least squares (nls) function in the R statistical software package (v 2.9.1) and threshold densities or numbers were found by solving the fitted function for x for a given y (probability of TB persistence = 0.01 or 0.05). This approach enabled prediction of TB persistence across a range of possum abundance but we also expected stochastic or chance events to affect TB persistence when possum numbers were very low so we plotted persistence probabilities as contour lines against the patch variables density and size to identify any combinations of these variables that might determine persistence. In these plots sensitivity to possum density is indicated by vertical contours (when density is on the x-axis) and sensitivity to possum number is indicated by angular contours connecting the x- and y-axes (since number is the product of patch density and patch size).

4.2 Patches in context

TB persistence simulations in realistic landscapes were run for two areas in the Hawkes Bay: Patoka and Timahanga (Fig. 1, Table 2). The landscapes were extracted from national maps of possum carrying capacity (K) at 50-m resolution generated from the underlying habitat classes and indigenous forest types described by ECOSAT. Spatially-referenced trapping data from these two areas was supplied by the Hawke's Bay Regional Council. These data described the location of possum trap sites and the location of traps that caught possums. We assumed that the number and location of the trapped possums was indicative of the abundance and home range locations of the possum population in the trapped area and used this as a starting point for the model simulations. This was achieved by placing a 100-m buffer around the trapped (operational) area to define the extent of the trapped population (indicated by purple line in Fig. 1) and using the trap locations of possums as coordinates for the home range centres of the modelled population. A minimum 5-km buffer was placed around the extent of the trapped population to define the total simulation area (indicated by the aerial photo inset in Fig. 1). Possum populations in the buffer area were proportional to the carrying capacity of the cell they resided in, set to approximately 0.08 of K to simulate an

area-wide residual trap catch index (RTCI) of 2%. Preliminary simulations were done to determine what value the disease transmission coefficient (β) should take to produce 2% TB prevalence at equilibrium (i.e. carrying capacity) under the assumption of density-dependent disease transmission. For the Patoka simulation this was $\beta = 0.7$, for Timahanga $\beta = 0.72$. Simulations were initialised with a 2% TB prevalence.

A habitat patch was defined as a collection of adjacent cells with positive possum habitat carrying capacity values. The minimum patch size was 50 x 50 m (0.25 ha) i.e. the resolution of the carrying capacity maps. A map of possum habitat patches was generated using a moving window algorithm (Johnson et al. 2004) applied to the carrying capacity map to assesses whether the focal cell had a positive carrying capacity ($K > 0$) and if any of the eight adjacent 50 x 50-m cells also had positive carrying capacity. If so, it lumped them together in the same 'patch'. The expected number of possums per patch at carrying capacity (=sum of K values over all cells in a patch) was used to generate a control mask whereby patches with an expected number greater than a threshold number of possums (identified from the first set of simulations) were part of the control area but those patches with less than the threshold number per patch were not controlled.

Simulations were run for 5 years under three scenarios: no control; control of all patches to a 2% RTCI threshold; and control to 2% RTCI only in those patches defined by the control mask above. Control to a 2% RTCI threshold involved annual assessment of RTCI by simulating possum trapping across the landscape (40 trap-lines, 200m long with 10 traps per line); control was then imposed if this RTCI measure was equal to or greater than 2%. After 5 years the presence and level of TB in the simulated population was assessed and the locations (x,y coordinates) of any infected possums identified so the location and attributes of the patch they inhabited could be assessed.

Table 2 Description of simulation areas

	Patoka	Timahanga
Total area of simulation (ha)	94917	22922
Area of possum habitat in total simulation (ha)	60430	19608
Area of possum habitat excluding patches with <8 possums at carrying capacity (ha)	58250	19434
Average K in possum habitat in total area (per ha)	2.42	2.85
Number of habitat patches	2188	193
Area of largest habitat patch (ha)	54339	19046
Area trapped (ha)	11539	1840
Area of possum habitat in trapped area (ha)	4558	998
Area of possum habitat in trapped area excluding patches with <8 possums at carrying capacity (ha)	4101	936
Average K in possum habitat in trapped area (per ha)	2.02	2.55
No. possums trapped	70	86

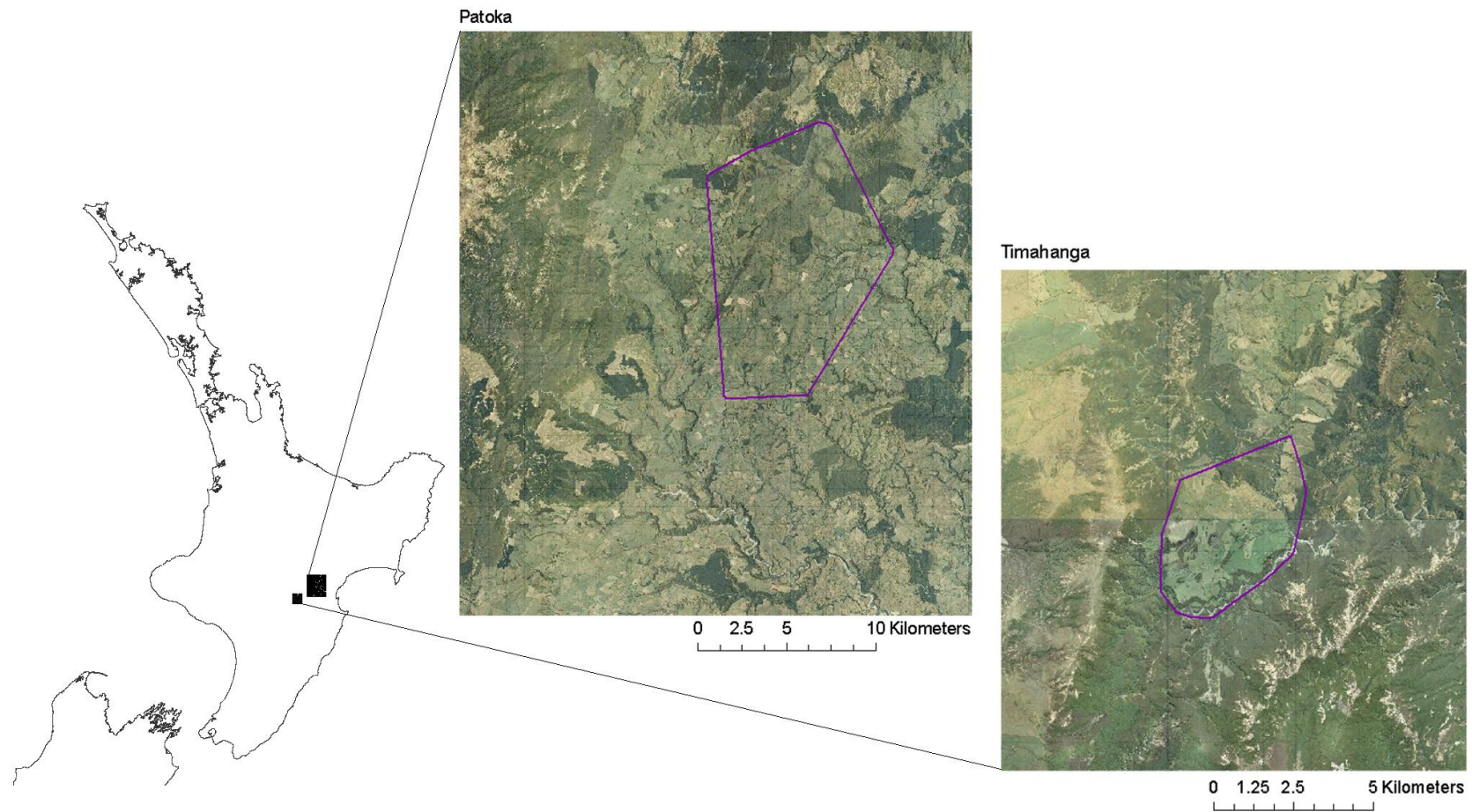


Figure 1 Location and aerial photos of Patoka and Timahanga sites used in real landscape simulations; purple lines show extent of possum trapping (operational) areas.

5 Results

5.1 Patches in isolation

Density-dependent transmission, no immigration

TB persistence for 5 years showed a non-linear relationship with possum *density* (Figs. 2a & 2c); whereas the relationship with the total number of possums in a patch varied with patch size (Figs. 2b & 2d). This is not surprising since the transmission mode was assumed to be density-dependent. For the 5% prevalence simulations, the fitted relationship depicted in Fig. 2a predicted that at a threshold of approximately 4 possums per ha there was a 0.05 probability of persistence and at 1.6 possums per ha a 0.01 probability of persistence (Table 3). Under the assumption of 2% prevalence at equilibrium these predicted thresholds were only slightly higher at 4.3 and 1.7 possums per ha resulting in 0.05 and 0.01 probabilities of persistence, respectively (Fig. 2c; Table 3).

However, contour plots of changes in persistence with both density and patch size showed some sensitivity of persistence to the *number* of possums in the patch (Fig. 3a). Hence more than 8 possums per patch, whether a patch of 1 ha with a density of 8 per ha or a patch of 8 ha with a density of 1 per ha, resulted in a greater than 0.01 probability of TB persistence assuming 5% prevalence at equilibrium (see light blue contour Fig. 3a). The relationship was not so clear for the 2% prevalence simulations – at low densities (1 possum/ha) a large patch size (>21ha = minimum of 21 individuals per patch) was required to give a 0.01 probability of persistence, but at a density of 4 possums per hectare all patch sizes (minimum of 4 individuals) gave a greater than 0.01 probability of TB persistence (Fig. 3b).

Realised possum density in the isolated patches declined with decreasing patch area (Figs. 2a & 2c; Figs. 3a & 3c) probably due to the effects of demographic stochasticity at low possum abundance. Relative patch densities, expressed as realised abundance divided by the patch carrying capacity, averaged $N/K=0.87$ for the largest (25ha) patches whilst those for the smallest (1 ha) patches were lower at around $N/K=0.31$.

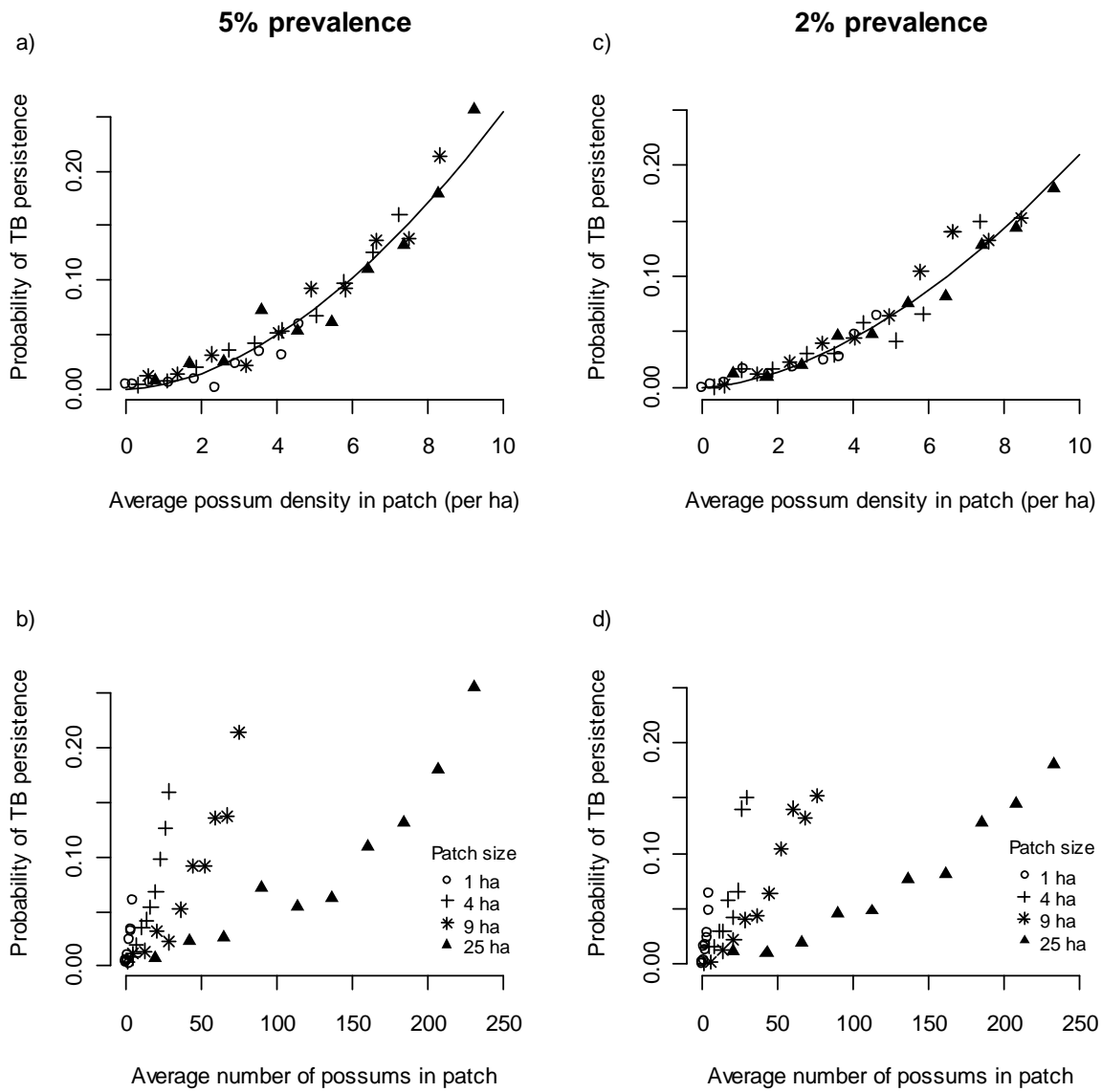


Figure 2 Probability of TB persistence in isolated habitat patches with change in possum density (panels a and c) and possum number (panels b and d) under the assumption of density-dependent transmission and a disease transmission coefficient of $\beta = 0.279$ (to give 5% prevalence at equilibrium, panels a and b) and $\beta = 0.258$ (to give 2% prevalence at equilibrium, panels c and d). The solid line in panels a and c shows the fitted curve used to calculate the threshold densities in Table 3.

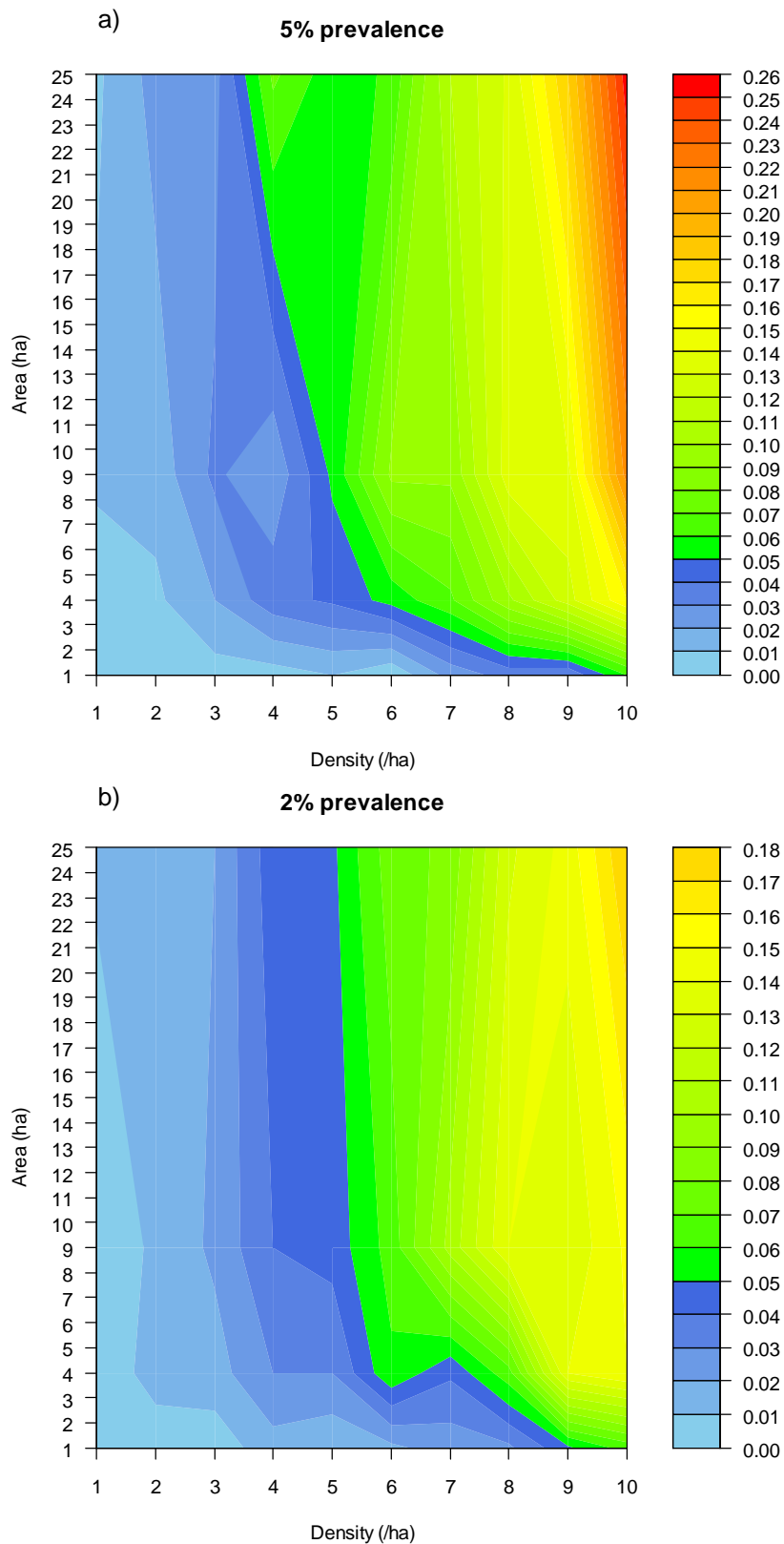


Figure 3 Probability (shown as colour) of TB persistence in isolated habitat patches of varying patch size and possum density under the assumption of density-dependent transmission and a disease transmission coefficient of $\beta = 0.279$ (to give 5 % prevalence at equilibrium, panel a) and $\beta = 0.258$ (to give 2 % prevalence at equilibrium, panel b).

Frequency-dependent transmission, no immigration

Under the assumption of frequency-dependence, persistence showed a better relationship with possum *numbers* (Fig 4b & 4d) rather than possum density (Fig 4a & 4c), the opposite of that observed in the density-dependent transmission simulations. Again this is what we would expect given the model of transmission assumed. The fitted relationship between TB persistence and possum number predicts that more than 0.9 possums per patch results in a 0.01 probability of persistence, or more than 4.1 possums a 0.05 probability of persistence under the assumption of 5% prevalence at equilibrium (Fig. 4b; Table 3). The predicted threshold numbers were only slightly higher under the assumption of 2% prevalence at equilibrium at 1.2 possums and 4.7 possums per patch to give 0.01 and 0.05 probabilities of persistence respectively (Fig. 4d; Table 3).

The threshold numbers derived from the fitted relationship seem illogical since they predict a threshold of one possum when the patch is only one seeded with one infected possum whose chances of surviving 5 years are approximately 0.004 implying a poor fit of the relationship at low numbers. Indeed the contour plots revealed higher threshold numbers than those derived from the fitted relationship. More than three possums per patch resulted in a 0.01 probability of persistence, or more than nine possums a 0.05 probability of persistence under the assumption of 5% prevalence at equilibrium (Fig. 5a). The threshold numbers were only slightly higher under the assumption of 2% prevalence at equilibrium at around 3 and 10 possums per patch to give a 0.01 and 0.05 probability of persistence respectively (Fig. 5b; Table 3). This implies a minimum proportion of susceptible possums in a patch ‘population’ of 0.67 (2/3) and 0.89 (8/9).

In all the scenarios there seemed to be enhanced persistence at *densities* of around 3 possums per hectare (Fig 4a & 4c), although this was obvious only in the bigger patches (9 & 25 ha). Three possums per hectare is the inflexion point for the non-linear contact rate function so there is a local maxima in contacts at this density (Fig 12 in Ramsey and Efford 2005) resulting in enhanced persistence. It was probably not manifest in the smaller patches because there is not as much latitude within a small patch for possum home ranges to expand or contract substantially.

Table 3 Predicted threshold possum abundance per habitat patch to give 0.01 or 0.05 probabilities of TB persistence over 5 years assuming 2 or 5 % TB prevalence at equilibrium. Thresholds were derived by fitting the function $y = axb/1+cx$ to the modelled probabilities of persistence (y) then solving for $x =$ possum density for the density-dependent transmission simulations or $x =$ possum number for the frequency-dependent transmission simulations.

Threshold possum density (density-dependent transmission)		
Probability of TB persistence	2% TB prevalence	5% TB prevalence
0.01	1.7	1.6
0.05	4.3	4.0
Threshold possum number (frequency-dependent transmission)		
Probability of TB persistence	2% TB prevalence	5% TB prevalence
0.01	1.2	0.9
0.05	4.7	4.1

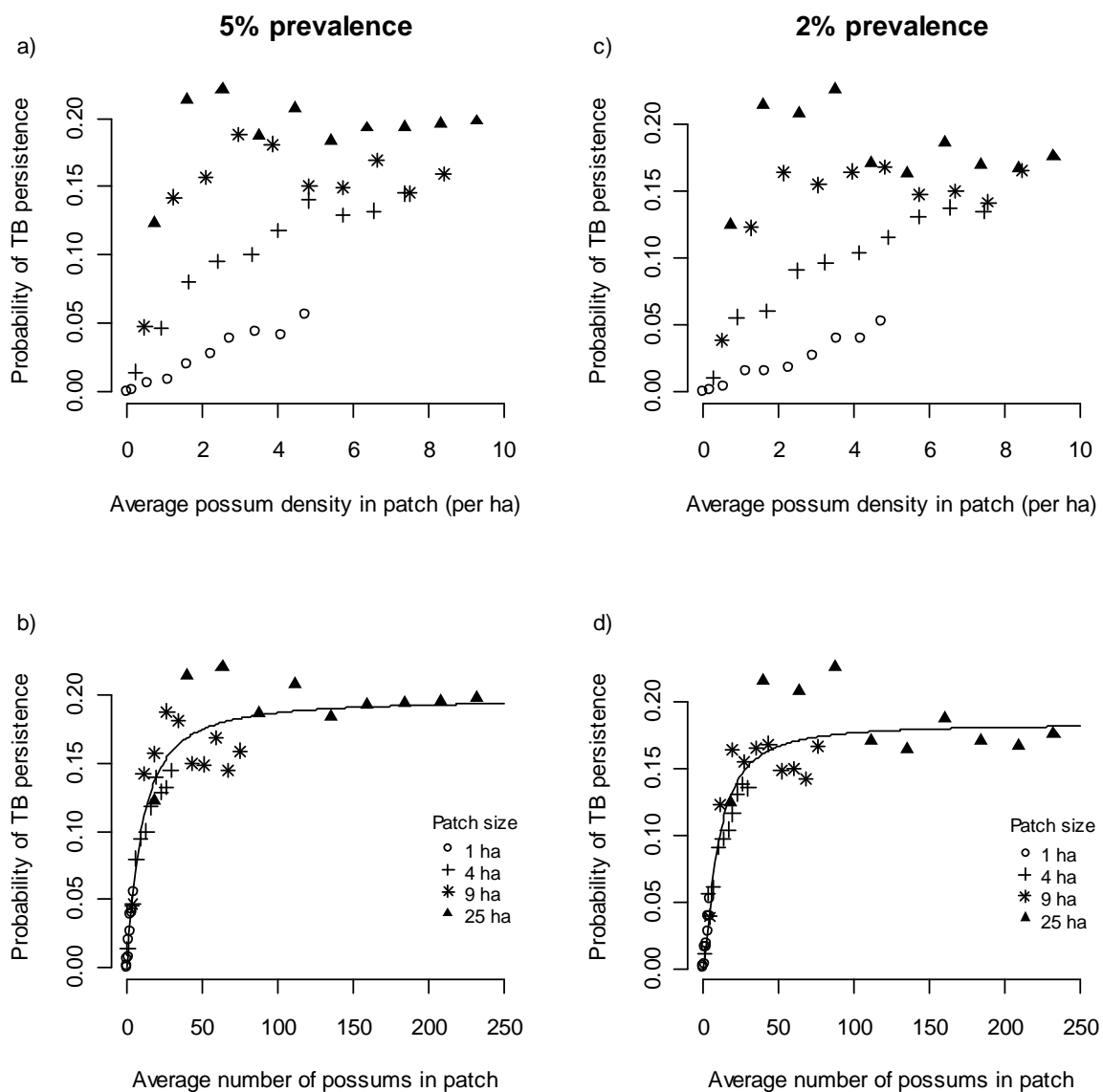


Figure 4 Probability of TB persistence in isolated habitat patches with change in possum density (panels a and c) and possum number (panels b and d) under the assumption of frequency-dependent transmission and a disease transmission coefficient of $\beta = 0.707$ (to give 5% prevalence at equilibrium, panels a and b) and $\beta = 0.695$ (to give 5% prevalence at equilibrium, panels c and d). The solid line in panels b and d shows the fitted curve used to calculate the threshold numbers in Table 3.

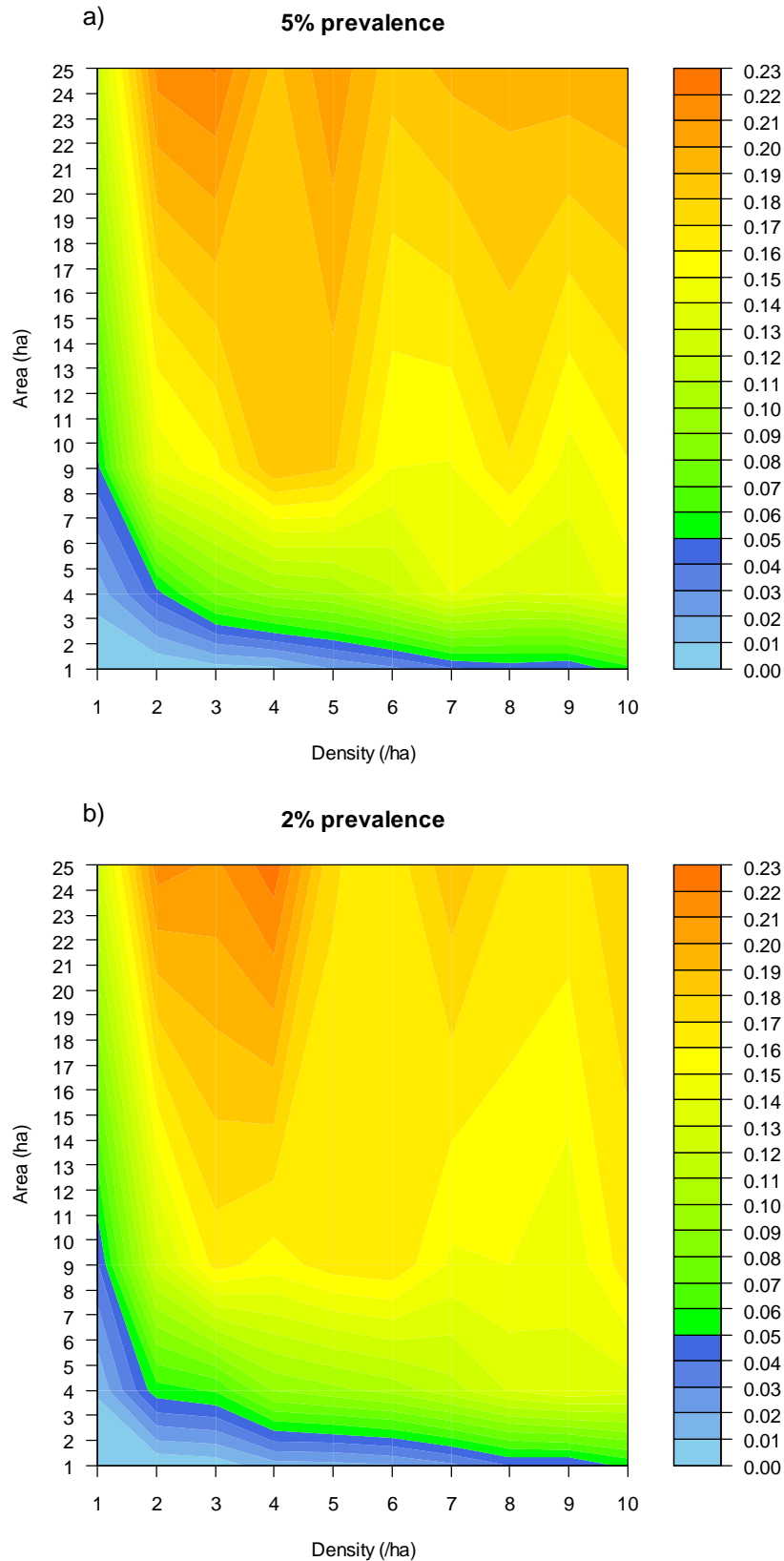


Figure 5 Probability (shown as colour) of TB persistence in isolated habitat patches of varying patch size and possum density under the assumption of frequency-dependent transmission and a disease transmission coefficient of $\beta = 0.707$ (to give 5 % prevalence at equilibrium, panel a) and $\beta = 0.695$ (to give 2 % prevalence at equilibrium, panel b).

Frequency-dependent transmission, 0.05 annual probability of an infected immigrant arriving at patch

Including an annual probability of immigration produced a similar-shaped response as simulations with no immigration, but overall persistence was increased (i.e. shifted up the y-axis by the rate of immigration assumed (Fig. 6: results from 0.05 annual immigration probability only presented).

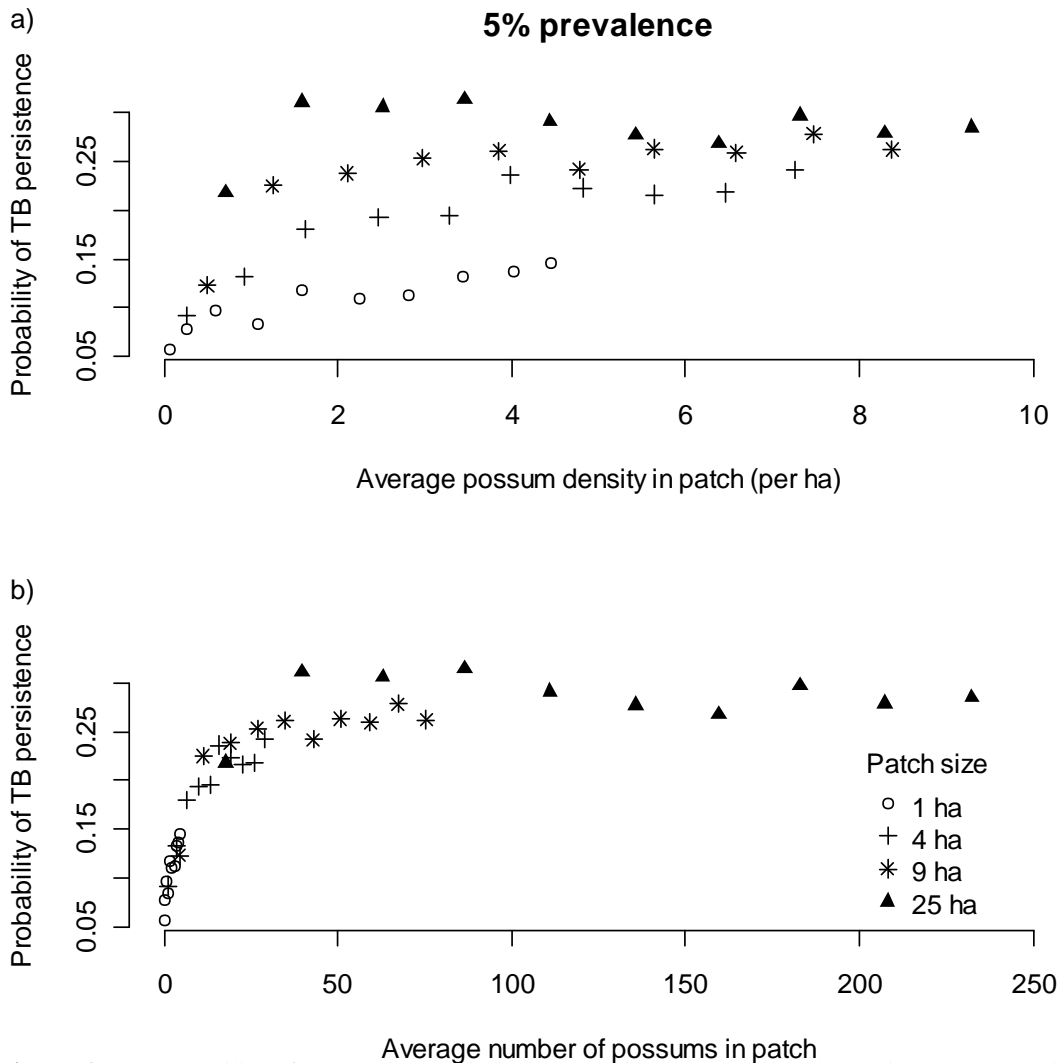


Figure 6 Probability of TB persistence in isolated habitat patches with change in possum density (panel a) and possum number (panel b) under the assumption of frequency-dependent transmission and a disease transmission coefficient of $\beta = 0.707$ (to give 5 % prevalence at equilibrium) and a 0.05 annual probability of an infected possum migrating to patch.

5.2 Patches in context

For both landscapes, most (90% for Patoka, 97% for Timahanga) possum habitat was part of one large patch spanning the simulation area (indicated by the dark teal colour in Figs. 7 & 8). This was because we classified habitat patches as contiguous areas where possum carrying capacity was predicted to be greater than zero, thus the main patch depicted in Figure 7 or 8 is made up of 50 x 50-m cells all connected by possum habitat. Consequently, most of the infected possums present after 5 years were distributed across the main habitat patch. Under the no control scenario, 97.3% and 99.6% of infected possums were located in the main patch for the Patoka and Timahanga simulations, respectively (Figs. 7a & 8a). For the Patoka no-control simulations, 0.5% of infected possums were located on patches below the patch population size threshold (8 possums per patch at carrying capacity). Under control this proportion actually increased to 0.9% with area-wide control and 6% with targeted patch control. However the average number of infected possums was reduced by 95% under both control scenarios (Table 4), so in terms of absolute numbers the risk of a small patch being inhabited by an infected possum was much less. For the Timahanga simulations, 0.2% of infected possums were located in patches below the patch population size threshold when there was no control. Control resulted in an overall 97-98% reduction in the number of infected possums (Table 5) and no infected possums were located in patches below the patch population size threshold.

Targeting only those patches with a carrying capacity of 8 or more possums for control resulted in a similar reduction in overall possum density as area-wide control (Tables 4 & 5). But the probability of TB persisting for 5 years and the average number of infected possums at the end of 5 years was slightly higher under targeted patch control compared with area-wide control (Tables 4 & 5). Under targeted control, there was a 2181 ha and 174 ha reduction in the area controlled for the Patoka and Timahanga simulations respectively, representing a proportional saving of 4% and 1% in control costs *ceteris paribus*. Looking at the trapped area in isolation, targeted control resulted in a 10 and 6% reduction in the area controlled and thus control costs for Patoka and Timahanga respectively.

Five-year TB persistence in the trapped areas was much lower than in the total area for both sites (Tables 4 & 5). This was because there was proportionally less possum habitat in the trapped areas compared with the total area (0.40 vs 0.64 for Patoka, 0.54 vs 0.86 for Timahanga) and the average possum carrying capacity within these areas was lower than the overall mean (Table 2). Infected individuals were rarely located in the trapped areas and when they were they tended to be around the edges which were part of the main patch for that site (Figs. 7 & 8). The average possum density in the trapped area after 5 years was 0.013 per ha for the Patoka site and 0.038 per ha for the Timahanga site under area-wide possum control to a 2% RTCI target (Tables 4 & 5). Assuming a large area of uniform habitat this can be converted to an RTCI measure using the relationship estimated by Ramsey et al. (2005), which gives an estimated RTCI of 0.6% and 0.7% for Patoka and Timahanga trapped areas respectively.

Table 4 Summary statistics for Patoka 5-year TB persistence simulations under 3 different control scenarios. Probabilities were calculated as the number of simulations where TB was present after 5 years divided by the total number of simulations (1000).

	No control	Area-wide control to 2% RTCI	Targeted patch control to 2% RTCI*
Probability of TB persisting over total area	0.994	0.228	0.255
Average no. infected possums over total area	7.92	0.34	0.40
Average possum density over total area (per ha)	0.45	0.05	0.05
Average prevalence over total area	0.00029	0.00011	0.00011
Probability of TB persisting in trapped area	0.056	0.006	0.005
Average no. infected possums in trapped area	0.068	0.008	0.005
Average possum density trapped area (per ha)	0.14	0.01	0.02

* Patches targeted were those with a carrying capacity of 8 or more possums per patch.

Table 5 Summary statistics for Timahanga 5-year TB persistence simulations under 3 different control scenarios. Probabilities were calculated as the number of simulations where TB was present after 5 years divided by the total number of simulations (1000).

	No control	Area-wide control to 2% RTCI	Targeted patch control to 2% RTCI*
Probability of TB persisting over total area	0.888	0.077	0.090
Average no. infected possums over total area	3.62	0.09	0.11
Average possum density over total area (per ha)	0.54	0.06	0.06
Average prevalence over total area	0.00035	0.00007	0.00008
Probability of TB persisting in trapped area	0.061	0.004	0.003
Average no. infected possums in trapped area	0.079	0.004	0.003
Average possum density trapped area (per ha)	0.37	0.04	0.04

* Patches targeted were those with a carrying capacity of 8 or more possums per patch.

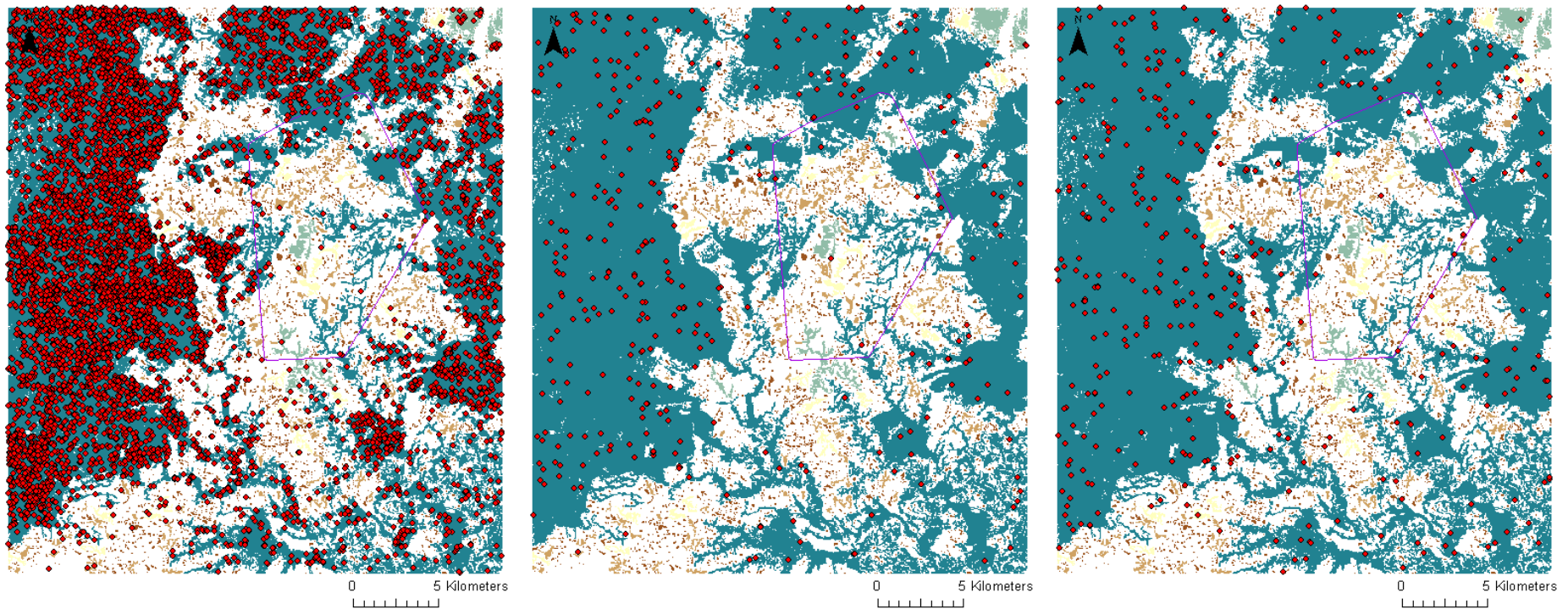


Figure 7 Location of infected possums from Patoka simulations under a) no control, b) area-wide control to 2% RTCI threshold, c) control to 2% RTCI threshold in patches with >8 possums at equilibrium. Note this is the distribution of infected possums at year 5 for all 1000 simulations, the average number of infected possums per simulation at year 5 was 7.92, 0.34 and 0.40 possums for control scenarios a, b and c respectively.

Map legend

Number of possums per patch at carrying capacity

- <8
- 8-50
- 50-100
- 100-1000
- >1000
- Trapped area

• Location of infected possums

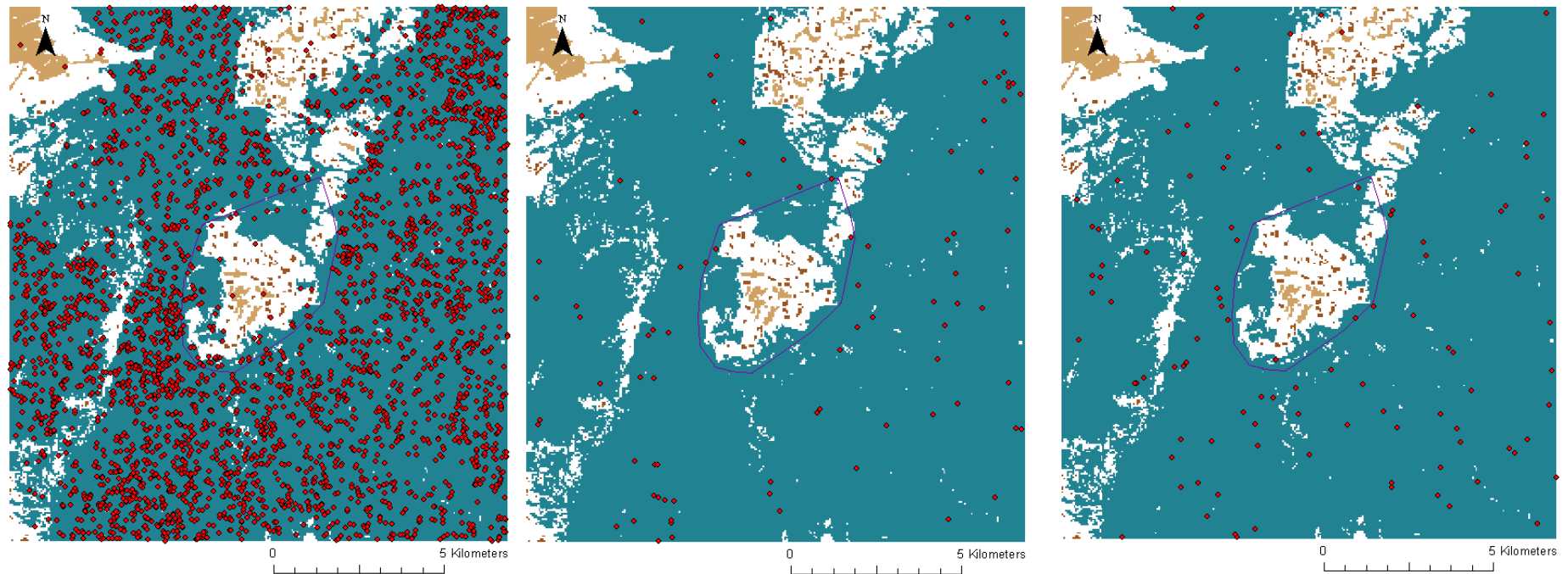


Figure 8 Location of infected possums from Timahanga simulations under a) no control, b) area-wide control to 2% RTCI threshold, c) control to 2% RTCI threshold in patches with >8 possums at equilibrium. Note this is the distribution of infected possums at year 5 for all 1000 simulations, the average number of infected possums per simulation at year 5 was 3.62, 0.09 and 0.11 possums for scenarios a, b and c respectively.

Map legend

Number of possums per patch at carrying capacity

 <8


 8-50

 50-100

 100-1000

 >1000

 Trapped area

 Location of infected possums

6 Conclusions

This project has determined the probability of TB persistence in theoretical isolated patches and in patches that are part of a fragmented landscape. The probabilities for the various patch configurations should be interpreted relative to each other rather than as absolute probabilities because they are sensitive to the value of the disease transmission coefficient (β), which has never been empirically measured. Rather the value of β was adjusted to produce the desired disease prevalence at equilibrium (carrying capacity). In general, the higher the disease prevalence, the more infected possums there are in the population and the less chance there is of stochastic disease ‘fade-out’ due to demographic stochasticity. The threshold number of possums for a given probability of persistence was less under the assumption of frequency-dependent transmission than density-dependent transmission (3 versus 8 possums per patch, respectively). This is because frequency-dependence assumes contacts are maintained at low densities which might occur, for example, if male possums contact the same number of females during the breeding season regardless of density. A positive relationship between cattle reactor rates and TB prevalence in sympatric possum populations has been argued to support the notion of density-dependent transmission (Barlow 1991). However Hone and Donnelly (2008) contended this relationship could also be produced in a two species model (cattle and badgers) with frequency-dependent transmission in the wildlife host (badgers). Measured contact rates between free-ranging possums showed a non-linear convex-up relationship with possum density during the breeding season (Ramsey et al. 2002), a period which probably provides the most opportunity for disease transmission. Ramsey and Efford (2010) concluded that the transmission type for possums is likely to be something in between frequency- and density-dependent transmission and their model (which is also the one used here) does have some elements of both. This is because the transmission rate is assumed to scale with density (density-dependent transmission) but the overlap between possum home ranges sets the contact rate and home ranges are assumed to scale with possum density so that contacts are maintained at low densities as possums expand their home ranges.

Accepting these caveats and assuming the normal possum-TB model default values (5% prevalence at $K=10$, density-dependent transmission) then simulations indicate that for there to be a less than 1% chance of disease persisting in an isolated patch over 5 years, patches of possums should not contain more than 8 possums, either as 8 possums in one hectare or 8 possums over 8 hectares. If we assume 2% prevalence and density-dependent transmission then the threshold for persistence is related more to patch density than total number, so that a patch density of more than 4 possums per hectare would be required to result in a more than 1% chance of persistence regardless of patch size. At a low patch density of 1 possum per hectare (when possums are uniformly distributed) more than 21 individuals would be required to result in a greater than 1% probability of TB persistence. Threshold numbers were less (≈ 3 possums) for frequency-dependent transmission simulations, indicating an infected possum needs at least 2 other susceptible possums to infect, for TB to persist in the patch for at least 5 years. These probabilities were for patches in isolation, but TB can be ‘imported’ by infected possums dispersing from other patches to the focal patch. If immigration of infected possums occurred at a constant rate to a patch the probability of TB persistence was simply the sum of the probability of persistence if the patch was isolated plus the annual probability of immigration. In reality this immigration rate will not be constant as it will be a function of the density, size of, distance to, spatial arrangement and disease status of neighbouring patches.

Here we assessed a habitat patch's potential to harbour infected possums on the basis of carrying capacity or the maximum density of possums it could support which in turn is based on vegetation type. We used carrying capacity because it is an indicator of abundance that could be evaluated before going into the field to do possum control and the information is easily extracted from GIS layers of vegetation type. In this respect it is a conservative measure since possum numbers are likely to be much lower than their potential maximum if there has been previous control in the area. If detection surveys (e.g. wax tags or chew cards) conducted just prior to control indicated an absence of possums in certain habitat patches and the patches were sufficiently isolated from neighbouring source patches then these patches could also be excluded from control.

To assess whether thresholds derived from patches in isolation could be applied to a landscape with realistic patch structure we simulated real landscapes using maps of possum habitat carrying capacity to define patches. These simulations showed that most of the landscape in these areas could be described as one large patch in terms of possum habitat and most infected possums are located in this large patch whether the area is controlled or not. Because most of the landscape was part of one large patch, excluding those patches that could not support more than 8 possums resulted in a less than 4 % reduction in the total area requiring control. There was a slight increase in the probability of TB persistence in the targeted compared with the area-wide control scenarios although the difference in probabilities was less than 0.03 and because control under both strategies would span a longer period than the 5 years simulated here the difference would probably be even less with time as TB declined within the possum population. Infected possums were occasionally detected in the small (<8 possum) patches indicating these patches were sufficiently connected to other patches to receive immigrants. Examining just the trapped areas, there was a 6% chance that TB would persist in those areas if there was no control to prevent the possum population recovering. With either area-wide or targeted control this probability dropped below 1%. However, if a 6% chance of TB persistence over a 5-year period was an acceptable risk to managers, for areas like those simulated here, i.e. with a low proportion of possum habitat, overall low habitat carrying capacities, and RTCs at or below 2%, the interval between control operations could be increased to at least 5 years, providing significant cost savings.

We may have been overly simplistic in these simulations by defining patches purely on the basis of possum habitat and ignoring the functional connectivity of the landscape which takes into account how possums perceive and interact with the landscape structure. In the model, possum dispersal distances are described by a gamma distribution with a mean dispersal distance of 2 km for male possums and 1km for females, but the gamma distribution has a 'long tail' so dispersal distances of >5 km are feasible. Dispersal distances are therefore large relative to the cell size used to assess habitat connectedness (50 x 50 m) and a patch that we defined as isolated because it is surrounded by non-habitat may not be functionally isolated because the distance to a nearby patch is well within possum dispersal capabilities and the non-habitat may pose no barrier to possum movement. Habitat patches may even be connected by day-to-day home range movements; field observations suggest bi-modal home ranges, where possums den in one area and move to another area to forage, are common even in non-patchy landscapes (Cowan & Clout 2000). The movement capabilities of possums suggest we have underestimated connectivity with our habitat patch maps but defining the functional connectivity of a given landscape will require an improved understanding of how possum movement and home range behaviour is influenced by landscape structure. This will

enable us to better define whether a patch is isolated and a low risk for harbouring infected possums and thus whether it needs to be controlled.

In summary, we have defined threshold population sizes for TB persistence in isolated patches but, without being able to probabilistically define whether a patch is functionally isolated in a real landscape, we are unable to provide a general rule on whether to control a patch or not. For the landscapes simulated, patches were highly connected on the basis of habitat alone and less than 4% could be omitted from control operations using a critical patch size rule. Given that we probably underestimated connectivity because the scale of possum dispersal and home range movements are large relative to our isolation distance, and the small numbers of possums predicted to be necessary in patches to sustain TB, there are likely to be very few ‘patches’ that do not require control. Consequently, programme managers and control contractors should not assume some habitat patches can be missed or eliminated from control coverage.

7 Recommendations

- If habitat type and patch size suggests a patch is unlikely to support more than 8 possums then such areas should be considered as low risk.
- Further research is required to understand how possum movement and home range behaviour is affected by landscape structure so we can better define the functional connectivity of the landscape.
- Empirical estimates of the disease transmission coefficient (β) are required to give more accurate probabilities of TB persistence.
- Control costs could be reduced by spelling areas from control if there is robust trap-catch data indicating RTCIs are at or below 2% and possum habitat is sparse.

8 Acknowledgements

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