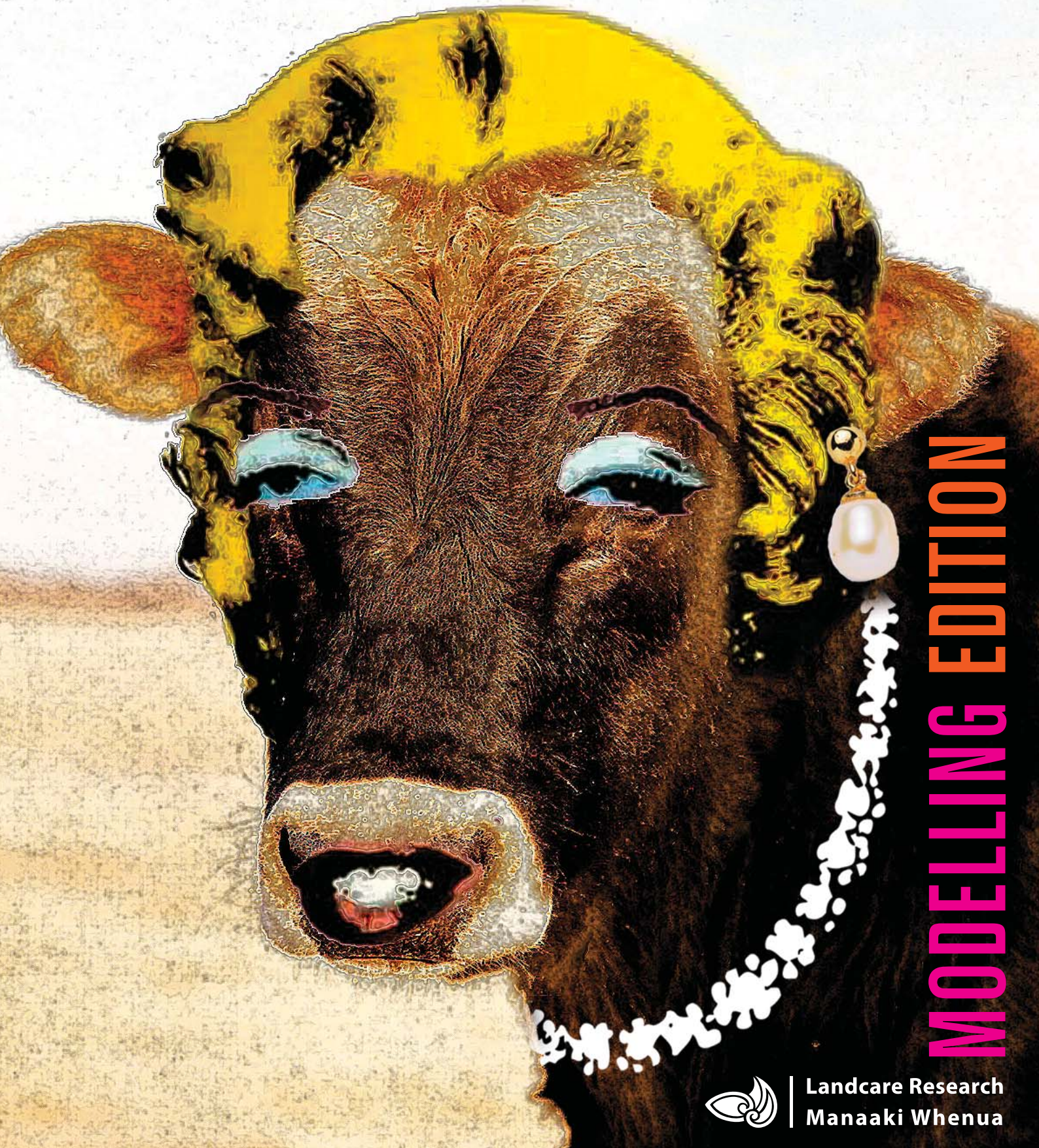


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Front cover - with apologies to Marilyn Monroe and Andy Warhol.

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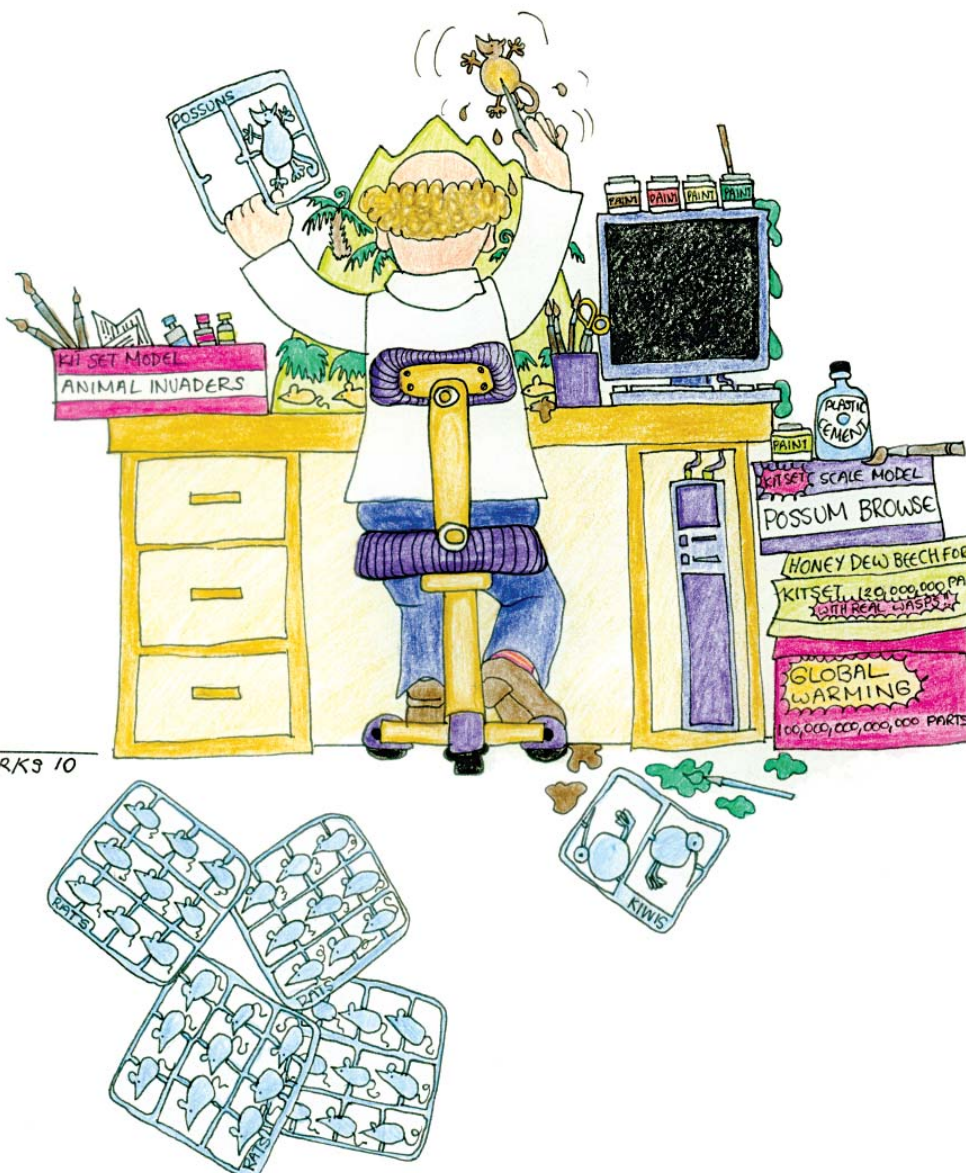
Ecological models – their form and function

Mention ecological modelling and many people run screaming in horror. For some, this response is due to visions of bearded ecologists working with imaginary and irrelevant data, but for most it's because people think modelling is full of complex mathematical equations that are far too difficult to comprehend. Mandy Barron offers a different perspective and here seeks to explain and encourage their wider use.

Although equations can be daunting at first, Mandy reports that if you persevere with them, they provide a far more precise, concise and universal method of expressing a hypothesis about how an ecological system works than any long-winded verbal

or written description. The first step in model development – writing it out – can be a useful exercise in itself because it forces researchers to clarify their mental model, make their assumptions explicit and to identify any knowledge gaps. Unlike their runway counterparts, i.e. fashion models, ecological models are not ornamental but are developed to understand and explain field or laboratory observations and to make predictions about how systems respond. For example, Whitehead and Tompkins (pp. 12–13) determined which mode of transmission best described the epidemiology of a new disease in Tasmanian devils in order to predict its impact on devil populations.

Thus, models are an abstract description or generalisation of a system. They do not, nor should they attempt to describe *all* of the complexity and heterogeneity in a natural system, as by the time this is done, the need for the model would have long since passed. The mark of a good model is that it is useful, i.e. fit for the purpose intended, be that explaining patterns in data, generating testable hypotheses, or identifying pivotal processes or parameters that need more data (e.g. Jones et al., p. 16, are collecting data on the breeding success of grey-faced petrel to build a population model that can then be used to assess the effects of rats on bird abundance). Modelling is an indispensable tool for ecological sciences where it is often difficult, impossible, too expensive or unethical to conduct replicated, manipulative experiments, because it allows notional experiments to be conducted or a variety of management interventions on modelled systems to be examined (e.g. Warburton, pp. 14–15, models the profitability of harvesting possums for fur over a range of initial possum densities).



Besides the equations, another aspect that puts people off modelling is the jargon that arises from the diversity of models available (Fig.). People often draw a distinction between “statistical” or “empirical” models versus “theoretical” or “mechanistic” models. The former are fitted to data gathered as part of an experiment and are used to explain patterns and draw inference particular to that system (e.g. Gormley et al., pp. 10–11, on distribution modelling of sambar deer), while the latter use mechanistic functions to describe general ecological processes and are used for understanding and prediction.

Systems can be modelled in “continuous time”, which calculates rates of change in infinitesimally small time-steps, using differential equations, and is useful when

modelling populations of species that have overlapping generations. Alternatively systems can be modelled in “discrete time”, which, as the name implies, models the state of the system at relatively large time-intervals, using difference equations, and is useful when modelling populations of species that have only one generation per annum.

Another dichotomy is between “deterministic” and “stochastic” models. For a given set of parameter values, a deterministic model will produce the same results every time whereas a stochastic model will draw the value for a model parameter from a probability distribution and thus will produce different results with each run.

“Analytical” models are usually theoretical models where the mathematical equations can be solved algebraically to understand the model’s behaviour (e.g. Holland, pp. 6–7, explores the consequences of changing possum density and foraging behaviour on mortality rates of kāmahi in a herbivory model). Often models are too complex to solve directly and/or include stochasticity (random behaviour), so they can only be determined by “simulation”, which means running the model multiple times, usually over a range of parameter values, then collating and analysing the outputs (e.g. Shepherd et al., pp. 22–23, in his description of the national possum model).

There’s also a new class of model gaining popularity that promises to bridge the gap between statistical and theoretical models, but unfortunately also has its own jargon! “Bayesian” statistical models essentially involve updating “prior” or previously held beliefs in a hypothesis (formulated as a model with known or unknown parameters) in light of new observations. The updated probability is the probability of the hypothesis being true given or conditional on the observed data. For example, Nugent (pp. 20–21), uses Bayesian analysis to provide managers with a posterior probability that TB has

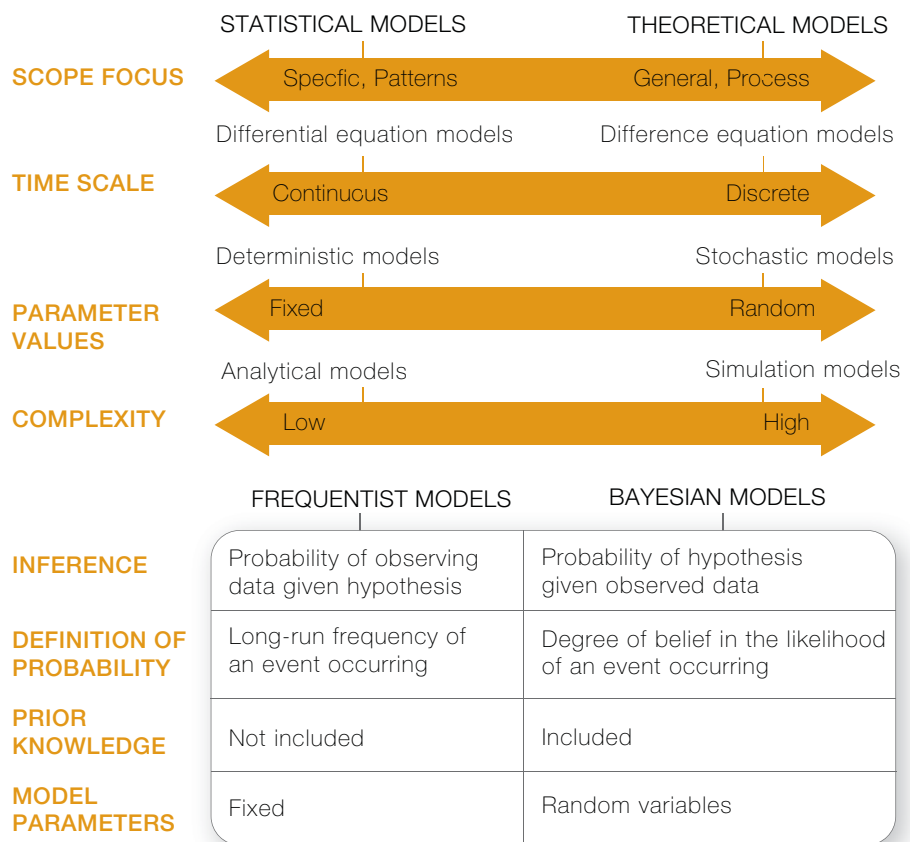


Fig. A schematic of model types, where model attributes are listed in the left hand column, and arrows define the scale of the attribute and the model type in relation to that scale.

been eradicated from wildlife vectors in an area, given negative surveillance and testing results. Using a similar approach, Parkes (p. 17) estimates the probability that the eradication of a target pest has occurred given no further animals are found. A key difference between Bayesian inference and classical (frequentist) inference is that Bayesian analysis assumes model parameters are random values whereas frequentist analysis assumes model parameters are fixed, true quantities (Fig.). This means Bayesian analyses can accommodate uncertainty at all levels in the modelling process: in the model parameters, in the process being modelled, and in the observation of that process (e.g. Anderson (pp. 8–9) included observation error in his Bayesian analysis of pig home range use). This hierarchical approach is handy for ecological data, which often

comprise piecemeal observations measured at different scales and thus don’t conform to the assumptions of frequentist statistical models.

The above has been a brief overview of common modelling terminology but in reality there are as many different model “types” as there are ecological questions. Mandy believes that there are models to fit every situation and that good science and management demand their wider use.

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Fuchsia trees killed by possum browse at Haast, South Westland.

Predicting where and when *possum* browse will kill trees

interacting processes at different spatial scales, from individual leaves to tree canopies, through to large areas of mixed forest.

Browse damage occurs when part of a leaf is eaten by a possum, and the FBI records the ratio of whole to partially browsed leaves in the tree canopy. For this reason, the model incorporates the within-canopy foraging strategy of possums, such as browsing entire or partial leaves indiscriminately, or only browsing entire leaves, leaf tips or petioles, or new growth.

The timescale is also important. While trees may be able to regenerate after a one-off, severe, defoliation event (e.g. storm damage), continual and preferential browsing by possums can have a detrimental effect on foliage growth rates and lead to tree death. The model has been used to quantify how foliage growth rates of kāmahi change with browsing damage, and to estimate mean leaf life span from FBI data. This is a crucial part of the framework, since leaf turnover removes evidence of historical browse.

At the tree scale, light browsing does not generally make any difference to canopy health, but heavy browsing clearly does so. When browsing exceeds some threshold, the model shows that the tree is unable to regrow foliage fast enough to replace the leaves lost to both browse and leaf-fall, and total defoliation and death are inevitable. This proves that browsing alone can kill kāmahi, with an average sized tree dying if more than about 6,000 leaves or about 10% of its foliage (<1 kg dry weight, or <2% of a typical possum's annual foliage consumption) are eaten annually. Once a tree has passed the browsing threshold, possum control may not be enough to reverse canopy decline.

Possums choose to eat foliage from an individual tree depending on the palatability, nutritional quality and toxin levels of its foliage, and the variety of other foods available. Hence, to predict how possum damage drives tree mortality at a site means large-scale foraging strategies must be incorporated into the model. FBI data alone cannot tell managers why spatial browsing patterns are so heterogeneous, but such data can be used to estimate foraging behaviours. For example, the proportion of kāmahi at a site showing no sign of browse can be used to estimate the degree of preference for individual kāmahi trees of similar size. If more large trees than small show heavy browse damage (as is normally the case), there must be an underlying preference for feeding in the canopies of large trees, over and above the proportion of food such trees provide within an area.

To predict tree mortality at a new location, minimal new data are required, including diameter at breast height, foliage cover, and browsing damage indices from a sample of trees, and a single estimate of possum density. Pen and her colleagues used such data from two North Island locations to test the model's predictions, and found that their model reproduces annual kāmahi mortality patterns well. Future development of the model will broaden the scope to more native tree species, and incorporate drivers of possum population and foraging dynamics.

This work was funded by Landcare Research's Capability Funding.

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Possums have been implicated as major drivers of the loss of biodiversity in forests in New Zealand. Although possums favour non-foliar foods such as energy-rich flowers and fruits (and such browsing may hinder long-term forest regeneration), foliage browsing is a significant cause of dieback and mortality of native tree species.

Untangling quantitative, causative relationships between possum density, observable damage and tree mortality is difficult, not least because such data are highly variable, both within and among forest sites. For example, while both Landcare Research and the Department of Conservation use the Foliar Browse Index (FBI) method to assess forest tree condition, it provides only snapshots of forest health. Pen Holland and colleagues have been using FBI data to formulate and parameterise a *mathematical model* of foliage growth, turnover and consumption, (Fig.) to answer two questions:

- How much of a tree's foliage do possums have to eat in order to kill it?
- To what level does foliage consumption by possums have to be reduced in order to protect trees at a particular location from browse-induced mortality?

The model framework is based on

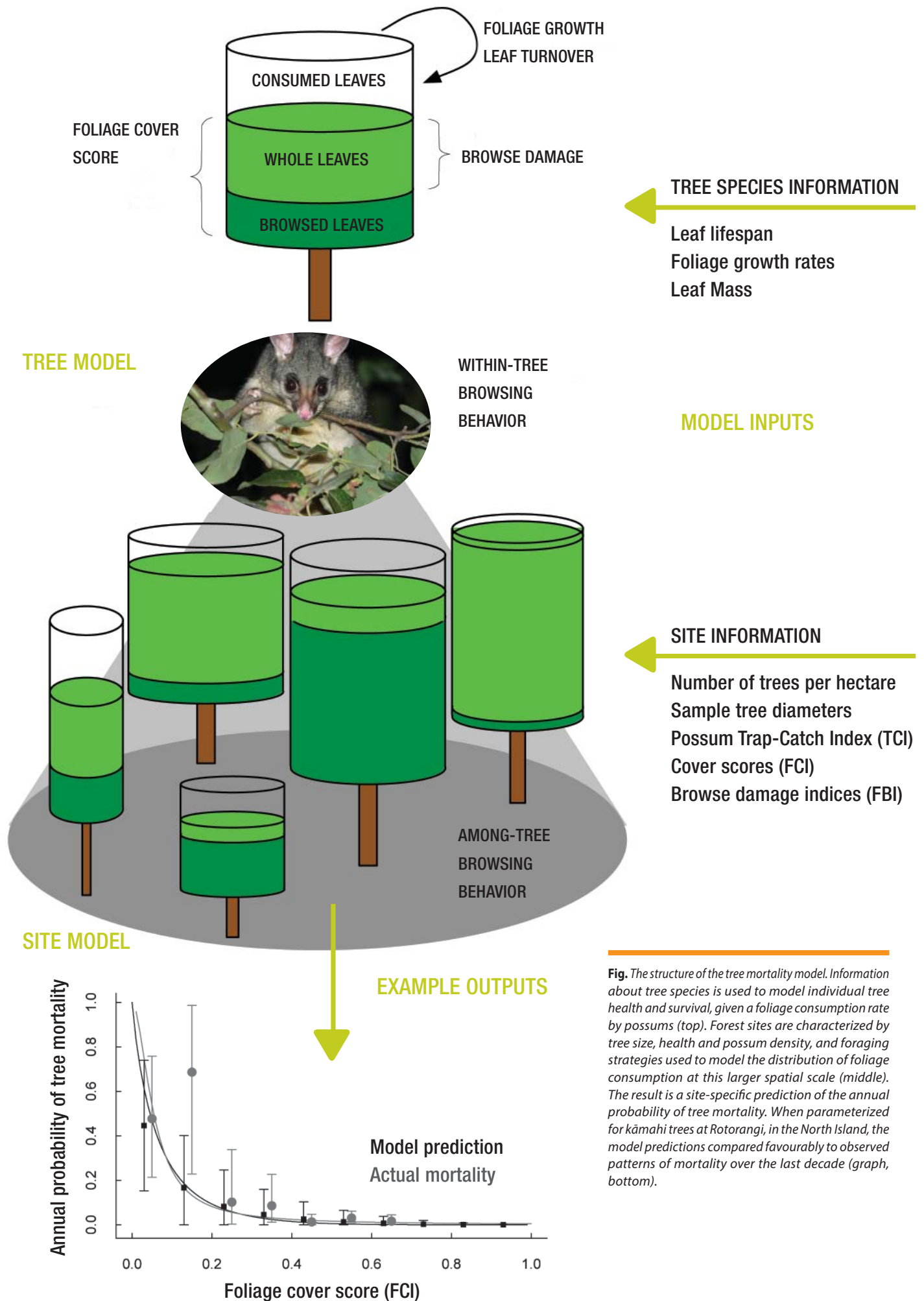


Fig. The structure of the tree mortality model. Information about tree species is used to model individual tree health and survival, given a foliage consumption rate by possums (top). Forest sites are characterized by tree size, health and possum density, and foraging strategies used to model the distribution of foliage consumption at this larger spatial scale (middle). The result is a site-specific prediction of the annual probability of tree mortality. When parameterized for kāmahi trees at Rotorangi, in the North Island, the model predictions compared favourably to observed patterns of mortality over the last decade (graph, bottom).





Analysis of home-ranges of pigs assists in their eradication from Auckland Islands

Pigs have been released on islands worldwide to provide food for castaways, hunters and as livestock. However, they are omnivores and consequently pose a serious threat to native flora and fauna. Pigs can affect the survival and recruitment of native plants through their consumption, rooting up and trampling. They also disperse exotic plant propagules and accelerate soil erosion and consequent sedimentation in waterways. Successful eradication of pigs from islands therefore has potential for high biodiversity gains, but the extreme terrain and/or thick vegetation often found there makes hunting and trapping physically difficult and expensive. There is therefore a growing need to understand the ecology of pigs in different island habitats to increase the efficiency of eradication efforts.

The Auckland Islands in New Zealand's subantarctic zone is a good example of a very isolated archipelago with terrain likely to make any eradication of pigs difficult. The main Island only is inhabited by pigs, and it is large (46,000 ha), mountainous and located 310 km south of Stewart Island (Fig. 1). The climate is characterised by persistent westerly winds and annual precipitation of approximately 1780 mm. Pigs were introduced in 1807 and were widely distributed by 1880. Dietary studies have suggested they prefer living in the

tussock vegetation occurring on higher land and potentially migrate to the coast in winter. Both of these behaviours may make eradication easier.

Dean Anderson used Department of Conservation location data from Argos telemetry collars deployed on 15 pigs on Auckland Island to address two objectives:

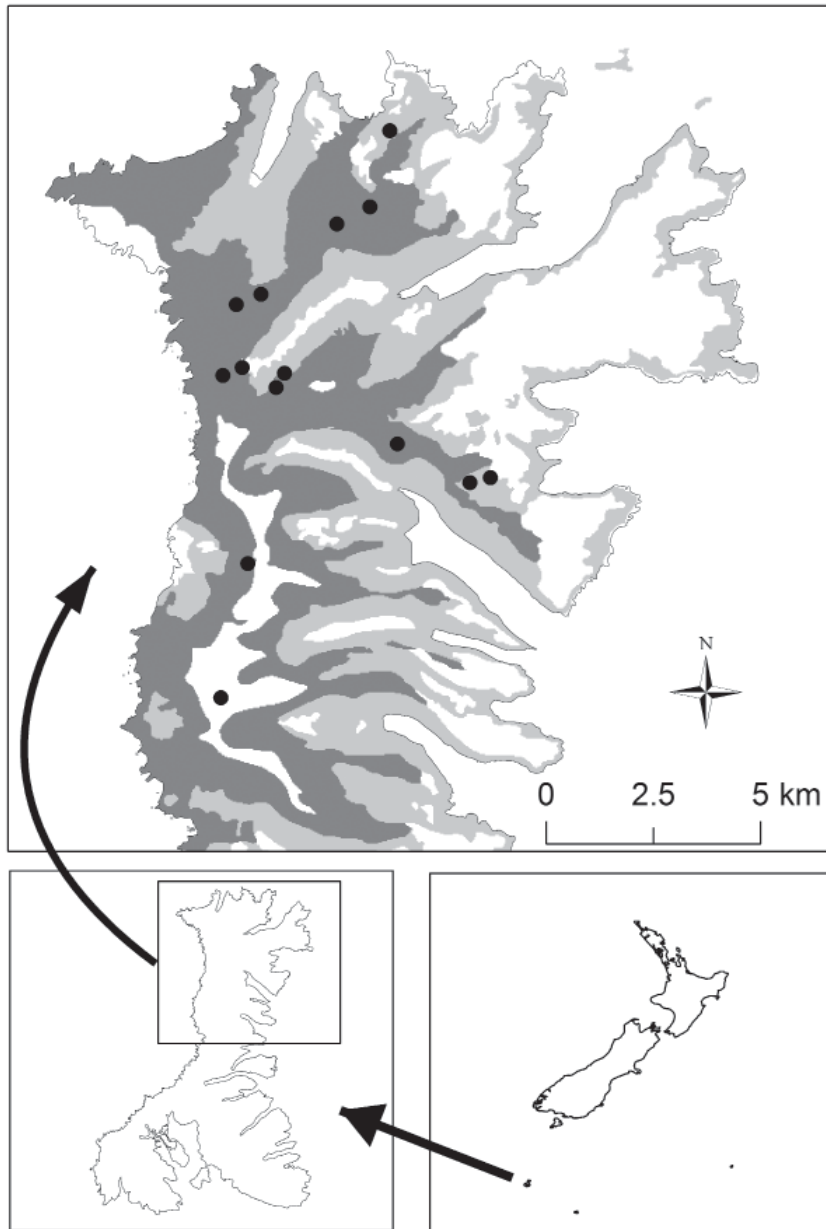
- To quantify home-range sizes across sex-age classes, and examine how these vary with vegetation cover; and
- To develop a resource-selection model that describes how pigs select various attributes of the environment.

Dean's analyses showed that home-range size varied from 1.37 – 32.8 km² (mean = 10.05 km², SD = 9.0 km²). The mean range sizes for males and females were 10.93 km² and 8.89 km² respectively, but the difference was not significant. Home-range size increased with increasing tussock cover. While home-range centres are not an indicator of home-range use, they were all located in or next to tussock cover (Fig. 1), suggesting a preference for this habitat, perhaps due to ease of movement relative to that in scrub.

A *hierarchical Bayesian analysis* of resource-selection showed that pigs generally do not migrate to the coast in winter as previously

thought (although one pig did so in June; see Fig. 2). Results also demonstrated a strong attraction for tussock cover and for north-facing slopes, and repulsion from scrub vegetation. The pigs had the tendency to make direction reversals in 1-day time intervals, which resulted in a criss-crossing pattern of home-range use, rather than directional persistence around range edges. The Bayesian approach also allowed Dean to account for the varying levels of telemetry error among the location data, and permitted the use of all the data and more accurate inference of the results.

It is clear from this analysis that eradication operations of pigs on Auckland Island need to put all the animals at risk by seeking them out, rather than waiting for them to come down to the coast. Because of access issues, this is a difficult task, but one that can be made less arduous by focusing efforts in tussock vegetation and to a lesser extent on north-facing slopes. If traps are used, they can be spaced further apart in areas with high tussock cover (where their ranges are greater) than in areas with low tussock cover. Hunters should use the knowledge that the different ranging patterns in tussock and scrub cover will influence the density of their 'sign'. Further, the tendency of pigs to make direction reversals with one-day time intervals rather



than roaming along home-range edges with directional persistence may be of assistance in planning for their eradication. However, Dean believes these patterns of movement and habitat use are likely to change as the population declines and as the pigs become wary of hunters and trapping devices. As the pigs adapt to the pressure of the eradication efforts, control staff will have to adapt to altered patterns of pig movements.

This work is funded by the Department of Conservation.

Dean Anderson

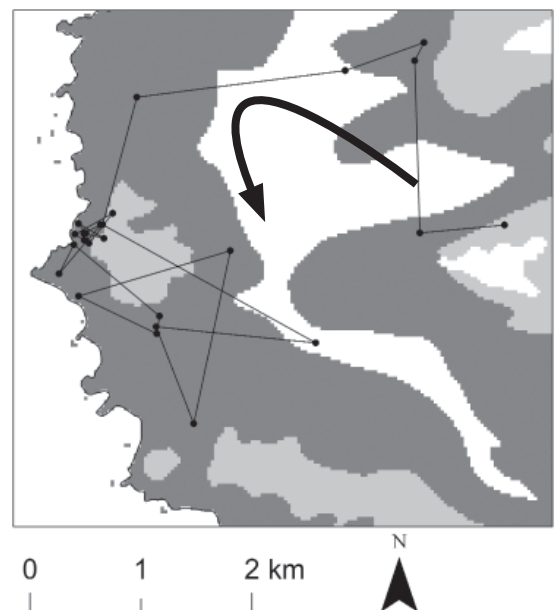
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Department of Conservation

Fig. 1. The study location on Auckland Island. Tussock and scrub habitat are depicted as dark and light grey respectively. All other land covers are grouped together as white. Black dots show the home range centres of the radio-collared pigs.

Fig. 2. The movements of one pig showing clear selection for tussock vegetation (tussock = dark grey; scrub = light grey; and alpine = white). This animal unusually also demonstrated a movement toward the coast followed by moves inland.





A female sambar deer at a camera-trap during a presence/absence field survey.

Distribution modelling for managing sambar deer in Victoria

Sambar deer were released in the 1860s in Victoria, Australia, and have subsequently spread across much of the State. Such expansion is of concern because of the potentially negative impacts the deer may have on native biodiversity and agriculture. Cost-effective management of sambar deer, as for any exotic species, requires knowledge of their current and potential distributions (i.e. areas of suitable habitat both occupied and unoccupied).

The time and cost to conduct comprehensive surveys of wildlife across large areas such as Victoria (237,629 km²), can be prohibitive. And even if it could be done, how would anyone know if an area was suitable habitat if a species had not yet had a chance to colonise there?

Fortunately, there is a method to predict future population distributions: *predictive distribution modelling*. The idea is based on the assumption that a species has its own environmental niche, i.e. it will live in areas that meet a certain range of environmental conditions related to biophysical variables such as temperature, rainfall, type of vegetation, and distance to water.

The approach involves developing a statistical model that describes the relationship between site occupancy (the presence or absence of a species at a small number of sampled sites relative to the total possible number of sites) and the biophysical variables at those sites. If these so-called 'predictor' variables are available for all sites, then the statistical model can be used to predict the habitat suitability of sites that are not surveyed.

Andrew Gormley, working with Dave Forsyth and others at the Arthur Rylah Institute, Department of Sustainability and Environment (DSE), in Victoria, used this approach to determine the current and potential distributions of sambar deer in the State. For the purpose of their field sampling and modelling, Victoria was divided into a grid of cells of 2x2 km, resulting in 56,764 cells. Fieldwork in 80 cells detected sambar deer in half of them (*Fig. 1a*). However, although sambar deer are clearly common and widespread in Victoria, they are typically nocturnal and live in dense forest, making them hard to detect. To minimise the chance of missing sambar deer during each survey, three different

detection methods were used in each cell:

- Faecal pellet counts (x3) along randomly placed 150-m survey lines
- Sign surveys (x1) involving searches for sambar, their wallows, tree-rubs and tracks, along a 400-m trail or watercourse
- Heat-in-motion remote cameras (x2) left out for 3 weeks at the start and end of the sign-survey trail

Twelve biophysical variables were potentially useful predictors of sambar deer occupancy. The Victorian State Government's Geospatial Database Library was used to calculate 'spatial layers' for each biophysical variable and hence the variable's value at every cell across Victoria. Next, statistical modelling determined the relationship between sambar deer and the biophysical variables, and this relationship was 'projected' onto every cell to produce a map of habitat suitability for sambar deer in Victoria (*Fig. 1b*). Finally, the map was partitioned into areas of suitable and unsuitable habitat, with the suitable habitat further divided into occupied and unoccupied range (*Fig. 2*). The occupied range was estimated as the utilisation distribution calculated from all recorded

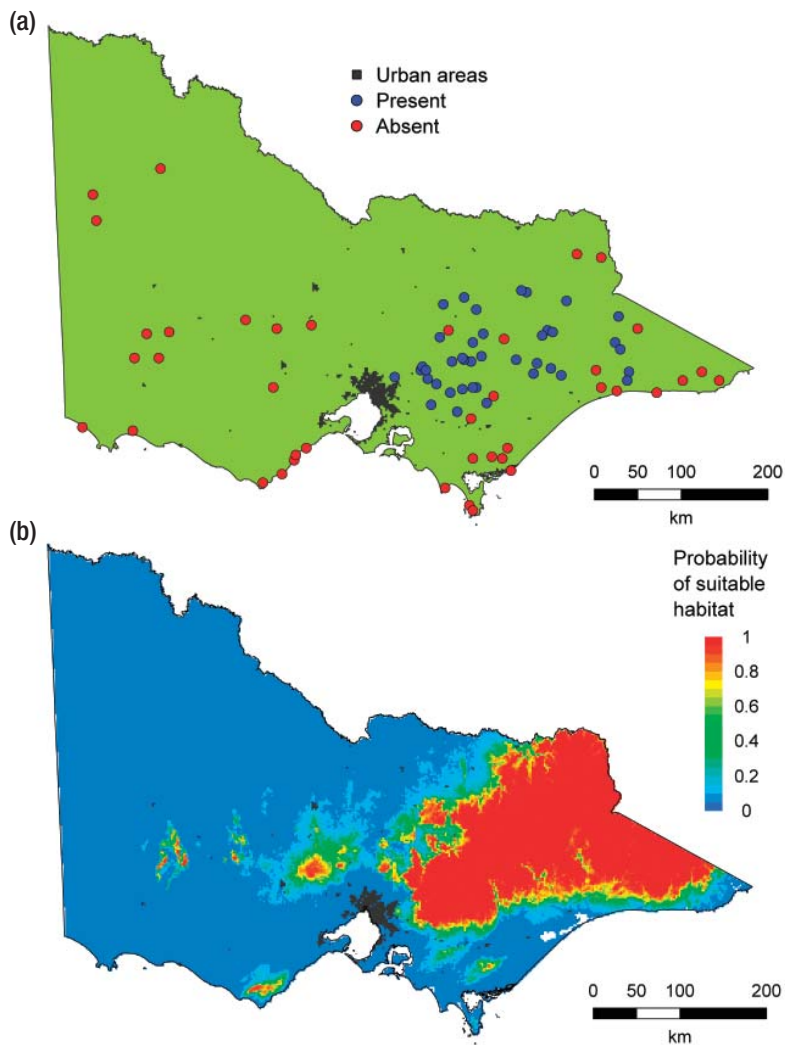


Fig. 1. Maps of Victoria (a) showing field-site location, with sambar deer presence (blue) and absence (red) indicated, and (b) habitat suitability for sambar deer.

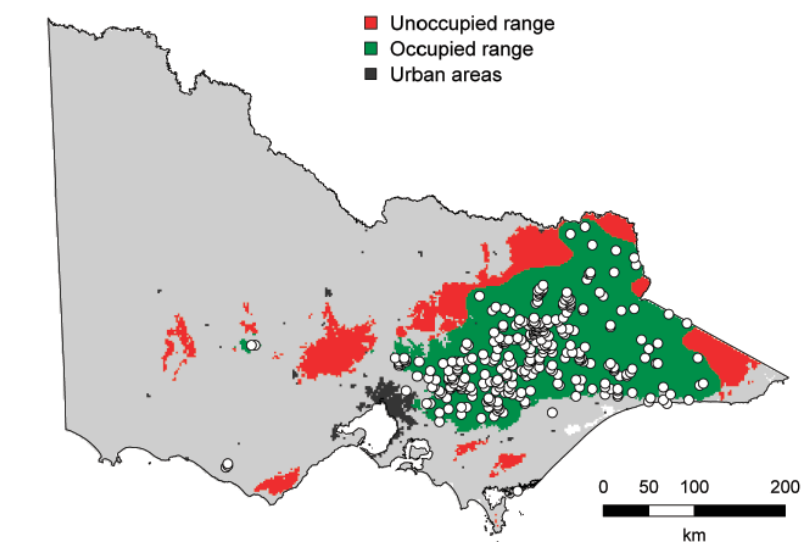


Fig. 2. Sambar deer range in Victoria: areas deemed to be unsuitable sambar deer habitat are grey, unoccupied range is red, and occupied range is green with circles showing sambar deer locations recorded from the *Atlas of Victorian Wildlife*.

sightings of sambar deer that have been entered into DSE's *Atlas of Victorian Wildlife*. The results indicate that sambar deer presently occupy about 74% of their potential range in Victoria.

The analysis identified several discrete areas of suitable habitat that are currently unoccupied (Fig. 2). Establishing surveillance monitoring in such areas may enable new populations to be quickly detected and appropriate management actions to be implemented.

Predictive distribution modelling is a tool that managers can use to estimate current and potential distributions of invasive species, and can be applied to any plant or animal taxon. It can also be used to better target control and/or containment actions in occupied range and establish surveillance monitoring to detect incursions into unoccupied range. It is inevitable that some areas of unsuitable habitat will be incorrectly deemed as suitable and vice versa. The method attempts to minimise these errors and at the same time provide a practical method for estimating habitat suitability at large spatial scales.

This study was funded by the Department of Sustainability and Environment, Victoria (Land Management Branch), the Department of Primary Industries, Victoria (Invasive Plants and Animals Branch) and Parks Victoria.

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Predicting the impacts of facial tumour disease on populations of Tasmanian devils

Wildlife diseases can lead to significant losses of individuals over short periods of time and may ultimately result in extinctions either directly or indirectly by making populations more vulnerable to other threats such as predation or habitat loss. Understanding the potential impacts of disease outbreaks is thus essential for effective conservation management. When knowledge about a disease is scarce (e.g. where it has newly emerged), *mathematical modelling* can be used to indicate what impacts *could* occur based on the information available.

Tasmanian devil populations are threatened by a fatal infectious disease known as devil facial tumour disease (DFTD). The disease causes malignant facial tumours, limiting an individual's ability to feed, and typically results in death within 6 months of infection. Signs of DFTD were first detected in north-eastern Tasmania in 1996 and the disease has since spread over most of the species' range, leading to major population declines. This has raised questions about the potential long-term impact of DFTD on devil populations.

To gain an insight into what this impact is likely to be, and hence indicate the most appropriate strategies for managing the

disease, Dan Tompkins and Amy Whitehead have been using an *epidemiological mathematical model* of disease dynamics to investigate whether or not (and, if so, how) the transmission of DFTD between devils is related to population density. This is one of the key questions to ask for any wildlife disease. Many diseases are 'density dependent'; that is, transmission rates decrease as population size decreases. Where this is the case, diseases generally 'fade out' as populations decline and hence are self-limiting. However, if disease transmission is independent of density, they can potentially have much greater impacts on host populations.

The model simulated a population of devils and contained information about population age and sex structure, in addition to individual infection status (*Fig. 1*). Such complexity is required to realistically model DFTD in devils as the disease is strongly believed to be transmitted via biting linked to breeding (i.e. male–male transmission associated with competition for mates and male–female transmission during mating).

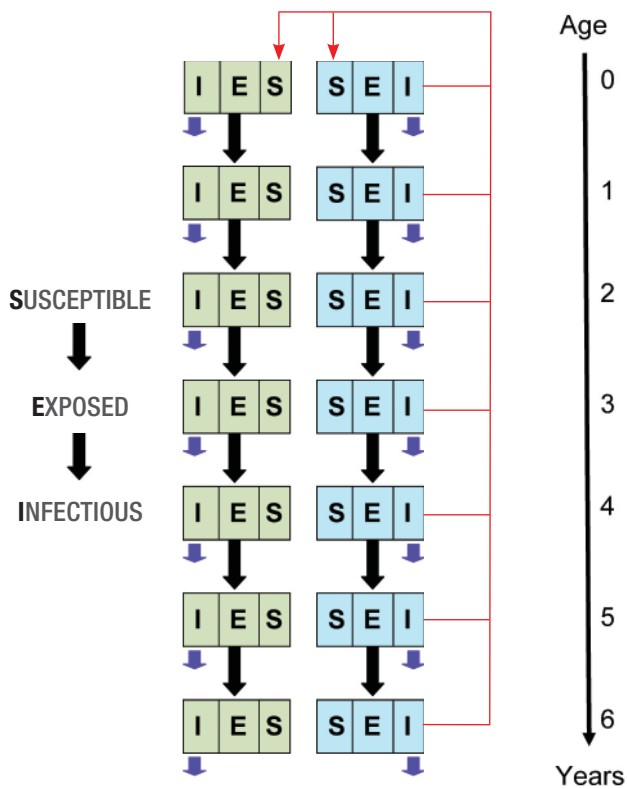
To investigate whether DFTD transmission is density dependent or density independent, a range of different mathematical functions

for the transmission process known from other diseases were modelled to assess which function (or combination of functions) best simulated disease dynamics observed in the field. The models also predicted the associated change in population size of devils over 50 years to assess the likelihood that DFTD would lead to their extinction.

Out of the transmission functions assessed, two provided the closest fit to the best available field data on disease prevalence (i.e. the proportion of infected individuals) from an infected population of devils in Freycinet National Park, Tasmania (*Fig. 2*); namely 'frequency dependence' (a density-independent function commonly associated with sexually transmitted diseases in which transmission rate is related to the *proportion* of infected individuals) and 'combined frequency and density dependence' (background density-dependent transmission occurring year round with an additional higher rate of frequency-dependent transmission during the breeding season).

Dan and Amy's modelling exercise strongly indicates that at least some, if not all, transmission of DFTD is independent of density. As a consequence, the disease is





not likely to be self-limiting through fade-out as populations decline, but could potentially cause rapid population decline (and perhaps) extinction. The model predicts that populations are likely to fall below 10% of their original size within a decade of infection being detected (Fig. 2). This conclusion reflects field observations to date. Hence, if the goal is to conserve devils in the wild, management intervention that can limit the impact of the disease in the wild is needed immediately. Longer term options such as vaccination or breeding for resistance could take well over a decade to achieve – by which time, it would most likely be too late.

This work was funded by Landcare Research Capability Funding.

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Fig. 1. Model of DFTD infecting Tasmanian devils. Green and blue compartments denote male and female animals respectively. Thick black arrows indicate the flow of animals between model compartments, red arrows indicate production of offspring by breeding adults, and short blue arrows indicate losses due to mortality (both natural and disease induced).

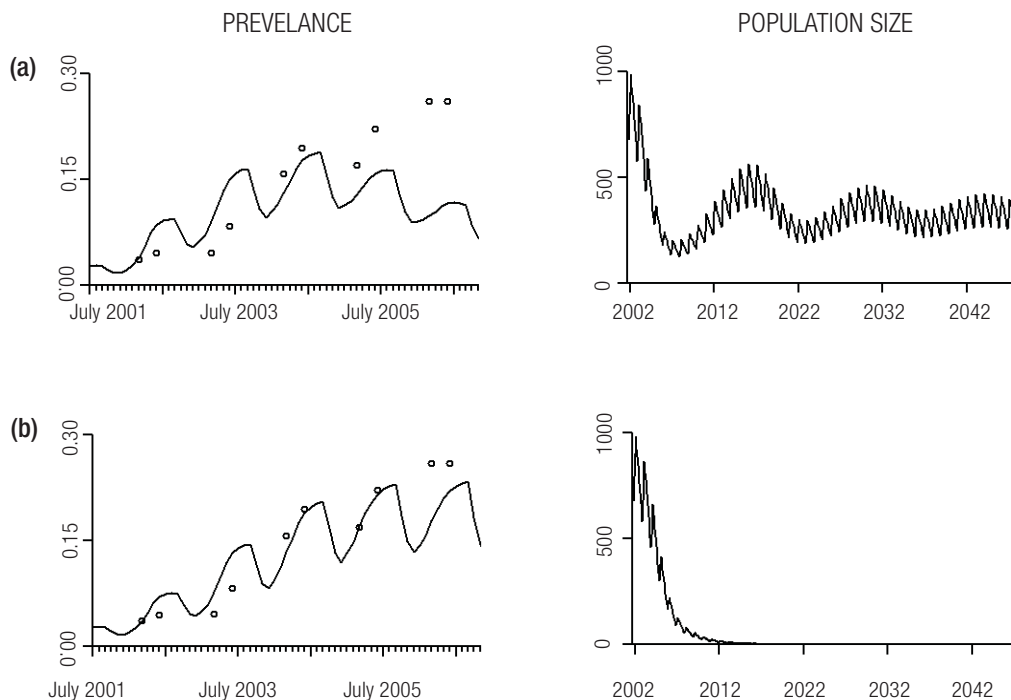


Fig. 2. Predicted DFTD dynamics under (a) density-dependent and (b) frequency-dependent transmission (combined density and frequency dependence not shown). The left column shows estimated DFTD prevalence (solid line) plotted against observed prevalence (points), while the right column shows predicted population trends.



Can the possum fur industry contribute to possum control programmes?

Possums are killed as pests in official control programmes and also harvested as a resource by commercial operators seeking their fur and skins.

Possums have been harvested for their fur in New Zealand since 1921. The industry peaked in 1981 when 3.4 million skins were exported. Since then, demand for fur-on skins has been weak, but has been replaced by an increasing demand for plucked fur that is woven with merino wool to produce high quality yarn (e.g. Merinomink™, Perino™). The demand for plucked fur has grown about 10% per annum over the last 7 years (Fig. 1).

The use of plucked possum fur as a component in blended yarn is now well established with the New Zealand yarn industry estimated to be worth \$50–70 million per annum. To service the demand for fur, about 1.5 million possums are now harvested each year, with about 80% of the fibre being processed into yarn for manufacturing into garments in New Zealand.

Because possums are controlled extensively in New Zealand for both the management of bovine TB and for protection of conservation values, the yarn-based industries are concerned about security

of supply and the 'waste' of fur when possums are killed in control operations. Consequently, commercial fur hunters ask how can the fur industry and pest control agencies work together for their mutual benefit?

To determine whether fur harvesting can provide a sustainable livelihood for trappers 'competing' for possums with the possum control industry, Bruce Warburton has developed a *spreadsheet model* that integrates the price paid for fur, and the catch rate most likely achieved by trapping, given the prevailing density of possums. The model assumed (1) a hunter's income of \$1,250 a week, (2) that hunters checked 200 traps per day, (3) that \$5 worth of fur was recovered on average from each possum, and (4) that the catch on trap lines declined each night at a given rate (derived from catch-rate data from lines trapped for up to 7 nights). The model also assumed a starting density of possums (indexed using a trap-catch rate), and was varied over the range found in the field (e.g. 0–80%). For the example shown below, the model used a starting density (trap catch) of 50% (Fig. 2).

In this example, the catch on the first night was 100 possums (i.e. 50% of 200 traps) and accumulated each night (yellow line) at a declining rate because of the decline in capture rate (blue line). By the sixth night of trapping, the catch had declined to 10% (blue line on graph).

The trapper can use one of two strategies: (1) try to maximise profit (i.e. return on effort), or (2) try to maximise the number of possums harvested (and therefore reduce the population to as low a level as possible). If they choose option (1), the model suggests they should stop when the catch rate has fallen to 25%, i.e. at point (c) when the difference between the numbers



Models wearing Merinomink™ garments made from a mix of possum fur and merino wool.

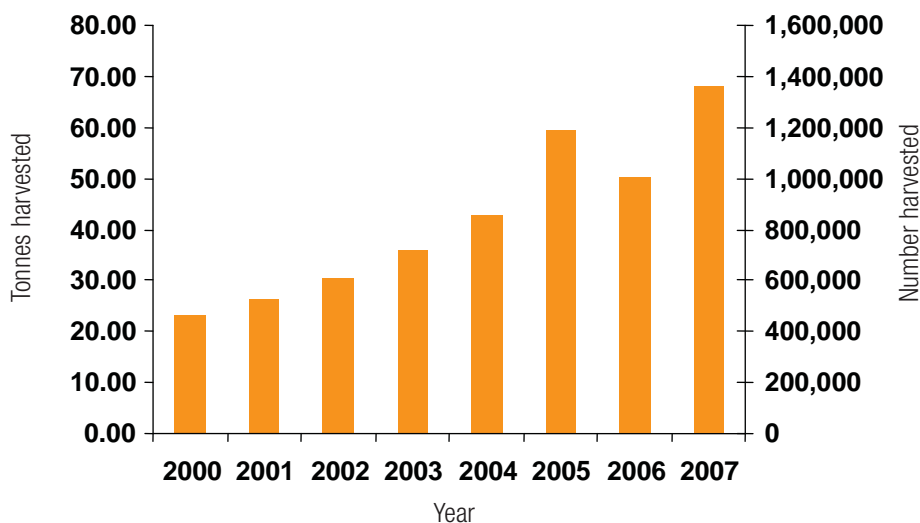


Fig. 1. Possum fur harvested from 2000 to 2007, with the number of possums harvested based on the weight of fur taken (assumed 20 possums equate with c. 1 kg of fur).

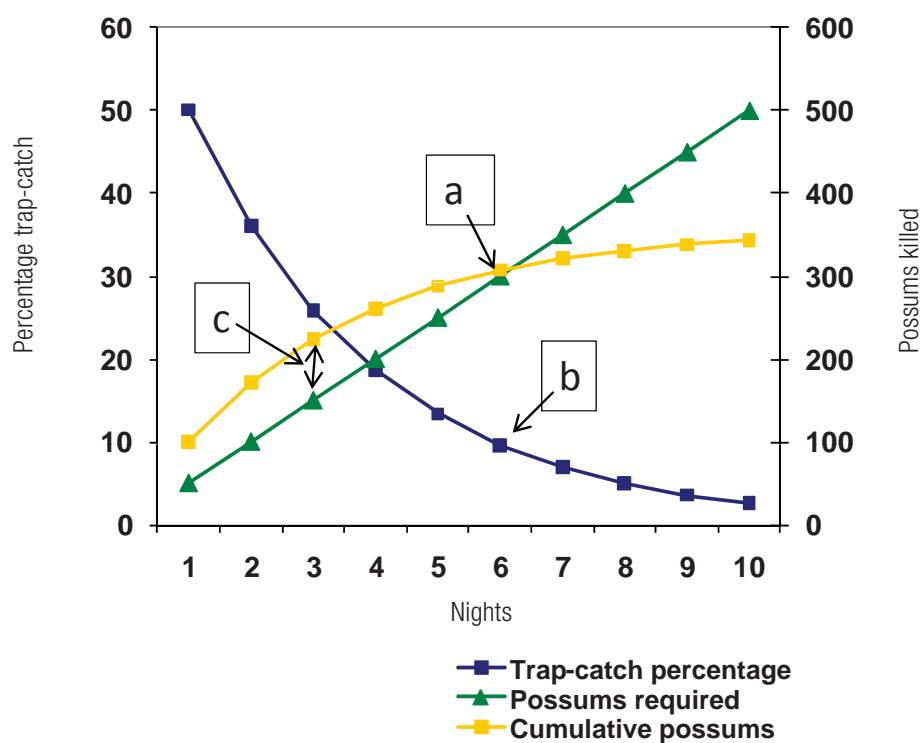


Fig. 2. Relationship between cumulative catch per night, number of possums required for a sustainable industry, and resulting trap-catch index. At point (a), the number of possums caught equals the minimum number of possums required to generate an acceptable income, and trapping for more nights would result in the trapper making a loss. When the trapper gets to point (a) on night 6, the trap-catch index has been reduced to point (b), which is about 10%. The point where the difference between the cumulative catch and the number of possums required (i.e. the rate of return on effort expended) is maximised is also shown (c).

caught and what they need to achieve their desired income is maximised. If the trapper chooses option (2) then they can continue to trap through to night 6 when their cumulative catch equals the possums required to match the income target set of \$1,250 a week. If they trap beyond this point they will operate at a loss. At point (a), they would have reduced the catch level down to about 10% and be getting a very low rate of return on their effort expended.

So does such modelling help managers planning official control operations? If the example given above is applied uniformly across a block where official control is planned, there may be some conservation benefits to plant and animal species that are moderately susceptible to possum browse or predation, but no benefits to more vulnerable species. However, it is unlikely there will be any benefits for the managers of TB control operations because possum numbers need to be reduced to levels indicated by a trap-catch of about 2% to eliminate any transmission of the disease between them.

At present Bruce is working with the Hawke's Bay Regional Council to try and find effective ways to integrate harvesting for fur into official control programmes. He believes his model goes some way to providing a better understanding of what possum densities (as indexed by trap catch) trappers for fur can economically operate down to, and how the conflict between possums as pests and possums as a resource can be resolved.

This work was funded by an Envirolink Grant (HBRC53)

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Restoring Ririwha (Stephenson Island)

Introduced rat species have significant impacts on seabird populations around the world through their predation on eggs and chicks. This is particularly so for breeding colonies on islands. One example of such predation occurs on Ririwha, an island owned by Ngā Uri o Whakakii (a hapū of Ngāpuhi) off Whangaroa Harbour, Northland, which has remnant populations of burrowing petrels and also kiore (Polynesian rat) and Norway (brown) rats, the former in large numbers. The hapū, via the Ririwha Restoration Trust, have asked Phil Lyver and Chris Jones to determine the effect of rats on egg survival and breeding success of oi (grey-faced petrel) populations and to develop population models to predict the recovery of oi in the absence of rats. This work is in line with Ngā Uri o Whakakii's plan to eradicate rats from Ririwha to allow the restoration of its native plants and animals.

The island has, until recently, been used for farming and is still stocked with sheep, which are maintained to help manage the introduced grasses, kikuyu in particular, that cover much of the island. Small remnants of native vegetation persist in gullies and around the coastal margins.

Oi are of cultural significance to northern iwi, and once formed the basis of widespread customary harvest. However, their present numbers make such harvest unsustainable. Restoration of the small remaining oi populations on Ririwha is likely to be achieved only by removing the rats. It is hoped that the knowledge gained by Chris and Phil from this work (and from the eventual rodent eradication programme) will complement the team's other research on sustainable harvesting of oi on the Aldermen Islands and Moutohora (Whale Island), and will guide the management of the birds' recovery on Ririwha.



Kev Drew using a burrowscope on Ririwha Island to check oi (grey-faced petrel) burrows for chicks.

The team is looking at how egg survival and breeding success of oi vary in both time and space relative to the presence of rats. Prior to the proposed island-wide eradication of rats, the researchers have set up trapping grids, including 120-m-wide buffer zones, over two remnant breeding colonies to remove all rats while the birds are laying and incubating. Breeding success of oi is being monitored using fibre-optic cameras, or 'burrowscopes', which allow observers to detect breeding birds, eggs or chicks deep inside the birds' burrows. Results from the trapped areas will be compared with those obtained from similar grids in other colonies where the rats are monitored but not trapped.

As well as being used to compare breeding success of oi in the presence and absence of rats in the same season, the untrapped areas will eventually be used to compare the breeding success of oi over time as the rat eradication programme (under the guidance of John Parkes) gets underway. The breeding performance of oi will be monitored for 3 years and the resulting data will be used in simple stage-based population growth models to predict the trajectory of the birds' recovery.

The project is in its early stages, but the team has already carried out rat trapping at the two removal sites (c. 2 ha) for the 6 weeks of the oi breeding season when eggs and young chicks are most vulnerable to

predation by rats. In just over 12,000 trap-nights, over 400 kiore were removed from the two grids. Both the researchers and the hapū are keen to find out how much this has contributed to the breeding success of oi in those small colonies as a forerunner to future island-wide eradication of rats, and both groups have high hopes for the ongoing restoration of Ririwha and its native biodiversity.

The Trust's long-term vision is one of co-existence of people and native species to maintain historical and traditional practices in and around the island. Mike Sheehan of the Trust believes that such restorative initiatives provide a continuity of past and future practices that will, in turn, allow for new and developing technologies to stimulate growth and new opportunities.

This work is funded by the Foundation for Research, Science and Technology (Programme C09X0908: Te Hiringa Tangata-Bicultural Restoration of Coastal Forests using Sea Birds).

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Start and stop rules in PEST ERADICATION

Eradication is usually the preferred option to manage pests because it (a) eliminates any future impacts, (b) may allow the damage from past impacts to ameliorate, and (c) does so at a one-off cost. However, judging whether eradication is possible is often not straightforward. Managers can use two approaches to see whether eradication is feasible. Firstly, they can look at precedents: who has succeeded before against this pest under similar circumstances? Secondly, they can analyse whether the necessary conditions for success can be met: can all the pests be put at risk and killed faster than they can replace their losses, is immigration unlikely or manageable, do the benefits outweigh the costs, and is eradication socially acceptable?

Having decided that eradication is feasible, managers have two strategies they can use, depending on the pest species of concern and the control tools available. For some pests, eradication can be achieved by a single, one-hit control event that kills the entire population, e.g. aerial baiting of rodents on islands. For others, eradication is achieved by successive control events that eventually reduce the population to zero, e.g. ground-based hunting of ungulates or trapping of stoats. These two strategies force managers into two quite distinct decision points that determine different planning and research needs – when to start and when to stop.

For the first strategy, everything must go right 'on the day', so meticulous planning and review before the operation are best practice. That is, start rules are the key. The operation itself provides no (or at best limited) information on success or failure. For managers to measure this they have to check for survivors, and if any exist they have to be located and removed. However, there are problems with doing this immediately after an aerial operation – absence of evidence does not mean absence of survivors and the only way to increase certainty of success is to diligently look for survivors throughout the entire operational area. A second problem is that the detection of a survivor at one point does not provide information on their presence or absence at other places, and unless the response to a point location is to repeat the broad-scale control everywhere as a precaution, the only

other way to check for 'success' is again to look everywhere. Both these options are costly so the normal process is to wait and see if pests have survived by allowing time for their population to recover and become obvious – and then repeat the eradication attempt. The problem with the absence of information provided by the control method per se is that the causes of failure are often difficult to prove and managers have to rely on weight-of-evidence diagnoses.

Recently, several pest eradication projects based on aerial poisoning have either not met their start rules, or have failed despite concerns about aspects of their start rules. For example, the rodent and rabbit eradication on Australia's subantarctic Macquarie Island planned for 2010 was halted (and hopefully just postponed until 2011) as bad weather precluded the helicopters used to sow the poison bait from flying during the window of time when non-target birds at risk from the baiting were absent. In contrast, the kiore eradication on Hawaii's Lehua Island had reached such a stage of planning (and regulatory commitment) that it was attempted and failed despite less than ideal conditions (unexpected rainfall causing a flush of vegetation and abundant food for the rats) and constraints (restrictions on baiting along the coast).

The second strategy, successive removal events, provides managers with information from the control events. Control effort, numbers of animals removed, their location, sex, age, and reproductive condition can all be measured as the campaign proceeds. Such information allows managers to adapt their plans and improve their chances of eventual operational success. The problem is thus not the start rules but when to stop and declare success.

In recent years Dave Ramsey, John Parkes and their co-workers have been using *Bayesian modelling* approaches (which allow for the generation of statistical likelihoods based on partial information) with data collected during such projects to (a) measure the probability that the lack of further animals killed or caught by the control tools (or detected in monitoring devices) equals no animals present, and (b) to

prescribe how much more monitoring is required and where it should be applied, to increase this probability to some level of comfort to decision-makers so they can stop all control.

For example, Island Conservation, a California-based NGO, has been attempting to eradicate feral cats from San Nicolas Island in California. Most cats were trapped over a year and this, along with searches of cat sign and the use of fixed cameras, provided data to calculate whether eradication had been achieved once no further cats were detected. Analysis of the data towards the end of the campaign suggested there was a 95% chance that between one and four cats remained, and as it transpired two further cats were detected and removed. The model that predicted this two-cat outcome had a 25% chance of being correct. The model allowed managers to design their stop-rule monitoring to limit the chance of falsely declaring eradication and/or to optimise the trade-offs between the costs of extra monitoring and the costs of falsely declaring success (see Ramsey et al. in the publication list in this issue).

A research area of growing interest is whether the approaches used on San Nicolas Island can be applied in a cost effective way to locate and kill survivors immediately after aerial eradication attempts.

This work was funded by The Nature Conservancy and Island Conservation (USA).

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Incorporating uncertainty in modelling the probability of freedom of *bovine tuberculosis*

Eradication of disease from an area is a discrete event; it either occurs or does not (e.g. 'heads' in a coin toss). If we find a diseased animal, we know for certain that the eradication attempt failed. Unfortunately, if we do not find a diseased animal, we cannot be certain that the eradication attempt actually succeeded. The best we can do is to predict the probability of eradication success. Such modelling assumes that the more we search for the disease without finding it, the more confident we can be that we have succeeded.

There are now fewer than 90 cattle and deer herds infected with bovine tuberculosis (TB) in New Zealand, a drop of over 95% since 1994. Predicting the probability of TB eradication from particular areas enables limited resources to be allocated to areas where there is insufficient surveillance data and where success is less likely. Modelling TB freedom is complicated because of inherent sources of uncertainty, and the fact that the disease can be harboured by and transmitted between livestock (cattle and deer) and wildlife (possums).

Here, Dean Anderson and his colleagues describe recent research aimed at modelling the combined probabilities of freedom of TB freedom for *both* livestock and wildlife, and how they account for uncertainty in the predictions generated.

Management decisions on whether to declare eradication success are based on predicted probabilities of freedom exceeding a specified threshold (e.g. > 0.95 probability of freedom). Standard probability calculations are used to combine the probabilities of freedom in livestock 'AND' wildlife, which results in a combined probability that is lower than the probabilities for the individual populations (*Fig. 1*). Consequently, predicted probabilities for both populations have to be well above the target threshold for the combined overall probability of freedom to surpass the threshold. Figure 1 illustrates how the individual population probabilities

exceeded the threshold in 2008, but the combined probability did not reach the mark until 2009 (due to intensified surveillance).

The lines in *Fig. 1* suggest that the team is certain about the predicted probabilities of freedom in livestock, wildlife and for the whole area. In reality, such probabilities are mean predictions from a model, and as such only represent a 'best guess'. Consequently, sources of uncertainty are incorporated in the model. For example, field tests to detect TB in livestock are imperfect (e.g. the standard caudal-fold skin test used on cattle only has an 82% (95% CI = 74–90%) chance of detecting TB in an infected animal). Similar uncertainty exists in the tests used on wildlife, and also in the probability of disease transmission and capture. The level of uncertainty is indicated in the confidence intervals of the predicted probabilities of TB freedom.



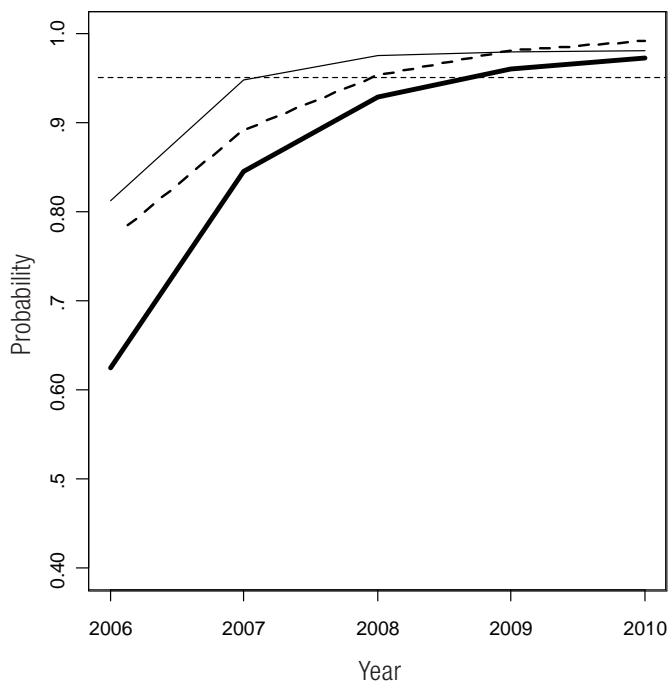


Fig. 1. Predicted mean probability of freedom from TB over time for livestock (thin line), wildlife (dashed line), and for both combined for the area (bold line). Only when the probability of freedom is sufficiently high (>95%) for both populations will the combined probability exceed the threshold (i.e. year = 2009).

Graphically representing the combined probability as a distribution (or histogram) allows Dean and his colleagues to assess this uncertainty. For example, two different surveillance scenarios could result in equal and satisfactory mean predicted probabilities of freedom (0.95), but very different levels of uncertainty (as measured by the 5th quantile; Fig. 2). Where there is high uncertainty, there is a high risk of being wrong in declaring the area disease-free. In contrast, where there is low uncertainty, or high confidence, the risk of being wrong in declaring eradication is relatively low. If managers are unsatisfied with the level of uncertainty associated with the predictions, additional surveillance will increase the accuracy and certainty in the model predictions.

Deciding how much extra disease management and/or surveillance is needed is always going to be difficult. The modelling described here can be used within a resource-allocation framework (see Nugent, pp. 20–21) to compute the amount of additional surveillance and/or wildlife control necessary to minimise the ‘net expected cost’ of being wrong (i.e. the joint cost in dollars of surveillance and renewed eradication operations). Minimising the cost of being wrong must include sources of uncertainty so that decisions are based on reliable model predictions.

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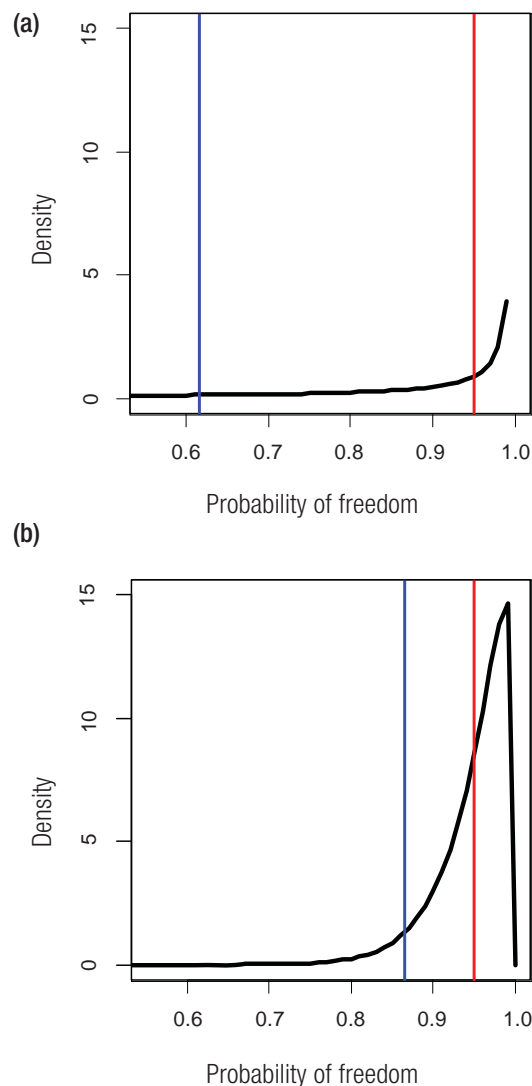


Fig. 2. Two different surveillance scenarios with predicted probability of TB freedom expressed as a distributions with means = 0.95 (red lines). (a) Scenario with high uncertainty in predictions as indicated by the low peak near the mean and low 5th quantile (0.62; blue line). (b) Scenario with low uncertainty in predictions as indicated by the high peak near the mean and relatively high 5th quantile (0.86; blue line).





What is the most cost effective path to TB freedom?

The current national bovine tuberculosis (TB) control strategy focuses on reducing and maintaining low possum densities in areas with infected livestock, and the testing and movement control of cattle. This strategy has successfully reduced the number of infected cattle herds from over 1,400 in 1994 to fewer than 90 now. The Animal Health Board now proposes to eradicate TB from all wild animal populations over 2.5 million hectares of New Zealand by 2026. This ambitious but achievable goal will depend on a 'proof of freedom' framework designed by Landcare Research. This framework provides an objective assessment of the probability that TB has been eliminated from an area (P_{NoTB}), based on recent control of wildlife vectors of the disease and lack of detection of TB in livestock, possums, or other wildlife sentinel species.

Under this framework, an area will be declared TB-vector free when P_{NoTB} is greater than some predetermined risk-management threshold (e.g. 95% probability that TB has been eliminated) that represents a low risk of operational failure (i.e. a 5% chance that TB is still present in wildlife vectors). When P_{NoTB} is still below the threshold, undertaking further possum control will increase the probability of achieving eradication. However, TB may

have already been eradicated, and all that is needed to prove this is additional wild animal surveys. Obviously a key need is to know which option to choose for any specified area. For example, should funding be used to kill more possums or to survey sentinel species such as wild pigs and deer for TB? Both strategies will help increase P_{NoTB} , but which would be most cost efficient?

To explore these complex resource-allocation questions, Graham Nugent, Pen Holland and colleagues are using the TB-freedom problem outlined above as the initial, and arguably one of the simplest, of several case studies (including island and disease eradication problems) to construct *whole-system models* to simulate all the key components of the Resource Allocation Framework (RAF) outlined in Fig.

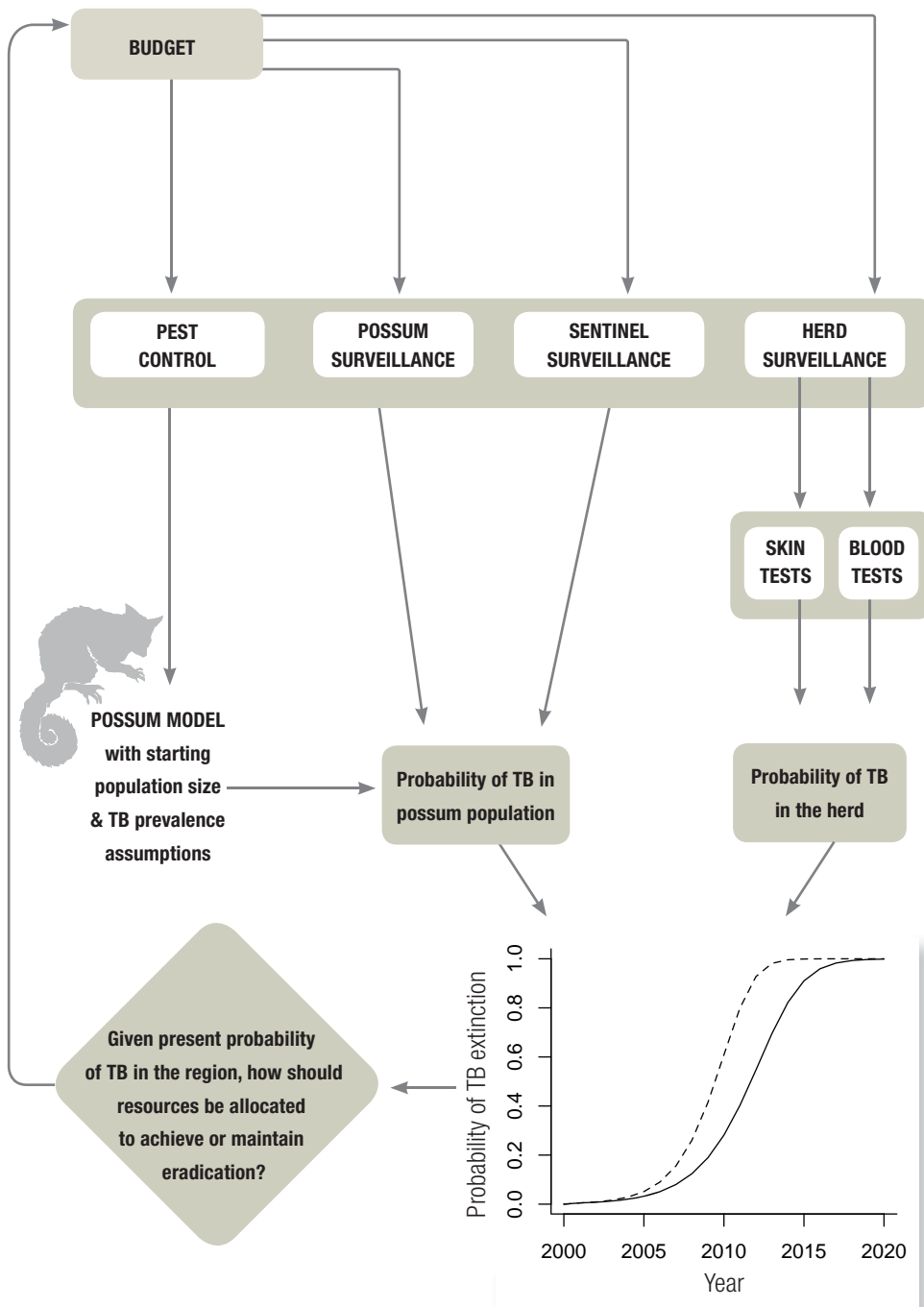
Data from the Blythe Valley (North Canterbury) is used here to illustrate how such a RAF will help TB managers. TB emerged in cattle herds in the Blythe Valley in the 1990s, and possum control began in 2000. By 2004, annual ground control of possums had reduced the number of infected herds to low levels but TB was still present in cattle. Intensive annual possum trapping continued until 2008 when just 16 possums were caught from 6105 trap

nights. Simulating this possum control history in a model of TB epidemiology in possums predicted a 99% likelihood that TB had been eliminated from possums as early as 2005.

Despite that prediction, TB was still present in cattle in 2005, making it prudent to assume there was still a 50:50 chance that infection was present in wildlife populations of either possums or ferrets. However, using data from trapping and from necropsies of possums and ferrets undertaken over the next three years, the Proof of Freedom Framework predicted a >95% likelihood that TB had been eradicated by 2008. One of the most important factors contributing to this high probability of eradication was the large amount of data from traps that caught no possums. If there is a zero catch rate at a trap site, there is a near-zero chance TB could persist within a 200–300 m radius of that site, because there are too few possums to maintain the disease.

Since 2007, no infected cattle have been found in the Blythe Valley. With hindsight, the last few cases of TB in cattle in 2005–2007 were probably animals that didn't react to the TB test or were due to within-herd infection. If so, TB was probably eradicated from possums by 2005 (as predicted by the Possum-TB model).





However, a further \$256,000 was spent on pest control, arguably for no benefit if TB had already been eliminated from wild animals. The obvious difficulty is that managers had no way of confirming that TB had been eliminated, so their decision to continue precautionary control was sensible. Nevertheless, some of the expenditure could have been saved if there had been an earlier shift away from simply killing possums toward both killing possums and using the wildlife surveillance data to 'prove' TB was absent.

The aim is therefore to develop whole-system models that will enable TB managers to allocate funding among control and surveillance strategies, in order to maximise the rate of TB eradication and to provide timely confirmation of success. Graham and his colleagues consider that a whole-system model for TB will improve the allocation of control and surveillance resources and thereby improve eradication efficiency.

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Fig. Resource (Funding) Allocation Framework (RAF) for rapid confirmation of TB freedom. The funding available can be allocated solely to killing possums or to some mix of possum surveillance (necropsy for TB), sentinel surveillance, and cattle surveillance (testing). These other activities provide information as to where an area sits along the TB-extinction curve. The RAF will be used to simulate and predict how funding should be allocated between activities that will most cost effectively eliminate TB and 'prove' that it has been eradicated from wild animals.



The National Possum Model – involving more than 30 million individuals

The National Pest Management Strategy for bovine TB in New Zealand proposes three options for managing wildlife vectors: containment of the pests, rollback of the disease, and disease eradication. Under all three scenarios, accurate, real-time and future predictions of possum abundance will be critical in order to make management decisions. Also possums have significant environmental impacts as they defoliate trees and prey on the eggs and chicks of native birds. Conservation efforts could be coordinated better if the Department of Conservation, regional councils and private groups have a more complete, up-to-date picture of when and where possums are being controlled. James Shepherd and his colleagues have developed a prototype individual-based model predicting the abundance of possums nationally: the National Possum Model. The model uses open-source GIS software and integrates existing land cover maps, jurisdictional boundaries, and control area boundaries. The model will be delivered and updated over the Web. However, users will need to input data on possum control in order to receive useful current and future population predictions.

Based on estimates of possum density and home-range size, the model describes the behaviour of individual possums located explicitly in a map of their habitat; hence it is referred to as an 'individual-based model'. Each individual has an Easting and Northing coordinate representing the notional centre of its home range. Each home range is assumed to be fixed, unless the possum 'decides' to disperse. Key events in an individual's lifetime comprise birth, death, and dispersal, and these are simulated as stochastic (random), competing Poisson processes, i.e. there is uncertainty in the timing of each event. It is assumed that births and deaths are affected by the local density of possums. In the model, the population density of possums is represented by a map that is the sum of the intensity of home-range use

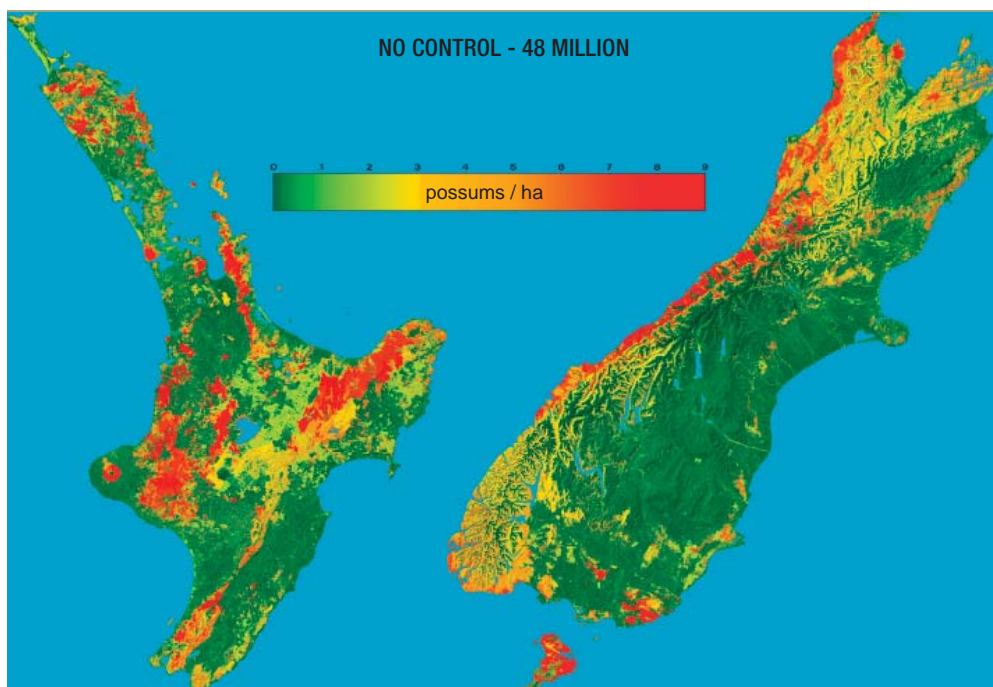


Fig. 1. Modelled equilibrium density of possums without control.

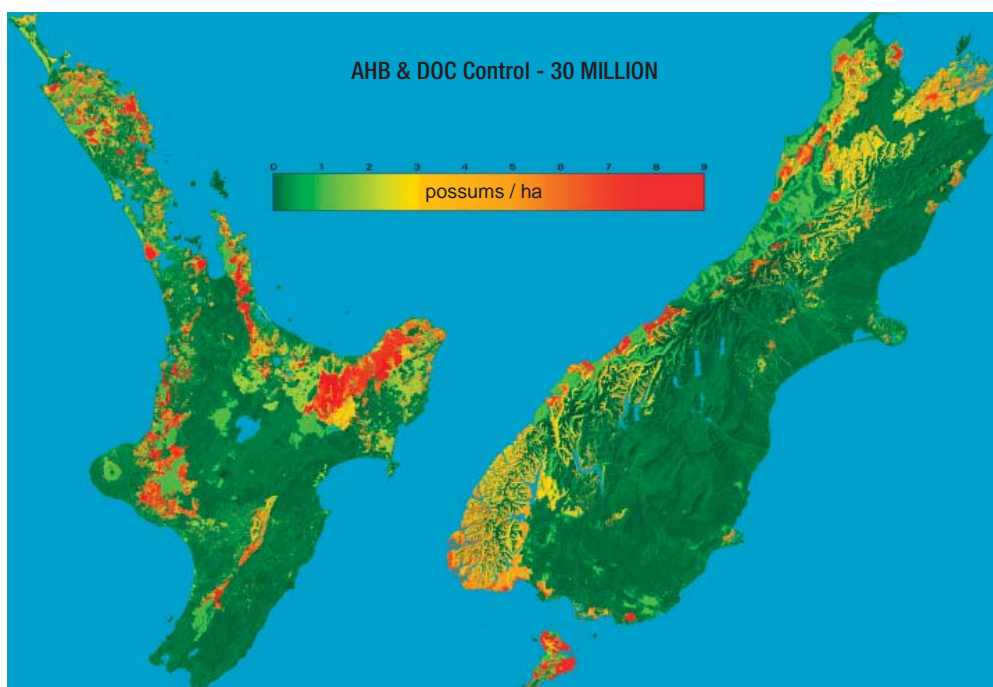


Fig. 2. Modelled density of possums following control programmes by the Animal Health Board and the Department of Conservation in 2008 and 2009.



by all individuals. Possum carrying capacity (i.e. maximum density) varies across the landscape and is predicted from detailed habitat maps derived from satellite imagery (Fig. 1). Births in the model occur as a single 'pulse' each year.

Due to the random nature of events in a possum's life, a single run of the model provides only one of many possible 'realisations' of changes in the possum population. Predictions require many individual model runs with different random starting values to build up a distribution of results from which the mean and spread of behaviour is drawn. This type of modelling is often termed *Monte Carlo simulation* and is computationally intensive. Typically, a prediction for the outcome of a possum

control programme, for example, is created from 500 model 'runs'. While this amount of processing does seem prohibitive, each run is independent and can therefore be carried out simultaneously on a cluster of computers set up to work as a single coherent unit. Eventually James and his team intend to move their modelling to a nationally based, high performance computing network. The equivalent of a true super computer will enable the complete suite of Monte Carlo simulations to be undertaken in the same time it takes for one run of the model on a desktop computer.

The National Possum Model will provide detailed and realistic forecasts of possum abundance, now (Fig. 2) and at regular time

intervals into the future. In other words, it will be a dynamic, continuously updated, national map of possums. To achieve this will require user input of the extent and effectiveness of recent control programmes to 'reset' possum numbers locally and to update the national prediction (Fig. 3). An important part of the process will be managers providing feedback to modellers when predictions differ from reality, so access to pre-control monitoring data will be invaluable. It is expected that the effectiveness of the model will be improved by many areas of Landcare Research's current research: satellite image processing and subsequent classification of land vegetation cover, understanding the relationship between vegetation cover and possum density, and improving model parameters for home range distribution and dispersal of possums through analysis of possum movement behaviour using GPS collars.

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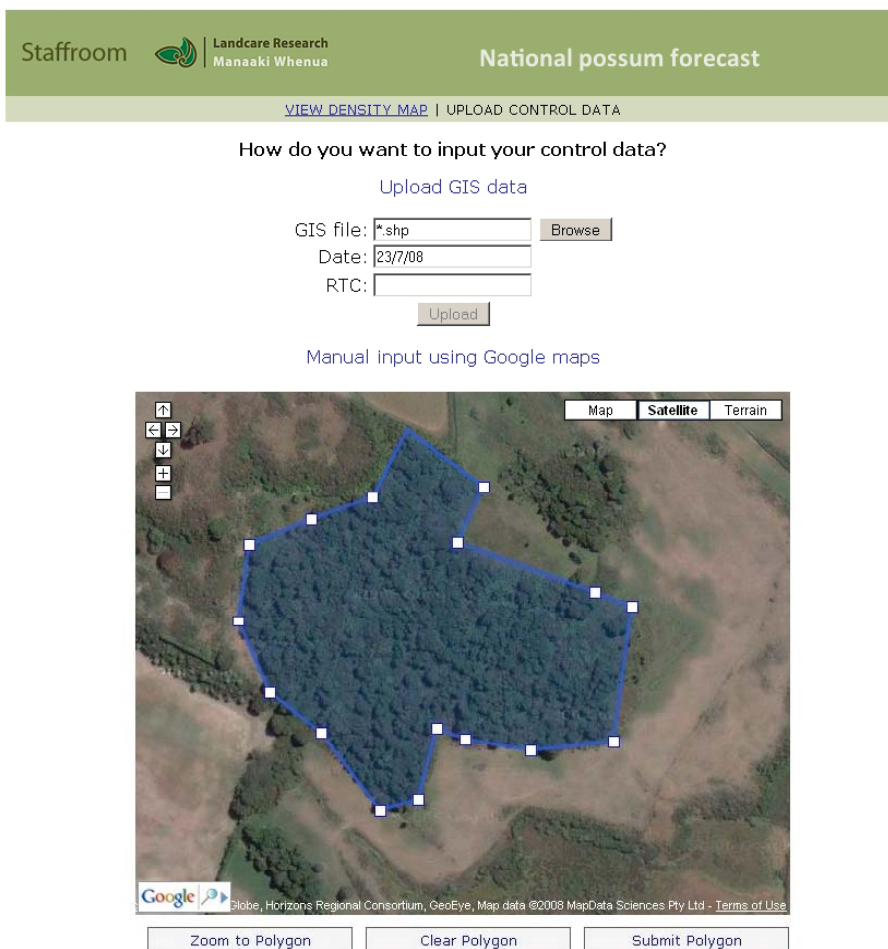


Fig. 3. Example of a web page for submitting the results of a recent possum control programme.



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