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Habitat case studies: islands

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Islands have earned the ironic distinction as the most fertile crucibles and most fatal pitfalls of evolution.
William Stolzenburg, *Rat Island* (2011)

Introduction

Many important issues in conservation biology are more clearly visible on islands than on continental mainlands. Islands are natural laboratories for demonstrating the dynamic nature of life and the consequences both of natural selection and of the human conquest of planet earth (Cook et al. 2006). In recent years, islands have also been places where large-scale experiments in the conservation of endemic species and the management of invasive species have led to huge practical advances in conservation biology. The literature on conservation on islands is enormous, and in this chapter we summarize a few of the key topics that concern island managers worldwide, with exemplary case studies from the islands shown in Figure 12.1.[1]

Conservation biogeography

The view that the patterns and principles of biogeography could serve as a 'cornerstone of conservation biology' is fundamental to the new discipline of conservation biogeography (Lomolino 2004, 2006; Whittaker et al. 2005; Richardson & Whittaker 2010). A brief summary of the key historical developments in island theory helps to illustrate the extent of its applications to endangered species conservation

[1] We use the term 'island' to mean an area of land completely surrounded by water. For discussions of marine habitats, see Chapter 9, and for mainland fragments, see Chapter 21. We consider primarily the land-breeding vertebrate faunas of islands, but only because there are fewer consistent and comparable databases available on plants and invertebrates.

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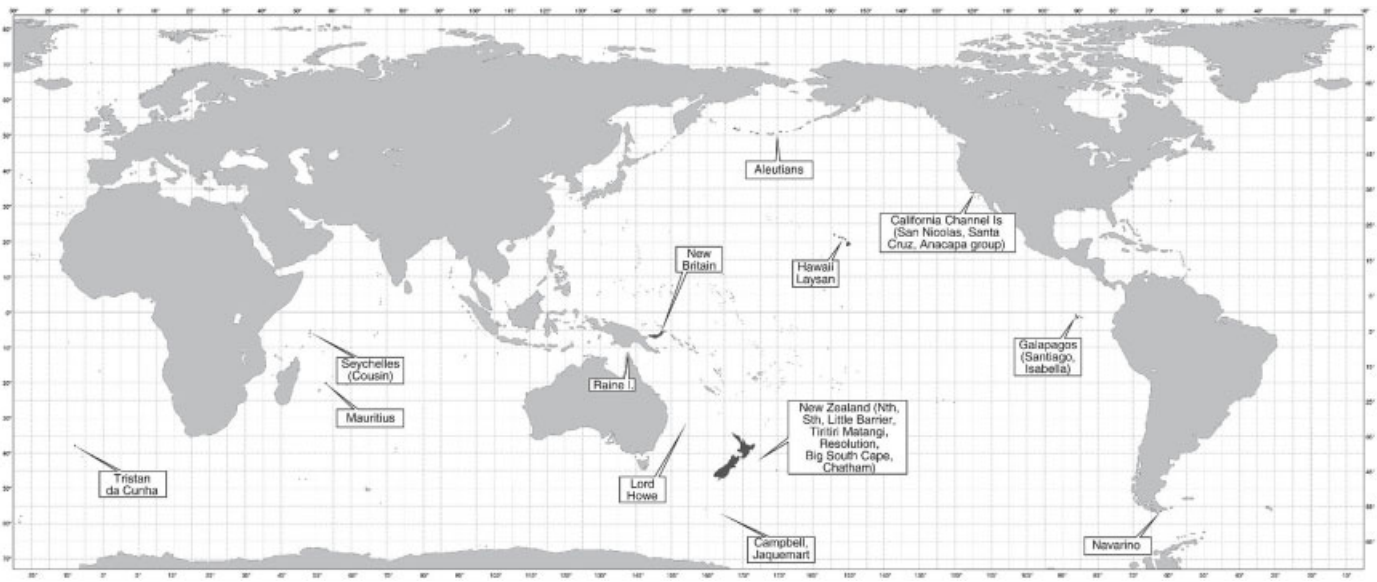

Figure 12.1 World distribution of islands mentioned in the text.

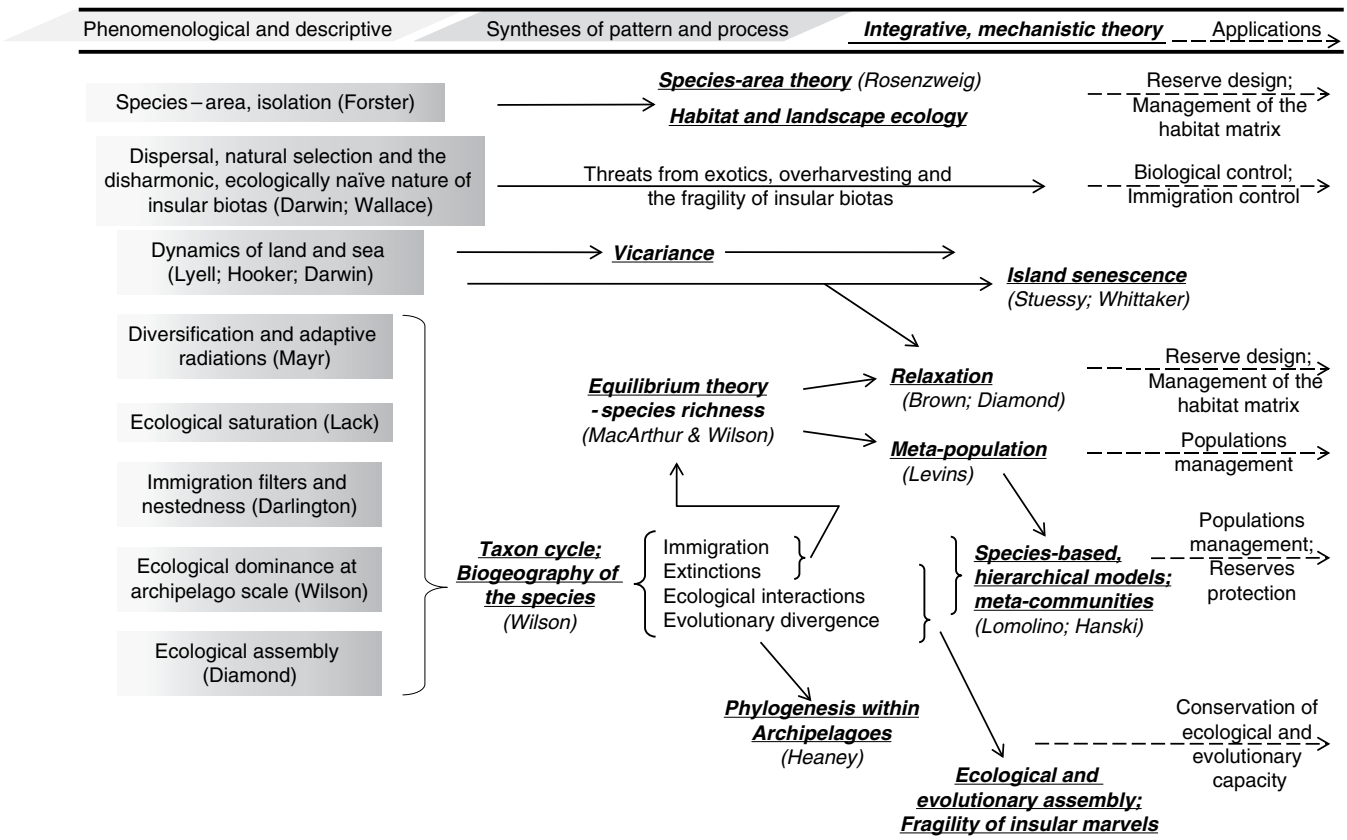

Figure 12.2 Summary of the historical development and influence of theoretical and applied island biogeography. The most fundamental contributions are listed on the left in rough chronological order, and suggest linkages from largely descriptive (light shaded boxes) or synthetic works on pattern and process (darker shading), to more integrative, mechanistic theories (bold, underlined italics) and their applications (dashed arrows). For summaries of the theories mentioned, see Box 12.1. Figure drawn by Mark Lomolino.

Box 12.1 Brief summary of some key theories and models of island biogeography

General definitions

Vicariance biogeography: a set of explanations for distributions of biotas that attribute disjunctions (broad gaps in species occurrences) to the splitting of areas (such as that caused by continental drift) rather than long-distance dispersal (Hooker 1866).
Taxon cycle theory: a comprehensive explanation of the predictable ecological and evolutionary changes in insular populations following their colonization of isolated islands (Wilson 1959, 1961).
Equilibrium theory of island biogeography: an explanation for patterns in species number among islands based on the assumptions that a relatively stable equilibrium is achieved between the processes of immigration of new species and extinctions among those already present (MacArthur & Wilson 1963, 1967).
Faunal relaxation model: explains exceptions to the equilibrium theory, which arise where immigrations and extinctions proceed on such different time scales that an equilibrium number of species is unlikely (e.g. for some biotas on land bridge islands following climate driven changes in sea level) (Brown 1971; Diamond 1972).
Model of dynamic disequilibrium and phylogenesis: an explanation for diversity of insular biotas based on the assertion that phylogenesis (evolutionary diversification) interacts in a complex manner with island area and isolation and, in turn, with extinction and immigration, and should therefore be modelled as a separate process driving biotic dynamics of insular biotas (Heaney 2000).

Demographic/ecological models

Metapopulation/metacommunity models: applications of genetic and demographic models for predicting distributions and persistence of species populations among patchily distributed habitats or true islands, based on the assumption that populations are linked by dispersal among patches (islands) (Hanski 2005, 2010).
Species-based, hierarchical model: an explanation for patterns in species distributions, diversity and species composition among islands based on the assertion that these patterns result from predictable patterns of variation in immigration abilities, resource requirements and interspecific interactions among species (Lomolino 2000).

Island senescence models

A model of ontogeny of insular floras: an explanation for the sequence of predictable changes in species diversity and genetic diversity based on how anagenesis and cladogenesis should vary with characteristics of the species, heterogeneity of habitats and age of the islands (Stuessy 2007).
Geological (general) dynamic model: a comprehensive explanation for changes in species diversity on particular islands as geological processes generate changes in their area, elevation and carrying capacity and, in turn, changes in the fundamental processes of immigration, extinction and speciation (Whittaker et al. 2008).

(Figure 12.2). We emphasize that any distinctions we make between empirical, conceptual and applied approaches are arbitrary, because even the earliest descriptive accounts also included comparisons with similar patterns, and speculations on the underlying causes. As Poincaré (1952) pointed out, 'Science is built upon facts much in the same way that a house is built with bricks; but the mere collection of facts is no more a science than a pile of bricks is a house'. None of the biogeographers we feature here, or those who contributed to the development of biogeography and its descendant disciplines, were simply dutiful collectors and cataloguers of facts.

History and development

The earliest foundations of island biogeography were laid by Johann Reinhold Forster, a naturalist on Cook's HMS *Resolution*, 1772–1775. He described two of the most general patterns in nature – that isolated systems have fewer species than those on the mainland, and that diversity on islands increases with their size (Forster 1778). His explanations for these patterns – the tendency for larger islands to provide more resources and a greater diversity of habitats – established lines of research that would eventually lead to species-area theory,

habitat ecology and management, landscape ecology, and the theory of the assembly of biological communities and regional biotas (Box 12.1; see also Figure 12.2).

Darwin and Wallace both pointed to the remarkable products of evolution in isolation, including birds that had lost the power of flight, and to these and countless other species that had become ecologically naive in the absence of mainland competitors and predators (Darwin 1839, 1860; Wallace, 1876). Lyell and Hooker recognized the similarity of plant assemblages in regions now isolated by southern hemisphere oceans (those now known to have formerly comprised the ancient supercontinent of Gondwanaland). Rejecting long-distance dispersal over water, they invoked geological dynamics – the emergence and subsequent submergence of extensive land bridges that once connected isolated continents and oceanic islands (Lyell 1834; Hooker 1866). While their proposed mechanism – dispersal across now submerged oceanic land bridges – was incorrect, their dynamic view of ancient life inspired later models of historical biogeography including vicariance, island senescence and the relaxation of insular biotas (Brown 1971; Diamond 1972). The same dynamics can be applied to predict the declines in biological communities, as previously expansive and continuous systems are reduced and fragmented ('insularized') in the face of environmental changes (see Chapter 21).

These observations and early theories nurtured the insightful and synthetic contributions of the early to middle 20th century by Ernst Mayr (1942, 1954), David Lack (1970), Philip Darlington (1957), Edward O. Wilson (1959, 1961) and Jared M. Diamond (1975a). These authors shared the view that diversification and assembly of insular biotas were strongly influenced by ecological interactions and differences among species in niches, ecological and competitive dominance, and the dispersal capacities of potential colonists. The taxon cycle theory of E.O. Wilson (1959, 1961) telescoped the theories of invasions and ecological dominance among continental biotas to invasions and ecological shifts of particular lineages along 'radiation zones' in archipelagos, and then down to within-island scales (Lomolino & Brown 2009). Wilson's idea of a taxon cycle uses each of the fundamental processes influencing assembly of insular biotas – immigration, extinction, evolution and ecological interactions – to produce a theory hypothesizing that isolated archipelagos were initially depauperate and disharmonic (unbalanced, or lacking taxa that typically dominate mainland communities, e.g., mammalian carnivores), then were colonized by a small subset of species that soon became entrained in a cycle of increased ecological and evolutionary specialization, which ultimately ended in extinctions of their descendant lineages. These extinctions were driven by continued colonizations and ecological divergence of new lineages as they or their descendants eventually out-competed more ancient and now overspecialized species. Wilson's concepts of the ecological dominance of invaders and their threat to native, insular biotas shared much with Darwin and Wallace's earlier observations on the fragility of island life, and foreshadowed the development and continued intensification of programmes to eradicate exotic, insular populations of invasive pests (discussed below).

Wilson's subsequent collaboration with the mathematical ecologist Robert MacArthur reversed the trend toward increasingly more integrative theories in favour of those that put a premium on generalization by simplicity. MacArthur & Wilson's (1963, 1967) equilibrium theory of island biogeography, while retaining the taxon cycle's assumption of recurrent immigration and extinctions, succeeded in explaining general species-isolation and species-area relationships without referring to ecological interactions, differences among species or evolution. Their equilibrium model saw the diversity of insular communities as a balance between recurrent immigrations and extinctions, which were direct functions of island isolation and area, respectively. Community ecologists and conservation biologists applied MacArthur & Wilson's model and, in particular, its assumption

of an equilibrium between immigrations and extinctions, to develop mathematical and graphical models for predicting faunal collapse and the prospects of preservation of biotic diversity under alternative scenarios of habitat loss and fragmentation (Harris 1984; Rosenzweig 1995). Best known and most controversial among these applications were a set of alternative, geometric designs for nature reserves (Diamond 1975b; Wilson & Willis 1975). Debates over these alternative prescriptions were often contentious (see Chapter 21) but had little positive and lasting effect on conservation biology.

Recent advances

Ironically, the most enduring and significant works influencing the equilibrium theory on island biogeography and the conservation of isolated communities were those that attempted to reintegrate fundamental processes distilled out of Wilson's taxon cycle theory during the conceptual development of the equilibrium model. These included the models that added non-equilibrial conditions generated by long-term dynamics of landscapes and seascapes, e.g. the relaxation models of Brown (1971) and Diamond (1972); the island senescence models of Stuessy (2007), Whittaker and his colleagues (Whittaker et al. 2008), and other models that emphasized demographic, genetic and ecological differences, and interactions among species, e.g. metapopulation models and species-based and metacommunity models, including those of Lomolino (2000) and Hanski and his colleagues (Hanski and Gilpin, 1997; Hanski, 2005), all summarized in Box 12.1.

Still lacking from these more recent models, but we think essential for understanding the natural character of insular biotas, is a reintegration of evolutionary processes in island theory. Evolutionary divergence has been at the core of historical biogeography at least since Hooker's anticipation of vicariance biogeography, and Darwin's dispersalist and centre of origin theories. Insights from historical biogeography, however, had less influence on the early development of conservation biology than did practical experience in wildlife management (Caughley 1994).

Exemplary case studies in conservation phylogeography such as those by Heaney (2000, 2004, 2007) have demonstrated the importance of phylogenesis to both conceptual and applied island biogeography. If we are to conserve the natural character of insular biotas, it seems essential that conservation programmes be guided by empirical patterns and their underlying processes, i.e. the influence of ecological interactions (among natives as well as exotics) on the distributions, abundances, niches and evolution of native species. The marvels and perils of life on isolated, initially depauperate oceanic islands are the products of diversification, adaptive radiations and evolutionary interactions within a small subset of the mainland biota. The absence or paucity of most species that usually dominate mainland communities, and the relatively intense competition from conspecifics and from an unbalanced assemblage of other long-distance colonists drive character release and displacement and, in turn, convergence on the size, growth form, and trophic and metabolic strategies of absent species. The ultimate consequence is the evolution of insular anomalies including giant shrews and rodents, dwarfed proboscideans and ungulates, flightless and often giant birds, lizards that become 'supergeneralists' as pollinators and seed dispersers, and the evolution of woodiness and tree-like stature in otherwise herbaceous lineages of plants, all described in recent books (Whittaker & Fernandez-Palacios 2007; Lomolino et al. 2010). Different rules apply to the equally fascinating assembly and ecology of marine species using islands as breeding platforms (Box 12.2).

Conservation management on islands

Caughley (1994) proposed a fundamental distinction between two main threads of conservation biology, distinguished by, among other things, their origins, their theoretical significance

Box 12.2 Significance of islands to marine vertebrates

Islands, often naturally lacking terrestrial predators, provide many significant breeding sites for air-breathing marine vertebrates, e.g. pinnipeds, marine turtles and seabirds. The biodiversity importance of these breeding aggregations is threefold. First, single breeding colonies can support great hosts of animals gathered from across vast areas of ocean, e.g. Raine Island, Australia, may host >100,000 breeding green turtles (*Chelonia mydas*), possibly as many as live in the whole Atlantic (Limpus et al. 2003). Second, isolation of breeding sites has lead to important endemism even among wide-ranging species, e.g. the Tristan da Cunha archipelago hosts at least four endemic species of seabirds (the Tristan albatross *Diomedea dabbenena*, yellow-nosed albatross *Thalassarche chlororhynchus*, sooty albatross *Phoebetria fusca* and great shearwater *Puffinus gravis*), all considered globally threatened (Hilton & Cuthbert 2010). Third, the large numbers of marine vertebrates can play important ecosystem engineering roles at their breeding sites, e.g. seabirds acting as conduits of nutrients from marine to terrestrial ecosystems (Polis & Hurd 1996) or affecting soil dynamics via burrowing (Mulder & Keall 2001).

Concentration and isolation define some of the major conservation concerns for these groups. The seasonally predictable distribution of numerous large vertebrates has permitted high levels of exploitation over the last 500 years. Key examples of overexploitation include sealing to near-extinction of fur seals in the southern oceans (Richards 2003), and overfishing extensive enough to cause significant shifts in food webs (Jackson et al. 2001). More than 90% of recent avian extinctions have been of island species, mainly due to predation by invasive mammals (Atkinson 1985; Steadman 1995). Seabirds are especially vulnerable (Hilton & Cuthbert 2010) so invasive species eradication efforts on islands (detailed below) are often undertaken, at least partly, for seabird restoration. Predicted climate change has the potential to affect breeding marine vertebrates in various ways, including loss of key coastal habitats or whole breeding islands through sea level rise (Baker et al. 2006) or through disruption of thermally determined sex ratios (Hawkes et al. 2009). A key consideration is whether animals breeding on islands have the potential to adapt by shifting to nearby, more suitable habitats.

and their technical methods. The *small-population paradigm* is concerned with the effects of small numbers on the chances of extinction, whereas the *declining-population paradigm* is concerned with identifying the reasons why a population becomes small. The dangers of being a small population are intrinsic, whereas for declining populations the focus is less on the distressed population than on the agents of decline. Both are relevant to the theme of protecting island biota, in combination with a special branch of theoretical biology focused specifically on islands.

Both paradigms assume that the main aim of conservation biology is to prevent extinctions, but they have developed more or less independently. Ideas about declining populations are based on decades of practical wildlife management experience. If the causes of a particular decline can be identified in time, experienced field managers can often mitigate or reverse them without reference to, or in the absence of, any useful theory. Ideas about small populations, such as risk of population extinction, population viability and extinction vortices, have their origins in both demographic and population genetic theory, and are often helpful for predicting which populations are or could be especially vulnerable to less manageable stochastic processes. The best rescue remedies, for example the one developed for the island fox (*Urocyon littoralis*) (Bakker et al. 2009), use a combination of both but with an element of defiance that refuses to give up on cases that should in theory be hopeless. When the Mauritius kestrel (*Falco punctatus*) got down to four individuals in 1974, the ICBP was ready to give up on it but a determined captive breeding programme led by Carl Jones succeeded so well that the species' 'Endangered' label was removed in 1994 (Quammen 1996).

Declining populations

The declining- and small-population paradigms are not independent, since a declining population often becomes a small population, and then

a locally extinct one, but declining populations may have more options than small ones. For example, the decline of the endemic Galapagos rail (*Laterallus spilonotus*) on Santiago was rapidly reversed by eradication of feral goats and pigs (Donlan et al. 2007). By contrast, the last 122 kakapo (*Strigops habroptilus*), a large, slow-breeding parrot endemic to New Zealand (Fidler et al. 2008), are vulnerable to environmental stochasticity, genetic drift and inbreeding depression, which are less easy to manage.

Diamond (1989) identified four main causes of decline to extinction, all of which are often illustrated on islands: overkill, habitat destruction and fragmentation, impacts of introduced species, and chains of extinction.

Overkill rapidly removed many large, slow-breeding species from remote islands as soon as human explorers, traders and colonists found them. In early postglacial times, nine species of moa (Aves: Dinornithiformes) inhabited the two main islands of New Zealand, which totals about the same area as Britain (Bunce et al. 2009); all were lost after Polynesian colonists arrived in about 1280 AD (Wilmshurst et al. 2008), probably within a century (Holdaway & Jacomb 2000). Similarly, 36 species of giant tortoise have been harvested to extinction on islands around the globe since the Pleistocene (Hansen et al. 2010).

Habitat destruction can range from 100% loss of lowland coastal areas, caused by the rapid post-Pleistocene rise in sea level, to the widespread contemporary logging of tropical forests on islands supporting many endemic species. Diamond (1984) showed that the species most affected by island drowning were those on the smallest islands, those with the largest body size, and those with the most carnivorous or specialist food habits – all characteristics associated with small population size. On New Britain, the largest island of the Bismarck Archipelago (Papua New Guinea), 12% of the original forest was lost in only 11 years (1989–2000), and continued losses are now jeopardizing 21 species of threatened or near-threatened forest birds (Buchanan et al. 2008).

Invasive species often prey on naive native faunas (Hilton & Cuthbert 2010), but do not have to be predatory to be disastrous (Macdonald et al. 2007). Exotic herbivores can reach huge numbers capable of replacing an original forest with grassland, making extinctions of resident forest-adapted endemics inevitable. For example, on Laysan Island (370 ha) in Hawaii, European rabbits (*Oryctolagus cuniculus*) introduced before 1904 destroyed virtually all vegetation by 1923, and reduced five endemic taxa of birds to remnants, from which three never recovered (Caughley & Gunn 1996).

Chains of extinction are observed when a change in status of one species makes life impossible for a different species. Rabbits can kill island populations of seabirds by supporting large populations of feral cats (Courchamp et al. 2000). Abundant exotic prey, feral pigs (*Sus scrofa*), enabled native golden eagles (*Aquila chrysaetos*) to colonize the California Channel islands, where their predation indirectly threatened an endemic island fox (Box 12.3).

Small populations

The concept of a minimum viable population rests on two separate but linked ideas, one derived from genetics and the other from population dynamics, both agreeing that small populations are always at much greater risk of extinction than larger ones. A widely quoted general rule for animals predicts that at least 50 *breeding* individuals are needed to stave off inbreeding depression, and 500 for long-term security against extinction by genetic drift (Franklin 1980). Total populations need to be larger. Inbreeding coefficients estimated for 182 non-endemic and 28 endemic island populations confirmed that breeding groups on islands are usually more inbred than their mainland relatives (Frankham 2005). In small populations, mating between close relatives is frequent, which causes H, the proportion of heterozygous loci in an average individual, to drop to dangerous levels.

Box 12.3 Recent innovations in island restoration

Methodological advances in island restoration, including unique financial instruments, strategic plans and the application of existing and new technologies, have allowed successful removal of entire suites of invasive vertebrates from larger and larger islands. Many of these approaches, first pioneered in New Zealand (Bellingham et al. 2010), are exemplified by recent eradications of invasive mammals in South and North America, as follows.

Project Isabella

Project Isabella is perhaps the most comprehensive invasive mammal eradication programme conducted to date. The goal was to remove invasive ungulates from Santiago Island (58,465 ha), plus the northern portion of Isabella Island (Galapagos). First, >18,000 pigs were removed from Santiago over a 30-year period. At this stage, the goats were ignored, because their intense browsing kept habitats open, facilitating pig removal (Cruz et al. 2005, 2009). Completion of this stage of the plan was followed by the development of a comprehensive strategy for a large-scale, rapid goat eradication campaign, financed by donations from numerous sources totalling US$6.1 million, administered by the Global Environment Facility to the Ecuadorian government. A systematic design used a mixture of methods (ground hunting with and without hunting dogs, and aerial hunting from helicopters), and the efficiency of each method was constantly assessed. The island was divided into hunting zones that varied in size, depending on the removal method (Lavoie et al. 2007) (Figure 12.3). GPS and GIS tools allowed close daily monitoring and confirmation of each stage of the work.

Importantly, this adaptive management strategy took into account the behavioural reactions of both the target animals and the human operators. First, animal behaviour was exploited by the use of the Judas goat, a sterilized individual (male or female) fitted with a radio collar which when released will always search for a herd to join. It is then relocated, every goat not collared is killed and the Judas left to find new companions. Later refinements of this method included the creation of the even more lethal Mata Hari females, 'sexed up' with reproductive hormones to prolong oestrus (Campbell et al. 2007). Mata Hari goats were particularly adept at leading hunters to males, resulting in a shortage of breeding males that reduced female reproductive output. This effect was critical during the crucial latter part of the eradication effort, when density-dependent increases in production could compensate for hunter-induced mortality.

Second, the influence of human behaviour on eradication efficiency was minimized by a keen understanding of the operators' response to one method of ground hunting, the *rastrillo*. Akin to a deer hunting drive, *rastrillo* involves placing hunters 100–150 m apart in a line and systematically covering a hunting block. This method was initially very effective, but prolonged use caused hunters to become disillusioned and less keen to succeed. A switch back to free-range hunting instilled a competitive air among the hunters that then increased efficiency (Cruz et al. 2009).

The net result was that >79,000 goats were removed in less than 4.5 years (Cruz et al. 2009). This campaign was the largest and most 'savvy' approach ever devised to eradicate large ungulates from an archipelago of enormous biological and social importance.

California Channel Islands

On Santa Cruz Island (25,000 ha), the largest of the Channel Islands off the coast of southern California, USA, foraging and soil disturbance by pigs directly endangered native plants, and indirectly endangered the endemic island fox (*Urocyon littoralis*) by attracting a shared predator, the golden eagle (*Aquila chrysaetos*). Eagle predation had a disproportionate effect on the foxes, driving them toward extinction (Roemer et al. 2002). By the deliberate and sequential deployment of different methods of accelerating intensity, 5036 pigs were removed in ~14 months (Parkes et al. 2010). Innovations in this and related programmes included sampling designed to detect when the last animal was removed, and modelling that yielded a framework linking population viability analysis with risk assessment to allow flexible management tactics (Morrison et al. 2007; Bakker et al. 2009).

Removing invasive rodents is 2–3 times more expensive per unit area covered than removing large ungulates (Martins et al. 2006). So another first for the California Channel Islands was the eradication of black rats (*Rattus rattus*) from Anacapa Island (actually a group of three small islands) despite the presence of an endemic rodent species (Howald et al. 2009). The chosen tool was aerial spreading of Brodifacoum, an anticoagulant rodenticide that would kill all rodents and probably cause secondary poisoning of raptors and other species. The operation proceeded in three phases: (1) conservation practitioners first captured and confined peregrine falcons

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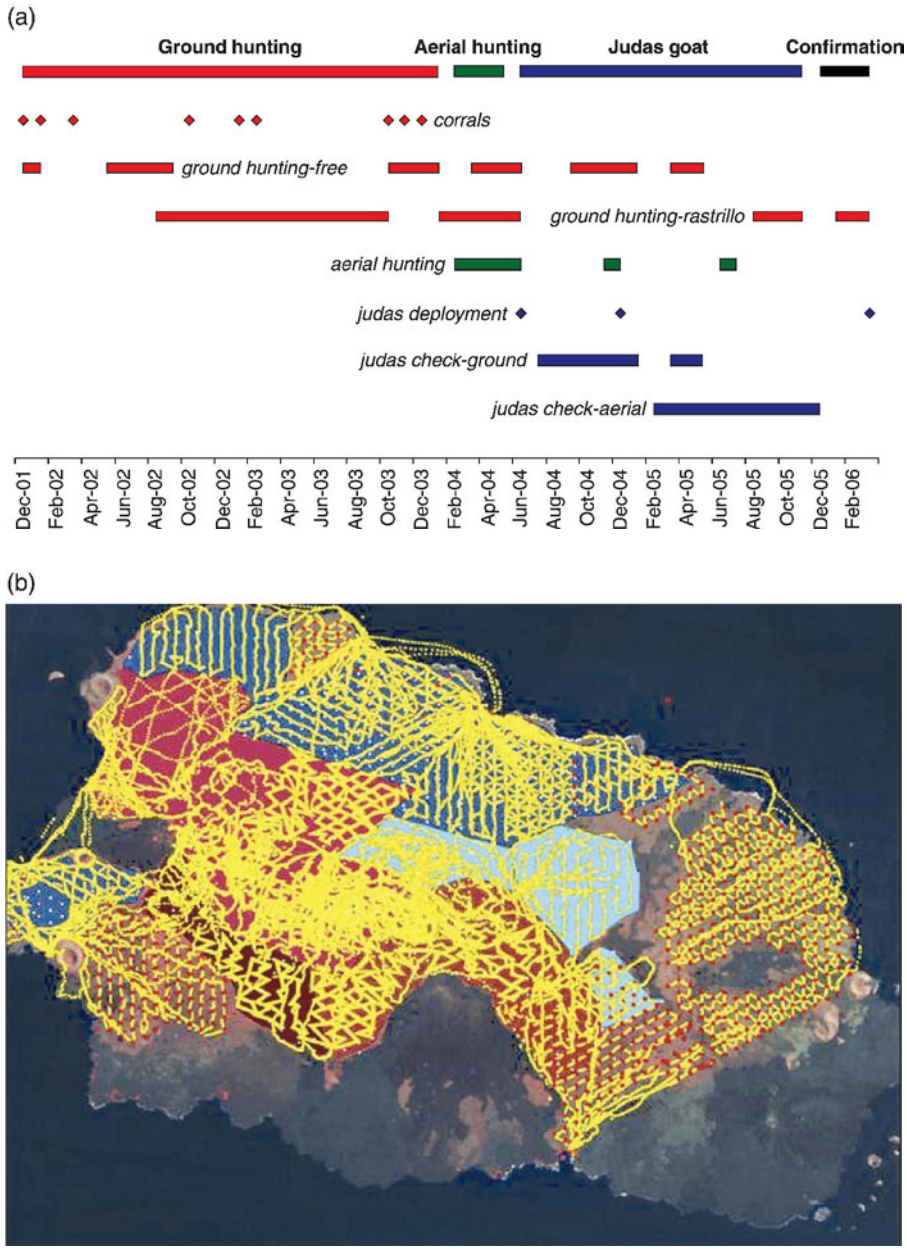

Figure 12.3 (a) The schedule of techniques adopted to eradicate feral goats from Santiago Island, Galapagos Islands, Ecuador. (b) An example of the coverage of Santiago Island by ground-hunting over the course of the eradication campaign. The southern and eastern portions of the island were too steep to be hunted on foot, so these areas were patrolled by helicopter. Figures courtesy of C.J. Donlan.

(*Falco peregrinus*), a listed species, and created a conservation strategy to collect and captive-breed the endemic Anacapa deer mouse (*Peromyscus maniculatus anacapae*); (2) the toxin was spread by helicopter; and (3) monitoring to verify environmental degradation of the remaining toxin determined when it would be safe to release the peregines and reintroduce the deer mice across the three islets (Pergams et al. 2000; Howald et al. 2009).

Low *H* is not always fatal, because genetic diversity can be maintained in other ways, as illustrated on many of the islands shown in Figure 12.1. The individual foxes (*U. littoralis dickeyi*) sampled on San Nicolas Island were virtually identical in DNA fingerprints and microsatellite profiles, but the major histocompatibilty complex, the region involved in microparasite defence, has maintained genetic variation owing, in part, to intense selection (Goldstein et al. 1999; Aguilar et al. 2004). In practice, emergency rescues of tiny and inbred island populations often do succeed. The case of the Mauritius kestrel quoted above is not the only such example. The Chatham Island black robin (*Petroica traversi*) recovered (assisted by translocation and cross-fostering) from the lowest possible number, a single breeding female in 1976, to an unmanaged population of >250 by 2003, because the risk of extinction from total loss of habitat was much more immediate than the risk of inbreeding depression (Jamieson et al. 2006). After rats reached the last refuge of another endemic species, the South Island saddleback (*Philesturnus carunculatus carunculatus*) on Big South Cape Island about 1962, the last remnant group of 36 birds was whisked out of danger in the nick of time. Later genetic management and translocations restored the stock to c.1200 birds spread among 15 island populations (Hooson & Jamieson 2004). The North Island subspecies of the saddleback (*P. c. rufusater*), which was also secured from extinction by a long history of repeated translocations from a single surviving group, provides one of the best documented examples of how serial bottlenecks can reduce genetic diversity in small founding populations (Lambert et al. 2005).

Analyses of minimum viable populations (MVP) examine small populations in terms of population dynamics, to estimate the expected time to extinction of an isolated group with specified characteristics. Almost all islands are too small to maintain any species of larger-bodied resident vertebrates in numbers large enough to provide for adaptation in response to future environmental changes (Soulé 1980; Frankel & Soulé 1981), and most islands are too small even to prevent extinction of large-bodied species in their current form for the next 100 years. Even the simple preservation of unmanaged viable populations of moderate-sized birds requires astonishingly large areas, e.g. about 10,000 ha for the North Island brown kiwi (*Apteryx mantelli*), a flightless bird of 2–3 kg body weight (Basse & McLennan 2003). Conversely, for invertebrates on islands, the potential for future evolution is more likely to be limited by habitat deterioration (New 2008). The stark difference in potential for successful preservation and prospects of future evolution between the vertebrates and invertebrates is seldom acknowledged.

Invasive species

Past a certain point, declining and small populations of vertebrates become linked by the extinction vortex, summarized by Caughley (1994) as a five-step process: 1. declining mate choice, hence more close-relative matings; 2. reduced heterozygosity in the offspring; 3. more lethal recessive alleles exposed to selection; 4. reduced fecundity and increased mortality; 5. reduced numbers and further restriction in mate choice. On islands, this often irreversible sequence of events can be set off by various events, often a combination of human-induced habitat destruction and the arrival of an invasive species.

New arrivals are a natural and ongoing part of the dynamic equilibrium controlling numbers of species on islands. Not all new species arriving on an island become hugely abundant invasives (Macdonald et al. 2007), and not all invasive species become damaging pests, but those that do may change species compositions and simplify community dynamics. They are the most common cause of the declining species syndrome. The chances of establishment of a new population vary; for ungulates, they are directly proportional to propagule size (Forsyth & Duncan 2001).

Pest eradication

To achieve at least temporary eradication of any population, three conditions are absolutely non-negotiable: (1) all individuals, or at least all of one sex, must be at risk of removal; (2) they must be removed faster than they can be replaced; and (3) any future arrivals must be prevented (Parkes & Murphy 2003). Failure to meet these conditions turns an eradication attempt into an exercise in sustained harvesting. The last few pest individuals are always the hardest and the most expensive to find, so success often depends on switching among standard technologies, e.g. from poisoning to introducing disease to shooting to trapping (Bloomer & Bester 1992), or by developing a new technique (see Box 12.3).

The third condition for eradication is easier to meet on islands than elsewhere, which is why successful island eradications are becoming routine, even of small pests on large islands. Removing Norway rats from 11,216 ha on Campbell Island (see Figure 12.1), once regarded as impossible, was achieved by aerial toxic baiting within 3 weeks in 2001 (Towns & Broome 2003; Bellingham et al. 2010). The marriage of strategy, technology and innovation has permitted huge advances in speed and efficiency, best illustrated by Project Isabella (see Box 12.3). Such advances make land area no longer limiting to pest eradication on uninhabited islands, but human residents unsympathetic to the programme or with domestic conspecifics can provide refuges which make eradication much more challenging (Ratcliffe et al. 2009).

The huge benefits of a well-planned and complete island eradication are becoming commonplace, e.g. the recovery of Cook's petrels (*Pterodroma cookii*) after the removal of cats and Pacific rats (*Rattus exulans*) from Little Barrier Island (Rayner et al. 2007). Additional and totally unexpected benefits can surprise everyone. Less than 5 years after Norway rats disappeared from Campbell Island, a previously unknown remnant colony of snipe, an undescribed species of *Coenocorypha* which had survived the rat invasion camped out on tiny (19 ha) Jacquemart Island offshore, recolonized the main island (Baker et al. 2010).

Successful eradication depends primarily on isolation from reinvasion. A systematic survey of 83 studies in which islands were defined by total area, not isolation of the area cleared of pests (Smith et al. 2010), concluded that post-breeding population sizes of birds were not improved on islands up to 2000 km^2. Such large islands are no different from mainlands if they are not treated as a single unit and if the cleared area is not protected from reinvasion. Much smaller islands than this have been vital in conservation provided the predators never got back to them. Fortunately, a theoretical model suggests that the benefits per unit of expenditure are higher if directed towards a larger number of relatively small islands (Brooke et al. 2007), despite the challenges and limitations of protecting small populations discussed above.

Mesopredator release, an increase in numbers of a previously less common predator from further down the food chain (Russell et al. 2009), can add indirect costs to a successful island eradication by inducing complex interactions among the remaining pests, including goats, pigs, cats, rats or rabbits, and mice – all often distributed to islands around the world by early explorers. For example, removal of cats from Little Barrier Island *reduced* the breeding success of Cook's petrels, owing to the consequent booming numbers of Pacific rats (*Rattus exulans*). This effect was reversed only when the rats were also removed (Rayner et al. 2007).

Species regarded as pests by conventional conservation management may be seen differently by indigenous people. *Rattus exulans* is valued by some Maori groups as a *taonga* (tribal treasure), so proposals to remove it from Little Barrier Island were preceded by translocation of some individuals to an alternative island (Ruscoe & Murphy 2005). Intense public debate focussed on conflicts between value judgements and science have so far prevented eradication of

North American beaver (*Castor canadensis*) from Navarino Island, Chile (Haider & Jax 2007). Large carnivores provide many more examples of the same problem (see Chapter 7).

Translocations and reintroductions

Island archipelagos are ideal locations in which to establish metapopulations of an endangered species, often by multiple transfers or assisted recolonizations from one or a few remnant sources to new locations, within or outside their former range. Archipelagos offer an escape from the risk of total loss and, in a world where large conservation islands are very scarce, they are often the best available option. The disadvantage of establishing several small populations is balanced by the great advantage of increasing the breeding stock and maximizing the genetic diversity of the species (Grueber & Jamieson 2008). Among 116 reintroductions analysed by Fischer & Lindenmayer (2000), success was associated with using a wild rather than a captive source population, releasing large propagules (>100 individuals) and removing the cause of the original population decline (see Chapter 22).

Source populations must not be overharvested, and the new location must not have the same limitations as the old one. The Seychelles warbler *Acrocephalus sechellensis* thrived after translocation from Cousin Island, where insects were few, to two islands with abundant insects (Komdeur 1994). The earliest translocations of kakapo to Resolution Island in 1894 (Hill & Hill 1987) failed at the time because stoats (*Mustela erminea*) swam the narrow channel (525 m) separating Resolution from the South Island. When a well-planned new programme of stoat eradication began in 2008 (Elliott et al. 2010), it removed 258 stoats in the first 2 weeks (New Zealand Department of Conservation, unpublished), and is ongoing.

Critically endangered island species retrieved from the brink of extinction by captive breeding, and later reintroduced to their native habitats, include, besides the Mauritius kestrel, the Lord Howe Island woodhen (*Tricholimnas sylvestris*) and the Hawaiian goose or nene (*Branta sandvicensis*) (Caughley & Gunn 1996). Conservation authorities now manage island translocations to maximize the genetic health of reintroduced populations, and monitor the results at least until the new populations stabilize (Armstrong et al. 2002; Taylor et al. 2005; Cardoso et al. 2009).

Island restoration

Restoration programmes attempt to return an island to a state approximating its condition at some point in the past. The focus is the whole island ecosystem rather than any particular species, which means that restoration programmes on severely damaged islands have to be long term, often starting with replanting of vegetation native to the area. On Tiritiri Matangi Island, near Auckland, >280,000 trees were planted over 9 years (1984–93), mostly by volunteers, and increasing numbers of native bird species are being translocated there as the forest matures. The island has developed as an open sanctuary, demonstrating that community participation in conservation is not only possible but strongly desirable, and is now being imitated elsewhere (Miller et al. 1994; Ogden & Gilbert 2009). Spontaneous recovery of native vegetation, including species not seen for years, is also possible if a sufficiently diverse seed bank survives and re-establishment is not prevented by lack of pollinators or dispersal agents (Weerasinghe et al. 2008).

Even without replanting, the restoration possibilities opened up by large-scale pest eradications are often spectacular (Towns et al. 1997, 2006; Towns & Broome 2003; Bellingham et al. 2010). Costs can be roughly estimated in advance if the island area (which accounts for 72% of the variation in expenses) and species to be eradicated are known. Costs have declined over time but increase with remoteness, so date and distance to the nearest main airport (a

measure of remoteness) can be used to help refine the first estimate (Martins et al. 2006).

Successful restoration should ideally aim to re-establish the original ecological and evolutionary processes of an island. For example, once rid of introduced Arctic foxes (*Vulpes lagopus*), several of the Aleutian Islands' seabird colonies were revived, and their guano fertilized and restored native vegetation communities that had been radically altered during their absence (Maron et al. 2006). But what if the native island fauna had been driven to extinction? How would these important processes be restored? Guidelines have now been developed on how to use extant taxa as ecological substitutes to replace extinct taxa and reinstate lost ecological and evolutionary processes (Hansen et al. 2010). For example, giant tortoises (e.g. *Geochelone* spp.) have been the targets of successful 'rewilding' efforts of islands (see Chapter 22).

Conclusions

Insular species are often ecologically naive to exotic competitors, predators and parasites, or imperilled by the loss of native pollinators, seed dispersers and other mutualists. Thus, in order to conserve not just the marvellous diversity but also the natural characters of island biota, the challenge is to manage fragile, insular assemblages successfully. That means not only attempting to minimize intense habitat destruction and alteration, such as logging, agricultural conversion and urbanization, but also reducing the threat from ecologically novel, exotic species while maintaining or replacing natural, ecological conditions that shaped the evolution of island life.

Facts and theories are different things, not rungs in a hierarchy of increasing certainty.

Stephen Jay Gould *Hen's Teeth and Horse's Toes* (1994)

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