

#32

MARCH 2019



Manaaki Whenua
Landcare Research

Kararehe Kino

ANIMAL PEST RESEARCH



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Published by: Manaaki Whenua
PO Box 69040
Lincoln 7640, New Zealand
ph: +64 3 321 9999

ISSN 1175-9844 (Print)

ISSN 1170-3016 (Online)

Photo credits:

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Editorial: Using quantitative models to gain insights in ecology

“ *Mathematics without natural history is sterile, but natural history without mathematics is muddled.* ”

John Maynard Smith

It is probably a fair assumption that people who are interested in the life sciences are not secretly yearning to learn and apply quantitative methods. Indeed, for many professional ecologists, mathematics and statistics were their least favoured subject areas during their training. However, because ecology typically involves trying to make sense of a complex system, we often require quantitative models to help us in that endeavour. A wide variety of quantitative modelling approaches are available, and this issue of *Kararehe Kino* presents a sample of these methods and how they can be applied to various wildlife management issues.

Some studies require *statistical models*. These are applied in studies that involve collecting data, where the statistical model is used to analyse that data so that the researcher can interpret the results in order to make reliable inferences about the study. Statistical models are often used in wildlife management to determine the success or otherwise of management. For example, we might collect data on stoat activity in a region before and after stoat control and use a statistical model to provide evidence that any observed change in activity [e.g. a decrease in stoat activity] is a result of the management intervention. Less common, but no less important, is conducting a power analysis before the field study is carried out. A power analysis gives the research team insight into how much field effort they need to undertake to answer their question. If you didn't find evidence for a change in stoat activity due to control, maybe you didn't measure it well enough! Cecilia Latham and Dave Latham [article 5] show that conducting a *a priori* power analyses can ensure resources are not wasted on poorly designed studies that would never answer the question of interest.

At other times we require *theoretical models*. These are often a simplified simulation model of the system being studied to help us understand the system and how its different components interact. These models can be used to tackle complex ecological problems. Pablo Garcia Diaz [article 3] used a simulation model to provide insight into potential reinvasion by ferrets in a large landscape. His approach illustrates how a simple, yet realistic, model can be used to explore the system process. Furthermore, by exploring how the results of the simulation respond to changes in the input parameter values, such models can help prioritise which field studies are required to better inform the model.

Statistical and theoretical models have the common aim of attempting to provide insight, whether to better understand an ecological process or to assess the success of a management activity. Such models are invaluable to land managers, helping them in their decision-making. For example, our intuition says that if we apply predator control then we will achieve biodiversity benefits. But more nuanced questions, such as how much control we need to carry out, how often, and where to apply it, are more difficult to answer. Models can be a useful tool to guide managers in answering these kinds of questions.

Dean Anderson and colleagues [article 4] used a simulation model to assess the most effective management strategy in order to increase populations of kiwi. Their model forecasts kiwi populations as a result of predator management by accounting for a range of interacting factors such as forest dynamics, and rat and stoat population trajectories.

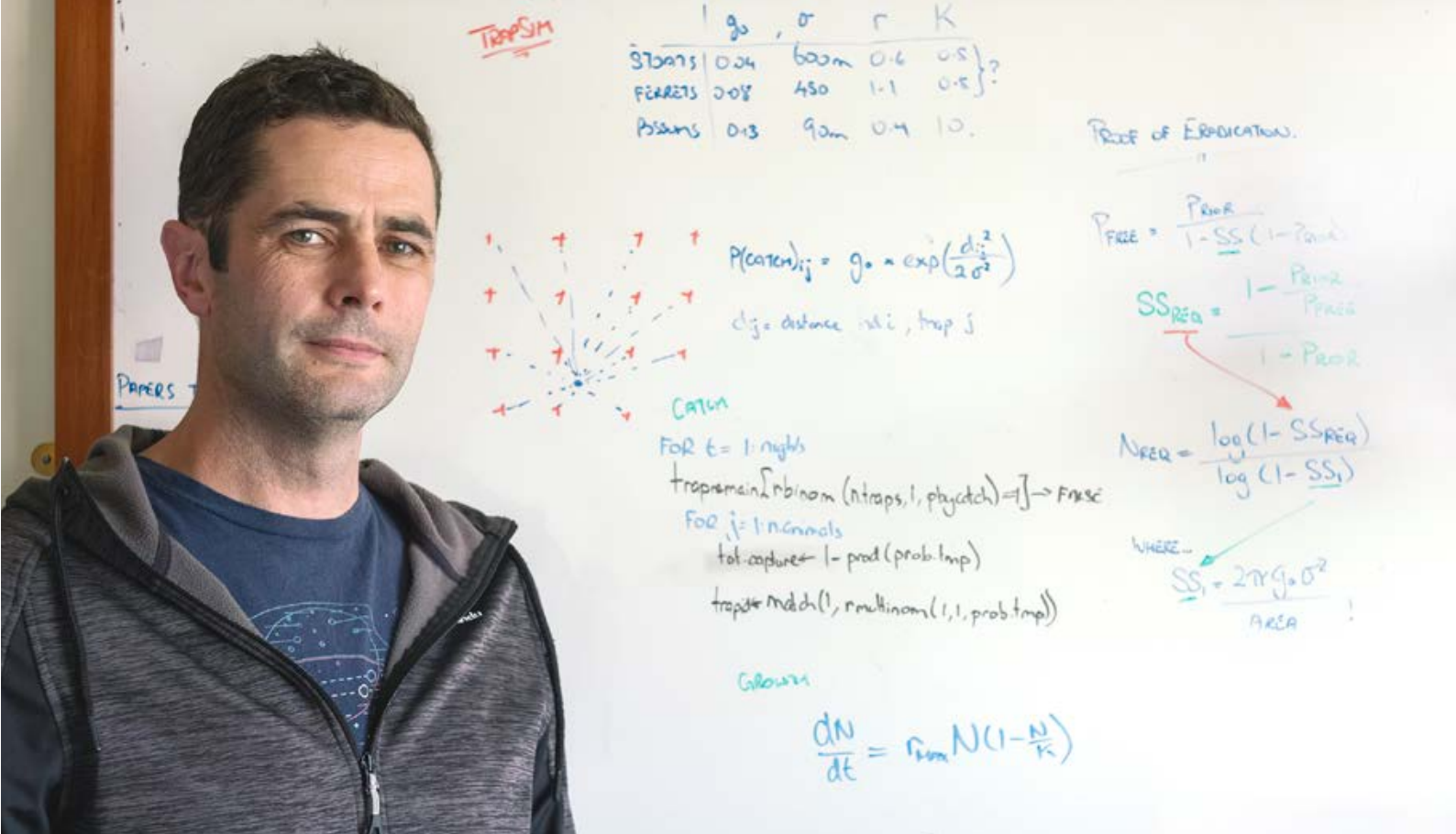
In a similar vein, Andrew Gormley and Bruce Warburton [article 8] constructed a model of predator trapping to help managers decide between the probable effectiveness of various large-scale trapping options. They have also constructed an online, easy-to-use version of a model called TrapSim, which allows managers to explore various scenarios without requiring them to have knowledge of the underlying model, or training in quantitative methodology.

When trying to eradicate a species, the issue of when managers can declare success is difficult: if the species is not detected, is that because it really has been eradicated or did the field team just not look hard enough? Dean Anderson et al. [article 6] have developed an analytical approach to help decision-makers decide when they can declare successful eradication, and they demonstrate its use on an eradication of Argentine ants on Kawau Island. Their approach is always for multiple surveillance methods to be included and enables managers to understand which of these methods is the most effective.

“ *Truth is much too complicated to allow anything but approximations.* ”

John von Neumann

Because ecological systems are complex, ecological models are necessarily a simplification of the actual system. Model complexity is a trade-off between simplicity and accuracy. Adding complexity will often improve the realism of a model, but it can make the model difficult to understand. In general, if we have two models with similar predictive power, the simplest one is the most desirable.



Andrew Gormley

This is not to say the simplest model is necessarily the best. For example, the current version of TrapSim mentioned above assumes that all individuals conduct themselves in the same way with respect to home range and how they interact with traps. But if that's not the case, does it matter? Giorgia Vattiato [article 7], a PhD student working with Rachelle Binny, is using a model to understand the potential effects of individual behavioural differences on the efficacy of predator programmes. Theoretical models such as these can help determine whether more complicated effects are worth including in the model, as well as providing managers with valuable information on the potential for the trapping programme to fail as a result of these individual differences.

Modelling is not confined to ecology, and is carried out in many disciplines. Network connectivity is a widely studied field in engineering with important applications to traffic management. Tom Etherington et al. [article 1] recently applied network connectivity research to invasive pests to help identify areas that can be targeted to ensure greater control efficiencies. Their work demonstrates how applying methods developed within other disciplines can be used to address ecological questions.

The opposite can also be true. Predator-prey models are commonly used in ecology to make inferences about the dynamics of two interacting species [e.g. fox and rabbit populations]. Bruce Warburton et al. [article 9] applied this ecological modelling framework to wild deer recovery, where helicopter hunters are the predator and deer are the prey. By accounting for the various financial costs, they provide a framework to easily assess the economic viability of wild deer recovery in New Zealand.

Models can be extended to include more than just ecological components. Decision-makers also have to consider economic and ethical factors, but accounting for these is inherently difficult. Bruce Warburton and Dean Anderson [article 2] present a framework that considers the probabilities of success of each of these factors with respect to a wildlife management programme. Modelling frameworks such as this that also account for ethical considerations will become increasingly relevant, especially as wildlife management moves even more into the public arena with national-scale programmes such as Predator Free NZ

“Essentially, all models are wrong, but some are useful.”

George Box

One final note: good quantitative models have the potential to help us better understand an ecological system as well as providing managers with a more objective way of making decisions. However, 'good' quantitative models rely on the availability of good data to develop and verify the reliability of the model. Quantitative models are a powerful tool, but they only work in conjunction with good information and are not a substitute for data. Garcia et al. [2019] have recently published a paper describing good practices in quantitative modelling for conservation management, and it is highly recommended as further reading.

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Prioritising pest control based on network connectivity

Resources for the control of invasive pests can be prioritised for certain sites in different ways, but one approach that has not received a lot of attention is prioritising sites based on landscape connectivity. This approach considers that as pests move around a landscape, targeting the parts of the landscape that act as critical junctions in a network of movement may help break a population into smaller more isolated sub-populations that are easier to control or eradicate.

Extending this analogy, imagine a road network you drive your car around. You know that some junctions are much busier than others because they connect many locations and are therefore more critical in maintaining the connectivity of the network. Traffic engineers use network connectivity models to find junctions in networks that are most important for allowing traffic to keep flowing. But if cars are viewed as invasive pests and roads as dispersal routes, then these same network connectivity methods could be used to find the critical junctions in a network of the movements of such pests. While traffic engineers protect critical road junctions to maintain traffic flow, pest managers could target their critical network junctions to reduce the spread of invasive pests.

Tom Etherington and his colleagues wanted to assess whether approaching invasive pest control using network connectivity could be an effective management technique. To do this in the real world would be difficult and costly because it would involve continuous monitoring of an invasive species population over large areas for long periods of time. Therefore, Tom and his colleagues used computer simulations of a virtual pest population breeding and dispersing around a network of habitat patches, upon which were imposed different control methods: one where control was random, one that controlled pests in a habitat close to another habitat, and one based on a network connectivity measure called 'betweenness centrality'. Betweenness centrality works by calculating the most direct dispersal route between all combinations of habitat patches, with the habitat patches occurring in more dispersal routes having a higher betweenness centrality (Figure 1).

The modelling indicated that using network connectivity to prioritise the control of invasive pests can be a more effective strategy than traditional pest control to reduce the size of a population of pests and the number of invaded sites. For example, using a network connectivity approach will have a greater impact for a given number of control sites, or achieve the same level of impact with fewer control sites (Figure 2), both of which indicate greater control efficiencies. However, these findings only apply when a network view of the landscape is appropriate, invasive pests are in the early stage of (re)invasion, and long-distance dispersal is limited. While encouraging, the findings are still theoretical, but future work will hopefully enable them to be examined in real landscapes.

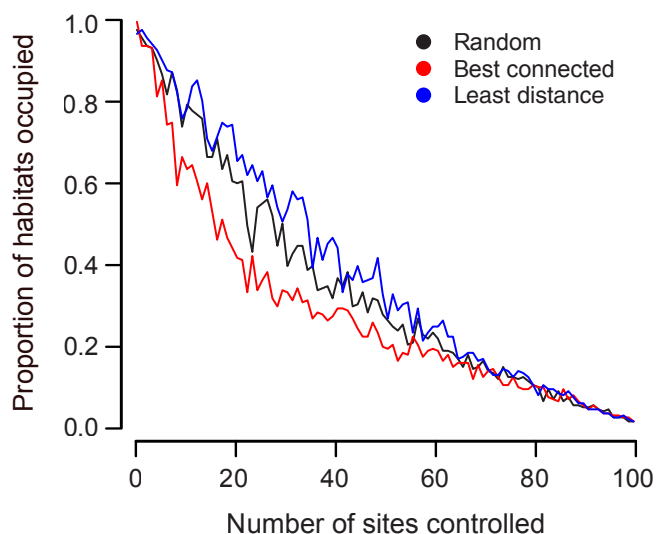


Figure 1. A hypothetical example of using network connectivity as a basis for pest control. A series of localised populations of an invasive pest species connected via dispersal pathways that form a network of populations across a landscape is illustrated above. If the connections are known or can be predicted, then a network connectivity metric, such as 'betweenness centrality', can be used to identify those localised populations that form critical junctions for dispersal around the network. Targeting such localised populations with higher betweenness centrality may break the network into smaller, isolated populations that are individually easier to control or eradicate.

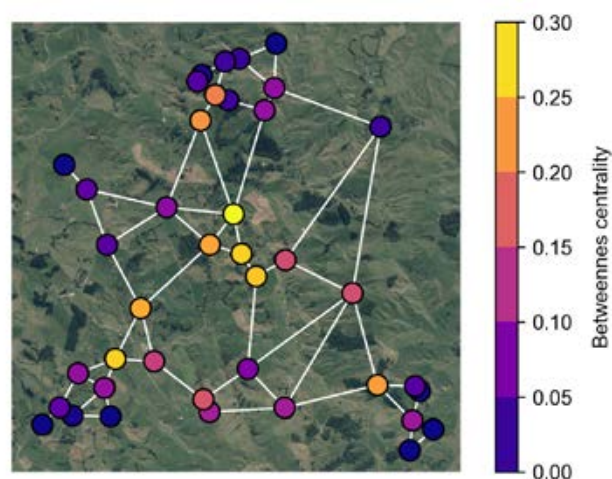


Figure 2. Effectiveness of control of invasive pests [as measured by the proportion of 100 occupied habitats at the end of the simulation] using the distance- and connectivity-based prioritisation strategies under different control intensity. Lines are medians from 30 model replications. When few sites are controlled, all methods perform equally poorly, and when nearly all of the 100 sites are controlled, all methods perform equally well. But as control effort increases, the connectivity-based approach provides the most efficient control strategy.

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Ecology, economics and ethics: the three Es required for sustained and effective vertebrate pest management

In New Zealand some introduced vertebrates are managed to limit their impacts on indigenous biodiversity, agricultural production, and infrastructure, and others for commercial and recreational harvest. Most of this management requires the use of lethal tools and techniques, and as a result wildlife managers are often challenged to justify their policies and actions on the basis of pest ecology, population dynamics and ethical acceptability. Unfortunately, most managers are poorly equipped to enter into informed discussion on what are often complex ethical and philosophical issues. For example, choosing and defending lethal control poses significant ethical challenges, and defending why populations need to be managed at all can raise significant philosophical challenges.

Most decisions that managers make related to ecology, economics and ethics have varying degrees of uncertainty, and here Bruce Warburton and Dean Anderson explore whether a probabilistic modelling approach can help managers frame and formalise adaptive management that integrates ecology, economics and ethics. Such formalisation will encourage managers to maximise the probability of achieving sustainable and effective wildlife management outcomes.

Ecological uncertainty

Managing wildlife can be inherently complex because individual species are part of broader multi-species communities, which in turn contribute to higher-level ecosystem processes. There are many examples of successful management actions delivering desired outcomes. For example, long-term suppression of ship rats, brushtail possums and stoats has resulted in significant population recoveries of threatened bird species, while reducing possum numbers alone has resulted in significant reductions in the number of cattle herds infected with bovine tuberculosis.

However, there are many failed programmes. Failures occur because managers often have insufficient knowledge about [1] species interactions, resulting in the release of meso-predators whose negative impact is as great or greater than that of the species controlled; [2] the relationship between pest density and impacts, resulting in inadequate reductions in pest density, and [3] the effectiveness of the control tools and strategies used.

Economic uncertainty

Managing wildlife has costs that managers need to consider when planning control programmes, either to decide how best to allocate limited funds across priority areas or how to allocate sufficient funds to achieve the desired outcome. There is a range of fixed and variable costs associated with managing wildlife, including planning, implementation,

non-target mitigation, addressing public needs, monitoring, compliance, and, where cost-benefit analyses are required, the monetising of conservation assets and benefits.

Ethical uncertainty

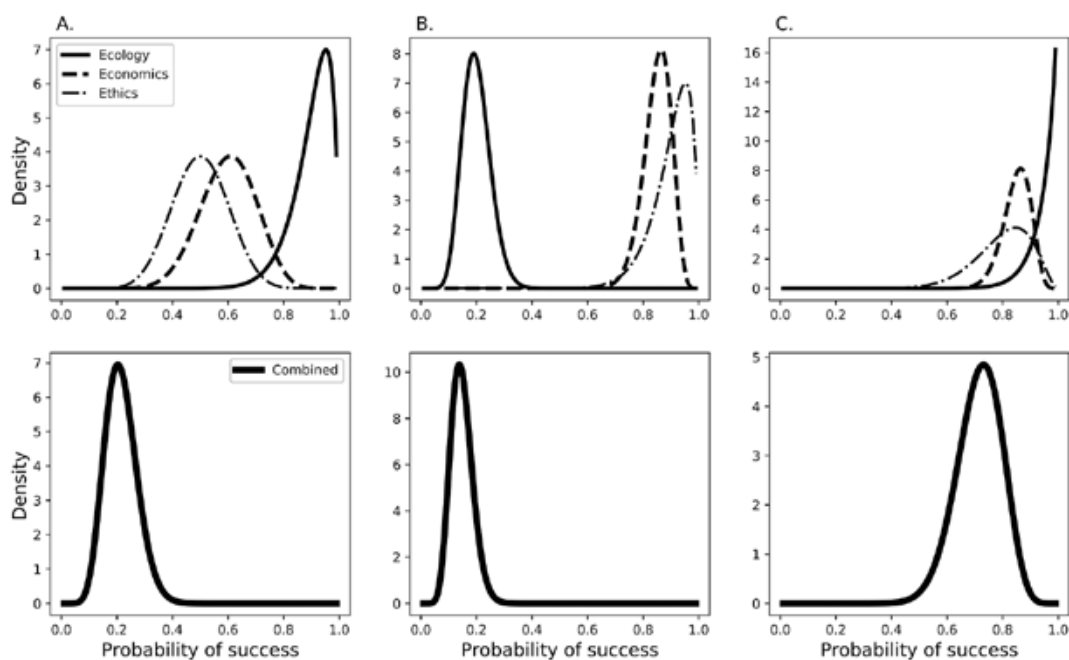
Wildlife management programmes often generate strongly polarised dialogue because of the diverse value sets held by stakeholders. Managers need to be aware of such differing values and recognise them as another level of uncertainty to account for. Managers faced with manipulating vertebrate species, especially if lethal methods are proposed, have both animal welfare and ethical issues to address. All lethal control methods have welfare costs (i.e. they cause pain or distress), ranging from fast-acting vertebrate toxins and kill traps that have the least welfare cost, to anticoagulant toxins and leg-hold traps that have significant welfare costs.

As a result, managers can be the target of vociferous opposition from stakeholders citing ethical issues, and although they are often passionate about protecting conservation or production values, they are often not well enough informed to respond to animal rights advocates and moral philosophers who claim the moral high ground by advocating non-lethal control methods. Utilitarians attempt to compare the costs to the benefits of managing pests, but in most ecological cases, although the welfare costs can be accounted for, it is often extremely difficult to measure the benefits, especially when they relate to non-sentient organisms such as plants, providing managers with another level of uncertainty.

Integrating ecological, economic and ethical uncertainty

Effective management strategies for wildlife issues hinge on the success of the 3Es for the duration of the project; that is, the continued success of ecological outcomes, financial and institutional support, and broad acceptance of the ethics of the actions undertaken. Given the inherent complexity and associated uncertainty, managers should modify their strategies as experience and new information are obtained.

Adaptive management guided by Bayesian uncertainty modelling is an evidence-based mechanism for arriving at and revising strategies to maximise the probability that management actions will achieve their objectives. Adaptive management provides a framework for formally and quantitatively incorporating the likely acceptance of the ethics of management actions into strategy development, especially when applied to the management of wild animals. Dean and Bruce have developed a conceptual approach



Results of three hypothetical management scenarios illustrating how the integration of 3E-component probabilities determines the overall probability of project success. In the upper panel of each scenario [A, B, and C], the probabilities of ecological, economic and ethical acceptance are decomposed into individual probability distributions. The product of these probabilities is shown in the corresponding lower panel and represents the overall probability of programme success.

for incorporating the 3Es into an adaptive management programme informed by Bayesian uncertainty modelling. Quantitative predictions of the probability of successful outcomes of each of the 3Es are made, and the probability of the overall success of a programme is the product of each of the 3E-component probabilities:

$$P[\text{overall success}] = P[\text{ecology}] P[\text{economics}] P[\text{ethics}]$$

The individual 3E-component probabilities are derived from data-driven or expert-parameterised models. Data-driven models are preferred and should replace expert-parameterised models as management programmes progress. Bayesian statistics are desirable because they take advantage of existing independent parameter estimates and expert insight of the system, and they update parameter distributions as more data are collected. Parameters are incorporated using probability distributions, not point estimates, to capture uncertainty in the understanding of the processes and predictions.

Three hypothetical examples are presented below to illustrate how this approach will lead to an overall probability of project success.

1. In the first example, the mean ecological, economic and ethical probabilities of success are 0.9, 0.6, and 0.5 respectively [see graph, scenario A, upper panel]. To obtain an overall probability of success that incorporates uncertainty, random variates from each component probability distribution are used to calculate the product [see equation]. This is repeated for 2,000 iterations to obtain the resulting distribution of the probability of success [see graph, scenario A, lower panel]. With two of the 3E-component probabilities equal to or slightly better than a coin toss, the overall probability of success has a likely value of 0.24.

2. In a second example, the mean probabilities of continued economic and ethical support are 0.9 and 0.85 respectively, but the mean probability of ecological success is only 0.2 [see graph, scenario B, upper panel]. Clearly the weak link is that the predicted ecological outcome for this strategy is unlikely to be sufficient, and the equation gives a most likely combined probability of success of 0.12 [see graph, scenario B, lower panel].
3. A third example illustrates that even with relatively high probabilities of success for the 3Es [means = 0.95, 0.85, and 0.80; see graph, scenario C, upper panel], the most likely combined probability of success for the program is 0.70 [scenario C, lower panel].

Do these relatively low joint probabilities mean that such programmes are unjustified? Not necessarily, as many will succeed, and adaptive management and research will discover innovative ways to increase each of the 3E-component probabilities to increase the combined probability of project success.

Conclusions

Managers will benefit from adopting this simple framework for managing vertebrate pests, and even if their first probabilities are based on expert opinion or degrees of belief, adaptive management using a Bayesian model will allow these probabilities to be updated. If nothing else, recognising that all three components have to be addressed when developing a sustainable pest management plan will be an improvement on the status quo.

This work was funded by Strategic Science Investment Funding.

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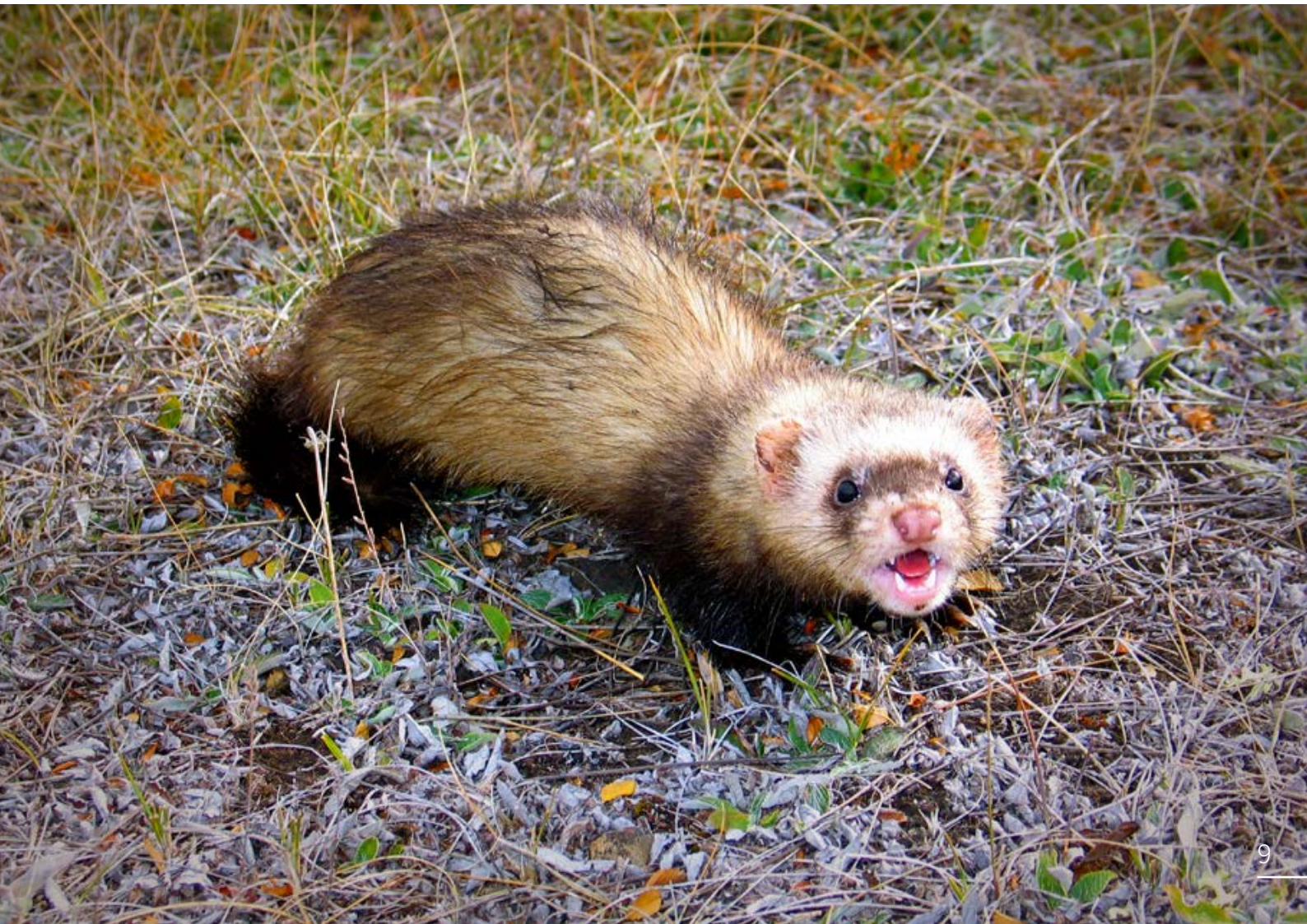
Using computer models to understand and forecast reinvasion by invasive mammals

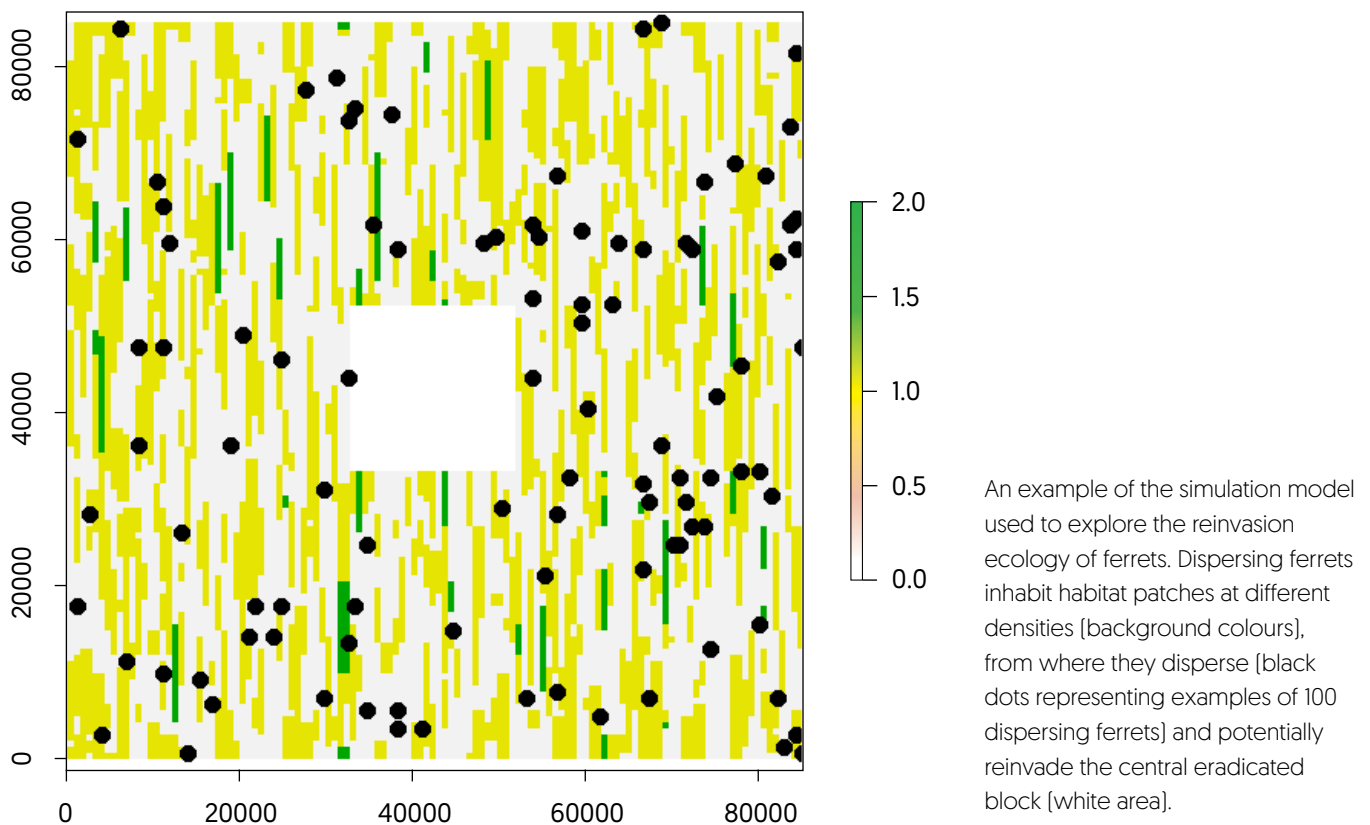
Preventing and effectively managing reinvasions is essential for the long-term viability and success of invasive species eradication and control interventions. It is a particularly formidable challenge in mainland scenarios where there are no natural barriers to hamper the spread and movement of potential reinvaders. The factors determining reinvasion pressure, measured as the total number of animals arriving in a managed area per year, and how managers better overcome the issues posed by such reinvasions, are the focus of ongoing research by Pablo Garcia-Diaz and Grant Norbury, in collaboration with other personnel from the Wildlife Ecology and Management team.

The complexity of the problem and the lack of information on the topic meant that a relatively simple modelling exercise would be a suitable starting point. Pablo and Grant developed a 'simulation' computer model, a simplified representation of reality that functions like a game, where animals move around

a virtual landscape following rules set by the researchers. By repeating the model multiple times (playing multiple games) using different values, it is possible to explore how reinvasion pressure responds to a range of potential virtual realities and how it depends on the settings established by the researchers. This approach will identify the most likely factors driving reinvasion pressure, and highlights knowledge gaps that need to be addressed to effectively manage reinvasions.

Pablo and Grant developed a proof-of-concept modelling framework, which they applied to a case study of reinvasion by juvenile feral ferrets in a large landscape (720 000 ha). In the middle of the landscape they included a large area (33 500 ha) where ferrets had been eradicated and kept free of reinvaders. The remaining landscape was divided into habitat patches where ferrets lived – patches that were the potential sources of reinvaders. The model specified that juvenile ferrets would disperse from these patches and move across





the landscape. The position of each dispersing juvenile ferret in the landscape was monitored for 120 days, and whenever a ferret arrived in the eradicated block it was scored as a reinvasion event. Two hundred repetitions of the model were undertaken, which took approximately 5 hours on a standard laptop computer. The modelling results showed very clearly that reinvasion pressure on the area cleared of ferrets was very high in the absence of management, and that reinvading ferrets were most likely to have come from those habitat patches closest to the eradicated block that harboured a high number of ferrets.

The model can be used to narrow down the number of unknown ecological variables needed to design appropriate fieldwork to obtain good information to update the model and make it more realistic and tailored to the particular context where intervention will take place. The first batch of model outputs will be used to guide field research, and the data will then be fed back into the model. Another batch of model runs will allow researchers to refine their recommendations for managing reinvasion pressure at landscape scales. Preliminary results clearly show that managing reinvasion pressure requires a landscape-level perspective that explicitly considers invasive mammals in the surrounding area. This updated model will be used to explore management alternatives and suggest cost-effective interventions to better tackle the risk of reinvasion.

Given that the same general principles of reinvasion ecology apply across most inland systems, this approach is likely to be beneficial for a range of invasive species management projects. In the short term, Pablo and Grant aim to include other species (e.g. stoats) in their model to see whether the same interventions can tackle multiple species simultaneously, or whether it is necessary to adapt separate management strategies for each targeted species.


More broadly, the example reported here showcases the power of modelling for tackling complex ecological problems. The process is to [1] begin by developing a simple, yet realistic, computer model to explore the processes underlying the problem, [2] use the outputs of the model to inform subsequent fieldwork and data collection to quantify the most sensitive ecological parameters, and, [3] revise the model using these newly acquired data to improve the reliability of the model predictions.

This work was funded by the Strategic Science Investment Fund provided by the New Zealand Ministry of Business, Innovation and Employment.

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Modelling supports nimble predator management for increasing kiwi populations over large areas

The recovery of the five species of kiwi is a national conservation priority. The great spotted kiwi, tokoeka and brown kiwi live in large tracts of forest and are experiencing population declines due to invasive predators. While the little spotted kiwi and rowi have low populations, their numbers locally have stabilised or are increasing due to effective predator management. Kiwi chicks are vulnerable to predation by stoats until the chicks reach a weight of about 1 kg. In the face of unmanaged predator populations, kiwi recruitment is reduced or stopped, which results in population declines.

The level of stoat predation on kiwi chicks is the result of a complex multi-trophic system that begins with forest production of seeds (Figure 1). Periods of high seed production, such as during masting in beech forests, provides an abundant food resource for ship rat populations, which rapidly increase. The pulse of such populations provides a rich prey resource for stoat populations, which subsequently increase in density and put kiwi at risk.

Currently, baiting with 1080 is the only cost-effective tool for controlling rats and stoats over very large areas, which must be done to reverse kiwi population declines. Stoats do not eat the 1080 baits, but 1080 acts to reduce the stoat population in two ways (as illustrated by the lack of an arrow from 1080 to stoats in Figure 1). First, stoats prey on rats that have eaten 1080 bait, and these 'toxic rats' act as a vector for getting 1080 into stoats, which then die from secondary poisoning. Second, baiting with 1080 reduces the rat population, which drives down the carrying capacity of stoats.

While the application of 1080 bait is *relatively* cost-effective, it cannot be applied everywhere and all of the time.

Therefore, a strategy is required to guide when and where it should be applied to achieve a growing kiwi population.

As a part of a Ministry of Business, Innovation and Employment-funded research project, Dean Anderson and John Innes have developed a broad-scale forecast model that captures the trophic dynamics of seed productivity, the rat and stoat populations, predator management with 1080, and kiwi population outcomes. The aim of the forecast model is to predict the likely change in kiwi population density over 20 years for a variety of alternative management strategies. The model incorporates stochastic forest productivity events (e.g. masts), dispersal and population growth of kiwi, rats and stoats and predation.

To illustrate the model, kiwi population dynamics were forecast across Fiordland National Park for 20 years in response to three different strategies for the deployment of 1080 bait. Predator management with 1080 cannot be conducted over the whole of Fiordland because of the costs involved, but it can be applied in management zones associated with the Department of Conservation's programme Save Our Iconic Kiwi (SOIK; Figure 2). The first strategy is 'reactive', in which an aerial 1080 operation is triggered in a given management zone by either rat-tracking rates (recorded in inked tracking tunnels) of at least 20%, or by 50% of the management zone being found to be in mast. The second strategy is '4-year prescriptive', in which each management zone receives a 1080 operation every 4 years, regardless of masting events or tracking tunnel rates. The third strategy is '3-year prescriptive', in which a 1080 operation occurs in each management zone every 3 years. Importantly, 1080 is never deployed outside the four management zones.

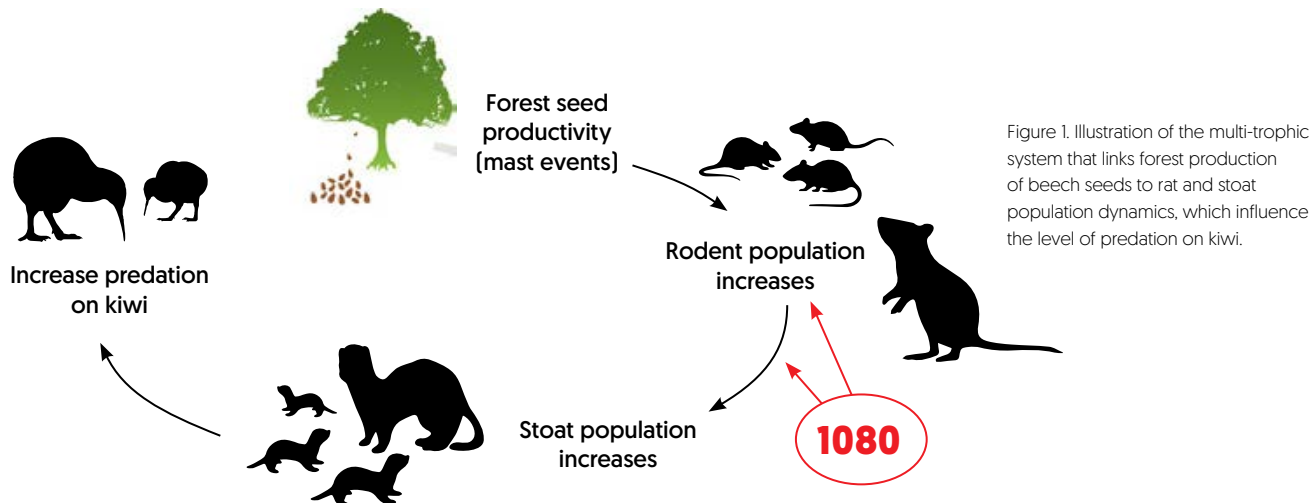


Figure 1. Illustration of the multi-trophic system that links forest production of beech seeds to rat and stoat population dynamics, which influence the level of predation on kiwi.

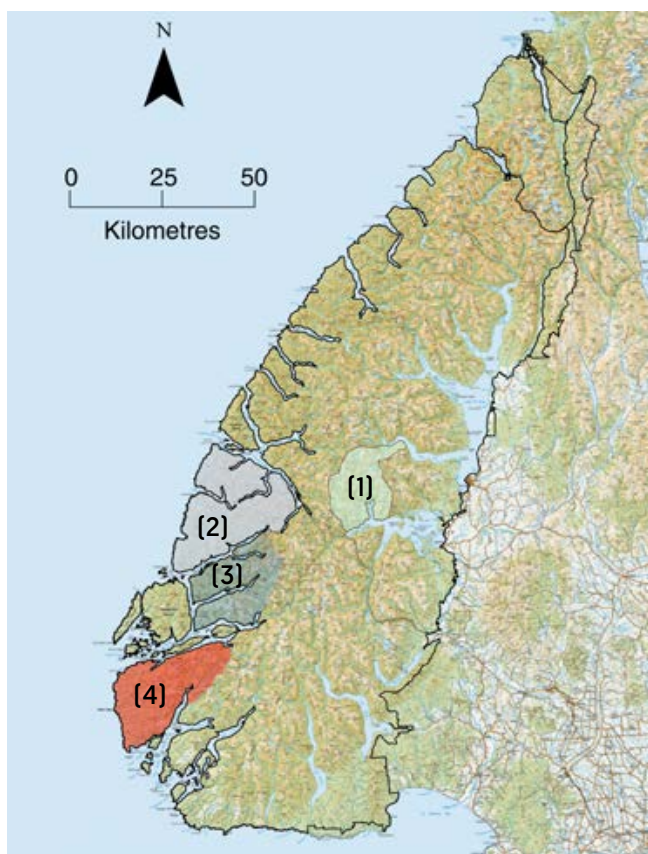


Figure 2. Map of Fiordland and the four Save Our Iconic Kiwi management zones: [1] Freeman Burn, [2] Mt Forbes, [3] Wet Jacket, and [4] West Cape.

Zone	Reactive	4-year prescriptive	3-year prescriptive
Freeman Burn	0.02	-0.01	0.02
Mt Forbes	0.12	0.01	0.11
West Cape	0.12	-0.04	0.06
Wet Jacket	0.10	-0.04	0.04
All Fiordland	-0.15	-0.16	-0.15
No. 1080 operations	29.36	20.00	26.00

Table 1. Results of the forecast model for the three management strategies. Displayed is the mean proportional change in the kiwi population in the four management zones and over all of Fiordland National Park. Also shown is the expected number of aerial 1080 operations for each management strategy.

The proportional change in kiwi population size over 20 years is forecast individually for each management zone and for all of Fiordland [see Table]. For the *reactive strategy*, the proportional change in the kiwi population varied across the four management zones from 0.02 in Freeman Burn to 0.12 in Mt Forbes and West Cape. This management strategy reversed the decline of the kiwi population and resulted in an increasing population, but the 0.12 proportional change equates to a per-annum population growth rate of approximately 0.5%, which is well below the potential maximum growth rate of 10% and the SOIK goal of 2% per annum. The expected proportional change in the kiwi population over all of Fiordland was -0.15, which indicates an ongoing population decline, despite increases in the SOIK-managed areas. The expected number of 1080 operations over the four management zones and over 20 years was 29.4.

The forecast kiwi outcome with the *4-year prescriptive strategy* was less favourable, with proportional population changes ranging from -0.04 to 0.01 [Table]. This suggests that letting beech forest areas go 3 or more years without predator control will result in damaging predation rates and decreasing kiwi populations. The required twenty 1080 operations in this strategy was clearly insufficient to meet management objectives. The *3-year prescriptive strategy* required 26 baitings of 1080 over 20 years and resulted in positive kiwi population growth in all management zones, but lower than that of the reactive strategy [see Table].

The forecast model provides an objective means to compare alternative broad-scale predator management strategies. The results of the modelling indicate that the best outcomes for kiwi result from a nimble management strategy that is reactive to annual stochasticity in masting and rat population density. The finding that kiwi population declines can be reversed with intensive management, but that growth rates are unlikely to meet the 2% SOIK goal, demonstrates that modelling can provide policy makers, management and the public with evidence-based expectations for favourable biodiversity outcomes as a result of predator management.

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Wielding power for pest control

Consider this scenario: introduced predators, like ship rats, are responsible for dwindling numbers of North Island robins at Hamburger Hill Scenic Reserve. An aerial poison operation reduces rat numbers by an estimated 95%, and managers want to determine the response of the robin population to reduced predation. There is optimism that robin survival will have increased by 40%, but hopefully by at least 20%. Data are collected and statistical analyses are carried out. The results are disappointing because there is no statistical support for increased survival. However, is there a chance that survival did increase by 40% or 20% due to rat control, but the researchers simply had insufficient 'statistical power' to detect it?

Statistical power is the ability to detect a significant difference or effect when one is present. For example, if robin survival had actually increased by 40%, could this increase be detected with the sampling design used? Power analysis has been advocated for many decades to improve research designs and aid the interpretation of statistical results, yet it remains unfamiliar or misapplied. Doing an *a priori* power analysis [i.e. before a study begins] helps researchers estimate the number of samples necessary to detect a biologically significant effect if one has occurred.

Statistical power depends on three inter-related components: [1] sample size, [2] α , which is the significance level, and [3] effect size. Increasing any one of these always increases

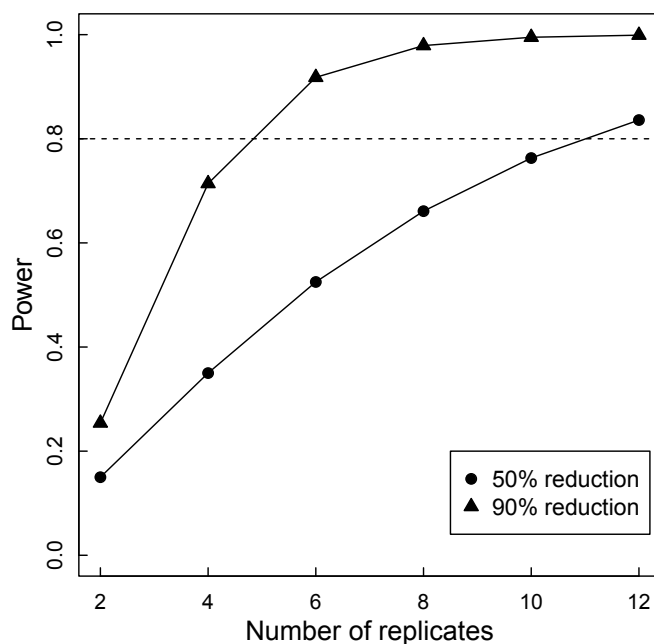


Figure 1. A power analysis aimed at detecting 50% and 90% decreases in the relative abundance of rabbits after poison control operations, obtained using camera traps in Otago. The dashed horizontal line is the recommended power level of 80%.

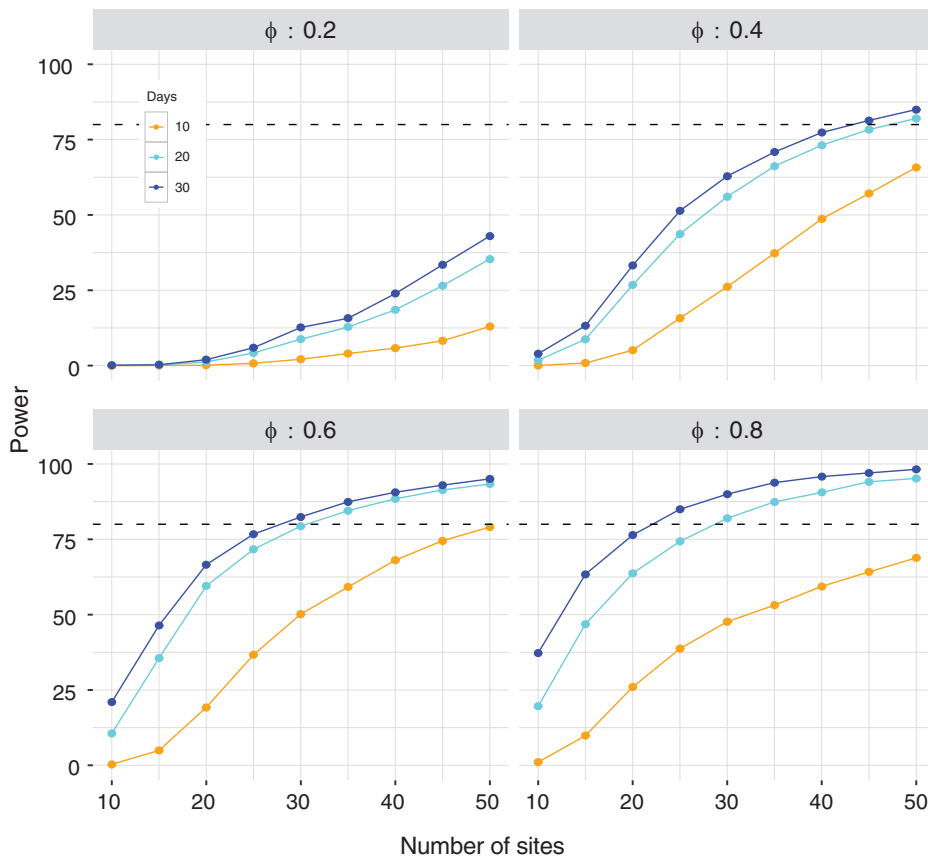


Figure 2. Estimated statistical power to detect a 90% reduction in the probability of occurrence of stoats after control in Taranaki Mounga. Simulations included variation in number of cameras, number of days of sampling, and pre-control probability of occurrence of stoats (ϕ). The dashed horizontal line is the recommended power level of 80%.

power, but α is generally set at 0.05 in order to reduce the chance of a type I error [which is rejecting a null hypothesis that is true]. The least understood of these components, effect size, is critical for calculating power. For the robin example, the effect sizes are 40% and 20%, and an increase in robin survival of 40% would be easier to detect than an increase of only 20%. Prior to monitoring survival, a power analysis should have been done to determine the minimum number of samples needed to reliably (i.e. with high power) detect an increase of 20% or 40% survival.

The data necessary to conduct a power analysis can be obtained from previous research, from a pilot study, or from a range of biologically probable values. Such an analysis ensures resources are not wasted by carrying out studies that are too small to reliably answer managers' questions. Here Cecilia Latham and Dave Latham use three local case studies to illustrate how statistical power analysis can be used to guide robust research and management.

Rabbits are a long-standing pest of dryland pastures in New Zealand. A key method for controlling them is through aerially applied 1080 poison, and it is generally assumed that 1080 operations reduce rabbit numbers by 95% or more. While quantitative data have shown that this is achievable, the outcome of an operation is often based on a more qualitative assessment. Dave Latham, Graham Nugent and Bruce Warburton examined the efficacy of rabbit control by

conducting a power analysis using data from a pilot study that assessed the accuracy of three methods (spotlight transects, vantage-point counts and camera traps) for monitoring rabbit relative abundance. Their key findings were that with moderate sampling intensity (either four 800 m spotlight transects, four vantage points, or six camera traps), all methods had good statistical power (83–95%) to detect large reductions in rabbit numbers (95%). There was, however, reduced power to detect smaller reductions (e.g. 50%); for camera traps, at least 12 units would be needed to reliably detect such an effect size (Figure 1).

Programmes to control mammalian predators across an increasingly large part of New Zealand are becoming a management reality as more regional authorities commit to the Predator Free 2050 initiative. As in the rabbit example, data from control programmes should instil confidence that pest numbers have been meaningfully reduced following intervention. Predators generally occur at much lower densities than rabbits, and so they require a higher sampling intensity to have sufficient power to detect a similar level of reduction. Al Glen and Cecilia Latham assessed the sampling effort needed to detect a 90% reduction in the post-control probability of occurrence of stoats for the Taranaki Mounga Project. The results indicated that a minimum of 45 camera traps deployed for at least 20 days would provide sufficient statistical power ($\geq 80\%$) to detect such reduction (Figure 2), but only if stoats initially occurred at 40% or more ($\phi \geq$

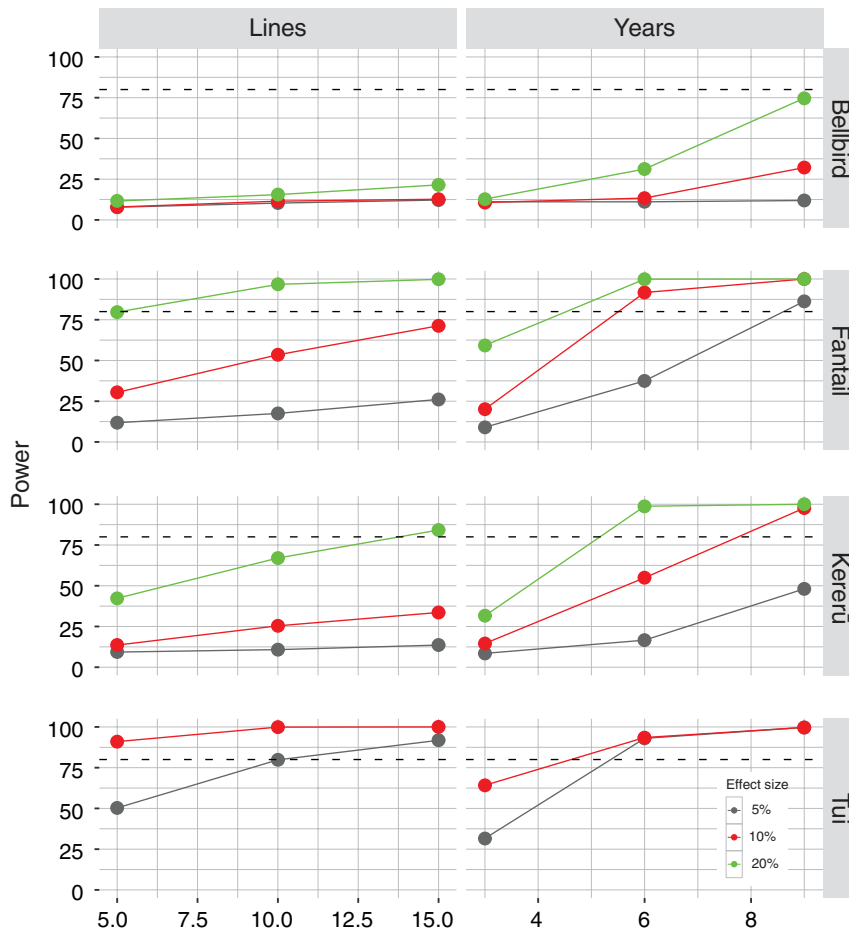


Figure 3. Power (with 95% confidence interval) to detect increases in the probability of occurrence of four bird species. Power was estimated by simulating changes in the number of lines or years surveyed. The dashed horizontal line is the recommended power level of 80%.



0.4) of the locations. However, if stoats were more sparsely distributed before control ($\phi < 0.4$), statistical power would be correspondingly low, regardless of the sampling effort.

Being able to confidently detect positive changes in biodiversity assets resulting from predator control is paramount to demonstrating that money has been well spent and that pest animals were not killed unnecessarily. When monitoring biodiversity assets, however, managers aim to detect effect sizes that are typically much lower (c. 10–20%) than those expected for control operations. Accordingly, sample effort needs to be larger, and this can be achieved by either increasing the number of sample sites and/or the duration of monitoring.

Cecilia Latham assessed these trade-offs by conducting a power analysis using 5-minute bird count data collected by Taranaki Regional Council around New Plymouth. The aim was to identify monitoring designs for the rural landscape between Mt Taranaki and the coast that would confidently detect annual increases of 5%, 10% or 20% in the probability of occurrence of native forest birds. The results indicated that for species like fantail and tūi, even the smallest effect size [5%] could be confidently detected after monitoring for a minimum of 9

years, whereas power to detect this effect size remained low for kererū (Figure 3). After 9 years, statistical power remained low for bellbirds irrespective of effect size. The number of years birds were monitored had a greater effect on statistical power than did the number of lines monitored (Figure 3).

Finding that some perturbation (such as predator removal) has had a statistically significant effect on the abundance or survival of their prey is not that informative: it is the magnitude of the effect caused by the removal and whether this is biologically significant that is important for wildlife management, conservation and adaptive management. An *a priori* power analysis is an important tool in this regard. It can inform the level of sampling intensity needed to detect a biologically meaningful effect, such as a sufficiently high level of robin survival to halt or reverse population decline. Cecilia and Dave recommend that statistical power analyses be done routinely to guide research planning.

This work was funded by Sustainable Farming Fund (Ministry of Primary Industries) and Taranaki Regional Council.

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Dave Latham

Using surveillance models to provide confidence in the eradication of Argentine ants



Surveys undertaken near the end of an eradication programme will often not find any target pests and the search results will consist of many zeros. But how do we know those zeros are real and there really are no pests left? Maybe some individuals have survived control but haven't been detected because they are so rare, and/or the search effort was insufficient to find them.

Some eradication programmes declare 'success' after a certain time interval during which the pest has not been found (e.g. 2 years). However, relying on a certain period is not useful unless the surveillance effort required to find a pest when at low density is specified. It is easy to find nothing when only a few surveys are undertaken, or when only part of the area is searched.

To answer the 'Are they true zeros?' question, surveillance sensitivity must be quantified in terms of the probability of detecting an organism if present. With this information managers can estimate the probability that eradication has been achieved and thus avoid prematurely declaring

success due to insufficient survey effort, or, conversely, avoid wasting resources on surveys when the pest has already been eradicated.

Darren Ward, Mandy Barron and Dean Anderson applied these concepts to the eradication programme for Argentine ants, *Linepithema humile*, on Kawau Island. Ants are recognised globally as significant exotic invaders. However, until recently relatively little had been published on the detectability of invasive ants, despite them being prone to poor detection because of their small size, variable foraging habits, cryptic nature, and strong association with human transportation. One species, the Argentine ant, is highly invasive and has been accidentally introduced by human trade to many countries throughout the world. They have invaded numerous open-canopy habitats, including coastal sage scrub and riparian woodland in California, matorral in Chile, fynbos in South Africa, subalpine shrubland in Hawaii, and oak and pine woodland in Portugal. Argentine ants are well established in northern New Zealand and are found in many types of open-canopy habitats, especially coastal ones, and increasingly on off-shore islands.

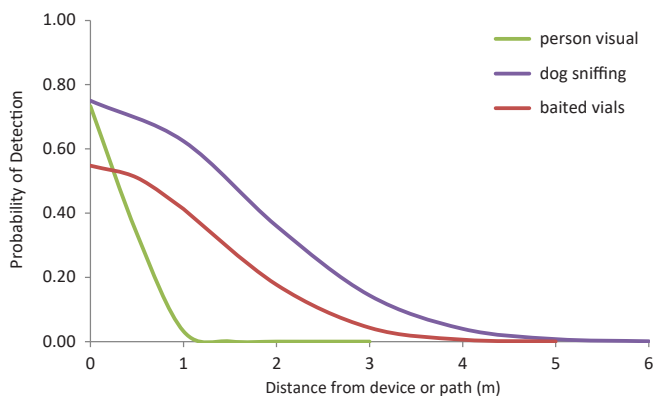


Figure 1. Half-normal function describing the probability of detecting an Argentine ant or nest with distance from a device (baited vials) or from a point along a path (visual search, sniffer dog).

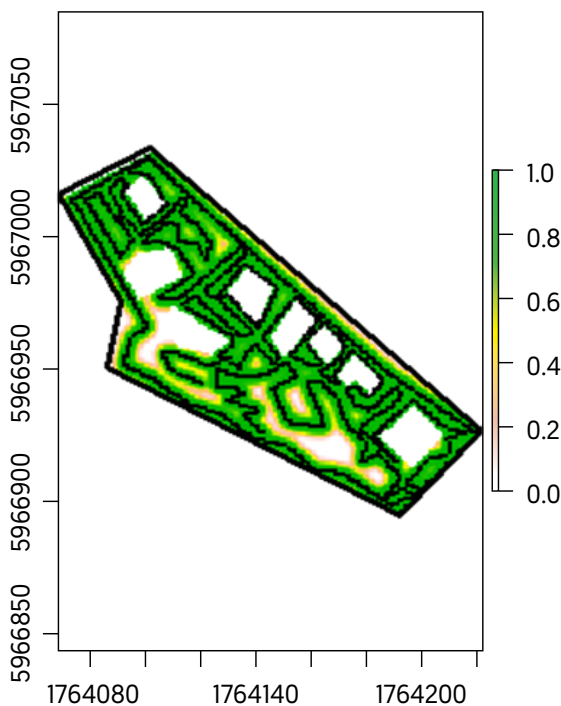


Figure 2. Combined system sensitivities for the detection of Argentine ants across the Schoolhouse Bay study area. Probability of detection ranges from high (green) to low (yellow) and zero (white). The large polygonal white areas are houses, which were excluded from analyses.

Darren and his colleagues used the spatially explicit surveillance data model developed by Dean and other colleagues to estimate the probability that Argentine ants had been eradicated from the Schoolhouse Bay area on Kawau Island in the Hauraki Gulf. This model quantifies the sensitivity of each search method using a maximum probability of detection parameter (assumed to be when the target pest is directly on the search path or at the detection device) and a spatial decay parameter describing the decline in detection probability with increasing distance from the device or searcher.

All search paths or device locations are used to calculate a combined probability of detection for that survey (i.e. the surveillance sensitivity) and a map of the surveillance coverage is produced. Each time a survey is done the surveillance sensitivity estimate is used to update the probability of ant eradication derived from the previous survey. For the very first survey a 'prior' probability of the ants being eradicated is derived from expert opinion or is left deliberately vague (e.g. 'likely to be somewhere between 20% and 80%').

For the Kawau Island ant eradication project there were four surveys following the spring 2012 poisoning of ants in the 3 ha of infested area at Schoolhouse Bay. Three surveillance methods were used for these surveys: visual searching, vials baited with non-toxic Inform bait, and a sniffer dog trained by Auckland Council. Several 'paths' were used to cover the entire Schoolhouse Bay area. These paths were documented with a GPS and used for all three surveillance methods. The spatial sensitivity parameters used are shown in Figure 1, with a sniffer dog having a greater search range than a human visually searching. A map of surveillance sensitivity for the combined methods of human searching, baited vials, and sniffer dogs is shown in Figure 2.

No Argentine ants have been detected at Schoolhouse Bay since the control operation in 2012. The estimated probability of eradication (POE) increased sharply as each survey was conducted. Analysis of the four post-control surveys estimated a median probability of eradication of 96% with a high level of confidence in the POE result. Sniffer dogs gave the highest probability of detection per path searched, and so the predicted number of surveys to reach a threshold POE of 95% was less using this survey method than with the other two methods.

Combined modelling of all surveys and sampling devices indicates there are several small spatial gaps that have received less survey effort. Such gaps might be a refuge for a small Argentine ant population. These gaps are generally on the north-facing slope behind the local residences and will be targeted for surveillance in future monitoring. Such spatially explicit models are vital to give confidence in eradication programmes, especially from highly valued conservation areas such as offshore islands.

This work was supported by the Auckland Council, the Northland Regional Council, and the Ministry of Business, Innovation Employment through funding of the Managing Invasives Portfolio at Manaaki Whenua – Landcare Research.

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How do behavioural differences in pests affect their trapability and eradication success?

New Zealand has a history of successful small mammal eradications from offshore islands. On the mainland, advances in pest-proof fencing technologies have made it possible to eradicate pests over relatively small areas and to protect against reinvasion. Since the announcement of the Predator Free 2050 goal in 2016 there has been increased interest in the development of new tools and strategies to improve the efficiency, effectiveness and scale of pest eradication operations.

Pest managers benefit from models that can make accurate predictions about the size and/or spread of a pest population over time or the outcomes of different management scenarios. For example, models that predict the number of trap nights required for successful eradication under a particular trapping regime can help managers choose an optimal trapping strategy. Such models usually take into account an animal's movements and use of space, reproduction rate and immigration patterns. What is seldom considered, however, is the possibility that different individuals within a population could exhibit consistent differences in their behaviour. Such differences could have considerable effect on the dynamics of a pest population, and on the effort required for its eradication.

It has been well reported, for example, that animals show varying degrees of boldness when confronted with new objects in their environment. While some animals are quick to approach and interact with unfamiliar objects (e.g. traps or toxic baits), others are more cautious, and a few are highly risk averse. These behavioural differences are a key challenge faced by managers attempting to eradicate – as opposed to suppress – pest populations down to the last individual. Current standard trapping methods often fail when a number of very 'shy' individuals are present in the target population because these individuals are unlikely to approach such control devices.

To study this problem and measure the effect of these behavioural differences on control programmes, Giorgia Vattiato, Rachelle Binny, Michael Plank and Alex James have built a model to simulate the evolution of a theoretical population of small mammal pests during a trapping regime. They compared predictions for both a homogeneous population (in which all individuals behave the same [i.e. have the same level of 'trap shyness']) and a heterogeneous population (in which individuals have different levels of trap shyness) to assess the extent to which behavioural variation

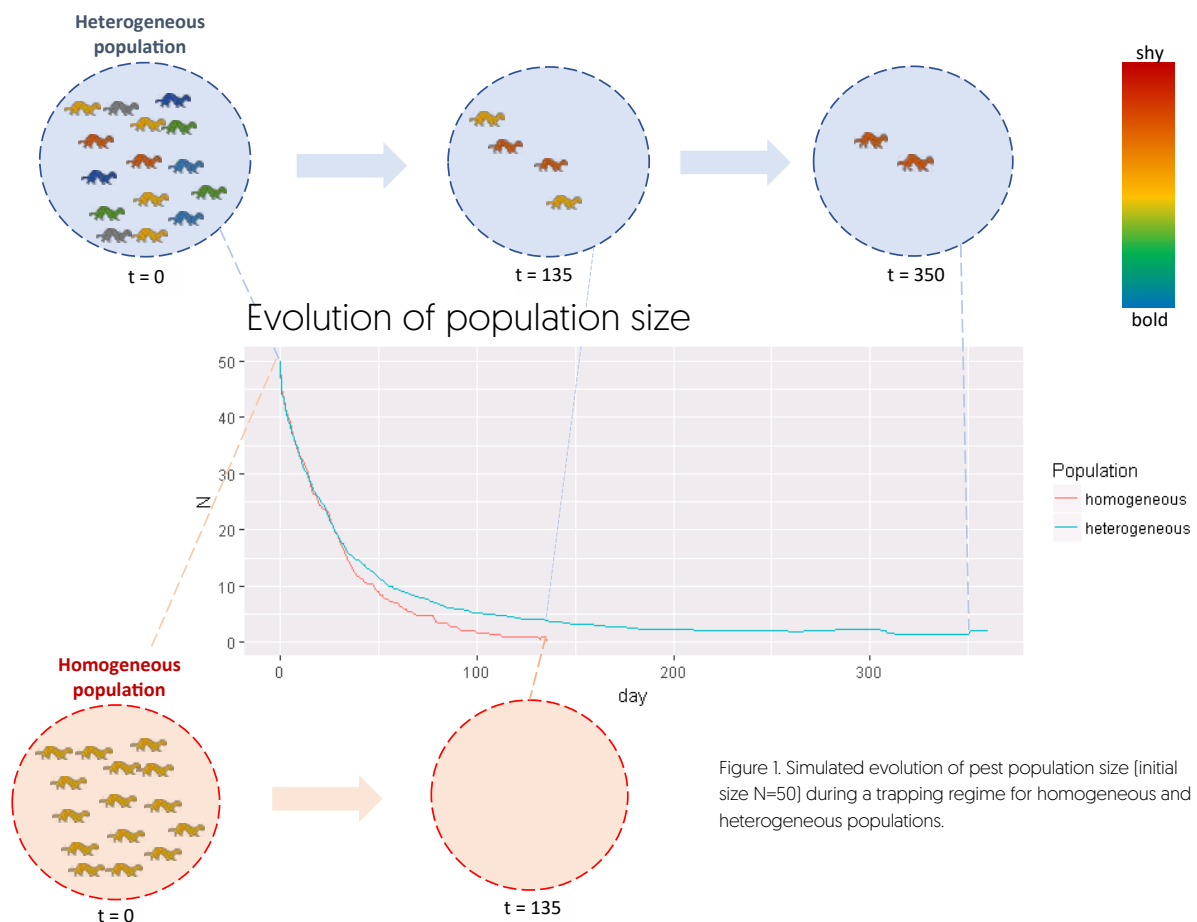


Figure 1. Simulated evolution of pest population size (initial size N=50) during a trapping regime for homogeneous and heterogeneous populations.

Eradication probability

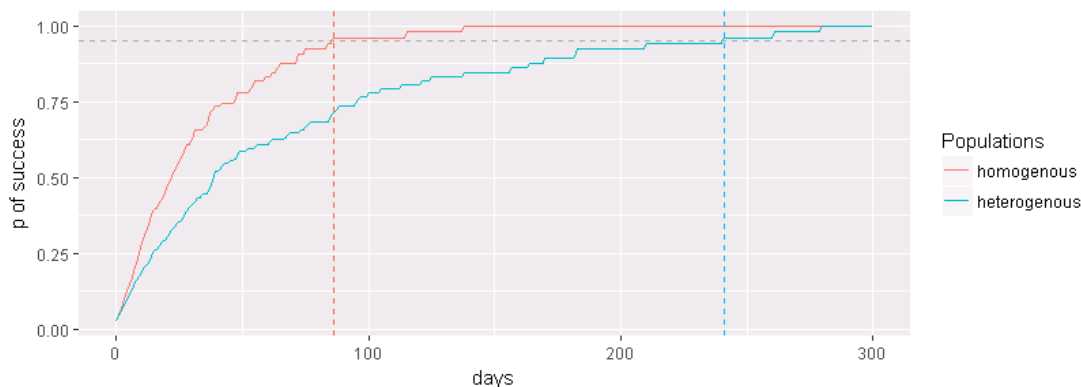


Figure 2. Simulated probability of eradication over the number of “quiet nights” since the last pest detection for homogeneous and heterogeneous population. The vertical dotted lines show the time when 95% probability of success is obtained.

matters. Their first simulation results (Figure 1) showed that, as expected, heterogeneous populations (blue line) take much longer to eradicate than homogeneous populations (red line) (more than 350 days versus 135 days, respectively) due to the presence of a few elusive individuals that are extremely difficult to capture.

Another challenge faced by pest managers is how to decide when during an eradication process one can be confident that the target population has been eliminated. Usually this decision is based on the number of ‘quiet nights’ (the time elapsed since a pest was last captured or detected). Giorgia and colleagues used their model to make predictions of this value, once again comparing results for homogeneous and heterogeneous populations (Figure 2). Again, there is a considerable difference between predictions for the two simulated population types, highlighting the importance of taking such behavioural variation into account in models for pest management. For example, in the overly simplistic model where it was assumed all animals were equally likely to interact with a trap (a homogeneous population), after about 80 quiet nights the probability of having successfully eradicated the population was 0.95. In contrast, for a heterogeneous population (with some trap-shy individuals) nearly 250 quiet nights would be needed to achieve the same probability of success.

So, how can these types of models be used to help design more efficient eradication procedures? So far the model has been used to simulate a theoretical pest population, using ecologically relevant but arbitrary parameters (e.g. the rate at which an animal moves through its home range). The next step is to calibrate the model for a particular pest species and landscape using data from a real pest population. The calibrated model could then become a useful tool to help design an effective eradication programme and to predict the time and probability of success for operations.

Even highly trap-shy individuals can be captured using more intensive trapping and baiting procedures or specially designed control devices. However, these methods are typically more expensive and/or labour-intensive and too costly for long-term use. The key to a successful and cheaper eradication programme could therefore lie in choosing the optimal time to switch from a standard control approach, which successfully kills the majority of a population, to a more intensive approach targeting any remaining individuals. The model could help managers identify this switch-point.

For example, as shown in Figure 1, the evolution of population size for the heterogeneous population shows a considerable deceleration after approximately 50 days, which indicates that most of the pests have been captured and that a change to a more intensive control method is necessary to eradicate the remaining, very trap-shy individuals. The approach outlined in Figure 2 could then be used to estimate the number of quiet nights needed for a high probability of eradication success.

The next steps in this work are to improve the model by adding more detailed landscape parameters (e.g. different terrains and vegetation types) to better simulate animals’ movements within their home ranges. Giorgia and her colleagues will also explore the idea of knowledge transmission among individuals of a population and through generations, to investigate the impact that learned behaviours might have on a population control programme.

This work is funded by Te Pūnaha Matatini, the CoRE for complex systems and networks.

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TrapSim: an online tool to help managers decide on a trapping regime

When faced with the task of managing predators at a landscape scale, there are a number of decisions land manager(s) must make. These include how many traps should be used, how far apart traps should be set, how often traps should be checked, and are traps needed that can catch/kill more than one animal before being reset? Deploying too few traps and/or not checking them frequently enough will defeat the aims of a control programme. In contrast, deploying too many traps and/or checking them too often will result in a high level of redundancy, ultimately wasting valuable funding. There is no 'one-size-fits-all' trapping regime: the optimal regime will differ in each case, and will depend on the goals of the programme as well as a number of species-specific factors. However, modelling can provide guidance for most control regimes.

How many to kill?

The goals of a predator-trapping programme are generally either eradication [which requires removing all individuals from a population and then defending the area from future incursions] or suppression [achieving and maintaining a population at a level that allows for biodiversity benefits]. For eradication, the rate of removal must exceed the rate of population growth of the target species in order for the population to eventually go to zero, whereas for suppression the rate of removal must at least match the rate of population growth in order to prevent an increase. In either case, it is important to have some knowledge about the population's growth rate.

Population growth rates depend on rates of survival, reproduction, immigration and emigration. For many species, maximum rates of increase have been estimated from previous studies, and these can be used to determine the approximate percentage of the population required to be controlled to achieve management goals. Populations with a

high rate of increase require a high proportion of the population to be killed and/or control to be carried out more frequently compared with that of a slow-growing population (Figure 1).

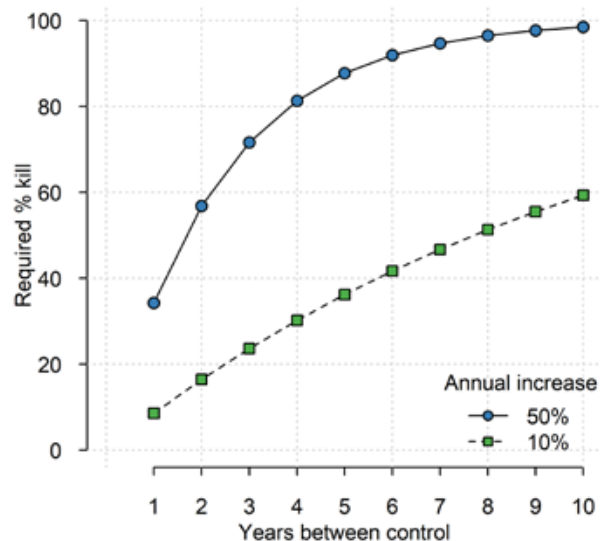


Figure 1. Relationship between the control frequency (years between control) and the required %kill to maintain a stable population under two levels of population increase.

What trapping regime?

Knowing the required level of control is a start, but the question of what trapping regime is needed to achieve that goal remains. The answer relies on a number of factors, including the size of individual animal home ranges, the probability of capture, population densities, and rates of by-catch of non-target species. If eradication is the goal, all individuals in a population must be at risk of being trapped, and so knowledge about likely home range sizes is important.

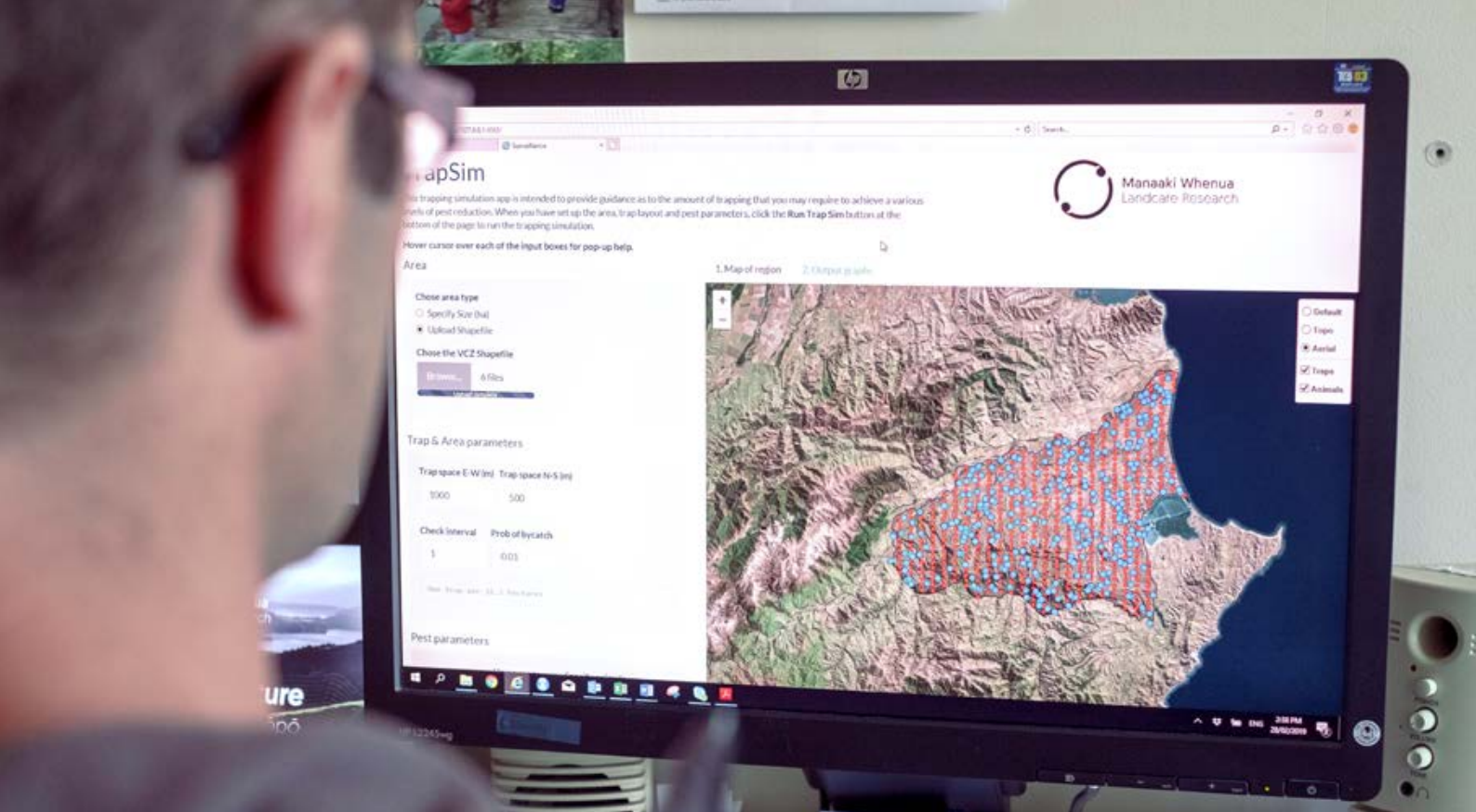


Figure 2. TrapSim showing the modelled outcomes from one simulated scenario.

For example, mustelids [ferrets and stoats] have home ranges of about 300 ha, whereas rats have home ranges of only about 3 ha. For mustelids, traps could be spaced 400 m apart and still theoretically achieve eradication, but for rats this spacing would mean that large groups of individuals would never encounter a trap. Where suppression is the goal some level of survivorship is acceptable, but it is still desirable to have all animals at risk of capture.

Knowledge of the size of the target species population is important to help inform both the time interval between checking and resetting traps and the trap capacity. Checking traps too often (e.g. nightly) when populations are low is a waste of resources, as there are likely to be very few if any traps to clear of carcasses. In contrast, checking traps too infrequently may result in many traps having been long triggered by pests and no longer able to catch remaining animals. It is also not just the target population size that is important: non-target animals such as hedgehogs are often caught in traps intended for stoats and ferrets, thereby taking those traps out of action until they are cleared and reset.

In terms of trap capacity, single-capture traps can only kill one animal before being physically cleared and reset, and may not be effective when population numbers are high. Setting multiple traps at each location (or even traps that self-reset) may be advantageous in some situations with high target species densities and/or high levels of by-catch. However, the increased cost may not be justified, especially when the size of the targeted population is low.

Decision tools

Even with perfect knowledge of these interacting factors, the best trapping regime is not always obvious. So how can managers decide on a trapping regime that will

meet their aims? Andrew Gormley and Bruce Warburton previously worked with Hawke's Bay Regional Council to develop an interactive trapping simulation tool to examine the effectiveness of various trap regimes on the capture of ferrets, stoats and cats within the Cape to City wildlife diversity restoration programme. The success of this work, as well as the increasing requests for guidance on other landscape-scale trapping programmes (e.g. Taranaki Mounga), indicated the need for a user-friendly and freely available version of a trapping simulation tool that could be generalised for any area and/or species.

This led to the development of TrapSim, an online 'ready reckoner' (<https://landcare.shinyapps.io/TrapSim>) that gives managers the ability to estimate the efficacy of proposed trapping regimes [Figure 2]. The user specifies the density of the target species, as well as parameters related to its/their home range, trappability and population growth, and can then investigate various trapping regimes by altering the trap spacing, trapping interval and likely by-catch. TrapSim removes some of the guesswork by enabling managers to explore the potential effectiveness of various trapping networks, allowing them to make more informed decisions. TrapSim is in continual development, and the next stage will include features such as habitat-specific home ranges.

This work was funded by Hawkes Bay Regional Council and the Ministry of Business, Innovation Employment through funding of the Managing Invasives Portfolio at Manaaki Whenua – Landcare Research.

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Economic aspects of New Zealand's wild deer recovery industry

Red deer were introduced into New Zealand in the mid to late 1800s and are now almost ubiquitous across both the North and South Islands. The commercial recovery and export of venison from wild-caught deer began in about 1958, but the industry did not grow significantly until about 1963, when helicopters were first used to harvest deer carcasses from alpine grasslands.

The wild deer recovery industry was highly competitive, with the number of deer harvested per year peaking at about 133 000 in 1972, and then declining to about 45 000 in the early 1980s, when live capture began to meet the demand for deer to stock farms (Figure 1). This new demand resulted in the price for a live hind (NZ\$3,000 in 1979) far exceeding that of a deer carcass. As a result, helicopter hunting again became economic for two to three years, before the demand for live wild deer declined and the capture industry essentially ceased. The harvesting of deer carcasses continued at a lower level.

The impact of harvesting on deer density varied between habitats, with the greatest reductions occurring in alpine grasslands and the lowest reductions in low-elevation forests. In some areas deer populations were reduced by 90 to 95% (as measured by faecal pellet group densities).

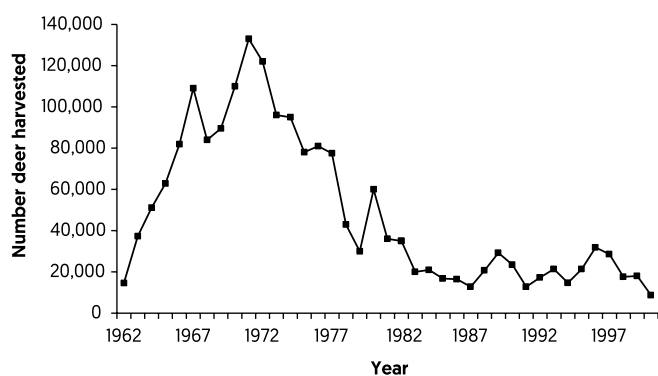


Figure 1. Annual harvest of wild deer, 1962–2000.

Between 2002 and 2004 the export market for wild-caught deer declined substantially, but then increased and stabilised at c. 16 000 annually. However, since 2002 most processed deer carcasses have come from deer farms (Table 1).

Since about 2004 the Ministry for Primary Industries has required all helicopter-based harvesters to use GPS to record their flight path and a waypoint for each deer shot. Because these data were readily available, Bruce Warburton, Dean Anderson, and Graham Nugent used them in a predator–prey functional response model to look at the deer densities required for helicopter operators to hunt profitably. The team

Table 1. Number of farmed and wild-caught deer carcasses processed, 2002–2015 [source:ASUREQuality – meat inspections]

Year	Farmed	Wild
2002	490 050	–0.01
2003	595 408	0.01
2004	722 595	–0.04
2005	814 446	–0.04
2006	774 081	–0.16
2007	627 031	20.00
2008	633 739	17 978
2009	484 801	21 444
2010	407 387	16 065
2011	436 832	17 894
2012	438 371	17 309
2013	457 372	16 628
2014	447 264	16 144
2015	421 108	16 842

obtained data from one helicopter operator flying an R44 helicopter at a cost of c. \$1,200 per hour for 10 hunts (Table 2), and used them to generate a type II functional response model, relating capture rate to detectable deer density:

$$F = \frac{aN}{1+ahN} \quad \text{where} \quad \text{eq 1}$$

F = per capita consumption rate (deer harvested per hour of helicopter time)

h = handling time (while gutting a carcass)

a = attack rate or rate of search (km²/h)

N = density of the prey (deer/km²).

To generate a value for attack rate, Bruce and his colleagues used the distance travelled per hour and an average search swathe width of 200 m (i.e. 100 m on each side of the helicopter). Because the team had no measure of detection probability, the density derived from equation 1 is the density of detectable deer, not the actual density. Based on the carcass price paid (averaged over 2005 to 2015; i.e. \$220), a helicopter hunt needed to harvest five or six deer per hour to be economically viable. Of the 10 hunts for which data were available, only two had fewer kills per hour than this (Table 2).

A functional response relationship between actual population density and hourly harvest rate (Figure 2) was established using historical faecal pellet count data, defecation rates, and harvest rates. It was found a harvest rate of 5.5 deer per hour (required for economic harvesting) was achievable in alpine habitats when deer densities are ≥4 per square kilometre (Figure 2).

Table 2. Parameters from GPS track logs and waypoints of deer killed from 10 hunts.

Hunt	Total time	Handling time [h]	Search time	Deer harvested	Consumption rate [F]	Avg hunting speed [km/h]	Attack rate [a]
1	4.85	1.80	3.05	40.00	8.70	54.40	10.90
2	6.70	3.20	3.50	73.00	10.90	40.10	8.00
3	6.50	2.00	4.50	70.00	10.80	53.50	10.70
4	5.10	1.50	3.60	68.00	13.30	77.10	15.40
5	6.95	2.38	4.57	40.00	5.70	57.30	11.50
6	5.30	1.40	3.90	14.00	2.60	87.30	17.50
7	3.90	0.50	3.40	19.00	4.80	101.60	20.30
8	2.42	1.00	1.42	29.00	11.90	45.50	9.10
9	2.75	0.63	2.12	25.00	9.10	58.60	11.70
10	2.50	0.83	1.67	25.00	10.00	70.80	14.20

The commercial red deer harvest industry has remained remarkably resilient in New Zealand. However, the demand for wild deer is largely influenced by the ability of farmed deer to supply the venison market. Because of a current shortage of farmed deer, the demand for wild deer has increased over the past 12 months.

The functional response modelling carried out for this analysis contained a number of assumptions:

- the attack rate was based on an assumed search swathe width of 200 m
- deer density was estimated using historical data on faecal pellet group density and harvest rates
- deer detectability was derived from the detectable density (not the actual density)
- helicopter operators need to fully recover their costs in every hunt.

The reliance on these (untested) assumptions highlights the need for their direct measurement to make the analysis more robust. For the last assumption, few, if any, helicopter operators are now solely reliant on wild deer recovery, and most are sustained by tourism and other commercial operations. As a result, operators can afford to harvest deer below its marginal cost, as long as their overall business is viable.

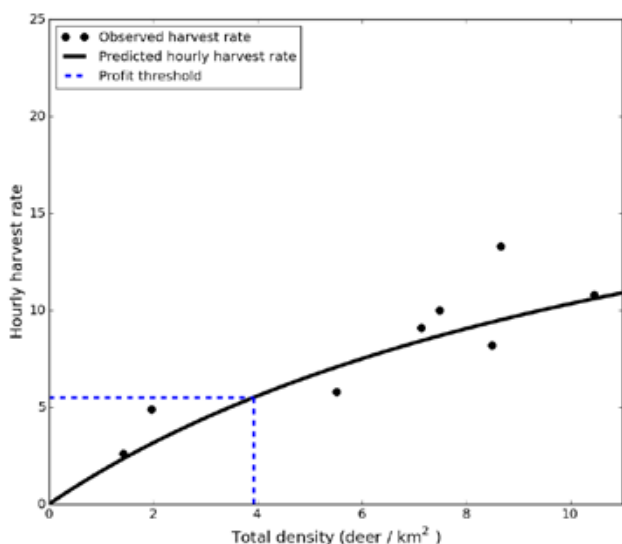


Figure 2. Relationship between hourly harvest rate and estimates of deer density. The dashed line shows the number of deer required per hour to provide an economic return (using an R44 helicopter) and the deer density needed to achieve that.



Recovering red deer carcasses in the Canterbury high country.

Most of the demand for venison can now be met from farmed deer, and demand for wild-caught deer is unlikely ever again to reach the levels seen in the 1970s and 1980s. Consequently, deer densities are likely to continue to increase in New Zealand, especially within forests. Where high deer densities occur in high conservation value sites, there may be an increasing need for some form of official agency-directed control. Conversely, in less sensitive areas there may be an opportunity to determine a sustainable yield for both commercial and recreational hunters. To ensure official control is optimised, the relationships between deer density and helicopter encounter and kill rates needs to be better understood.

The authors acknowledge the historical data collected and published by Chris Challies.

This work was funded by the Ministry of Business, Innovation and Employment.

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Dean Anderson

Graham Nugent

This study was fully reported elsewhere: see 'Some recent relevant publications'

Some recent relevant publications

Forsyth DM, Caley P, Davis NE, Latham ADM, Woolnough AP, Woodford LP, Stamation KA, Moloney PD, Pascoe C

2018. Functional responses of an apex predator and a mesopredator to an invading ungulate: Dingoes, red foxes and sambar deer in south-east Australia. *Austral Ecology* 43(4): 375–384. doi: 10.1111/aec.12575

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