It's often better to eradicate, but can we eradicate better?

E. S. Zavaleta
Dept of Integrative Biology, University of California, Berkeley, CA 94720, USA.
E-mail: zavaleta@socrates.berkeley.edu

Abstract Invasive species eradications have achieved important conservation gains the world over. Growing numbers of eradications take place, however, in complex and highly altered ecosystems with high risks of unexpected ecological effects. Ecosystems that contain multiple invaders, have lost one or more native species along with their functional roles, or have undergone long-term change to soil and other site conditions can respond to eradication with mixed results. The most common secondary outcome of a single-species eradication is the ecological release of a second (plant or prey) exotic species previously controlled by the removed species (herbivore or predator) through top-down regulation. Examples of a variety of other undesirable secondary outcomes also exist, challenging invasive species managers to develop tools for predicting and averting these "surprises." Most unexpected outcomes can be understood and anticipated through knowledge about species interactions and the general ecological rules that they follow. Several tools that already exist, including thorough pre- and post-eradication monitoring and restoration measures such as re-seeding, simply need to be applied more routinely in eradication projects. Other areas deserve to be carefully explored, such as formal but qualitative approaches to ecological assessment during the planning stages of an eradication project. As eradication moves from narrow invasive species management to actively pursuing and practicing restoration, it will be able to achieve clear conservation results in increasingly challenging settings without accidental, adverse effects.

Keywords Invasive species eradication; secondary effects; species interactions; food web; ecological release; restoration.

INTRODUCTION

Invasive species now pose an enormous threat to the world's biological diversity, second only to land-use change (Chapin *et al*. 2000). Several global trends – growing human populations, transport, and tourism, the weakening of trade barriers as trade volumes skyrocket; ongoing habitat loss; and climate and atmospheric changes – will likely increase the movement, establishment, and spread of exotics (Mooney and Hobbs 2000). If biological invasions go on unabated, crude estimates predict the eventual loss of at least 30-35% of the world's species (McKinney 1998).

We have an opportunity to overcome this bleak vision with a steadily growing arsenal of knowledge, tools, and techniques for preventing and undoing biological invasions and their harmful effects. The case studies in this volume document the latest advances in undoing biological invasions in critical areas for biodiversity conservation. Many of these cases illustrate that a range of invasive taxa, including vertebrate animals, plants and insects, can be eradicated from a diversity of regions around the world (e.g. Veitch 1974; Allwood *et al.* 2002; Burbidge and Morris 2002; Coulston 2002; Dixon *et al*. 2002; Flint and Rehkemper 2002). The conservation potential of the projects described in this volume is especially great because they focus on islands, which contain a disproportionate share of the world's unique species (Whittaker 1998) and are especially vulnerable to the impacts of invasions (Atkinson 1989; Simberloff 1995). These case studies illustrate that island invasive species eradications are already an important and effective way to protect native biota and ecosystems.

These case studies also present an opportunity to learn from experience. Eradications take place in increasingly complex ecological contexts – in settings affected by multiple invaders (e.g. Algar *et al*. 2002; Bullock *et al*. 2002; Carter and Bright 2002; Coulston 2002; Klinger *et al.* 2002; Micol and Jouventin 2002; Mowbray 2002; Roy 2002; Rippey *et al.* 2002; West 2002), long-term damage to native populations and ecosystem function (e.g. Brown and Sherley 2002), and other global environmental stresses such as climate change (IPCC 2001). These complexities mean that restoring native systems is not always as straightforward as removing an invader. They also mean that eradications are more likely to have unexpected, undesirable effects, such as the accidental release of other exotic populations (Zavaleta *et al*. 2001).

What can go wrong?

To some extent, eradications will always be single, unreplicated experiments, so there will always be some surprise outcomes (Simberloff 1995, 2002). My goal is to help reduce undesirable outcomes of eradications through an assessment of why they occur and how they can be prevented. Eradications fail for a variety of reasons, including non-target impacts of the eradication method itself (e.g. Morris 2002; Torr 2002) and failure to eliminate the target organism (e.g. Varnham *et al.* 2002; Hammond and Cooper 2002; Burbidge and Morris 2002; Lovegrove *et al*. 2002; Bell 2002; Parkes *et al.* 2002). Other authors provide excellent critical overviews of how to avoid these types of problems (Moro 2002; Burbidge and Morris 2002). Here, I focus on the problem of unwanted, secondary ecological consequences of *successful* eradications – releases of other exotic populations, declines in native populations following eradication, and the failure of na-

Pages 393-403 In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

tive biota and ecosystems to recover once target invaders have been removed. Aspects of this topic have been discussed elsewhere (Zavaleta *et al.* 2001); in this paper I discuss some specific, possible solutions to unwanted secondary impacts.

Species interactions – both among exotics and between exotic and native species – lie at the root of most of these post-eradication outcomes in these categories. In invaded ecosystems, exotic species interact with each other and with native species largely according to the same rules that govern all species interactions. In any ecosystem, populations of producers, consumers, and predators are in part controlled by one another through food web and other biotic interactions, including competition and provision of habitat (Hairston *et al.* 1969; Fretwell 1987; Polis and Strong 1996). Every invaded ecosystem is unique in some way, but every invaded ecosystem also follows, at least qualitatively, the same set of basic rules that all ecosystems do. With these basic ecological rules in mind, managers and eradication experts can make great gains towards anticipating, planning for, preventing, and mitigating the unexpected.

The types of species interactions that produce undesirable eradication outcomes can be viewed as falling into three classes. The first and largest includes trophic (food-web) and competitive interactions, both between exotics and natives and among exotic species themselves. Both competition and trophic interactions are large categories of species interactions important to eradication outcomes, but they are necessarily linked in many cases. For example, eradication of feral pigs (*Sus scrofa*) and sheep (*Ovis aries*) in Hawai'i removed herbivores that controlled exotic plant populations (food-web interaction). Competition between exotic and native plants became a more important structuring force in the absence of top-down control by feral herbivores, with mixed results (Scowcroft and Conrad 1992). The other two, smaller classes of species interactions – provision of habitat by one species for another, and indirect interactions through the alteration by one species of site conditions for another – are discussed near the end of this section.

Trophic and competitive interactions

The rules governing food-web interactions and their relative importance in different ecosystems have long been studied and debated. Research in a range of ecosystems has shown that both bottom-up and top-down regulation of populations of consumers and producers can play important roles (Pace and Cole 1996; Pace *et al*. 1999; Polis 1999; Terborgh *et al*. 1999). The importance of these forces has implications for interactions in invaded ecosystems. Bottom-up regulation of predators by prey (Polis 1999) implies that, among other things, removing an exotic prey species could reduce both exotic and native predator populations. On Santa Cruz Island, California, USA, ecologists anticipate that feral pig (*Sus scrofa*) eradication will reduce native golden eagle (*Aquila chyrsaetos*) populations that prey on the pigs (Roemer *et al.* 2002). In

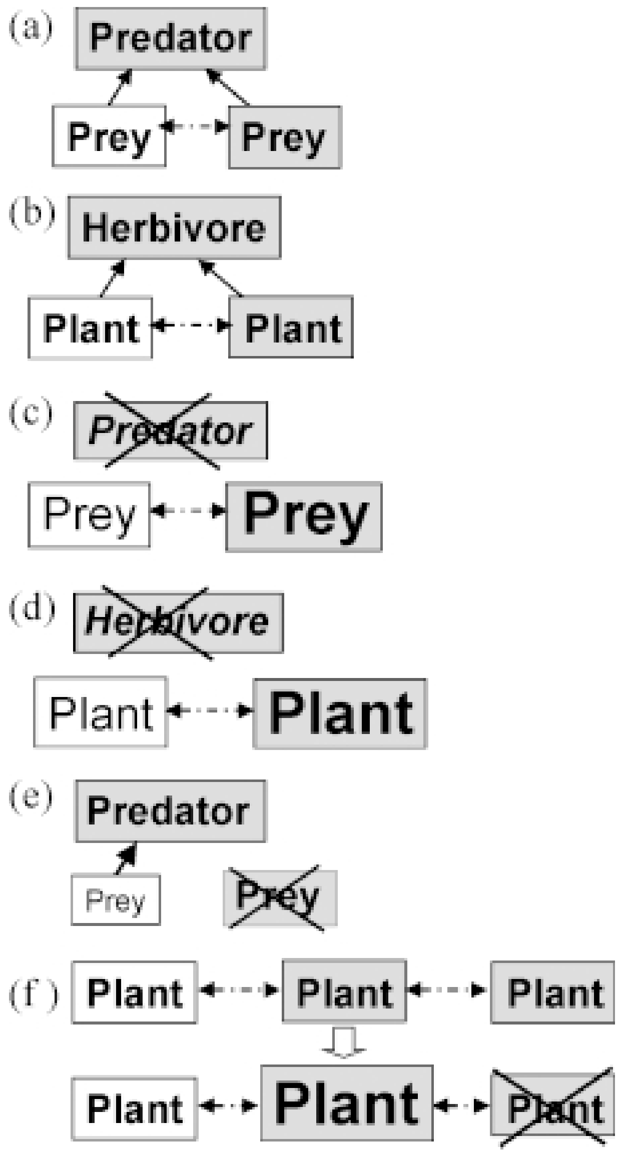

Fig. 1 Ecological release following removal of an exotic species. Grey boxes are exotics, white boxes are natives, dashed arrows indicate competition, and solid arrows point to consumers from the organism consumed. Font size indicates population size. In systems where (a) exotic predators consume both native and exotic prey or, (b) exotic herbivores consume both native and exotic plants, removal of the top consumer can lead to release of exotic (c) prey or (d) plant populations that can outcompete their native counterparts. In (e), removal of an exotic prey species from situation (a) leads an exotic predator to consume more native prey, a phenomenon known as prey-switching. In (f), removal of one exotic plant species leads to ecological release of a second exotic plant species, with no benefit to native plant populations. This phenomenon has been termed "the Sisyphus effect" by Mack and Lonsdale (2002). Figure adapted from Zavaleta *et al*. 2001.

this case, the reduction of the native raptor will be welcome; predation by pig-inflated golden eagle populations appears responsible for sharp reductions in endemic island fox (*Urocyon littoralis*) populations.

Similarly, top-down regulation of prey by predators (including regulation of plant populations by herbivores) (Terborgh *et al.* 1999) implies that removing exotic predators can increase populations of both native and exotic prey (Fig. 1a-d).

This kind of ecological release – of exotic prey or plants previously consumed by an introduced animal that gets removed – has occurred in a range of settings involving a range of exotic species (Fig. 1a-d). In some cases, an exotic predator controls populations of exotic prey species until the predator is removed. Mesopredator release, the rapid expansion of a prey population once top-down control by a predator has disappeared, could lead to negative effects if the expanded prey population competes with or consumes native biota. Eradications of feral cats (*Felis catus*) in the Orongorongo Valley, New Zealand (Fitzgerald 1988) and on Isabela Island, Mexico (C. Rodriguez, unpub. data) have led to increased populations of introduced rats. Merton *et al*. (2002) describe an explosive irruption of exotic crazy ant (*Anoplolepis gracilipes*) populations following, and possibly resulting from, the removal of rats from Bird Island in the Seychelles. Certain common invaders are known to feed on other exotic animals in a variety of settings. Data from Fitzgerald (1988) indicate that where introduced rabbits are absent, exotic rats generally make up more than two thirds of the diet of introduced cats on several islands where rats and cats co-occur (Fitzgerald 1988; Fitzgerald *et al.* 1991) (Table 1). On islands where introduced cats, rats, and rabbits all co-occur, rats make up a much smaller part of cats' diets – suggesting that in these settings, cats might be eating many rabbits instead of rats.

Table 1 Exotic rats in the diet of introduced cats on islands. Data from Fitzgerald (1988).

Islands without introduced rabbits	Occurrence of rats in diet (%)
Galapagos: Isabela	73
Galapagos: Santa Cruz	88
Lord Howe	87
Raoul	86
Little Barrier	39
Stewart	93
Campbell	95
Islands with introduced rabbits	**Occurrence of rats in diet (%)**
Gran Canaria	4
Te Wharau, NZ	3
Kourarau, NZ	Trace
Orongorongo, NZ	50
Mackenzie, NZ	2
Kerguelen	0
Macquarie	3

NZ=New Zealand
Reprinted from Zavaleta *et al.* (2001) with permission from Elsevier Science

Mesopredator release can potentially lead to cascading changes in entire ecosystems. On subantarctic Marion Island, pre-eradication studies found that feral cats fed heavily on exotic house mice (*Mus musculus*). The mice, in turn, ate large numbers of an endemic moth, *Pringleophaga marioni*, important to nutrient cycling on Marion (Bloomer and Bester 1990, 1992; Crafford 1990). Cat eradication could have released mouse populations, which in turn could have reduced moth abundance and subsequently changed patterns of soil nutrient availability.

Even more frequently, removal of an exotic herbivore releases populations of exotic plants from top-down control. Many islands have large numbers of exotic plants on them in addition to the more often focused-on exotic herbivores (e.g. Frenot *et al.* 2001). Bullock *et al*. (2002) describe how rabbit eradication from Round Island, Mauritius has increased plant biomass, but mainly by increasing the dominance of exotic species in the island's flora like *Chloris barbata* (North *et al.* 1994). Klinger et al. (1994, 2002) describe a similar outcome following the removal of sheep from Santa Cruz Island, U.S.A. On Santa Cruz vegetation cover has increased, but certain endemic plants species have declined, and exotic plants have proliferated in areas formerly grazed by the sheep. On nearby Santa Catalina Island, the removal of feral pigs and goats has increased plant diversity and vegetation cover, reducing potential for further topsoil erosion (Schuyler *et al.* 2002). However, exotic species contributed much of the gain in plant diversity and increased in both absolute and relative cover (Laughrin *et al.* 1994).

Only one exotic plant need be present in an ecosystem to pose a threat. The most dramatic exotic plant release described in this volume (Kessler 2002) involved a single species whose presence was unknown prior to exotic mammal eradication. Following removal of feral goats and pigs from Sarigan Island in the Commonwealth of the Northern Mariana Islands, the exotic vine *Operculina ventricosa* rapidly became superabundant. It now covers much of the island, but its effects on ongoing regeneration of the island's native forests and fauna remain unclear. On San Cristobal Island in the Galapagos, removal of feral cattle from areas containing suppressed populations of exotic guava (*Psidium guajava*) led to rapid development of dense, mature guava thickets (Eckhardt 1972). In a case like San Cristobal, herbivore removal can create a situation that for practical purposes may be irreversible. Browsers and grazers will consume guava seedlings and damage saplings, but they cannot reduce numbers of established, woody guavas once succession to these exotics has been allowed to progress.

In every one of these cases, successful eradication removed a damaging exotic from a threatened ecosystem. These cases make clear, though, that greater conservation gains are possible if these initial eradications are viewed as only first steps in a larger process of island restoration. In some settings with multiple invasions, ecological releases of other exotics can be anticipated, and steps can be taken to head off potential problems before, during, and after eradication. In others, unanticipated releases can be caught and managed effectively through a combination of contingency planning for surprise outcomes and post-eradication monitoring.

Diet switching and competition

Eradication of exotic prey without the simultaneous removal of introduced predators can also spell trouble when these predators are forced to switch their diets to native prey species (Fig. 1e). In New Zealand, introduced stoats (*Mustela erminea*) feed largely on introduced rats (*Rattus rattus*) and common brushtail possums (*Trichosurus vulpecula*) (Murphy and Bradfield 1992; Murphy *et al*. 1998). Efforts to reduce all three of these species together resulted in successful control of the rats and possums, but not the stoats. With the exotic prey species much reduced, the remaining stoats switched their diets to include more native birds and eggs. This type of prey switching, under the wrong circumstances, could potentially extirpate a native prey species in an island setting. Since removing the exotic predator first could lead to increased exotic prey abundance (Fig 1. a,c), whether to remove exotic predator or prey first can pose a serious quandary. The solution to this scenario depends on, among other things, the feasibility of a successful dual eradication; the ability of native prey populations to withstand temporary increases in predation; and the increased difficulty of successful prey eradication that would result from an exotic prey population expansion following predator removal.

Competition plays important roles in the responses of multiply-invaded ecosystems to eradications, both in concert with trophic links and on its own. When an exotic herbivore is removed from a multiply-invaded island, top-down control may cease to be the main force suppressing both exotic and native plant populations. In the new, herbivore-free setting, competition between native and exotic plants might play a bigger role in shaping who "wins." Invasive exotic plants often have life history traits such as large and frequent seed crops and short times to reproductive maturity (Mack 1996; Rejmanek and Richardson 1996). These can provide a competitive advantage over island natives and endemics, so that the winners of these "contests" at least in the short term are, unfortunately, often the exotics. Variations on this shift from top-down to competition-driven threats posed by exotics have followed pig, sheep, goat, rabbit, and other herbivore eradications on islands around the world, in the Channel Islands U.S.A, Mauritius, Oceania, the Galapagos, Hawaii, and Mexico, among other locations.

The removal or control of a single exotic plant species from an ecosystem containing multiple exotic plants can also produce competition-mediated releases, with discouraging results. Mack and Lonsdale (2002) provide several examples of exotic plant removals on land and in aquatic systems that appear to have led to increases of other exotic plant populations released from competition, with no clear benefits to native biota. Exotic plant removal may achieve desirable results only if all invasive species present are targeted together, or if native plants are actively restored to prevent other exotics from grabbing resources freed by the removal.

Habitat and indirect interactions

The second class of interaction that can complicate eradication planning and execution is a positive association between a native and an exotic species. Elsewhere in this volume, Carter and Bright (2002) describe how exotic but non-invasive Japanese red cedar (*Cryptomeria japonica*) plantations on the island of Mauritius provide refuges for native birds from introduced predatory macaques (*Macaca fascicularis*). In a case like this, removal of an exotic species (Japanese red cedar) would indirectly increase the impacts of another exotic species on endemics with high conservation value. In the western U.S.A, large areas of invasive saltcedar (*Tamarix ramosissima*) trees have replaced the historical riparian forest habitat of the endangered south-western willow flycatcher (*Empidonax trailii* var. *extimus*) (USFWS 1997). In these areas, the flycatcher now depends on the invasive saltcedar as nesting habitat. Large-scale removal of these saltcedar stands without accompanying native forest restoration could, some government officials argue, threaten the endangered songbird. Saltcedar control within the range of the flycatcher will likely need to include careful planning and restoration measures to meet the requirements of the U.S. Endangered Species Act.

A third class of species interaction, which can create a need for significant post-eradication restoration work, is an indirect negative effect of an exotic on native species that persists after the removal of the exotic. The clearest examples of this type of interaction involve exotic plants that alter site properties. Invasive iceplant (*Mesembryanthemum crystallinum*) salinises soils so much that native vegetation may not be able to recolonise after its removal (El-Ghareeb 1991; Vivrette and Muller 1977). Restoration of iceplant-invaded areas on Santa Barbara Island, Channel Islands National Park, U.S.A is expected to require substantial soil restoration measures beyond the removal of the exotic plant (Philbrick 1972; Halvorson 1994). Similarly, invasive trees and shrubs of the genus *Tamarix* in the south-western United States salinise streamside soils to levels not tolerated by many native organisms (Jackson *et al*. 1990; Busch and Smith 1995; Shafroth *et al*. 1995; Wiesenborn 1996). Nitrogen-fixing plants, such as invasive Scotch broom (*Cytisus scoparius*) and French broom (*Genista monspessulana*) in coastal California, U.S.A, can increase soil nitrogen availability over time (Bossard *et al*. 2000). When these species are removed from long-invaded sites, this high nutrient availability can increase site susceptibility to re-invasion by exotic annuals (K. Haubensak pers. comm.). In cases like these, altered site conditions might recover over time without intervention. Leaving these kinds of sites to recover on their own, though, can come at cost. Soil erosion, susceptibility to re-invasion, and an absence of forage and habitat for native animals all could create bigger and more costly management challenges than pursuing active site restoration from the start.

With eradications taking place in increasingly complex and altered settings, a wide range of unexpected outcomes are possible (Table 2). Some of these potential outcomes are less likely than others because the particular conditions required to produce them are rare, such as the case of a predator removal releasing exotic plant populations through cascading changes in ecosystem interaction webs. Others, such as the failure of a reduced or extinct native population to recover, or the ecological release of an exotic competitor or prey species, occur with undeniable regularity. Are these "side-effects" of well-intentioned eradications just noise around overwhelmingly successful conservation projects, or can they completely undo the good intentions of an eradication project and create even more serious problems? The answer is probably both, depending on context and on the steps taken to cope with them before and while they occur.

What we can do

Removing exotic species from ecosystems is rarely an end in itself. The ultimate goal of most eradications should be to restore the diversity and functioning of native ecosystems (but see Browns Island case (Veitch 2002)). Most practitioners now recognise this objective, so narrow definition of the goals of eradication is not really a problem. For instance, nearly every eradication case study in this volume specifies its goal in terms of allowing recovery, protecting native species, restoring biological diversity, or some other aspect of conservation.

What fewer of these case studies describe is an active pursuit of their conservation goals, through specific steps like restoration planning or monitoring. This may be partly because the focus of this volume is the process of eradication itself. Still, fewer than half of the case studies in this volume mention any pre- or post-eradication monitoring other than search for missed target individuals and immediate non-target effects. Given the explicit conservation and restoration goals of most eradication projects, this is surprising. Without pre-eradication evaluation of a project's context, managers cannot reliably avert or plan for the undesired side effects of eradication in a complex setting. Without at least some post-eradication monitoring, managers cannot possibly catch totally unanticipated side effects or know whether and when to implement contingency plans for dealing with undesired outcomes.

Table 2 Potential, undesired effects of exotic species removals. Removals of exotic plants, herbivores, and predators (top row) can alter interactions with other exotic and native species in an ecosystem (left columns) in ways that move the system further from a desired state (table cells). Exotic species removals can also be insufficient to permit natural ecosystem recovery, as when exotic plants have rendered site conditions inappropriate for native establishment. See text for further discussion. Bolded statements indicate outcomes documented by at least one case study discussed in this paper or elsewhere.

Species affected		Exotic species removed		
		Plant	Herbivore	Predator
Plant	exotic	**Competitive release**	**Top-down release**	Cascading release
	native	**Site alteration prevents recovery**	**Small population prevents recovery**	Loss of dispersal vector
Herbivore	exotic	Food switching to native plant	Competitive release	**Top-down release**
	native	**Loss of protection/habitat**	Small population prevents recovery	**Small population prevents recovery**
Predator	exotic	**Thrive in native vegetation**	**Switch to native prey**	Competitive release
	native	Loss of protection/habitat	Decline due to absence of prey	

Leveraging information to guide eradication

Without post-eradication follow-up, eradication experts as a community also cannot accumulate valuable knowledge about project outcomes. Cromarty *et al.* (2002) identify a need not only to define long-term restoration goals, but also to better understand the downstream effects of removing exotics. We need both of these pieces: only by understanding downstream effects can we determine how to meet those long-term goals, and only specific, defined long-term goals can consistently guide decisions that produce (mostly) the "right" downstream effects and not (as many of) the "wrong" ones. In the long run, knowledge accumulated through consistent follow-up monitoring is a major way for the global eradication community to improve and refine its techniques and to communicate the importance of invasive species removals to new and sometimes sceptical audiences.

While avoiding surprise outcomes and improving eradication techniques require understanding the ecological systems where eradications take place, this understanding has to come with the recognition that many islands are, to varying degrees, in states of crisis. There are costs to waiting for information to be gathered. As much as possible, research needs to be incorporated into actual conservation projects. Short-term, pre-eradication studies can provide useful insights into potential ecosystem responses to an invasive species removal. For example, careful, pre-eradication food trial experiments to quantify the plant food preferences of introduced rabbits on islands have qualitatively predicted plant community responses to rabbit eradication on small, simple islands with very few plant species and no other exotic herbivores (Donlan 2000). These kinds of studies may not work as well, though, in the complex settings where predictive tools are most needed. The same food preference trials yielded little information on islands with modestly diverse (<50 species) floras and multiple exotic herbivores (E. Zavaleta and B. Tershy, unpub. data) (Fig. 2). Constructing exclosures while exotic herbivores are still present can also provide a window into how vegetation might respond to herbivore removal in more complex settings. Interannual and spatial variability and time lags in community response, however, all limit the ability of one or a few years of exclosure data to predict an entire island's response over decades.

Fig. 2 A feral rabbit (*Oryctolagus cuniculus*) selects an exotic forb (*Tribulus cistoides*) over an endemic bunchgrass (*Aristida pansa*) in a food preference trial on Clarion Island, Mexico.

Within the planning of any given eradication, then, a better alternative to collecting large quantities of information in search of clear answers might be to identify the *minimum* information necessary to suggest wise decisions. Models exist for how to both identify and use minimum necessary information in this way. Qualitative assessment methods, such as decision trees (Reichard and Hamilton 1997) and rule-based models (Starfield *et al*. 1989; Starfield 1990) allow one to characterise a species or a whole system with little or no quantitative information. For example, the North American woody invaders decision tree of Reichard and Hamilton (1997) allows one to assess whether any woody species is safe to import based on yes/no answers to two to seven questions about its basic ecology. It should also be possible to improve decisions about island eradication planning with a qualitative understanding of key aspects of the island's condition and ecology. Basic knowledge of the exotic species present in a system, the likelihood for interactions among them and with native species, and the extent of damage they have caused can flag areas to consider more carefully in eradication planning. Figure 3 provides a rough example of what such a planning guide could look like for island eradications. It starts with three qualitative questions about the ecology of the island on which eradication is to take place:

- Is there (or could there be) more than one exotic species on the island?
- Has the target species eliminated or greatly reduced any native populations on the island?
- Has the target species altered site conditions in any long-term way, such as severe soil erosion or salinisation?

If the answer to any of these questions is "yes," planners could consider additional questions about the eradication and restoration process. Perhaps the most critical aspect of this process is the evaluation of tradeoffs before taking action: what are the worst-scenario costs of proceeding with no further planning or information? And what are the worst-scenario costs of waiting? In some cases the best strategy for avoiding disaster, such as an extinction, may still be to proceed with immediate eradication. In other situations, the best strategy may call for adding "surveillance" steps, such as post-eradication monitoring to catch unwanted changes early, or "action" steps, such as native species re-seeding/re-introduction in conjunction with exotic species removal (see Zavaleta *et al*. 2001) or simultaneous removal of more than one species (Murphy *et al.* 1998).

Often, the single best strategy, from a holistic conservation standpoint, will not be obvious because outcomes cannot be fully predicted. On Clarion Island in the Revillagigedo Archipelago, Mexico, exotic rabbit, sheep,

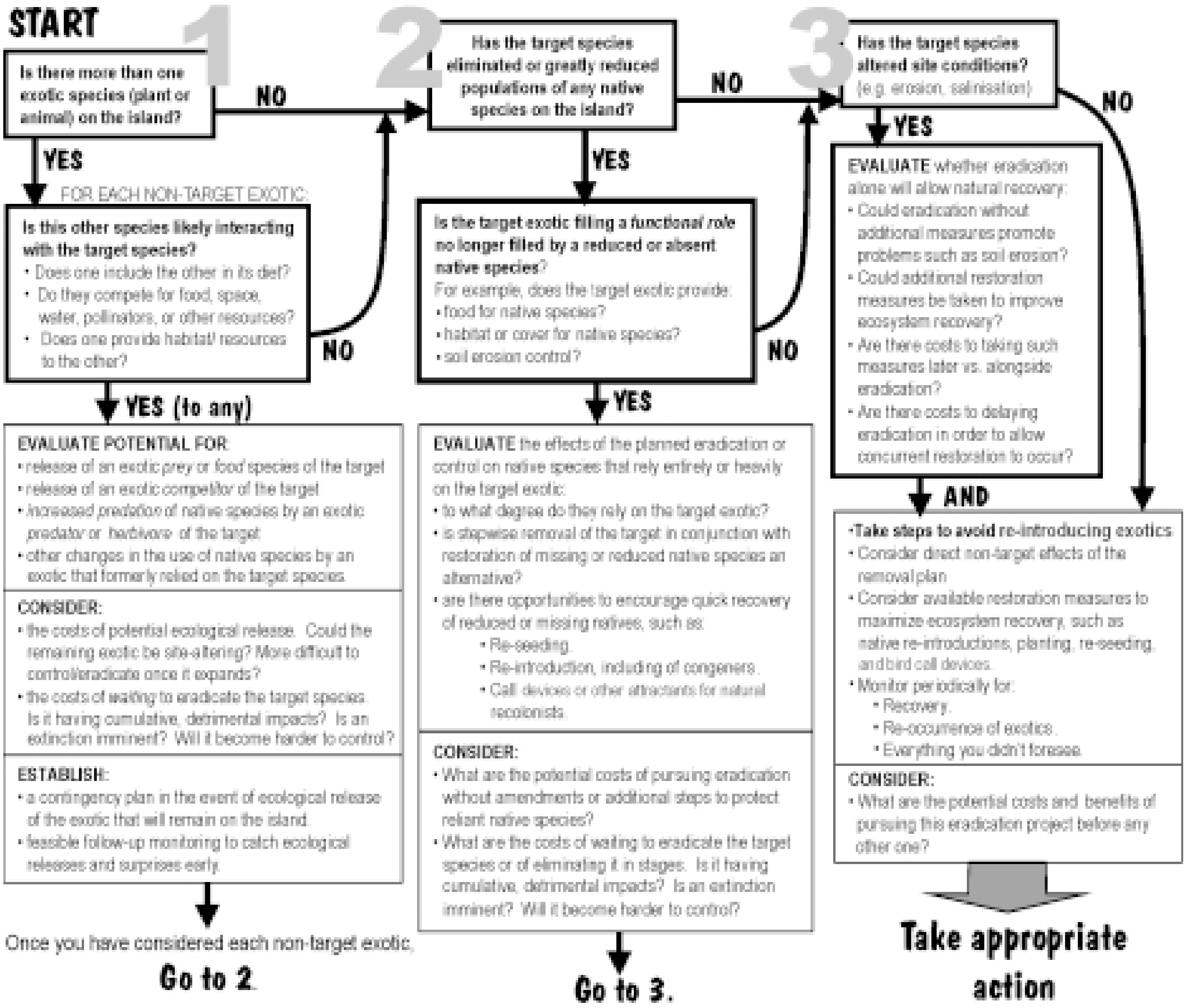

Fig. 3 A prototype planning guide for averting unexpected eradication outcomes on islands. To walk through issues to consider for a particular eradication project, start with the upper left-hand box (START). Use your yes/no answers to choose which arrow to follow from each *question box* (thick outline). When you reach a *guideline box* (thin outline), read through it then follow the arrow from it to the next step.

and pig eradication will almost certainly reduce widespread areas of bare soil throughout the island, stemming topsoil erosion and aiding recovery of heavily impacted native species such as a potentially endemic variety of *Opuntia englemanii* (Fig. 4; pers. obs.). However, small to significant (>1 ha) patches of up to seven new noxious exotic weeds, including Bermuda grass (*Cynodon dactylon*) and bufflegrass (*Cenchrus echinatus*), exist near the island's inhabited military garrison. If these exotic plants spread over large areas of the island when released from herbivory pressure, they may become impossible to ever remove. Little information exists, however, to suggest whether exotic plant release in this setting is a likely outcome. A pre-emptive, costly, multi-year weed eradication attempt before eradicating herbivores could safeguard against potential exotic plant spread but is riskier than immediate herbivore eradication from the standpoint of reversing declines in seabird populations, soil conditions, and certain native plant populations. The many unknowns complicating this weighing of options include how native and exotic plant species will respond to herbivore removal, whether the spread of new exotics would negatively affect island biodiversity and functioning more than feral herbivores do, and how imminent are threats of extirpation or extinction to certain native species.

Planners cannot, in this very typical kind of situation, presage the optimum path to complete island restoration. What they *can* do is to choose a first step wisely, identify outcomes to this step that they absolutely want to avoid, qualitatively evaluate the likelihood of such outcomes, and take steps to prevent them. Eradications have been a singularly effective conservation tool on islands; they have helped save numerous species from extinction and numerous ecosystems from collapse. Eradications can do more. As eradication advances in a technical sense, with ever-improving baits and traps, hunting strategies, and hard tools, its practitioners should also strive towards the state-of-the-art in an ecological sense. This means taking ad-

Fig. 4 Prickly pear (*Opuntia englemanii*), once widespread in the lowlands of Clarion Island, Mexico, now survives only on rocky outcrops that protect it from feral herbivores.

vantage of a different set of tools – monitoring, species reintroduction and translocation, revegetation and erosion control, and qualitative, systems-level ecology. It means placing more emphasis on achieving and verifying, not just identifying, long-term ecosystem restoration goals. As knowledge about the ecological context of eradications evolves alongside technical expertise, the conservation value of invasive species management can only grow.

ACKNOWLEDGMENTS

I thank H. A. Mooney and R. J. Hobbs for helping to spawn many of these ideas, and M. N. Clout, A. Saunders, B. R. Tershy, C. R. Veitch, and two anonymous reviewers for their helpful comments and advice. This project was supported by The Nature Conservancy's David H. Smith Fellowship program and the U.S Environmental Protection Agency STAR Fellowship Program.

REFERENCES

Algar, D. A.; Burbidge, A. A. and Angus, G. J. 2002. Cat eradication on Hermite Island, Montebello Islands, Western Australia. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 14-18. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Allwood, A. J.; Vueti, E. T.; Leblanc, L. and Bull, L. 2002. Eradication of introduced *Bactrocera* species (Diptera: Tephritidae) in Nauru using male annihilation and protein bait application techniques. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 19-25. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Atkinson, I. 1989. Introduced animals and extinctions. In D. Western and M. Pearl. (eds.). Conservation for the twenty-first century, pp. 54-69. Oxford, New York.

Bell, B. D. 2002. The eradication of alien mammals from five offshore islands, Mauritius, Indian Ocean. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 40-45. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Bloomer, J. P. and Bester, M. N. 1990. Diet of a declining feral cat *Felis catus* population on Marion Island. *South African Journal of Wildlife Research 20*:1-4.

Bloomer, J. P. and Bester, M. N. 1992. Control of feral cats on sub-Antarctic Marion Island, Indian Ocean. *Biological Conservation 60*: 211-219.

Bossard, C. C.; Randall, J. M. and Hoshovsky, M. C. 2000. Invasive Plants of California's Wildlands. University of California Press, Berkeley.

Brown, K. P. and Sherley, G. H. 2002. The eradication of possums from Kapiti Island, New Zealand. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 46-52. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Bullock, D. J.; North, S. G.; Dulloo, M. E. and Thorsen M. 2002. The impacts of rabbit and goat eradication on the ecology of Round Island, Mauritius. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 53-63. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Burbidge, A. A. and Morris, K. D. 2002. Introduced mammal eradications for nature conservation on Western Australian islands: a review. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 64-70. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Busch, D. E. and Smith, S. D. 1995. Mechanisms Associated with Decline of Woody Species in Riparian Ecosystems of the Southwestern US. *Ecological Monographs 65*: 347-370.

Carter, S. P. and Bright, P. W. 2002. Habitat refuges as alternatives to predator control for the conservation of endangered Mauritian birds. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 71-78. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Chapin, F. S.; Zavaleta, E. S.; Eviner, V. T.; Naylor, R. L.; Vitousek, P. M.; Sala, O. E.; Reynolds, H. L.; Hooper, D. U.; Mack, M.; Diaz, S. E.; Hobbie, S. E. and Lavorel, S. 2000: Consequences of changing biodiversity. *Nature 405*: 234-242.

Coulston, G. J. 2002. Control of invasive plants on the Poor Knights Islands. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 79-84. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Crafford, J. E. 1990. The role of feral house mice in ecosystem functioning on Marion Island. Pages 359-364 in K. R. Kerry and G. Hempel. (eds.). Antarctic Ecosystems: Change and Conservation. Springer-Verlag, Berlin.

Cromarty, P. L.; Broome, K. G.; Cox, A.; Empson, R. A.; Hutchinson, W. M. and McFadden, I. 2002. Eradication planning for invasive alien animal species on islands – the approach developed by the New Zealand Department of Conservation. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 85-91. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Dixon, I. R.; Dixon K. W. and Barrett, M. 2002. Eradication of buffel grass (*Cenchrus ciliaris*) on Airlie Island, Pilbara Coast, Western Australia. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 92-101. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Donlan, C. J. 2000. Islands and introduced herbivores: using conservation to investigate top-down and bottom-up processes. M. A. University of California-Santa Cruz, Santa Cruz, CA.

Eckhardt, R. C. 1972. Introduced plants and animals in the Galapagos Islands. *Bioscience 22*: 587-590.

El-Ghareeb, R. 1991. Vegetation and soil changes induced by *Mesembryanthemum crystallinum* L. in a Mediterranean desert ecosystem. *Journal of Arid Environments 20*: 321-330.

Fitzgerald, B. M. 1988. Diet of domestic cats and their impact on prey populations. In D. C. Turner. (ed.). The domestic cat: the biology of its behaviour, pp. 123-146. Cambridge University Press, Cambridge.

Fitzgerald, B. M.; Karl, B. J. and Veitch, C. R. 1991. The diet of feral cats (*Felis catus*) on Raoul Island, Kermadec Group. *NZ Journal of Ecology 15*: 123-129.

Flint, E. and Rehkemper, C. 2002. Control and eradication of the introduced grass, *Cenchrus echinatus*, at Laysan Island, Central Pacific Ocean. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 110-116. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Frenot, Y.; Masse, L.; Gloaguen, J. C. and Lebouvier, M. 2001. Human activities, ecosystem disturbance and plant invasions on subantarctic Crozet, Kerguelen, and Amsterdam Islands. *Biolical Conservation 101*: 33-50.

Fretwell, S. D. 1987. Food chain dynamics: the central theory of ecology? *Oikos 50*: 291-301.

Hairston, N. G.; Smith, F. E. and Slobodkin, L B. 1969. Community structure, population control, and competition. *American Naturalist 94*:421-425.

Halvorson, W. L. 1994. Ecosystem Restoration on the California Channel Islands. In W. L. Halvorson and G. J. Maender. (eds.). The Fourth California Islands Symposium: Update on the Status of Resources, pp. 485-490. Santa Barbara Museum of Natural History, Santa Barbara.

Hammond, M. E. R. and Cooper, A. 2002. *Spartina anglica* eradication and inter-tidal recovery in Northern Ireland estuaries. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 124-132. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

IPCC. 2001. Working Group 1 Third Assessment Report. Cambridge University Press, Cambridge.

Jackson, J.; Ball, J. T. and Rose, M. R. 1990. Assessment of the salinity tolerance of eight Sonoran desert riparian trees and shrubs. Final Report Bureau of Reclamation, Yuma, AZ.

Kessler, C. C. 2002. Eradication of feral goats and pigs and consequences for other biota on Sarigan Island, Commonwealth of the Northern Mariana Islands. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species,* pp. 132-141. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Klinger, R. C.; Schuyler, P. T. and Sterner, J. D. 1994. Vegetation response to the removal of feral sheep from Santa Cruz Island. In W. L. Halvorson and G. J. Maender. (eds.). The Fourth California Islands Symposium: Update on the Status of Resources, pp. 341-350. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Klinger, R. C.; Schuyler, P. T. and Sterner, J. D. 2002. The response of herbaceous vegetation and endemic plant species to the removal of feral sheep from Santa Cruz Island, California. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 141-154. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Laughrin, L.; Carroll, M.; Broomfield, A. and Carroll, J. 1994. Trends in vegetation changes with removal of feral animal grazing pressures on Santa Catalina Island. In W. L. Halvorson and G. J. Maender. (eds.). The Fourth California Islands Symposium: Update on the Status of Resources, pp. 523-530. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Lovegrove, T. G.; Zeiler, C. H.; Greene, B. S.; Green, B. W.; Gaastra, R. and MacArthur, A. D. 2002. Alien plant and animal control and aspects of ecological restoration in a small 'mainland island': Wenderhom Regional Park, New Zealand. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 155-163. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Mack, R. N. 1996. Predicting the identity and fate of plant invaders: emergent and emerging approaches. *Biological Conservation 78*: 107-112.

Mack, R. N. and Lonsdale, W. M. 2002. Eradicating invasive plants: hard-won lessons for islands. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 164-172. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

McKinney, M. L. 1998. On predicting biotic homogenization: species-area patterns in marine biota. *Global Ecology and Biogeography Letters 9*: 297-301.

Merton, D.; Climo, G.; Laboudallon, V.; Robert, S. and Mander, C. 2002. Alien mammal eradication and quarantine on inhabited islands in the Seychelles. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 182-198. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Micol, T. and Jouventin, P. 2002. Eradication of rats and rabbits from Saint-Paul Island, French Southern Territories. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 199-205. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Mooney, H. A. and Hobbs, R. J. (eds.). 2000. Invasive Species in a Changing World. Island Press, Washington.

Moro, D. 2002. Comparison of baits and bait stations for the selective control of wild house mice on Thevenard Island, Western Austrailia. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 213-218. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Morris, K. D. 2002. The eradication of the black rat *(Rattus rattus)* on Barrow and adjacent islands off the north-west coast of Western Australia. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 219-225. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Mowbray, S. C. 2002. Eradication of introduced Australian marsupials (brushtail possum and brushtailed rock wallaby) from Rangitoto and Motutapu Islands, New Zealand. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 226-232. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Murphy, E. and Bradfield, P. 1992. Change in diet of stoats following poisoning of rats in a New Zealand forest. *NZ Journal of Ecology 16*: 137-140.

Murphy, E. C.; Clapperton, B. K.; Bradfield, P. M. F. and Speed, H. J. 1998. Effects of rat-poisoning operations on abundance and diet of mustelids in New Zealand podocarp forests. *NZ Journal of Zoology 25*: 315-328.

North, S. G.; Bullock, D. J. and Dulloo, M. E. 1994. Changes in the vegetation and reptile populations on Round Island, Mauritius, following eradication of rabbits. *Biological Conservation 67*: 21-28.

Pace, M. L. and Cole, J. J. 1996. Regulation of bacteria by resources and predation tested in whole lake experiments. *Limnology and Oceanography 41*: 1448-1460.

Pace, M. L.; Cole, J. J.; Carpenter, S. R. and Kitchell, J. F. 1999: Trophic cascades revealed in diverse ecosystems. *Trends Ecology and Evolution 14*: 483-488.

Parkes, J. P.; Macdonald, N. and Leaman, G. 2002: An attempt to eradicate feral goats from Lord Howe Island. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 233-239. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Philbrick, R. N. 1972. The plants of Santa Barbara Island, California. *Madrono 21*: 329-393.

Polis, G. A. 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos 86*: 3-15.

Polis, G. A. and Strong, D. R. 1996. Food web complexity and community dynamics. *American Naturalist 147*: 813-846.

Reichard, S. H. and Hamilton, C. W. 1997. Predicting invasions of woody plants introduced into North America. *Conservation Biology 11*: 193-203.

Rejmanek, M. and Richardson, D. M. 1996. What attributes make some plant species more invasive? *Ecology 77*: 1655-1661.

Rippey, E.; Rippey, J. J. and Dunlop, N. 2002. Management of indigenous and alien Malvaceae on islands near Perth, Western Australia. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 254-259. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Roemer, G. W.; Donlan, C. J. and Courchamp, F. 2002. Golden eagles, feral pigs, and insular carnivores: How exotic species turn native predators into prey. *Proceedings of the National Academy of Sciences 99*: 791-796.

Roy, S. S.; Jones, C. G. and Harris, S. 2002. An ecological basis for control of the mongoose *Herpestes javanicus* in Mauritius: is eradication possible? In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 266-273. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Schuyler, P. T.: Garcelon, D. K. and Escover, S. 2002. Eradication of feral pigs *(Sus scrofa)* on Santa Catalina Island, California, USA. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 274-286. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Scowcroft, P. G. and Conrad, C. E. 1992. Alien and native plant response to release from feral sheep browsing on Mauna Kea. In C. P. Stone, C. W. Smith, and J. T. Tunison. (eds.). Alien Plant Invasions in Native Ecosystems of Hawai'i: Management and Research, pp. 625-665. Univ. of HI Cooperative National Park Resources Studies Unit, Honolulu.

Shafroth, P. B.; Friedman, J. M. and Ischinger, L. S. 1995: Effects of salinity on establishment of *Populus fremontii*(cottonwood) and *Tamarix ramosissima* (saltcedar) in southwestern United States. *Great Basin Naturalist 55*: 58-65.

Simberloff, D. 1995. Why do introduced species appear to devastate islands more than mainland areas? *Pacific Science 49*: 87-97.

Simberloff, D. 2002. Today Tiritiri Matangi, tomorrow the world! Are we aiming too low in invasives control? In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 4-13. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Starfield, A. M. 1990. Qualitative, rule-based modeling. *Bioscience 40*: 601-605.

Starfield, A. M.; Farm, B. P. and Taylor, R. H. 1989. A rule-based ecological model for the management of an estuarine lake. *Ecological Modelling 46*: 107-119.

Terborgh, J.; Estes, J. A.; Paquet, P.; Ralls, K.; Boyd-Heger, D.; Miller, B. J. and Noss, R. F. 1999. The role of top carnivores in regulating terrestrial ecosystems. In M. E. Soule and J. Terborgh. (eds.). Continental conservation: scientific foundations of regional reserve networks, pp. 39-64. Islands Press, Washington.

Torr, N. 2002. Eradication of rabbits and mice from subantarctic Enderby and Rose islands. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 319-328. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

USFWS. 1997. Endangered and Threatened Wildlife and Plants: Final Determination of Critical Habitat for the Southwestern Willow Flycatcher. *Federal Register 62*: 39129-39147.

Varnham, K. J.; Roy, S. S.; Seymour, A.; Mauremootoo, J.; Jones, C. G. and Harris, S. 2002: Eradicating Indian musk shrews (*Suncus murinus*, Soricidae) from Mauritian offshore islands. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 342-349. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Veitch, C. R. 1994. Habitat repair: a necessary prerequisite to translocation of threatened birds. In Serena, M. (ed.). Reintroduction biology of Australian and New Zealand Fauna, pp. 97-104. Chipping Norton, Surrey Beatty & Sons.

Veitch, C. R. 2002. Eradication of Norway rats *(Rattus norvegicus)* and house mice *(Mus musculus)* from Brown Island (Motukorea), Hauraki Gulf, New Zealand. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species*, pp. 350-352. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Vivrette, N. J. and Muller, C. H. 1977. Mechanism of invasion and dominance of coastal grassland by *Mesembryanthemum crystallinum*. *Ecological Monographs 47*: 301-318.

West, C. J. 2002. Eradication of alien plants on Raoul Island, Kermadec Islands, New Zealand. In Veitch, C. R. and Clout, M. N. (eds.). *Turning the tide: the eradication of invasive species,* pp. 365-373. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Whittaker, R. J. 1998. *Island biogeography: ecology, evolution, and conservation.* Oxford University Press, Oxford.

Wiesenborn, W. D. 1996. Saltcedar impacts on salinity, water, fire frequency, and flooding. In Proceedings of the saltcedar management workshop, Rancho Mirage, CA., pp. 9-12

Zavaleta, E. S.; Hobbs, R. H. and Mooney, H. A. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends Ecology and Evolution 16*: 454-459.