Abstract  Invasive species can fundamentally alter island ecosystems, and eradication is often necessary to abate the threats they pose to native species. But just as the introduction of a species to an island can have profound ecological effect so too can its removal. While significant ecological effects are often the desired outcome of an eradication, unintended or undesired effects can also manifest. One such undesired effect may be that due to the ecological change following removal of a pest, a different pest becomes more of a threat or more difficult to manage. Such risks may be reduced by eradicating multiple pests simultaneously, or if sequentially, in a manner that anticipates trophic cascades and first exploits the ecological impact of one pest to help render another more susceptible to control. To illustrate, I present a case study from Santa Cruz Island (250 km$^2$), 40 km off Santa Barbara, California, USA. For nearly two centuries, non-native species caused widespread destruction of natural communities, until recent decades when the most damaging of them were removed – some sequentially, others concurrently. I review that history and outline strategic considerations based on the ecological relationships of the managed non-native species, which include sheep, pigs, golden eagles, and wild turkeys. This case study highlights how addressing pest management issues comprehensively can not only reduce cost and investment risk in island restoration programmes; it can also sooner abate key threats to often unique and often imperilled island biota.

Keywords: California, efficiency, eradication, planning, risk, Santa Cruz Island

INTRODUCTION

Invasive alien species can devastate island ecosystems and eradication is often necessary to protect native biota. Species targeted for eradication are typically those that have a profound impact on island resources, so it follows that their removal may have similarly profound effects. Dramatic ecological responses following eradication programmes have been observed (e.g., Howald et al. 2010), ranging from desired to undesired. These responses may or may not include those anticipated when the eradication was planned.

Perverse outcomes of eradications are perhaps more likely when there are multiple invasive species and the removal of one favours another (Zavaleta et al. 2001). Given the pervasiveness of invasive species and the severity of their impacts on naïve ecosystems, many, if not most, islands face multiple challenges from invasive species in need of management. In these situations, managers must determine how to invest limited funds to maximise desired outcomes, while minimising those that are undesired and or unexpected. However, this planning is frustrated by imperfect understanding of the myriad direct and indirect interactions in ecological communities. Modelling can be informative (e.g., Russell et al. 2009), but also unlikely to capture the full array of synergistic relationships, trophic complexity, and management constraints. Case studies can also be illuminating, although compared with single species efforts, the literature contains few examples where multiple invasive species have been managed.

Here I provide an overview of efforts to manage multiple invasive species over three decades on Santa Cruz Island, California, USA. Some of these pests were managed in series, others more or less simultaneously. Reviewing that history provides an opportunity to examine how understanding and exploiting the trophic relationships among pests and native flora and fauna can reduce the risks of perverse outcomes in eradication, and increase the efficiency of pest management and therefore island restoration.

CASE STUDY: SANTA CRUZ ISLAND

Santa Cruz Island is the largest of the eight Channel Islands off mainland southern California. The 250 km$^2$ island is co-owned and managed by The Nature Conservancy (TNC) and the United States National Park Service (NPS). The island has two rugged mountain ranges flanking a fault valley and experiences a Mediterranean-type climate of cool, wet winters and warm, dry summers. Vegetation communities are predominantly grassland, coastal scrub, chaparral, oak woodland, and pine forest. Four terrestrial nonvolant mammals are native to the island: island fox (Urocyon littoralis santacruzae), island spotted skunk (Spilogale gracilis amphiala), deer mouse (Peromyscus maniculatus santacruzae), and western harvest mouse (Reithrodontomys megalotis santacruzae).

For much of the past two centuries, Santa Cruz Island was used for ranching and agriculture. Sheep (Ovis aries) and pigs (Sus scrofa) introduced in the 1850s soon established feral populations that ranged throughout the island. Seven wild turkeys (Meleagris gallopavo) were introduced to the island in 1975. In 1978, TNC acquired 90% of the island. Channel Islands National Park was established in 1980, and in 1997 NPS acquired the remaining 10% of the island. Pest problems facing managers ranged from feral honeybees (Apis mellifera) and cattle (Bos taurus), to noxious forbs and weedy trees. Remarkably, there are no non-native rodents or feral cats.

Direct and indirect impacts of non-native ungulates have been implicated in threats to the survival of at least nine species of plants on the island (NPS 2002). In the late 1990s-early 2000s, the island fox population also underwent a precipitous decline. Golden eagles (Aquila chrysaetos), which had not previously been resident on the island, established a small population, likely due to an abundant food supply provided by feral pigs (Roemer et al. 2002). Incidental predation by eagles led to the Santa Cruz Island fox being listed as federally endangered in 2004.

Over the past 30 years of conservation management of the island, numerous programmes have been implemented to remove pests. Below I discuss some of those efforts and highlight lessons that may apply generally to island managers facing a similar need to control multiple species.

Managing pests in series

Sheep and cattle caused extensive degradation and destruction of native vegetation (Van Vuren 1981). In the 1980s, sheep were eradicated from 90% of the island (Schuyler 1993) and in the late 1990s from the remaining 10% of the island (Faulkner and Kessler 2011). Cattle were removed in 1988.

Release from herbivory triggered a dramatic vegetation response that had cascading ecological effect. Many native vegetation communities rebounded. For example, in 1985 bare ground and grassland covered nearly three-quarters of...
Feral pigs perhaps facilitated its spread via vegetation recovery began on Santa Cruz Island, there would have been greater efficiency of eradication at that time because there was less vegetation to conceal the pigs. On Santa Cruz Island, 77% of the pigs were dispatched by a shooter from a helicopter (Parkes et al. 2010). Given that aerial hunting is more efficient in open habitat, having more open habitat (Fig. 1) would likely have led to a programme that was more cost and time efficient.

Meanwhile, throughout the 1980s and 1990s, the population of wild turkey remained at 40–50 birds in the vicinity of the initial introduction (P. Schuyler pers. comm.). In the early 2000s, however, their numbers increased >5-fold from 46 in 1999 to 276 in 2006 (L. Laughrin, UC Santa Barbara, unpublished data). Various trophic relationships may have contributed to that increase: turkeys may have been released from top-down control following the decline of the island fox population; perhaps turkeys benefited from a bottom-up increase in resources with the recovery of native vegetation following the sheep eradication, decades prior, and the island was turning into better turkey habitat (Fig. 1). Although its cause was unknown, the turkey population trend was especially problematic with pigs having just been removed from the system. Feral pigs are opportunistic omnivores (Wilcox and Van Vuren 2009) that likely competed with turkeys for food such as acorns, invertebrates, and small vertebrates. The pigs also probably depredated eggs and poults of turkeys. Without pigs and with habitat quality improving, turkeys had few limits on abundance and dispersal, and so were on a trajectory of becoming more difficult to manage. Managers were concerned that a large population of turkeys, also opportunistic omnivores, could directly affect island resources and also have potentially serious indirect impacts as another food subsidy for golden eagles, which would exacerbate the threat to foxes (Fig. 2). For that reason, an intensive control effort was launched in 2006 (Morrison 2007). Monitoring suggests that today only two male “sentinel” turkeys remain on the island (unpublished data).

Managing pests concurrently

Direct and indirect relationships among pests brought a convergence of crises to Santa Cruz Island in the early 2000s. Feral pigs were pushing a number of plants precariously close to extinction, and their presence was subsidising a population of golden eagles that was driving the island fox to a similar fate (NPS 2003). In 2003, the fox population was estimated to be less than 100 (NPS 2003).

Multiple strategies were used to manage these issues (NPS 2003). In 1999, live capture and removal of golden eagles was initiated. In total, 32 free-flying eagles were captured, mostly in the first years of the programme; detection and capture efficiency declined considerably as the population was reduced (SCPBRG 2004; IWS...
In 2002, 12 foxes were placed in fenced enclosures to protect them from predation and to launch a captive breeding program; eventually the captive breeding program expanded to house approximately 20 paired foxes. Also in 2002 a programme was initiated to re-establish bald eagles (*Haliaeetus leucocephalus*) on the island (Sharpe and Garcelon 2005). Bald eagles had been extirpated from the Channel Islands in the mid-1900s likely due to pesticide contamination from marine-sourced food. It was hypothesised that territorial behaviour of the mostly piscivorous bald eagles could deter golden eagles from settling on the island (NPS 2002). Indeed, agonistic behaviour between these species of eagles became a key component of the overall fox recovery strategy.

Long-term success, however, depended upon removing feral pigs from the system. In 1999, preparations began for an eradication programme (Morrison et al. 2011). Planning for the eradication included assessments of ways in which trophic relationships might affect the likelihood of attaining the various management goals. For example, there was concern that the pig eradication could impaireagle capture efforts, because an abundance of carcasses might make killing them even less effective than it had already proven to be. To prevent carcasses of dispatched pigs from becoming a resource or attractant to eagles, the eradication contractor was required to move carcasses of any pigs dispatched in open areas into more densely vegetated areas where they would be concealed from foraging eagles. The greatest concern, however, was that the removal of the prey base provided by feral pigs would result in an intensification of hunting on island foxes by golden eagles. Some models suggested that that increased predation of foxes could have catastrophic consequences (Courchamp et al. 2003), leading some to advocate delay of the eradication program until all golden eagles had been removed from the island.

But delaying the eradication also had risks: What if the remaining eagles simply could not be captured (or killed, as some recommended)? What if removing pigs was in fact a prerequisite to being able to manage the last of the eagles? What if postponing the pig eradication effort jeopardised the ability to implement it at all, because the enabling factors that eradication projects need to succeed (see Morrison et al. 2011) would be difficult to reassemble? Managers assessed such questions on an ongoing basis. Ultimately, they decided to manage risks by advancing on multiple fronts: captive breeding of foxes; radio-collaring and frequent monitoring of a large portion of the wild fox population; population modelling and management planning for foxes (e.g., Bakker and Doak 2009); continuing efforts to capture golden eagles; removing the prey subsidy of feral pigs; re-establishing bald eagles; and maintaining materials on island to house more foxes in the event that predation rates became unsustainable and more foxes needed to be brought into temporary protective shelter. Thus, efforts to capture the remaining golden eagles were concurrent with the feral pig eradication.

As the onset of the pig eradication programme approached, sightings of golden eagles became exceedingly rare; their presence was mostly indicated by mortality signals from radio-collars of dead foxes. Spatial and temporal patterns of dead foxes were used to hone searches for eagles, estimate activity centres, and find nests. Nests were an important component of the capture strategy because the behaviour of nesting eagles was more predictable and so exploitable. In 2006, the nest of the last known breeding pair on the island was located, within days of egg hatching (IWS 2006). Although the removal of the young from the nest would have eliminated the eagles’ immediate need to provision transportable (i.e., fox-sized) prey, nesting was allowed to continue to improve the likelihood of ultimately catching the parent birds. Monitoring of radio-collared foxes was intensive during this period, and it revealed a growing tally of dead foxes from the vicinity of the nest. However, population models indicated that the overall fox population could withstand that associated increased mortality. Approximately seven weeks later, both parent birds (and their chick) were captured and removed from the island (Morrison 2007). The remains of 13 island foxes were found in the nest (Collins et al. 2009).

The strategy of multiple concurrent pest management efforts appears to have been successful. Today, pigs are gone; there is no evidence golden eagles breed on the island; all of the foxes have been released from the captive facilities; and resident bald eagles breed on the island. The fox population is intensively monitored, and even though foxes are still occasionally depredated by (presumably resident) golden eagles, the fox population has very high annual survival rates (96.2% +/- 0.022, 80% CI) and is rebounding (736 +/- 254 adults, 80% CI in 2008; V. J. Bakker, unpublished data). It is important to underscore that none of these efforts was guaranteed to succeed, and the fox-pig-eagle management crisis put considerable strain on the capacity of island managers. Facing such uncomfortably high stakes and dynamic circumstances, managers were fortunate to have a diverse group of external scientists and partners providing perspective (and often spirited discussion) on various alternatives for management. As a consequence, they were ultimately accountable for their decisions, having relevant and constructive input was invaluable for the necessarily adaptive implementation of the programme.

Current emphasis in pest management

Santa Cruz Island is now free of un-managed introduced mainland vertebrates. Intensive monitoring of island foxes continues. This includes maintaining an array of radio-collared foxes that serve as "sentinels" for predators and disease (Bakker and Doak 2009). With the near decade-long extinction crisis at bay, the focus can now move to other resource management priorities, such as revising biosecurity protocols to protect investments. Now that soil disturbing pests (pigs) are out of the system, comprehensive weed management programmes are underway (Knapp et al. 2009) with greater confidence in enduring returns.

Vegetation recovery on the island (Fig. 1) should bring continuing benefits to native species. For example, increased tall vegetation will likely reduce the vulnerability of foxes to aerial predators. Nevertheless, there is a need to remain vigilant for undesired effects. Wildfire, for example, was probably historically uncommon on the islands (Anderson et al. 2009). However, increasing fuels, including flashy non-native grasses, and human activity (e.g., public access) may increase likelihood of ignition. Vegetation recovery may yet usher in other trophic cascades involving pests. For example, invasive Argentine ants (*Linepithema humile*) currently occur in a few localised infestations on the island (see Randall et al. 2011). Argentine ants are limited by availability of water and sugars, and actively tend honeydew producing aphids and scales. As shrub cover increases, so might vegetation suitable for honeydew producing species. Increased higher stunted vegetation may also increase water inputs into the island ecosystem via moisture capture from fog – an otherwise desired positive feedback cycle for the island, but one that could also facilitate the invasion of Argentine ants.

HINDSIGHT

If we were to go back in time on Santa Cruz Island with the technological and methodological sophistication available in today’s eradication “tool box”, and ask how best to invest (always) limited resources to restore the island, we might ask two questions. The first is whether there is a “trophically strategic” sequence that the myriad pest
issues should be engaged. That sequence would be aimed at reducing the potential for pests to contribute to perverse outcomes, and at using the impact of one species to render others more tractable. In this regard, sheep might be considered a “keystone pest” on Santa Cruz Island as they suppressed weeds and probably affected habitat quality for pigs and turkeys. With hindsight, the turkeys should have been removed when they were still incipient invaders. If pigs were also removed ahead of sheep, it is possible that their numbers might have been lower and the feasibility of hunting and monitoring would have been enhanced due to the greatly reduced cover. While it is doubtful that fennel could have been fully eradicated, management to contain its spread was surely possible.

The second question we might ask is whether there would be benefits in engaging the pests concurrently. A comprehensive and concurrent approach would have had numerous benefits, including prevention of some of the observed perverse cascades, setting the island sooner on a recovery trajectory, and cost efficiency. Concerning the latter, when managers of Santa Cruz Island hired a professional wildlife management team to conduct the feral pig eradication, they brought in the island specialisation personnel and equipment, including a small helicopter. That expertise and resource was subsequently deployed to control turkeys and capture eagles. Use of capacity already on island for these other projects reduced the need to mobilise wholly separate efforts. It also made it possible to integrate the activities of the different projects and so reduce costs often encountered in projects like these that need to be implemented adaptively; teams often needed to wait for opportunities to engage that were unpredictable (e.g., some golden eagle capture strategies depended upon particular weather conditions and fortuitous sightings of birds).

Programmes designed to concurrently manage multiple pests can lead to greater effectiveness as well as efficiency. For example, as the pig eradication programme was transitioning from hunting to monitoring, some members of the pig hunting team were trained to identify priority pest plants, and tasked with mapping weeds island-wide using their helicopter, GPS, and database management expertise. The helicopter helped increase efficiency in mapping (Knapp et al. 2009) and in treating remote infestations that would have otherwise gone undetected or been difficult or unsafe to access. A co-benefit of this effort was that while conducting the weed work, the team also surveyed for pig sign – and so enhanced confidence that pigs had been eradicated. Ideally, synergistic activities like these that leverage limited funds to accomplish multiple restoration objectives would be built into programmes from the outset.

All that said, managers did have some constraints on their ability to sequence eradication efforts differently. For example, TNC was not authorised to control pigs until after it attained full property right in 1987. Moreover, the technological and methodological advances that today make concepts like concurrent multi-taxa eradication on an island of this size feasible were not yet established. Thus, this retrospective is not intended to critique decisions that were made. Rather, it is to take advantage of a vantage provided by multiple decades of eradication efforts to extract lessons that might inform future programmes.

DISCUSSION

The various pest management programmes on Santa Cruz Island have been essential to the protection of the island’s unique native flora and fauna. That is not to say there have not been undesired or unanticipated effects. Given the degraded state of many islands and the complexity of their community dynamics, the unexpected should be expected. Planning must therefore be rigorous, and there needs to be strategic investment in monitoring so that risks to island resources can be identified and managed.

I acknowledge that this overview is largely anecdotal. There may be many hypotheses to explain apparent cascades, and causality can be difficult to determine (e.g., Bergstrom et al. 2009a, b; Dowding et al. 2009). The surprising and experimental demonstration is necessary to demonstrate some of the trophic relationships discussed here were mostly absent. This lack of comprehensive monitoring is not atypical; it reflects the real resource constraints many island managers face. When action is imperative and funding is limited, an unfortunate trade-off is often research and monitoring. Fortunate for the conservation management of Santa Cruz Island is that the island is the focus of much ecological research, so the monitoring investments managers could afford were augmented by the work of external scientists who helped keep a pulse on the system and brought to light issues requiring management attention. This is important because cascades can play out over very long timeframes (e.g., Fig. 1) and anticipating the variables important to measure can be difficult. It would have been arguably impossible, for example, to predict that the pig eradication might lead to the island specialisation of carnivore predation or extinction of foxes due to hyperpredation by a novel predator.

When there are gaps in monitoring, however, questions about effects of management actions can linger. For example, did the availability of carcasses during the sheep eradication on Santa Cruz Island and or the pig eradication on Santa Rosa Island provide the initial food subsidy that drew golden eagles to the island? Possibly, but the evidence suggests no. Many golden eagle nests on the islands have been excavated. Analyses of prey remains have not revealed sheep remains in nests from Santa Cruz Island or pig remains in those from Santa Rosa Island (Collins and Latta 2005). The more likely effect of sheep on the foxes was the destruction of vegetation cover that increased the exposure of the foxes to a novel aerial predator.

One strategy to reduce the risk of perverse outcomes is to leave fewer pests in the system that can go awry. Holistic pest management programmes may help reduce risk of perverse cascades (Zavala et al. 2001). But what also should be recognised are the efficiencies that can result from a comprehensive and strategically sequenced programme. If one pest plays a transformative role in the system, e.g., top down control of vegetation and therefore habitat quality for other pest species, that impact might be a means by which those other pest species can be managed more efficiently and effectively. Even those pests that seem relatively innocuous (like the small population of turkeys probably did before the fox crisis) might best be proactively engaged. Conclusive demonstration of adverse effects of pests should not be the threshold for intervention on an island: it was not known the extent to which, if at all, the turkeys would serve as a prey resource for golden eagles and exacerbate the risk to foxes. The precautionary principle was sufficient for action, as addressing pests early in their invasion may bring far fewer cascading consequences than doing so after a long period of ecosystem alteration.

Exploiting synergies among pest management projects might also improve the quality of the efforts relative to them being conducted separately. For example, the certification monitoring required at the end of the feral pig eradication contract was extensive (see Parkes et al. 2010). The hunters were obligated to search intensively for pigs despite the high likelihood none would be found. Months of such searching can strain morale. But by shifting the emphasis of the hunters – who by then were practically instinctually cued to see pig sign – to include other projects (like weed mapping), hunters were more focused in the field and managers were able to get both “products.” The best demonstration of the benefit of synergistic activities was that the last pig dispatched on the NPS property was
detected by the hunters while they were surveying for golden eagles—not pigs.

Fortunately, island managers today can benefit from considerable advances in eradication science and practice when planning to engage multiple pest problems. Eradication professionals have honed approaches to address many pest taxa through a range of effort combined with the use of multiple pests in an effectively single mobilisation may often be possible. With today’s approaches, and adequate investment (e.g., in aerial support), it is conceivable that if we were presented again with a problem like Santa Cruz Island C 1980, what took multiple decades might well have been completed in a few years and for considerably less overall expense.

Exploiting trophic relationships among pests can be an important strategy for increasing the return on investment of limited conservation resources and increasing the pace and scale of island restoration (see Saunders et al. 2011). This case study suggests ways that pest eradication efforts might be strategically sequenced into more compressed and comprehensive programmes that will help manage complexity, reduce risk, and increase efficiency in meeting conservation goals. Enhancing the resilience of island ecosystems by effectively addressing multiple pest problems is imperative for the protection of many native species—especially in an era of increasing global change and uncertainty.

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