See discussions, stats, and author profiles for this publication at: https://www.researchgate.net/publication/288933370

Prioritizing eradication actions on islands: it's not all or nothing

Article *in* Journal of Applied Ecology · June 2016 DOI: 10.1111/1365-2664.12599

CITATIONS		READS					
35		483					
7 authors, including:							
Ø	Kate Helmstedt		Justine D. Shaw				
	Queensland University of Technology		The University of Queensland				
	33 PUBLICATIONS 365 CITATIONS	-	65 PUBLICATIONS 3,409 CITATIONS				
	SEE PROFILE		SEE PROFILE				
	Michael Bode		Aleks Terauds				
	University of Melbourne		Australian Antarctic Division				
	169 PUBLICATIONS 5,638 CITATIONS		85 PUBLICATIONS 2,486 CITATIONS				
	SEE PROFILE		SEE PROFILE				
Some of the authors of this publication are also working on these related projects:							

a Invertebrate monitoring on sub-Antarctic Islands following invasive mammal eradications View project

Collaboration for Environmental Evidence (CEE) View project



Prioritizing eradication actions on islands: it's not all or nothing

Kate J. Helmstedt^{1,2*†}, Justine D. Shaw^{3,2}, Michael Bode^{4,5}, Aleks Terauds³, Keith Springer⁶, Susan A. Robinson⁷ and Hugh P. Possingham^{2,8}

¹School of Mathematics and Physics, University of Queensland, St Lucia Qld 4072, Australia; ²ARC Centre of Excellence for Environmental Decisions, School of Biological Sciences, University of Queensland, St Lucia Qld 4072, Australia; ³Antarctic Conservation and Management, Department of the Environment, Australian Antarctic Division, Kingston Tas. 7050, Australia; ⁴School of Botany, University of Melbourne, Parkville Vic. 3010, Australia; ⁵ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville Qld 4812, Australia; ⁶Tasmania Parks and Wildlife Service, PO Box 126, Moonah Tas. 7009, Australia; ⁷Invasive Species Branch, Department of Primary Industries, Parks, Water and Environment, Biosecurity Tasmania, Newtown Tas. 7008, Australia; and ⁸Department of Life Sciences, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY, UK

Summary

1. Many highly diverse island ecosystems across the globe are threatened by invasive species. Eradications of invasive mammals from islands are being attempted with increasing frequency, with success aided by geographical isolation and increasing knowledge of eradication techniques. There have been many attempts to prioritize islands for invasive species eradication; however, these coarse methods all assume managers are unrealistically limited to a single action on each island: either eradicate all invasive mammals, or do nothing.

2. We define a prioritization method that broadens the suite of actions considered, more accurately representing the complex decisions facing managers. We allow the opportunity to only eradicate a subset of invasive mammals from each island, intentionally leaving some invasive mammals on islands. We consider elements often omitted in previous prioritization methods, including feasibility, cost and complex ecological responses (i.e. trophic cascades).

3. Using a case study of Australian islands, we show that for a fixed budget, this method can provide a higher conservation benefit across the whole group of islands. Our prioritization method outperforms simpler methods for almost 80% of the budgets considered.

4. On average, by relaxing the restrictive assumption that an eradication attempt must be made for all invasives on an island, ecological benefit can be improved by 27%.

5. *Synthesis and applications.* Substantially higher ecological benefits for threatened species can be achieved for no extra cost if conservation planners relax the assumption that eradication projects must target all invasives on an island. It is more efficient to prioritize portfolios of eradication actions rather than islands.

Key-words: decision theory, eradication, feral cats, integer programming, invasive species, island conservation, optimization, resource allocation, threatened species, trophic cascade

Introduction

Eradicating invasive species from uninhabited islands offers substantial benefits to conservation. Island species have unique, divergent evolutionary histories, and as a result, islands hold a disproportionate percentage by area of global biodiversity (Kier *et al.* 2009). Unfortunately, the same unique factors that lead to high biodiversity – small size and isolation – have meant that a higher proportion of extinctions have occurred on islands, primarily due to invasive vertebrates (Simberloff 1995; Courchamp, Chapuis & Pascal 2003). Threats to these ecosystems and their biodiversity from predation, competition and habitat destruction by invasive species remain high (Kier *et al.* 2009; Medina *et al.* 2011; Spatz *et al.* 2014), motivating invasive species eradication projects. Eradication efforts have focused largely on islands because of their high bio-

^{*}Correspondence author. E-mail: katehelmstedt@berkeley.edu [†]Present address: Department of Environmental Science, Policy and Management, University of California Berkeley, Berkeley, CA 94720, USA

diversity and vulnerability. In addition, islands do not suffer from the high likelihood of reinvasion that large, connected continental sites experience, greatly increasing the likelihood of a successful and enduring eradication.

The success of island eradication projects is not guaranteed (Gregory et al. 2014), and any conservation efforts on islands can be unusually expensive given their restricted access and limited infrastructure (Martins et al. 2006; Donlan & Wilcox 2007). Therefore, it is imperative that limited funds are appropriately allocated to maximize the expected conservation outcomes while considering the likelihood of success. Numerous studies have proposed methods (of varying complexity) for prioritizing eradications of invasive species from suites of islands. All previous prioritization exercises make the same critical assumption that only a single, all-or-nothing option is available to managers on each island. They constrain their recommendations to a single choice, similar to reserve selection in conservation planning, where an island is either selected for invasive species eradication or it is not (Possingham, Ball & Andelman 2000). Many assume that managers will always eradicate all invasive vertebrates from islands (e.g. Brooke, Hilton & Martins 2007; Hilton & Cuthbert 2010; Donlan, Luque & Wilcox 2015), foregoing the opportunity to eradicate only invasive species that give the highest benefit for the money spent (Game, Kareiva & Possingham 2013). Other studies only consider eradication of a single invasive species across many islands (e.g. Nogales et al. 2004; Ratcliffe et al. 2009; Capizzi, Baccetti & Sposimo 2010; Harris et al. 2012), making inherent assumptions about which invasive species has the greatest impact on each island. As we will show, considering more than one action on each island can substantially increase potential ecological benefits.

The cost and feasibility of invasive species eradications have frequently been omitted when prioritizing eradication programmes across multiple islands. The decision not to include or consider the cost of candidate projects forces the implicit assumption that either all projects have equal cost, or that budgets are unlimited (Nogales et al. 2004; Donlan & Wilcox 2007; Ratcliffe et al. 2009; Harris et al. 2012; Dawson et al. 2015). This is a risky assumption in any conservation planning project, but particularly when considering conservation on islands where costs can be extremely high. Omitting cost ignores opportunities to rapidly and relatively cheaply eradicate invasive mammals from numerous small and logistically simple islands. When feasibility (the probability of successful eradication) is included in existing prioritization schemes, a false dichotomy is often created by considering only binary success depending on island attributes: below a certain threshold, success is guaranteed, and above the threshold, success is impossible (e.g. Harris et al. 2012; Donlan, Luque & Wilcox 2015; Dawson et al. 2015). While this approach will bias priority setting away from islands where eradication is very difficult, it is overly simplistic (in fact many failed eradications are on small, inshore

islands, see Gregory *et al.* 2014) and misses an opportunity to choose islands that are difficult but very rewarding for conservation. The ability to balance risk and benefit is an essential element of rational asset management and cannot be achieved simply by ignoring high-risk options (Joseph, Maloney & Possingham 2009; Game, Kareiva & Possingham 2013).

We extend the island prioritization problem to include a more realistic suite of options on each island, as well as the costs and feasibilities of each option. This extends the existing invasive species eradication literature in two ways: first, we consider partial successes of eradication (acknowledging that if multiple invasives are targeted for eradication on the same island, it is possible that some will succeed while others fail). Second, on each island we consider the option to target any combination of invasive species while intentionally leaving others. We will show that this increased complexity has measurable benefits and delivers higher conservation outcomes for limited budgets than more simplistic prioritization schemes. Our method reveals several efficiencies that cannot be obtained by using the existing suite of optimization methods. Rather than focusing on islands as management units, our method targets different subsets of invasive species on islands. The method allows for complex ecological processes (i.e. trophic cascades) such as competitive release, mesopredator release, prey switching and invasional meltdown to be considered and accounted for. Prioritizing portfolios of eradication actions better reflects the variety of options available to managers and considers the range of ecological processes that can result from perturbing an insular system. This prioritization method would be useful for decision-making agencies deciding how limited funds should be allocated between defined projects, for example allocating funds within a region (Dawson et al. 2015).

We illustrate our framework using case studies of 23 distinct portfolios of actions on four uninhabited Australian islands that have all recently undergone successful vertebrate eradications: Macquarie, Tasman, Faure and Hermite islands. We then generalize the results of our case study by applying the method to a large number of randomly generated island data sets. We demonstrate that allowing managers to choose from among multiple portfolios of actions on each island provides a substantially higher conservation benefit compared to alternative, less flexible prioritization methods.

Materials and methods

We aim to achieve the greatest conservation benefit to a group of islands by determining which groups of invasive species (if any) should be eradicated from each island for a fixed budget to benefit species of conservation concern. When considering more than one action on an island (e.g. baiting for rats and shooting goats), the actions are grouped into 'action portfolios'. An action portfolio represents more than just the sum of its parts; it includes cost, feasibility and outcomes of the contributing actions. This approach creates potential efficiency gains both economically (e.g. if logistic costs such as transport are shared) and through increased probability of successful eradication (where interactions between pest species are strong).

Despite management intentions, an island may transition into an undesirable state following an eradication attempt. This removal of part of an ecological network can result in complex and detrimental ecosystem processes, potentially affecting all species of concern (Courchamp, Chapuis & Pascal 2003). Even when attempting to eradicate all invasive species present, eradication of each species has the potential to fail. This may be due to technical/logistic failures (e.g. bad weather, inadequate bait coverage) or the demographic stochasticity of eradication. Any invasives remaining from the eradication attempt will reduce the realized conservation benefit of the project. Therefore, when attempting to eradicate any group of invasive species on an island, all possible combinations of potential successes and failures need to be considered as potential future states. The probability of an island transitioning into a new invasive species state after a specific action is mathematically defined in Appendices S1 and S2 in Supporting Information.

OBJECTIVE

With unlimited funds, an optimal eradication plan would typically aim to eradicate every invasive species from every island, spending as much money as it takes to be certain of eradication. However in reality, budgets are limited and therefore conservation objectives must be clearly defined to determine how best to allocate funds. For fixed budget B, our method provides the maximum conservation benefit across the entire system of islands by considering three important factors: (i) the ecological benefit, (ii) the economic cost and (iii) the feasibility of each eradication action. We combine these factors by calculating the expected ecological benefit (indicated by E below): the benefit of a suite of invasive species remaining after eradication multiplied by the probability that those invasives remain after the eradication attempt. Even highly influential eradications will not contribute much to the total expected ecological benefit if they are unlikely to be successful.

The optimal portfolio of actions maximizes the objective:

$$\max_{A \in \mathbb{R}^I} \sum_{i=1\dots I} \mathbb{E}[U(y_{i1})|y_{i0}, A_i]$$

subject to the budgetary constraints (budget *B*):

$$\sum_{i=1...N} c(A_i) \le B.$$
eqn 1

 $U(y_{i1})$ is the biodiversity benefit achieved when island *i* is in the invasive species state y_{i1} (see Appendices S1 and S3 for details of calculation), and $c(A_i)$ is the cost of action portfolio A_i . This objective function includes any negative outcomes resulting from unintended states reached if part of the eradication campaign fails.

We focus on eradication campaigns that aimed to improve the state of predefined 'species of conservation concern' based on species listed in the IUCN Red List (IUCN 2014) and the EPBC Act List of Threatened Fauna (EPBC Act 1999). We also included Fairy Prions *Pachyptila turtur* on Tasman Island (which do not occur on either list), due to the conservation value of this

very large colony (BirdLife International 2014). Invertebrates or plants could easily be included if data were available. To illustrate our method, we calculate the ecological benefit of an action portfolio by the population increase of all species of conservation concern (see Appendix S3). However, many different utility functions could be used. In order to capture the species' relative rarity without using an arbitrary scoring system, we convert the population increases to percentages of the current global population. This weighs endemic species and important global populations highly and places less emphasis on more common species. To calculate the increase in abundance of each species of concern, we determined through expert elicitation or from the scientific literature the equilibrium population size in the initial state (all invasives present) and each potential future state (see Appendices S1 and S3).

DATA REQUIREMENTS

Carefully prioritizing eradications of invasive species requires a good understanding of the ecosystem of each island. For each portfolio of actions this includes a cost estimate and the likelihood that the portfolio would result in the successful eradication of each invasive species targeted. These likelihoods of success combine to give the probability that the island will transition into each particular future invasive species state (Appendix S1). Additionally, the impact of each potential remaining group of invasive species in the native ecosystem needs to be quantified and incorporated into the utility function in Equation 1 (see Appendix S3). This requires insight into not only the impact of each invasive species on each species of concern, but also how the absence of an invasive species might affect other invasive species populations. These insights might come from detailed ecological studies on species recovery (Ringler, Russell & Le Corre 2015; Buxton et al. 2016), predictive modelling techniques (Raymond et al. 2011), or expert elicitation (Sutherland & Burgman 2015).

COSTS OF ACTION PORTFOLIOS

The cost not only of each individual eradication but of each combined portfolio is required to capture potential cost-sharing between actions. Mixed rodent eradications are an effective example of shared costs: the baits can be dropped simultaneously (sharing the helicopter costs), but more animals will require more baits, either with a repeated bait drop or at a higher density. This cost for the whole action portfolio, $c(A_i)$, is applied in Equation 2 to ensure the chosen action portfolios can be achieved with the given budget (see Appendix S4).

THREE PRIORITY-SETTING METHODS

We prioritize eradications of invasive vertebrates from a case study of four islands using the 'action portfolio' framework described above. For a range of given budgets, we calculate the most beneficial set of actions that can be performed by exhaustively exploring potential combinations of eradication actions (although a heuristic method such as simulated annealing would be useful for larger problems, Van Laarhoven & Aarts 1987). We compare our method to two approaches that make many of the same assumptions as previously published prioritization methods. In both cases, we prioritize the eradication actions with the alternative method but assess the outcome in the same way for all

736 K. J. Helmstedt et al.

methods. We draw no comparison to single island or single invasive species studies (e.g. Capizzi, Baccetti & Sposimo 2010; Raymond *et al.* 2011), focusing instead only on multiple invasive species across multiple islands. The first method we compare prioritizes islands rather than actions: every invasive species must be targeted if an island is chosen in the priority set. In this 'all-ornothing' method (Brooke, Hilton & Martins 2007; Dawson *et al.* 2015), the action is to either eradicate everything if the island is chosen, or eradicate nothing. Islands may still contain some combination of invasive species after the eradication attempt.

We will compare these two methods to a third, less complex alternative method wherein we choose which species to eradicate on particular islands based on the cost-efficiency of each invasive species eradication, independent of the other invasive species. This is a simpler attempt to consider more than one potential action on each island. Each invasive species is considered a candidate for eradication, but only in isolation. This 'rank-and-sort' method does not take into account interactions between invasive species and considers each invasive species on each island separately, using the cost-efficiency (i.e. the expected ecological benefit of the single species eradication divided by the cost). For any given budget, the eradications are chosen by a greedy prioritization algorithm. In order, the algorithm steps down this ranked list selecting invasive species to eradicate (without recalculating the benefits) until the entire budget is allocated.

CASE STUDY

We use case study specifics (e.g. costs, probabilities of success and the measure of ecological benefit) to illustrate the process, flexibility and performance of our eradication prioritization, rather than recommending how the method should be parameterized in future applications. We analyse a hypothetical project comprising four Australian islands (see Table 1 for details), each of which underwent a successful eradication attempt. This case study is intended to illustrate the utility of considering multiple eradication options on each island rather than a retrospective critique of eradication programmes. We implement our framework for this case study (see Appendix S5 for a detailed description of how the case study was applied to each phase of this framework) and test the robustness of the results on a randomized set of islands (see Appendix S6). We elicited population estimates from experts for each island in a series of workshops (Appendix S3). As it is difficult to predict with confidence how species of conservation concern will respond to combinations of invasive species that have never occurred on the island, for the case study we utilized population estimates from experts for each of the islands (a technique frequently used in conservation planning, Kuhnert, Martin & Griffiths 2010; Martin et al. 2012). Although making these estimates may require time and money in future applications of this method, it is unlikely to require more than a small

Table 1. The four Australian islands included in this case study. Here, we list invasive species on each island and their individual eradication costs (from Martins *et al.* 2006) and probabilities of success (from Gregory *et al.* 2014) and the species of concern present on each island and their Latin names and conservation status. An attempt cannot be made to eradicate from Macquarie Island without also eradicating rats

	Invasive species			Species of concern		
Island	Name	Cost (AU\$)	Probability of eradication	Common name	Latin name	Status
Faure 58 km ²	Cats	\$659 043	0.641	Banded hare-wallaby*	Lagostrophus fasciatus	V§
	Goats	\$397 112	0.970	Burrowing bettong*	Bettongia lesueur	$\mathbf{V}^{\$}$
	Sheep	\$775 200	0.980	Greater stick-nest rat*	Leporillus conditor	$\dot{\mathbf{V}}^{\$}$
	Sheep	<i>Q110</i> <u>2</u> 00	0,000	Shark-bay mouse*	Pseudomys fieldi	V [§]
				Western-barred bandicoot*	Perameles bougainville	EN [‡]
Macquarie 128 km ²	Cats	\$1 289 885	0.604	Antarctic tern	Sterna vittata	EN [‡]
*	Rats	\$1 231 831	0.834	Black-browed albatross	Thalassarche melanophrys	$\mathbf{V}^{\$}$
	Rabbits	\$1 286 177	0.633	Blue petrel	Halobaena caerulea	V^{\ddagger}
	Mice	N/A	0.836	Grey-headed albatross	Thalassarche chrysostoma	NT [‡]
		,		Grey petrel	Procellaria cinerea	NT^{\ddagger}
				Light-mantled albatross	Phoebetria palpebrata	NT^{\ddagger}
				Macquarie shag	Phalacrocorax atriceps purpurascens	\mathbf{V}^{\S}
				Northern giant petrel	Macronectes halli	$\mathbf{V}^{\$}$
				Sooty shearwaters	Puffinus griseus	NT^{\ddagger}
				Southern giant petrel	Macronectes giganteus	$\mathbf{V}^{\$}$
				Wandering albatross	Diomedea exulans	V^{\ddagger}
Tasman 1.2 km ²	Cats	\$24 395	0.794	Fairy prion	Pachyptila turtur	$\mathbf{V}^{\$}$
Hermite 10.2 km ²	Cats	\$150 672	0.716	Spectacled hare-wallaby [†] ,*	Lagorchestes conspicillatus	\mathbf{V}^{\S}
	Rats	\$143 890	0.892	Golden bandicoot [†] ,* Black-and-white fairy wren [†]	Isoodon auratus Malurus leucopterus leucopterus	\mathbf{V}^{\S}

*Reintroduced populations (within historical range).

[†]Barrow Island subspecies.

[‡]IUCN Red List status.

[§]EPBC conservation status.

V, vulnerable; EN, endangered; NT, near threatened.

percentage of the costs required for eradicating multiple invasive species from multiple islands. Estimating these additional parameters also increases the uncertainty in the model, but even uncertain estimates are preferable to the unrealistic assumption that either all eradications in a campaign are successful or all fail.

We use a statistical estimator for feasibility, based on invasive species type and island size [although Gregory *et al.* (2014) recommends using island ruggedness rather than island size when possible]. We also use a statistical estimator for cost based on island size and latitude (Martins *et al.* 2006 and Appendix S4; also see Holmes *et al.* 2015). It was not possible to determine the costs for each individual invasive species eradication from the expert-elicited costs of past eradications on these islands. Using a statistical estimator allows us to separate these eradications easily and to normalize the cost estimates between islands (avoiding differences in accounting between departments over many years). These cost estimates do not reflect the actual funds spent on these eradications.

Results

Prioritizing portfolios of actions resulted in better or equal biodiversity benefit compared to the other two methods tested (Fig. 1). We prioritized the islands at budgets from zero up to the maximum cost (i.e. performing all eradication actions on all islands) (Table 2). In 79.5% of the budgets considered, the 'action portfolio' prioritization method outperformed the 'all-or-nothing' method, providing a 27% higher mean ecological benefit. In this case study, attempting to eradicate all invasive species from each island has a positive expected benefit even though undesirable states may be reached if some actions in the portfolio fail. With enough money, both the 'action portfolios' and 'all-or-nothing' methods recommend attempting to eradicate all invasive species from all islands.

The 'rank-and-sort' method (Fig. 1, dotted line) performed poorly for most budgets. This method calculates

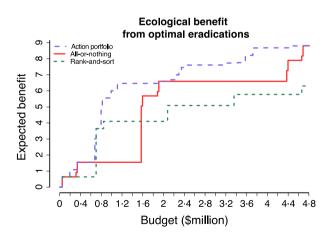


Fig. 1. The expected ecological benefit from the best eradication programme (an increase in the population of each species of concern as a proportion of their global population) chosen by applying three different prioritization methods: (1) 'action portfolio' (dashed line), (2) 'all-or-nothing' (solid line), (3) 'rank-and-sort' (dotted line).

Table 2. The ten most cost-efficient prioritizations (from a total of 1023) for the two priority-setting methods: all-or-nothing eradications and action portfolios. Bold indicates that only complete sets of invasives are targeted for eradication attempts; subsets in italics are the most cost-efficient subset on that island

Prioritization	'All-or-nothing' rank	'Action portfolio' rank
Tasman	1	1
Faure (cats, goats), Tasman	_	2
Faure (cats, goats)	_	3
Faure (cats, goats),	_	4
Tasman, Hermite (cats)		
Tasman, Hermite (cats)	_	5
Faure (cats, goats), Tasman, Hermite (all)	_	6
Faure (cats, goats),Tasman, Hermite (rats)		7
Faure (cats, goats), Hermite(cats)	_	8
Faure (cats, goats), Hermite (all)	-	9
Faure (cats), Tasman	_	10
Hermite	2	13
Faure and Tasman	3	21
Faure, Tasman and Hermite	4	23
Faure	5	25
Faure, Hermite	6	27
Faure (cats, goats), Tasman, Macquarie (cats)*	-	28
All actions, all islands	8	210
Faure, Tasman, Macquarie	9	230
Faure, Hermite, Macquarie	10	241
Macquarie	15	655

*The most cost-efficient eradication programme that includes an action on Macquarie Island.

the benefit of eradicating each invasive species in isolation (with no consideration of species interactions) and simply adds these benefits when considering eradications of multiple species. This method substantially underestimates the benefit of eradicating some invasive species because their eradication alone provides no net benefit. This occurs particularly in cases where no threatened species can coexist with one of the invasive species. For example, all species of concern are locally extinct on Faure Island when cats are present, so there is no benefit to species of concern of eradicating goats if cats are left on the island. This simple 'rank-and-sort' method does not consider invasive species interactions, so the benefit of eradicating goats is always considered zero. This method will therefore never recommend eradicating goats, even in an action portfolio in unison with cat eradication, illustrating that it is imperative to use a method that includes invasive species interactions (see Fig. 2a). This ranking method performs well at low budgets when these combinations of invasive species are not a factor because they exceed the budget, but it performs very poorly at mid- to high budgets. It never outperforms the action portfolios method.

When prioritizing using the action portfolios method, it is almost always optimal to intentionally leave some inva-

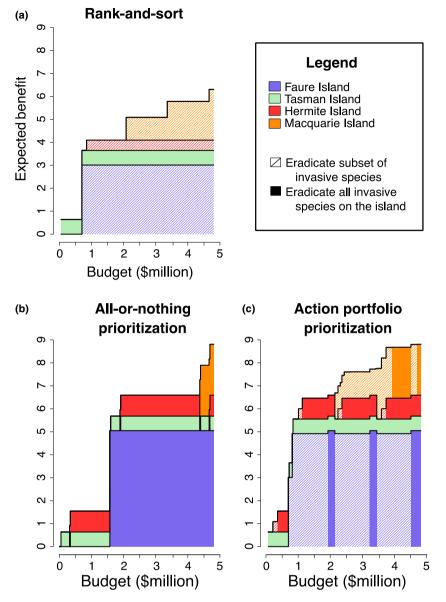


Fig. 2. The ecological benefit achieved by the optimal eradication programme recommended by each of the three priority-setting methods at varied budgets. Each coloured bar represents the ecological benefit contributed by each island (see the legend for colours). A solid colour indicates that all invasive mammals should be eradicated from that island. A hatched colour indicates that the optimal solution advises only attempting to eradicate some invasive species from the island.

sive species on at least one island (Fig. 2). The flexibility gained is best seen at key budgets when a single eradication action falls within the budget, but an entire suite of invasive species on an island does not. The action portfolios method allows managers to drop the least efficient actions and still achieve high conservation benefits on that island for much lower costs. AU\$700 000 is insufficient to eradicate all the invasives on Faure Island. However, cats can be eradicated from Faure for that budget, achieving 60% of the potential conservation benefit on that island (Fig. 2c at AU\$700 000). Using the all-or-nothing method, which does not allow the flexibility to leave goats and sheep, none of that benefit can be achieved for a budget less than \$1.2 million (Fig. 2b at AU\$1 200 000).

The efficiency of leaving some invasive species on some islands to free resources for other partial eradications is evident also at higher budgets. Once the budget is large enough to eradicate everything from Faure, Tasman and Hermite islands, there is the potential to gain significant benefit from the eradication of just cats on Macquarie Island with a total budget of AU\$2.43 million (using the cost estimates of Martins *et al.* 2006). It would cost a considerably larger budget (AU\$4.3 million, more than 1.75 times the investment) to achieve the same additional benefit with the 'all-or-nothing' prioritization method.

There are instances of imperceptibly small expected benefits of eradication attempts in this case study, for example mice on Macquarie Island (Fig 2b at a total budget of AU\$3.8 million) or sheep on Faure Island (Fig 2b at AU\$2.1 million). The expected benefit of an eradication attempt can be low for two reasons: relatively low ecological benefit compared to the other invasive species (sheep on Faure Island), low feasibility compared to other invasive species or a combination of both (mice on Macquarie Island, where to date mice had not been identified as a major threat to species of concern – unlike other sub-Antarctic islands Angel, Wanless & Cooper 2009; Jones & Ryan 2010). The advantage of leaving these invasives on

an island is particularly obvious when it is very expensive to eradicate them: 75% of the total possible benefit for the entire four-island system can be achieved for AU\$1.8 million. For perspective, this saving is enough to eradicate the whole complement of invasives from Hermite, Faure and Tasman islands twice over.

Discussion

Existing methods for prioritizing island eradications impose strong constraints on conservation decision-makers; if an island is chosen as a priority, managers only have a single option (Brooke, Hilton & Martins 2007; Ratcliffe *et al.* 2009; Capizzi, Baccetti & Sposimo 2010; Nogales *et al.* 2013). We have shown that intentionally leaving some invasive species on islands can increase overall potential conservation benefits. In any optimization scenario, restricting the available options cannot result in better outcomes. Sometimes the best solution will satisfy the restrictions, in which case the restricted and the unrestricted problem would find the same solution. However in many cases (especially in this study), the optimal solution breaks the restrictions and would not have been found by a restricted decision-maker.

With no funding limitations, managers should eradicate all invasives from all islands at the same time (Glen et al. 2013). Where trade-offs are required, our prioritization method allows funding to be directed to cost-effective eradications of invasive species that cause the greatest and most immediate ecological harm. The flexibility of our framework provides significant gains for budgets where not all invasives can be successfully eradicated due to budgetary constraints (or inadequate technology) and so trade-offs must be made. For example, if cats had not been eradicated from Macquarie Island in the years prior to the expensive (and technologically difficult) rabbit and rodent eradications, several species of high-conservation seabird would have become extinct (Robinson & Copson 2014). This pressing need, reiterated by our results, does not imply that mice are not harmful on Macquarie Island. In fact, they do affect many ground-nesting seabirds (see Appendix S3 and discussions in Bergstrom et al. 2009; Dowding et al. 2009), but with a limited budget the most cost-efficient species (cats on all islands) should be eradicated with priority. Conservation is a field constrained by budgets, and so the ability to trade-off and increase benefits that can be achieved with small budgets is pragmatic. When prioritizing the eradication of a single species from multiple islands (e.g. black rats, Capizzi, Baccetti & Sposimo 2010), prioritizing actions is equivalent to prioritizing islands).

Previous studies have avoided more complex prioritization methods due to the difficulty in predicting ecosystem responses. Ecosystem science and modelling techniques are rapidly improving the ease and reliability of these predictions and are likely to continue developing. The understanding of species interactions and food web dynamics are increasing (Raymond *et al.* 2011; e.g. Eklöf, Tang & Allesina 2013). Our aim here was to illustrate the utility of a more detailed, nuanced prioritization framework. Future applications should apply the most up-to-date techniques to predict the ecological responses of systems to changes in composition, such as structured qualitative modelling techniques (Hunter et al. 2015). By applying these structured, transparent modelling techniques we can more accurately capture the increases in population that are controlled by invasive species removal rather than the myriad other threatening processes facing threatened species. These methods can ease reliance on expert estimation and literature review for predicting the current and potential future population estimates. The estimates require a detailed knowledge of the ecological interactions on the islands, and a willingness and ability of experts to forecast into unknown states (see Courchamp, Chapuis & Pascal 2003 for discussion on the complexity of eradications from islands). Any attempt to predict ecological responses to altered invasive species compositions is not perfect: many assumptions must be made, and it is important to maintain transparency throughout the entire parameterization process (e.g. see Appendices S1-S5).

Predictive statistical models for cost (Martins et al. 2006) and feasibility (Gregory et al. 2014) proved useful for our case study. Statistical models are useful when considering either large numbers of islands, or (as is the case here) where the primary aim is to illustrate a decision support tool rather than a prescribed plan of action. These predictors force a compromise between specificity of results and ease of application. For example, the model to predict cost presented by Martins et al. (2006) does not capture the large shipping cost for Macquarie Island (a sub-Antarctic and therefore unusually remote island). These statistical models could be used for a first pass at a large number of islands, after which a detailed budget be created for a short list of islands and the prioritization method run again. We have not explicitly considered the possibility of reinvasion. The feasibility estimates from Gregory et al. (2014) include reinvasion as a failure, so we have implicitly included these results as predicted failures in our model. If different feasibility estimates are used, the prioritization method introduced here is not applicable for islands with high risk of reinvasion. Although they are often considered 'inland islands', reserves surrounded by predator-proof exclosures suffer from a constant threat of reinvasion and cannot be considered with this framework without additional detailed modelling (Moseby & Read 2006; Helmstedt et al. 2014).

The ecological benefits of conservation actions are not always measured relative to threatened species population increases. For example, the level of ecosystem service or species diversity might be the goal of an eradication programmes (and indeed was a factor in procuring funding for the Macquarie Island eradications). Our framework can use any of a broad class of benefit measures; the only requirement is that the invasive species group on an island is mapped to a single numeric benefit value. Benefit functions of this form are wide ranging: from simplistic (maxi-

740 K. J. Helmstedt et al.

mizing the number of invasive-free islands by using a binary benefit function) to complicated (combining multiple weighted objectives). It is not a trivial task to define the benefit function for an eradication programme; it is important that aims are clearly defined and that all stakeholders agree on the metrics of success. We do not aim to prescribe how island ecosystem functions should be weighted against, for example, a high-conservation-valuethreatened seabird population. These trade-offs and values will be different for every eradication programme.

Our aim was to illustrate the increased utility gained by considering a more realistic suite of management options. Given that we do not prescribe any actions, we have not considered uncertainty around the estimates we have used for ecosystem response, cost or feasibility. Changes in these parameters could certainly change the optimal solution, but are unlikely to change our main result: that it is frequently optimal to eradicate only subsets of invasive species from some islands. We have illustrated that this result is consistent by prioritizing actions across many groups of islands with randomized parameters (see Appendix S6).

Considering a more realistic suite of actions on each island increases the complexity of the prioritization over an 'all-or-nothing' approach, but the data requirements are not substantially greater. Even when using an 'all-ornothing' prioritization method, each individual eradication might fail, leading to unintended invasive species states. Population estimates for all species of concern under all of these potential future states are needed: the same number of population estimates as an 'action portfolios' approach. As long as the conservation goals are consistently defined and agreed on prior to the prioritization, the 'species of concern' can be chosen for any purpose. However, rules must be consistently applied to avoid definitional differences skewing the results.

One caveat to our treatment of undesirable invasive species states is that we assume that once a decision is made, all prescribed eradications will be undertaken. This is the case where all eradications occur simultaneously. However, this may not be the case on an island where an action portfolio can result in either a highly desirable or a highly destructive invasive species state. In that situation, a risk-averse manager might choose to perform one of the eradications (e.g. mice) and only then proceed with the others (e.g. cats) if successful. We do not model the optimal application of the prescribed eradication actions (Bode *et al.* 2013; Bode, Baker & Plein 2015).

Our use of four Australian islands that have undergone mammal eradications, funded by very different organizations and separated by up to 17 years should not be interpreted as a retrospective critique of management decisions, since each could have been the legitimate best choice of the relevant organizations at the time. Instead, they provided an opportunity to parameterize our model with realistic values, and therefore produce a representative estimate of the increased ecological benefit that can be realized by prioritizing actions rather than islands.

We illustrated the utility of our model using four islands, but given other developments in ecological modelling, this framework can potentially be applied to much larger prioritization efforts. This is particularly pertinent as our knowledge of ecosystem response to changes in community composition improves. We feel that this illustrative case study suffices to introduce both feasibility and the concept of prioritizing actions into the field. We hope future proposed eradication projects across multiple islands involving multiple species will combine this concept with detailed expert knowledge of all islands being considered to determine a complete and realistic set of priorities. Rather than emphasizing a return to pristine islands with no invasive mammals present, it is more important that we aim to eradicate those species that are destructive and can feasibly be eradicated.

Acknowledgements

We thank D. Algar, K. Morris from Department of Parks and Wildlife Western Australia, S. Legge from Australian Wildlife Conservancy, L. Gadd from DPIPWE Tasmania, the editors and two anonymous reviewers.

Data accessibility

R scripts are available in online Appendix S7.

References

- Angel, A., Wanless, R.M. & Cooper, J. (2009) Review of impacts of the introduced house mouse on islands in the Southern Ocean: are mice equivalent to rats? *Biological Invasions*, **11**, 1743–1754.
- Bergstrom, D.M., Lucieer, A., Kiefer, K., Wasley, J., Belbin, L., Pedersen, T.K. & Chown, S.L. (2009) Indirect effects of invasive species removal devastate World Heritage Island. *Journal of Applied Ecology*, 46, 73–81.
- BirdLife International (2014) Important Bird Areas factsheet: Tasman Island. BirdLife International, http://www.birdlife.org.
- Bode, M., Baker, C.M. & Plein, M. (2015) Eradicating down the food chain: optimal multispecies eradication schedules for a commonly encountered invaded island ecosystem. *Journal of Applied Ecology*, **52**, 571–579.
- Bode, M., Brennan, K.E.C., Helmstedt, K., Desmond, A., Smia, R. & Algar, D. (2013) Interior fences can reduce cost and uncertainty when eradicating invasive species from large islands. *Methods in Ecology and Evolution*, 4, 819–827.
- Brooke, M.D., Hilton, G.M. & Martins, T.L.F. (2007) Prioritizing the world's islands for vertebrate-eradication programmes. *Animal Conser*vation, 10, 380–390.
- Buxton, R., Taylor, G., Jones, C., Lyver, P.O.B., Moller, H., Cree, A. & Towns, D. (2016) Spatio-temporal changes in density and distribution of burrow-nesting seabird colonies after rat eradication. *New Zealand Journal of Ecology*, 40.
- Capizzi, D., Baccetti, N. & Sposimo, P. (2010) Prioritizing rat eradication on islands by cost and effectiveness to protect nesting seabirds. *Biologi*cal Conservation, 143, 1716–1727.
- Courchamp, F., Chapuis, J.L. & Pascal, M. (2003) Mammal invaders on islands: impact, control and control impact. *Biological Reviews*, 78, 347–383.
- Dawson, J., Oppel, S., Cuthbert, R.J., Holmes, N., Bird, J.P., Butchart, S.H., Spatz, D.R. & Tershy, B. (2015) Prioritizing islands for the eradication of invasive vertebrates in the United Kingdom overseas territories. *Conservation Biology*, 29, 143–153.
- Donlan, C.J., Luque, G.M. & Wilcox, C. (2015) Maximizing return on investment for island restoration and species conservation. *Conservation Letters*, 8, 171–179.
- Donlan, C.J. & Wilcox, C. (2007) Complexities of costing eradications. Animal Conservation, 10, 154–156.
- Dowding, J.E., Murphy, E.C., Springer, K., Peacock, A.J. & Krebs, C.J. (2009) Cats, rabbits, Myxoma virus, and vegetation on Macquarie

Island: a comment on Bergstrom et al. (2009). Journal of Applied Ecology, 46, 1129–1132.

- Eklöf, A., Tang, S. & Allesina, S. (2013) Secondary extinctions in food webs: a Bayesian network approach. *Methods in Ecology and Evolution*, 4, 760–770.
- EPBC Act (1999) Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act). Office of Legislative Drafting and Publishing (OLDP) (ed. A. Government). Canberra.
- Game, E.T., Kareiva, P. & Possingham, H.P. (2013) Six common mistakes in conservation priority setting. *Conservation Biology*, 27, 480–485.
- Glen, A.S., Atkinson, R., Campbell, K.J., Hagen, E., Holmes, N.D., Keitt, B.S. *et al.* (2013) Eradicating multiple invasive species on inhabited islands: the next big step in island restoration? *Biological Invasions*, 15, 2589–2603.
- Gregory, S.D., Henderson, W., Smee, E. & Cassey, P. (2014) Eradications of vertebrate pests in Australia: a review and guidelines for future best practice. *PestSmart Toolkit publication*, 76 pp. Invasivse Animals Cooperative Research Centre, Canberra, Australia.
- Harris, D.B., Gregory, S.D., Bull, L.S. & Courchamp, F. (2012) Island prioritization for invasive rodent eradications with an emphasis on reinvasion risk. *Biological Invasions*, 14, 1251–1263.
- Helmstedt, K.J., Possingham, H.P., Brennan, K.E.C., Rhodes, J.R. & Bode, M. (2014) Cost-efficient fenced reserves for conservation: single large or two small? *Ecological Applications*, 24, 1780–1792.
- Hilton, G.M. & Cuthbert, R.J. (2010) Review article: the catastrophic impact of invasive mammalian predators on birds of the UK overseas territories: a review and synthesis. *Ibis*, **152**, 443–458.
- Holmes, N.D., Campbell, K.J., Keitt, B.S., Griffiths, R., Beek, J., Donlan, C.J. & Broome, K.G. (2015) Reporting costs for invasive vertebrate eradications. *Biological Invasions*, 17, 2913–2925.
- Hunter, D.O., Britz, T., Jones, M. & Letnic, M. (2015) Reintroduction of Tasmanian devils to mainland Australia can restore top-down control in ecosystems where dingoes have been extirpated. *Biological Conservation*. **191**, 428–435.
- IUCN (2014) IUCN Red List of Threatened Species. Version 2014. IUCN, http://www.iucnredlist.org.
- Jones, M.G.W. & Ryan, P.G. (2010) Evidence of mouse attacks on albatross chicks on sub-Antarctic Marion Island. *Antarctic Science*, 22, 39–42.
- Joseph, L.N., Maloney, R.F. & Possingham, H.P. (2009) Optimal allocation of resources among threatened species: a project prioritization protocol. *Conservation Biology*, 23, 328–338.
- Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J. & Barthlott, W. (2009) A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences*, **106**, 9322–9327.
- Kuhnert, P.M., Martin, T.G. & Griffiths, S.P. (2010) A guide to eliciting and using expert knowledge in Bayesian ecological models. *Ecology let*ters, 13, 900–914.
- Martin, T.G., Burgman, M.A., Fidler, F., Kuhnert, P.M., Low-Choy, S., McBride, M. & Mengersen, K. (2012) Eliciting expert knowledge in conservation science. *Conservation Biology*, 26, 29–38.
- Martins, T.L.F., Brooke, M.D.L., Hilton, G.M., Farnsworth, S., Gould, J. & Pain, D.J. (2006) Costing eradications of alien mammals from islands. *Animal Conservation*, 9, 439–444.
- Medina, F.M., Bonnaud, E., Vidal, E., Tershy, B.R., Zavaleta, E.S., Josh Donlan, C. *et al.* (2011) A global review of the impacts of invasive cats on island endangered vertebrates. *Global Change Biology*, **17**, 3503– 3510.
- Moseby, K.E. & Read, J.L. (2006) The efficacy of feral cat, fox and rabbit exclusion fence designs for threatened species protection. *Biological Con*servation, **127**, 429–437.
- Nogales, M., Martín, A., Tershy, B.R., Donlan, C., Veitch, D., Puerta, N., Wood, B. & Alonso, J. (2004) A review of feral cat eradication on islands. *Conservation Biology*, 18, 310–319.
- Nogales, M., Vidal, E., Medina, F.M., Bonnaud, E., Tershy, B.R., Campbell, K.J. & Zavaleta, E.S. (2013) Feral cats and biodiversity conservation: the urgent prioritization of island management. *BioScience*, 63, 804–810.
- Possingham, H., Ball, I. & Andelman, S. (2000) Mathematical methods for identifying representative reserve networks. *Quantitative Methods for*

Conservation Biology (eds. S. Ferson & M. Burgman), pp. 291-306. Springer, New York.

- Ratcliffe, N., Mitchell, I., Varnham, K., Verboven, N. & Higson, P. (2009) How to prioritize rat management for the benefit of petrels: a case study of the UK, Channel Islands and Isle of Man. *Ibis*, **151**, 699–708.
- Raymond, B., McInnes, J., Dambacher, J.M., Way, S. & Bergstrom, D.M. (2011) Qualitative modelling of invasive species eradication on subantarctic Macquarie Island. *Journal of Applied Ecology*, 48, 181–191.
- Ringler, D., Russell, J.C. & Le Corre, M. (2015) Trophic roles of black rats and seabird impacts on tropical islands: mesopredator release or hyperpredation? *Biological Conservation*, 185, 75–84.
- Robinson, S.A. & Copson, G.R. (2014) Eradication of cats (*Felis catus*) from subantarctic Macquarie Island. *Ecological Management & Restoration*, 15, 34–40.
- Simberloff, D. (1995) Why do introduced species appear to devastate islands more than mainland areas? *Pacific Science*, 49, 87–97.
- Spatz, D.R., Newton, K.M., Heinz, R., Tershy, B., Holmes, N.D., Butchart, S.H. & Croll, D.A. (2014) The biogeography of globally threatened seabirds and island conservation opportunities. *Conservation Biology*, 28, 1282–1290.
- Sutherland, W.J. & Burgman, M. (2015) Policy advice: use experts wisely. *Nature*, 526, 317–318.
- Van Laarhoven, P.J.M. & Aarts, E.H.L. (1987) *Simulated Annealing*. Springer, Dordrech, the Netherlands.

Received 7 September 2015; accepted 8 December 2015 Handling Editor: Don Driscoll

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Figure S1. Potential outcomes from an attempt to eradicate all invasive species (cats, rats and mice) from an island.

Figure S2. The mean performance of 500 simulated four island system comparing: our novel method prioritizing packages of actions (dashed line) and whole island eradications (solid red line).

Appendix S1. Mathematical methods.

Appendix S2. Case study feasibilities.

Appendix S3. Case study ecological benefits.

Table S1. Tasman Island population estimates.

 Table S2. Macquarie Island population estimates.

Table S3. Faure Island population estimates.

 Table S4. Hermite Island population estimates.

Appendix S4. Case study costs.

Appendix S5. Case study application.

Appendix S6. Robustness analysis.

Appendix S7. R code.