

Direct Impacts of Seabird Predators on Island Biota other than Seabirds

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Introduction

“... I have not found a single instance ... of a terrestrial mammal inhabiting an island situated above 300 miles from a continent or great continental island; and many islands situated at a much less distance are equally barren.”

(DARWIN 1859)

“He who admits the doctrine of special creation of each species, will have to admit, that a sufficient number of the best adapted plants and animals have not been created on oceanic islands; for man has unintentionally stocked them from various sources far more fully and perfectly than has nature.”

(DARWIN 1859)

Since Darwin's time, islands have been celebrated for having highly endemic floras and faunas, in which certain taxonomic groups are typically overrepresented or underrepresented relative to their abundance on the nearest continents (Darwin 1859, Wallace 1911, Carlquist 1974, Whittaker and Fernández-Palacios 2007). Sadly, island endemics in many taxonomic groups have suffered a disproportionately large number of the world's extinctions, and introduced mammals have frequently been implicated in their decline and disappearance (Vitousek 1988, Flannery and Schouten 2001, Drake et al. 2002, Courchamp et al. 2003, Steadman 2006).

Of the many mammalian predators introduced to islands, those having the most important impact on seabirds are cats, foxes, pigs, rats, mice, and, to a lesser extent, dogs and mongooses (discussed extensively in Chapter 3). These predators can be divided into two groups: superpredators and mesopredators. Superpredators (e.g., cats and foxes) are carnivores, relatively large, and able to consume all life stages of their prey (including other, smaller predator species). They are also prone to overconsumption of prey, necessitating diet-switching, or potentially leading to

the extinction of the superpredators themselves (Eberhard 1988, Courchamp et al. 2003, Ritchie and Johnson 2009; see Chapter 9 for a more detailed discussion of prey-switching). In contrast, mesopredators (e.g., pigs and rodents) are more generalist, omnivorous species. Mesopredators are often limited in the life stages of prey that they can consume (e.g., only eggs or chicks), and may themselves act as alternative prey for superpredators.

This chapter has two main purposes. The first is to ask what direct effects the aforementioned seabird predators have on island species other than seabirds, especially arthropods, mollusks, amphibians, reptiles, land birds, mammals, and plants. (Impacts on seabirds are discussed in Chapter 3; for indirect effects, see Chapter 9). The second purpose is to ask, within each of these island taxa, what determines a species' vulnerability to seabird predators. To address these questions, information has been gathered from many systems—not all of which are strictly “seabird islands,” though most are islands, and all are places where the predators are not native—with the expectation that the predators' effects will be at least as great on seabird islands as they are elsewhere. Of course, many other species of animals and plants have been introduced to islands and caused impacts highly relevant to the ecology, conservation, and management of seabird islands—but they are beyond the scope of this chapter.

The Predators and Their Effects

Effects of ecological interactions between introduced predators and island species may be negative, positive, or neutral for the island species. Here, we consider direct effects to be those that are not mediated by a third species or through a species' effects on environmental resources. Seabird predators are well known for their direct negative effects on island animals through predation, and on plants through herbivory or physical disturbance. In some restricted cases, however, the introduced predators may have direct, positive effects on island animals. For example, they may act as prey for island raptors. They may also act as reproductive mutualists for plants by effecting pollination or seed dispersal—though it may be more common for them to have negative, indirect effects on plants and animals when predation or herbivory disrupt mutualistic interactions between native species (Nogales et al. 2006, Traveset and Richardson 2006, Traveset et al. 2009, Kaiser-Bunbury et al. 2010).

It is often difficult to assess the impacts of introduced predators, because most methods used to study them involve inherent limitations. Diets have been assessed mainly by analysis of stomach contents, but also through experimental feeding trials, stable isotope analysis, and examination of middens (an accumulation of discarded or inedible remains of an animal's meals). Each method is valuable, but inherently biased, so results must be interpreted with caution. For example, stable isotope ratios of a predator's tissues can estimate the amount of animal food in the diet, but can neither identify which animals were eaten nor determine whether they were taken by predation or scavenging. Analysis of stomach contents can

identify species eaten, but again, cannot distinguish between predation and scavenging. Dietary evidence from middens is biased in favor of species that leave durable remains (Campbell et al. 1984). Feeding trials in captivity necessarily offer a limited choice of foods in an unnatural setting. These methods work best when used in combination (see also Chapter 3).

Another difficulty in evaluating a predator's impact is that even when the sign of an ecological interaction is known, its strength and ecological or evolutionary significance may not be. For example, evidence that a rat eats and destroys some seeds of a plant species is not necessarily evidence that it destroys enough to affect the species' population size or evolutionary trajectory. And in some cases, high levels of seed predation may even be associated with enhanced recruitment of plants (Klinger and Rejmanek 2010). In addition, species that make up only a small component of a predator's diet may nevertheless be severely impacted. For example, Clark (1981) determined that although birds made up only 6% of the diet of just 15% of ship rats (*Rattus rattus*) in Galápagos thorn scrub, this level of predation could still account for the loss of 34 birds·ha⁻¹·mo⁻¹, a rate that might easily result in species decline. In many cases, a predator's impact has been inferred by comparing islands that have predators and islands that lack them, or by comparing sites before and after the introduction or eradication of predators. In such cases, even when an unambiguous impact can be demonstrated (i.e., when the presence or abundance of a predator is negatively correlated with the presence or abundance of an island species), it is often unclear whether the mechanism involves direct effects such as predation, or indirect effects such as resource competition or trophic cascades. In many cases, the overall impact of a predator is likely to be the net result of several different direct and indirect effects, each of which may be positive or negative for one or more species (Fukami et al. 2006, Kurle et al. 2008, Mulder et al. 2009, Grant-Hoffman et al. 2010). Finally, effects of introduced predators are often difficult to disentangle from the concurrent effects of other changes to island ecosystems; these include other introduced plants and animals, direct exploitation of island species by humans, and the changes to habitats and disturbance regimes that accompany human colonization (Wilmschurst et al. 2008, Anderson 2009, Prebble and Wilmschurst 2009). In summary, the clearest data on predator effects are likely to result from combinations of observational, experimental, and historical approaches (Drake and Hunt 2009).

CATS

Since its domestication in the Middle East about 9,500 year ago, the domestic cat (*Felis catus*) has traveled with humans to most parts of the world and established feral populations in a wide variety of habitats on remote or uninhabited islands that harbor great biodiversity (Fitzgerald 1988). Cats were often introduced to islands to control previously introduced rabbits (*Oryctolagus cuniculus*) and rodents. Some of the cat's characteristics, such as its promiscuous mating system, high fecundity, and ability to exploit novel environments, facilitate invasion of islands. On the different islands where it has been introduced, this relatively small

(1.1–5.8 kg; Long 2003) carnivore is an opportunistic hunter of a wide variety of prey, including more than two hundred species of mammals, reptiles, birds, and insects (E. Bonnaud personal communication). Where present, introduced mammals (mainly rabbits, rats, and mice) generally constitute most of the biomass ingested by cats. However, on oceanic islands where these prey are scarce or absent, birds, reptiles, and invertebrates assume major importance. Consumption of birds is especially important on islands located far from continents. The importance of reptiles in the feral cat diet is generally greatest on islands located in the tropics and subtropics (Fitzgerald 1988). The greatest frequency of reptile remains in feces has been recorded in Tenerife (Canary Islands), where an endemic lizard (*Gallotia galloti*) is frequently preyed upon (Nogales and Medina 2009). Little detailed information has been published on the impact of cats upon invertebrates on islands. In the case of the Canary Islands, perhaps the insular region where the diet of feral cats has been studied most thoroughly, a total of 32 species of prey have been identified, 47% of which were endemics (Medina and García 2007, Nogales and Medina 2009). However, these invertebrates contribute a low quantity of biomass to cat diets. The main invertebrate component of the diet consists of large insects such as Orthoptera and Coleoptera. On islands where cats' biomass intake consists predominantly of non-native mammals such as rodents and rabbits, the deleterious impacts produced by cats on other native species may be exacerbated via hyperpredation (the situation in which an introduced prey species that is adapted to high rates of predation allows a population of an introduced predator to grow to a point where it drives a native, alternative prey species extinct.)

Predation by feral cats has important impacts on seabirds and many other vertebrates on islands worldwide (Moors and Atkinson 1984). More than 15 species of reptiles, 30 mammals, and 100 birds are threatened by feral cats on islands (Medina et al. unpublished data). Cats have led to the extinction of insular vertebrates, some of them endemics (Nogales et al. 2004). Native mammals, especially rodents, have frequently been consumed on the islands of Baja California, the Galápagos, and the Caribbean. For example, a species of hutia (*Geocapromys thoracatus*) became extinct through the combined direct effects of feral cats and rats on Little Swan Island, Honduras (Flannery and Schouten 2001). Furthermore, endemic rodents (*Nesoryzomys* spp. and *Oryzomys* spp.) from the Galápagos have suffered dramatic declines and extinctions because of introduced cats and rats (Dowler et al. 2000). On the islands off Baja California, cats have been partially responsible for the extinctions (or near-extinctions) of at least 10 rodent taxa (Mellink et al. 2002).

With regard to land birds, feral cats are responsible for the extinction of at least 33 species (Lever 1994). Although many families of passerine and non-passerine birds are affected, perhaps the most notorious example is the Stephens Island wren (*Traversia lyalli*) in New Zealand; the last remaining population of this species was driven to extinction by feral cats in 1894 (Fuller 2000, Galbreath and Brown 2004). Furthermore, on Socorro Island (west of Mexico) the extinction in the wild of *Zenaida graysoni* (Socorro dove), and the drastic reduction of the endemic passerine *Mimodes graysoni* following the

introduction of cats by a military garrison in the late 1950s are especially noteworthy (Jehl and Parks 1983).

Feral cats have also caused the extinction or decline of insular reptiles on many tropical and subtropical islands. Local reptile extinctions attributed to cat predation have been documented in iguanas (*Brachylophus* spp.) and skinks (*Emoia* spp.) in Fiji (Gibbons 1984) and iguanas (*Cyclura* spp.) on Caribbean islands (Mitchell et al. 2002). Furthermore, other reptiles, such as the endemic giant lizards (*Gallotia gomerana*) from La Gomera (Canary Islands), are on the verge of extinction, with cat predation suspected as the major cause (Nogales et al. 2001). Away from tropical and subtropical areas, in New Zealand, the tuatara (*Sphenodon punctatus*) and 40% of lizard species are largely confined to off-shore islands free of introduced predators (Townes and Daugherty 1994). In summary, feral cats are considered to be one of the 100 worst invasive species in the world (Lowe et al. 2000), and active management has been considered essential in order to eliminate or at least minimize their pernicious effects on islands (Nogales et al. 2004).

Finally, although predation has been the main and most visible direct effect of feral cats on islands, they also have other cryptic, indirect ecological effects, such as disease transmission and food competition (see Chapter 9). Another effect is the alteration of ecological and evolutionary processes: more than 100 seeds from at least eight fleshy-fruited plant species were found in 1047 scat groups of feral cats in the Canary Islands (Nogales et al. 1996). These seeds, which were in the guts of the lizards preyed on by the cats, demonstrate the potential for cats to alter native seed dispersal systems. Another complex effect is the extinction of giant lizards by cat predation, which has led to some plants, such as *Neochamaelea pulverulenta* (Cneoraceae), being sub-optimally dispersed, and larger seeds (with better fitness) having low probability of dispersal by the medium-sized lizards now most common in the system (Valido 1999).

FOXES

Foxes are a widespread group of canids native to all continents except Australasia and Antarctica. Some species are specialized carnivores, while others are generalist omnivores that consume a wide range of animal and plant food (Hersteinsson and Macdonald 1996, Baker and Harris 2008). Humans introduced two highly carnivorous species, the arctic fox (*Vulpes lagopus*; 1.4–9.0 kg; Long 2003) and the red fox (*Vulpes vulpes*; 3.5–10 kg; Long 2003), to northerly islands as stock for the fur trade in the nineteenth century (Bailey 1993). The red fox was also introduced to large parts of the western United States in the seventeenth century, and to Australia in the nineteenth century, for recreational hunting (Rolls 1969, Kamler and Ballard 2002). Both species have had profound impacts on small islands and continental landmasses, with the most obvious direct effect being predation on native animal populations, frequently resulting in their actual or near extirpation (Bailey 1993, Dickman 1996, Kamler and Ballard 2002). The effects of predation are exacerbated by the foxes' caching behavior, leading to storage of large quantities of

Complex Predator Effects on Little Barrier Island

Location: Little Barrier Island (Hauturu), South Pacific Ocean, northeastern New Zealand **Climate:** temperate

Three mammalian predators were introduced to Little Barrier Island, or Hauturu (36°12'S 175°E; 28 km²). Pacific rats and (possibly) dogs arrived at some time after settlement of the New Zealand archipelago by Polynesians in about 1280 (Wilmshurst et al. 2008). Dogs were free-ranging over the island until their removal in about 1896 (Watson 1961). Cats arrived after contact with Europeans, during the late nineteenth century. The early effect of rats is unknown. However, after the arrival of cats, populations of burrowing seabirds were greatly reduced or extirpated (Townes et al. 2006), and a forest bird species, the saddleback (*Philesturnus carunculatus*) was lost from the island. Most likely, these losses and declines were the direct effects of predation.

The last cats were removed in 1980, and in 1986–1987, saddlebacks were successfully reintroduced and spread throughout the island, despite the continued presence of Pacific rats (Lovegrove 1996). However, species such as lizards and tuatara (*Sphenodon punctatus*) showed no evidence of recovery in 20 years after removal of cats. Other species showed continued or even accelerated declines. One such species was a huge (>30 g) flightless cricket, or wetapunga (*Deinacrida heteracantha*), which may have declined from the combined effects of rats and expanding populations of insectivorous birds (Gibbs and McIntyre 1997). More complex effects were documented for the wood rose *Dactylanthus taylorii*. This endemic, dioecious, parasitic plant is pollinated by another endemic species, the short-tailed bat (*Mystacina tuberculata*). However, the inflorescences are also attractive to Pacific rats. On Little Barrier Island, flowers were destroyed by the rats, resulting in periodic failure of the plants to set seed. Rats thus suppressed *Dactylanthus* through the combined effects of herbivory, resource competition with bats, and reduced seed dispersal (Ecroyd 1996). Other forest plants were also affected by Pacific rats, but largely through seed predation and browsing on seedlings. Campbell and Atkinson (2002) studied seedling recruitment in rat-proof exclosures on Hauturu and other northern New Zealand islands, as well as recruitment before and after Pacific rat removal. They found that the rats suppress recruitment in at least 11 species of coastal plants, reducing some to local extinction. This often appeared to be through destruction of seeds. However, rats consumed seeds, leaves, and underground stems of the palm *Rhopalostylis sapida*.

Pacific rats were eradicated from Hauturu in 2004 (Townes et al. 2006), which provides a mechanism for testing the observations made while they were present. So far, increased seedling density compared with nontreatment islands has been found for 13 species of forest plants (Campbell 2009), and there are reports of increased capture rates for selected species of skinks (H. Jamieson personal communication) and increased encounter frequencies of wetapunga (C. Green personal communication). There are also anecdotal reports of increased numbers of *Dactylanthus* plants (S. McInnes personal communication) and forest-inhabiting geckos (C. Green personal communication).

prey—for example, eggs or adult birds during the breeding season—in order to provide a food source during leaner winter months (Bailey 1993, Fay and Stephenson 1989, Hersteinsson and Macdonald 1996).

One of the clearest examples of the impacts of fox predation is seen in the Aleutian archipelago where, by the early twentieth century, many islands had at some stage been stocked with both species of foxes (Bailey 1993). Islands with large populations of birds were viewed as ideal locations because of the readily available food supply, but it was soon noted how rapidly such populations declined, and on many islands foxes died out after extirpating their prey base (Bailey 1993). Burrowing and surface-nesting seabirds were the principal avian components lost from these islands (see Chapter 3). However, the impacts on other ground-nesters, particularly colonially nesting species such as shorebirds, waterfowl, ptarmigan (*Lagopus* spp.) and even—on these often treeless islands—small passerines, have been equally severe (Bailey 1993). Consumption of nesting birds may place foxes in competition with river otters (*Lontra canadensis*) and native raptors on some Alaskan islands (Bailey 1993).

Although there are few precisely quantified changes in Aleutian bird numbers, the impacts of fox introduction and eradication are clear (Ebbert and Byrd 2002, Chapters 3 and 10). The Aleutian cackling goose (*Branta hutchinsii leucopareia*) survived only on three fox-free islands, with a population reduced to under 1000 birds (Byrd 1998). However, fox eradication, combined with natural population recovery and translocations (Ebbert and Byrd 2002), has raised the population to over 35,000 (Byrd 1998). The population size and breeding attempts of black oystercatchers (*Haematopus bachmani*) were significantly lower on the fox-invaded Simeonof and Chernabura Islands than on neighboring, fox-free islands (Byrd et al. 1997), and red-necked phalarope (*Phalaropus lobatus*) recolonized Ogluga and Skagul Islands after fox eradication (Day et al. 1979). The natural arrival of red foxes on Shaiak Island, after crossing sea ice, led to complete breeding failure of the eider (*Somateria mollissima*) and gull (*Larus* spp.) colonies there (Bailey 1993).

Fox predation of seabirds has indirectly caused shifts in entire plant communities of invaded Aleutian Islands, with the removal of marine nutrients resulting in a switch from grasslands to maritime tundra (Croll et al. 2005, Chapter 6). However, fox consumption of a wide range of intertidal animals and plants may also affect community structure and the transfer of nutrients and energy between marine and terrestrial systems (Carlton and Hodder 2003). Intertidal resources are particularly important in sustaining fox populations outside of bird breeding seasons, when alternative prey are often not widely available (West 1987). For example, consumption of marine invertebrates by arctic foxes on St. Lawrence Island, Bering Sea, increased during the winter (Fay and Stephenson 1989). Though the impact of fox predation on such resources remains unquantified, monitoring changes in these communities before and after fox eradication would provide opportunities to assess their impacts more rigorously (e.g., Donlan et al. 2002).

In the Falkland Islands, one of the few other island groups where foxes have been introduced by humans, evidence of their impacts is also circumstantial rather than strictly quantified. However, the deliberately released Patagonian fox (*Pseudalopex griseus*), currently present on five islands in the group, appears to have disrupted and reduced native bird populations (Varnham 2005). The widespread and devastating impacts of red foxes in Australia demonstrate that the significant effects are not confined only to small insular systems, and also suggest what could happen should foxes be released into other islands having native mammals or herpetofauna. Red fox predation has been a key reason for the local or total extinction of many marsupial and reptile species and sea turtle rookeries (Smith and Quin 1996, Burbidge and Manly 2002, Kinnear et al. 2002). Effects on other groups remain largely unquantified despite this species' known omnivory. Studies of fox stomachs can reveal significant numbers of invertebrates (e.g. Palmer 1995), and there are suggestions that foxes may act as vectors for invasive plants, but these remain poorly understood, yet potentially important, impacts. There has also been little investigation of the extent to which introduced foxes may be preyed upon by island raptors in the same way that the native Channel Islands fox (*Urocyon littoralis*) is heavily preyed upon by golden eagles (*Aquila chrysaetos*) in California.

The limited global range of fox introductions means that an understanding of their impacts and results of their control comes from a small number of sources. However, given the dramatic effects seen in these situations, and the fact that information of this kind remains the best predictor of the impact of an invasive species in a novel environment (Simberloff 2003), such impacts are likely to be repeated if foxes are introduced elsewhere. Such an unfortunate experiment may be underway in Tasmania, where the recent red fox introduction (Saunders et al. 2006), combined with the rapid reduction in the population of one of its few potential competitors, the Tasmanian devil (*Sarcophilus harrisii*; McCallum 2008), may have significant consequences for native mammals (Kinnear et al. 2002).

PIGS

Pigs (*Sus scrofa*) are ungulates (hoofed mammals) that originated in the islands of Southeast Asia, dispersed naturally to continental Asia and Europe, and were domesticated independently in multiple regions beginning around 9,000 years ago (Matisoo-Smith 2009). During the period between about 3000 and 800 years ago, the East Asian line of domesticated pigs was established throughout Remote Oceania (though not New Zealand or Easter Island) by the ancestors of the modern Polynesians (Anderson 2009, Matisoo-Smith 2009). Beginning about 500 years ago, feral populations of the European breeds of pigs became established on many islands following release by European voyagers. In the Pacific, the European breeds replaced the smaller, Polynesian varieties. Regardless of their origin, feral populations of pigs tend to revert to the ancestral phenotype, being leaner and more muscular and having longer, coarser hair than domestic pigs (McIlroy 2005).

Adult sizes of feral pigs range from 15–350 kg (Long 2003, McIlroy 2005). Today, feral pigs are found in the Atlantic, Pacific, and Indian Oceans, the Caribbean, and the Mediterranean, on islands ranging from the equator to the subantarctic (Auckland Islands; Matisoo-Smith 2009). Once present, pigs are able to spread throughout an archipelago by swimming between islands (Matisoo-Smith 2009). They exploit a wide range of habitats on islands—from the intertidal to 3,000 m in New Guinea—though their physiological requirement for water limits their ability to persist in very dry environments (Long 2003, McIlroy 2005). Although pigs are widely regarded as having serious negative impacts on islands, there are surprisingly few published studies that provide data on their effects (Ralph and Maxwell, 1984, Campbell and Long 2009, Busby et al. 2010).

Feral pigs are highly omnivorous. Animal prey typically comprises less than half of their diet, yet consumption of protein is important: it limits reproduction in adult females and growth in juveniles (McIlroy 2005). Pigs consume a wide array of animals, including earthworms, snails, insects, frogs, lizards, ground-nesting birds, small mammals, and carrion (Rollins and Carrol 2001, Long 2003, McIlroy 2005, Campbell and Long 2009). They root in the soil and shred logs while searching for invertebrates. Eggs and juveniles of quite large species of vertebrates are consumed, including tortoises, freshwater turtles, sea turtles, and birds (Eckhardt 1972, Fordham et al. 2006). Pigs also consume freshwater eels (McIlroy 2005) and intertidal invertebrates (Carlton and Hodder 2003).

Roots, stems, leaves, fruits, and seeds of terrestrial plants comprise the bulk of the diet of most feral pigs. Pigs often consume and destroy relatively large numbers of large seeds (Campbell and Long 2009). In Polynesia, they frequently destroy tree ferns by consuming their starchy stems (Diong 1982, McIlroy 2005, Campbell and Long 2009). Feral pig diets also include fungi and marine algae (Chimera et al. 1995). Whereas herbivory has serious impacts on plant community composition and structure, it is often difficult to separate its effects from those resulting from physical disturbances that pigs generate.

Feral pigs are unique among the introduced seabird predators in the extent to which they cause physical disturbance to their environments by trampling, creating wallows, destroying rotting logs, and rooting for food in the substrate (Ralph and Maxwell 1984, Vtorov 1993, McIlroy 2005, Mitchell et al. 2007, Campbell and Long 2009, Busby et al. 2010). Under some conditions, pigs may dig to depths of >1 m while rooting. The main direct effect of rooting, aside from predation and herbivory, is the uprooting of plants, many of which evolved in the absence of such disturbance. Even in pigs' native range in Asia, their rooting damages many plant species and alters community composition (Ickes et al. 2001, 2005). In Hawaii, where pigs are introduced, their disturbances are highly destructive in native forests and montane bogs (Spatz and Mueller-Dombois 1975, Diong 1982, Ralph and Maxwell 1984). In Hawaiian montane rain forest, tree seedling densities are lower where feral pigs are present than in exclosures lacking pigs (Drake and Pratt 2001, Busby et al. 2010). Rooting also affects the physical and chemical properties of the soil, which in turn indirectly affect the vegetation, seed bank, and soil microflora and invertebrates (Campbell and Long 2009, Vtorov 1993). Another key indirect

effect of rooting is erosion of soil into streams, and ultimately into coastal marine ecosystems (Eckhardt 1972, Campbell and Long 2009).

Pigs consume fallen fruits of numerous plant species, and disperse viable seeds of some of those that have protective seed coats (Ridley 1930). Because pigs' home ranges can extend up to 43 km² or more (McIlroy 2005), seeds may potentially be dispersed over quite long distances. This dispersal could benefit some island plant species. However, pigs are also implicated in dispersal of some invasive species, such as strawberry guava (*Psidium cattleianum*) in Hawaii (Diong 1982).

Pigs are an important prey item for native raptors on some islands. For example, golden eagles (*Aquila chrysaetos*) consume pigs on the Channel Islands of California (Roemer et al. 2001, 2002). And, while pigs are unlikely to be important in the diets of the native vertebrates that exist on many remote islands today, it is conceivable that before their extinction, large raptors such as the sea eagles (*Haliaeetus albicilla*) in Hawaii could have taken juvenile pigs as prey.

RATS

Probably no group of human-dispersed animals has invaded more islands or caused more destruction on them than these three commensal rats: Pacific rats (*Rattus exulans*), ship rats (*R. rattus*), and Norway rats (*R. norvegicus*; Atkinson 1985, 1989, Courchamp et al. 2003, Towns et al. 2006, Drake and Hunt 2009, Towns 2009a). These generalist rodents are found on island groups everywhere except in the high polar latitudes and, once present on an island, they spread from the intertidal zone to every vegetated habitat, including alpine shrubland 3000 m above sea level. Although it is often difficult to distinguish between the direct and indirect ecological effects of rats, the overall impact of their presence is undeniable (Towns 2009a, Varnham 2010).

The Pacific rat is native to southeast Asia. It was carried into the southwest Pacific Ocean by the ancestors of the modern Polynesians by at least 3000 years ago, and had reached even the most remote islands in Oceania: New Zealand, Rapanui (Easter Island), and Hawaii by 700 years ago (Harris 2009). The ship rat, a native of India, reached Mediterranean Europe at least 4000 years ago and was subsequently carried throughout much of the world in European ships between 1000 and 1700 AD (Harris 2009). The Norway rat, a native of northeast Asia, reached Europe in around 1700 AD, replaced ship rats on European ships, and spread rapidly throughout the world during the next 150 years (Harris 2009). Ship rats reappeared on ships in around 1850, and since then, both it and Norway rats have continued to be introduced to islands.

Although the similarities among the three rat species far exceed their differences, they are not completely alike. One of the main differences among them is body size, which typically ranges from Pacific rats at 60–80 g, to ship rats at 120–160 g, to Norway rats at 200–300 g, though all of these species sometimes reach much larger sizes (Atkinson and Towns 2005). There are also behavioral differences. For example, Norway rats are strong swimmers, while ship and Pacific

rats are progressively weaker (Atkinson and Towns 2005, Innes 2005a, 2005b). In contrast, the ship rat is such an excellent climber that it is often considered arboreal, while Pacific and Norway rats are progressively less adept (Twibell 1973, Atkinson 1985). And, though all three species create small runways, the Norway rat is the only species that commonly excavates extensive burrows and therefore has the potential to cause significant physical disturbance (Innes 2005a). These differences in size and behavior all contribute to subtle differences in ecological effects on island ecosystems.

All three rat species are opportunistic, generalist omnivores, whose diets vary among islands, habitats within islands, and seasons within a habitat (Daniel 1973, Clark 1981, Yabe et al. 2010, Ruffino unpublished data). Seasonal shifts in diet have been attributed to changes in food availability (Caut et al. 2008, Yabe et al. 2010), or to a requirement for greater protein (i.e., animal prey) for juveniles (Cole et al. 2000) or breeding females (Clark 1981). Though omnivorous, rats are selective in their choice of foods (Grant-Hoffman and Barboza 2010, Ruffino unpublished data); as a result, some species of plants and animals that are rare in the environment comprise a high proportion of food ingested, while others are ignored (Clark 1981). In some cases, the ability of an individual rat to exploit a complex food, such as a pine cone, can be transmitted culturally, through social learning (Terkel 1995).

All three rat species eat animals, though animals usually comprise less than half of their food intake (Fall et al. 1971, Wirtz 1972, Sugihara 1997, Cole et al. 2000). They prey upon a broad range of insects, land crabs, other terrestrial arthropods, annelids, snails, freshwater bivalves, amphibians, reptiles, birds, and bats, and they also consume carrion (Atkinson and Towns 2005, Innes 2005a, 2005b). Rats are able to kill adults of some vertebrate species, such as nesting birds (Towns et al. 2006) and crevice-roosting bats (Clark 1981), though with most large prey species it is typically the more vulnerable early life stages that are taken, such as bird and reptile eggs, unfledged chicks, and tortoise hatchlings (Clark 1981, Long 2003). In the intertidal zone, Norway rats consume mainly mollusks and crabs, but also echinoderms, fish, and algae (Carlton and Hodder 2003, Kurle et al. 2008).

The diets of introduced rats are typically dominated by plant material, including starchy underground storage organs, leaves, twigs, bark, sap, flowers, and, especially, fruits and seeds (Figures 4.1, 4.2; reviewed by Grant-Hoffman and Barboza 2010). In New Zealand, flowers of the rare, parasitic plant *Dactylanthus taylorii*, which is adapted for pollination by bats, are destroyed by Pacific rats but pollinated by ship rats (Ecroyd 1996). Evidence of seed predation is very common (Wirtz 1972, Moles and Drake 1999, McConkey et al. 2003, Harper 2005, Shaw et al. 2005, Grant-Hoffman et al. 2010), and seeds form a substantial part of the rats' diets in most habitats, yet quantitative evidence that consumption of seeds (or seedlings) limits plant recruitment is rare (Campbell et al. 1984, Meyer and Butaud 2009). Some of the best evidence comes from exclosure experiments demonstrating that *R. exulans* suppressed recruitment of 11 species on New Zealand offshore islands (Campbell and Atkinson 2002). However, recruitment limitation has more often been inferred from cases where high levels of seed predation were correlated

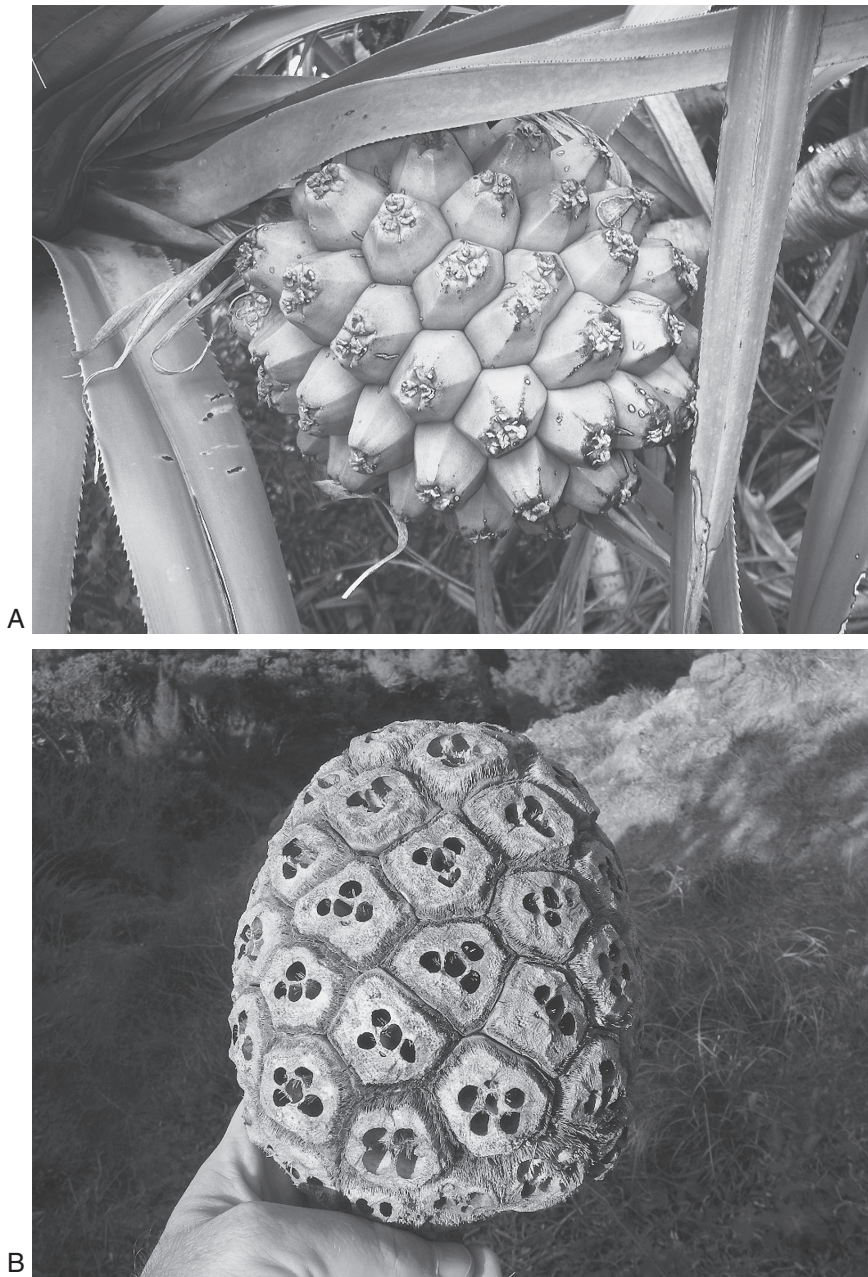


FIGURE 4.1 *Pandanus boninensis* (Pandanaceae) before (A) and after (B) seed predation by ship rats (*Rattus rattus*) on Ogasawara Islands, Japan.

Photo: D. Drake.



FIGURE 4.2 *Freycinetia arborea* (Pandanaceae) inflorescence before and after consumption by ship rats (*Rattus rattus*) on Oahu Island, Hawaii.

Photo: D. Drake.

with a lack of seedling recruitment. For example, where rats are present, the endangered Polynesian sandalwood (*Santalum insulare*) loses >99% of its seeds to predation and does not regenerate (Meyer and Butaud 2009).

Rats may sometimes disperse seeds of native plants. The rats carry much of their food to husking stations—sheltered sites where items can be consumed away from potential competitors or predators (Campbell et al. 1984). In some cases, undamaged or partially damaged seeds may be discarded in these sites and subsequently germinate (Campbell et al. 1984, McConkey et al. 2003, Abe 2007, Kawakami 2008, Perez et al. 2008, Shiels and Drake 2011). However, none of the three species of rats commonly store seeds in caches in the wild (Vander Wall 1990). Norway rats sometimes form larderhoards (caches containing large numbers of seeds in one place) in captivity, but such behavior is rare in the wild, and would be unlikely to result in significant plant recruitment even where it did occur (Abe 2007). Perhaps more significant is the potential for small seeds to pass through a rat's digestive tract unharmed, and thus be dispersed in feces. Whole, apparently undamaged seeds of a number of small-seeded plant species have often been noted in rat feces (Clark 1981, Cole et al. 2000). When ship rats consumed fruits containing seeds <1 mg in mass (New Zealand; Williams et al. 2000) or <1.5mm in length (Hawaii; Shiels 2011, Shiels and Drake 2011) the seeds of many species passed through the rats' digestive tracts with no decrease in viability. It is likely that the maximum size of seed that can escape damage by the teeth is related to the size of the rat species.

Introduced rodents are a common, and in some cases dominant component of the diets of native raptors such as owls in Chile (*Tyto alba*; Navarrete and Castilla 1993), owls (*Ninox novaeseelandiae*) and harriers (*Circus approximans*) in New Zealand (Atkinson and Towns 2005, Innes 2005a, 2005b), owls (*Asio flammeus*) and hawks (*Buteo solitarius*) in Hawaii, and owls (*A. flammeus*) and buzzards (*Buteo buto toyoshimai*) in the Ogasawara Islands (Kawakami 2008). It is not clear whether the rats are supplements to the birds' natural diets, or substitutes for native prey species that have decreased in abundance (Kawakami 2008). For at least some time after their arrival, rats must also have figured in the diets of some island raptors that are now extinct.

MICE

The house mouse (*Mus musculus* s.l.) is the most widely distributed introduced mammal in the world (Long 2003, Ruscoe and Murphy 2005). By 6000 years ago it had reached the Mediterranean after spreading along trade routes from its native India (Harris 2009), and it subsequently moved with Europeans as they explored the world. House mice now occupy nearly every environment where they could possibly survive, with the exception of those from which they appear to be excluded by intact communities of native rodents (Ruscoe and Murphy 2005). This wide distribution is aided by at least one physiological advantage that house mice have over commensal rats; because house mice can obtain most of their water directly from their food and make very concentrated urine, their water requirements are

low, and this allows them to occupy extremely dry environments (Ruscoe and Murphy 2005). House mice range in size from about 12–30 g, and are mainly terrestrial, though capable of climbing and swimming (Ruscoe and Murphy 2005). They dig burrows that damage peat-forming cushion plants on Marion Island (Angel et al. 2009), but it is unclear how common it is for such physical disturbance to negatively affect island plants.

In terms of their ecological role as invasive species, house mice have often been regarded simply as scaled-down version of rats, and therefore likely to have scaled-down impacts relative to those described in the previous section—but hard data are scarce. Emerging information suggests that when house mice are not limited by competition from introduced rats or predation by introduced carnivores, they may reach very high densities (Russell and Clout 2004, Caut et al. 2007) and have severe ecological impacts (Angel et al. 2009). House mice are more likely than rats to undergo sharp population increases after consuming the large numbers of seeds (and lepidopteran larvae) produced by masting trees in New Zealand (Murphy 1992, Fitzgerald et al. 1996, Ruscoe et al. 2005, Murphy 2005).

House mice are omnivorous, typically consuming roughly equal amounts of animal and plant matter, though totals may be skewed toward one or the other depending on variation in species abundance among habitats or seasons (Badan 1986, Miller and Webb 2001, Ruscoe and Murphy 2005, Angel et al. 2009). Diets have been assessed mainly on the basis of stomach contents of trapped animals, examination of food remains in the wild (e.g., discarded seed coats), and a few experimental feeding trials. The recorded diet of the house mouse is narrower than that of introduced rats, though this apparent difference may simply be a reflection of our relative lack of knowledge about mice.

The animal component of the house mouse diet consists mainly of insects, especially large, slow-moving prey such as lepidopteran larvae, though beetle larvae and spiders are also commonly eaten. Predation is often severe enough to limit insect populations, and has even resulted in local extinctions (Marris 2000). Mice forage on intertidal invertebrates (Navarrette and Castilla 1993). They also consume vertebrate prey and carrion, though much less commonly than rats do, and there is some evidence that house mice prey upon eggs and chicks of the Gough bunting (*Rowettia goughensis*; Angel et al. 2009). Overall, however, the documented negative effects of house mice on land birds are more commonly indirect, resulting from competition for invertebrate prey (Angel et al. 2009, Chapter 9).

The main plant parts consumed by house mice are typically the seeds of grasses and sedges, and the young stems of herbaceous plants, though exceptions are common (Long 2003, McIlroy 2005). For example, mice feed heavily on seeds of *Nothofagus* spp. and other trees in New Zealand, and can build to very high population densities following a mast year (Murphy 1992, Fitzgerald et al. 1996). There is little evidence that house mice disperse seeds (Williams et al. 2000), but this may be owing to a lack of investigation; it is likely that very small seeds could pass unharmed through mice that have consumed fruits.

House mice are taken as prey by the same raptors that take rats (Ruscoe and Murphy 2005), but their smaller size makes them vulnerable to smaller predatory

birds as well. For example, in New Zealand, they are eaten not only by raptors, but also by rails (*Gallirallus australis*) and kingfishers (*Halcyon sancta*).

Vulnerability of Island Biota

In their natural state, islands generally support only a limited range of mammalian predators, and terrestrial mammals of any kind (other than bats) are extremely uncommon on remote islands. Most island animals, therefore, have evolved in the absence of predation (or competition) from mammals, and are generally believed to be naïve, lacking the antipredator behaviors necessary to coexist with mammalian predators (Eckhardt, 1972, Blumstein and Daniel 2005, Whittaker and Fernández-Palacios 2007). Likewise, island plants have evolved in the presence of a limited suite of mammalian herbivores, and are assumed to lack defenses against herbivory or seed predation by them (Carlquist 1974).

ARTHROPODS (AND EARTHWORMS)

Our knowledge of the impacts of invasive predators on invertebrates lags behind that of other physically larger, more obvious taxa (St Clair 2011). There have been only a limited number of studies specifically focused on the impacts on invertebrates, so much of our knowledge is derived from the examination of predator stomach contents, or from anecdotally noted responses following eradications. The impacts have mostly taken the form of direct losses through predation, though there is a minor role for indirect effects through resource competition, and for physical disturbance leading to the disruption of microclimates—a factor that is clearly more important for this group than for larger animals. Species that appear particularly vulnerable are those that exhibit one or a combination of the following characteristics: large size, flightlessness, slow larval development, a need to descend to the ground for at least part of their life cycle, or production of olfactory social cues (making them more detectable to mammalian than avian predators).

Groups such as the New Zealand weta—large, flightless orthopterans—have been particularly badly affected because they exhibit all the characteristics associated with elevated risk. Many species have been extirpated from large parts of their original range, and translocated populations thrive only on islands free from introduced mammals (Watts and Thornburrow 2009). However, species which shelter in secure, inaccessible refuges have been able to coexist with rats (Gibbs 2009). Similarly, flightless Lepidoptera and their larvae are often preferentially consumed by mice, resulting in local or island-wide extirpation (Angel et al. 2009). Following the invasion of Frigate Island, Seychelles, by Norway rats, numbers of the large tenebrionid beetle *Polposipes herculeanus* declined by approximately 80% in five years, with impacts also suspected for large scorpions and millipedes (Parr 1999). Elsewhere, ship rats caused declines in endemic tenebrionid beetles in the Balearic Islands (Palmer and Pons 2001).

The initial impacts of rats on the invertebrates of previously mammal-free islands are probably most well documented in New Zealand (Gibbs 2009). Based on stomach contents, all three rat species consume earthworms, centipedes, beetles, weevils, cicadas, spiders, and stick insects, as well as the larvae of these, butterflies, and moths (Atkinson and Atkinson 2000). Mice are also efficient predators of invertebrates, and may have caused the extirpation of several insects from Lord Howe Island (Hutton et al. 2007) and the Antipodes Islands (Marris 2000). There are, thus, numerous examples where invertebrates have clearly benefited from the removal of introduced rodents (e.g., Atkinson and Towns 2001, Sinclair et al. 2005, Towns 2009b). Comparing island pairs with and without introduced mice suggests that mice strongly affect invertebrate species composition and abundance, as well as reducing mean body size through preferential consumption of larger individuals of several species (Angel et al. 2009). Although on one such pair, invaded Marion Island and mouse-free Prince Edward Island in the subantarctic, invertebrate numbers did not recover in mouse-exclusion plots. This was attributed to significant changes in the ecology of the island in the absence of seabirds (Van Aarde et al. 2004). However, as with many other species, quantifying the effects of rodent eradications on invertebrate populations, when there is no comparable preinvasion baseline, is clearly difficult, and removal of rats in particular often brings simultaneous benefits for insectivorous birds, which can then actually reduce invertebrate numbers, as occurred on Kapiti Island, New Zealand (Sinclair et al. 2005).

Although it might be expected that rats and mice would be the predators with the greatest impacts on invertebrates, larger predators such as foxes and cats, particularly juveniles, may also consume such prey in significant amounts (Palmer 1995, Gillies 2001), and all of the key seabird predators have been recorded consuming a wide range of intertidal invertebrates (Carlton and Hodder 2003). Pigs consume large quantities of earthworms (Chimera et al. 1995), and pig removal from Aorangi Island, Poor Knights group, New Zealand is estimated to have benefited at least 18 species of invertebrates (Towns et al. 2009b). Clearly, in terms of habitat alteration, pigs have the most significant impacts, although the specific nature of the effects that rooting, wallowing, and plant damage have on native invertebrate populations remain to be fully investigated (Medina and García 2007).

On many tropical islands, land crabs are keystone species, exerting strong effects on vegetation composition and nutrient deposition (Lindquist et al. 2009). However, again, there is limited experimental evidence demonstrating the impacts of introduced mammalian predators on these important species. Cats, rats, and mice have all been recorded consuming crabs of a variety of species (Carlton and Hodder 2003), and predation, particularly of smaller individuals, is likely to be important. On Clipperton Island (south of Mexico) the presence of pigs and, after they were eradicated, a reinvasion of ship rats, both led to declines in land crab numbers (Sachet 1962, Pitman et al. 2006, Box 4.2). After cats and rats were eradicated from Raoul Island, New Zealand both a land crab (*Geograpsus grayi*) and ghost crab (*Ocypode kuhlii*) reappeared after having been at undetectable levels

Ecosystem Feedback Effects of Introduced Predators

Location: Clipperton Island, Eastern Pacific Ocean

Climate: tropical

Clipperton Island (10°18'N 109°132'W; 1.6 km²) is a small, uninhabited desert atoll in the Eastern Pacific Ocean, belonging to France. People mined guano there from 1892 to 1917, and introduced the first widespread plants, coconuts (*Cocos nucifera*), and mammals, pigs. The introduced pigs preyed on the abundant seabird colonies, driving severe population declines, with only 500 brown boobies (*Sula leucogaster*) and 150 masked boobies (*S. dactylatra*) recorded in 1958 (Stager 1964). This lack of avian prey led to pigs switching their diet to consume the large orange land crabs (*Gecarcinus planatus*), which had otherwise been keeping the island vegetation-free, except for mature palms. The reduced grazing pressure resulted in an explosion in introduced weeds. However, pigs were eradicated by Ken Stager in 1958, facilitating a substantial recovery in the seabird and crab populations, and causing the atoll to revert back to its devegetated state.

By 2000, however, ship rats colonized the island from a nearby shipwreck. This accidental introduction negatively affected both the seabirds, particularly smaller species such as sooty terns (*Onychoprion fuscatus*), and the land crabs. Furthermore, it was hypothesized that the increase in exotic vegetation cover resulting from reductions in crab numbers enhanced the spread of rats through the provision of additional, more suitable, habitat. This, in turn, led to increased impacts on crabs and further reductions in grazing pressure (Pitman et al. 2006). Such facilitation between introduced rats and introduced plants triggered an “invasional meltdown” (Simberloff and Von Holle 1999), with significant direct and indirect impacts upon the island’s native fauna.

Thus, on Clipperton, while both introduced pigs and rats directly reduced breeding seabird populations, their direct impacts on other ecosystem components were also substantial. These impacts were both negative (crabs) and positive (plants), and resulted in additional indirect feedback, which further affected both seabirds and non-seabird ecosystem components.

(Bellingham et al. 2010). Rodents are also likely to act as competitors as well as predators of land crabs, consuming shared resources such as carrion and seeds.

Lastly, one of the greatest threats to many native invertebrates is the introduction of alien invertebrates, particularly a number of ant species (Plentovich et al. 2009). These, like rodents, act both as competitors and predators of many species, including large land crabs. This can affect species distributions (McNatty et al. 2009) and even change the entire ecology of an island (O’Dowd et al. 2003, Box 4.3).

LAND SNAILS

Introduced predators have been so successful and damaging on islands mainly because of their opportunistic capacities to exploit their novel environment, and especially their adaptive foraging behavior. Among invertebrates, land snails have suffered extremely high levels of predation. In the tropical Pacific, land snails have

BOX 4.3

Crazy Ants Cause Invasional Meltdown

Location: Christmas Island, Eastern Indian Ocean, Australia

Climate: tropical

As with many islands, Christmas Island (10°30'S 105°40'E; 134 km²) has suffered from the introduction of mammals such as house cats, ship rats, and Pacific rats, resulting indirectly in the extinction of both of its native rat species *R. macleari* and *R. nativitatis* (Wyatt et al. 2008), and declines in other native fauna. However, it is the crazy ant (*Anoplolepis gracilipes*), introduced sometime in the early 1900s, which has proven to have the most important effects on the island ecosystem. Like most introductions, it was considered benign, and was disregarded until multi-queen “supercolonies,” from 0.9 to 787 ha in size, emerged after 1989. The formation of supercolonies allowed the ants to reach very high local densities, and they began to have widespread impacts on almost every trophic level of the ecosystem, both directly and indirectly (O'Dowd et al. 2003).

Through overwhelming predation, crazy ants locally extirpated the red land crab (*Gecarcoidea natalis*), the dominant endemic forest floor consumer, indirectly releasing the crabs' regulation of seedling recruitment and litter breakdown. The crazy ant also created new associations with introduced honeydew-secreting scale insects, the farming of which resulted in high population densities of host-generalist scale insects and growth of sooty molds, leading to canopy dieback and even deaths of canopy trees (O'Dowd et al. 2003). The abundance of the ground-foraging emerald dove (*Chalcophaps indica*) is significantly reduced around supercolonies, and nesting success of the endemic Christmas Island thrush (*Turdus poliocephalus erythropleurus*) might also be negatively affected (Abbott 2006). Although not killing the endemic Abbott's booby (*Papasula abbotti*), which nests in the canopy of old-growth forest, the ants created such a disturbance that nesting sites were abandoned.

The combination of strong direct negative impacts of crazy ants on native crabs, and the protective benefit the ants provided to introduced scale insects, has created feedback loops with enormous consequences for the vegetation of Christmas Island, ultimately altering the entire ecosystem. This is an example of invasional meltdown (Simberloff and Von Holle 1999), a process in which multiple invasive species facilitate each other to the severe detriment of the native fauna and flora. Invasive ants are known to be a threat to biodiversity (Holway et al. 2002), and they are found on a number of other oceanic islands, though their impacts in many of these systems are only just emerging (e.g., Plentovich et al. 2009) or remain, as yet, unclear. However, similar direct impacts of crazy ants have been found in the Seychelles archipelago, where positive associations with scale insects led to negative impacts on trees (*Pisonia grandis*) and invertebrate communities (Hill et al. 2003).

undergone some of the greatest adaptive radiations on earth, giving rise to thousands of endemic species (e.g., Cowie 1995, 2004) with poor dispersal capacities and restricted ranges (e.g., *Partula* spp. in French Polynesia, Murray et al. 1988; *Powelliphanta* spp. in New Zealand, Meads et al. 1984). Hawaiian land snails are characterized by low fecundity (4–7 offspring per year), large birth size (4–5 mm), slow growth rate, late maturity (3–9 years), and long lifespan (>10 years; Hadfield

and Mountain 1980, Hadfield et al. 1993, Hadfield and Saufler 2009). Their high degree of endemism, low motility, and slow population growth rates have rendered snails highly susceptible to habitat destruction and predation by introduced predators (both factors have rendered roughly 90% of the Hawaiian snail species extinct; Lydeard et al. 2004).

Within the guild of introduced seabird predators, not only rats, house mice, and pigs, but also hedgehogs (*Erinaceus europaeus*), possums (*Trichosurus vulpecula*), ants (e.g., *Solenopsis invicta*), and crabs (e.g., *Carcinus* sp.) have been implicated in the decline and extirpation of Pacific land snails (e.g., Powell 1938, Solem 1976, Vermeij 1982, Chiba 2007, Brescia et al. 2008). Rodent damage to snail shells is often easily recognized because shells are typically gnawed in a characteristic pattern (Brooke 2000, Brescia et al. 2008), while pigs tend to break the shells into several large pieces (Brescia et al. 2008). Hence, quantification of rat predation on extinct New Zealand endemic island snails has been possible by the examination of subfossil shells and their damage characteristics (Brooke 2000). Rodents are the introduced seabird predators that by far have the most negative effects on snails (Hadfield et al. 1993, Brooke 2000, Chiba 2007), mainly because of their ecological plasticity and their widespread introduced ranges. Moreover, both ship rats and Pacific rats are proficient tree climbers (King 2005) and can learn from other rats to easily catch tree snails. Introduced predatory ants, however, may be much more likely to affect ground-dwelling snail species (e.g., Endodontidae, Solem 1976). On the island of Oahu, Hawaii, Hadfield et al. (1993) showed that rats preferentially prey upon larger snails (>15 mm for *Achatinella mustelina*). On the Noises island group of New Zealand, Moors (1985) observed a large number of rat-damaged juvenile shells—usually with the lower spirals chewed open, or the apex of the spiral removed. He hypothesized that the population declined because of heavy predation on juvenile snails, because adult shells are too massive to be opened. However, *R. rattus* has been shown to consume snails having a wide range of shell lengths (11.5–59 mm) when two introduced snail species (*Euglandina rosea* and *Achatina fulica*) of different sizes were offered in feeding trials, suggesting no size refuge from rat predation for these species (Meyer and Shiels 2009). Mice have been recorded eating entire *Placostylus* egg clutches under semi-natural captive conditions on the Isle of Pines, New Caledonia (Brescia 2004). Pigs eat both large juveniles and adults on the Isle of Pines. Brescia (2001) observed that in pig-invaded areas, *Placostylus* abundance was only half that of pig-free areas. Therefore, introduced seabird predators (especially mammals) appear to be potentially very harmful to snail populations through severe predation of eggs, hatchlings, and juveniles.

There has recently been a strong focus on studying the adaptation and evolution of native prey species in response to introduced predators (e.g., Mooney and Cleland 2001, Strauss et al. 2006; see review by Cox 2004). Some studies have pointed out behavioral and morphological responses of native mollusks to introduced predator pressure. For example, intertidal mollusks showed an adaptive phenotypic plasticity (increased shell thickness) when exposed to an increase in the abundance of a shell-crushing introduced predator, the green crab *Carcinus*

maenas (Vermeij 1982; Trussell and Smith 1999). Marine snails, *Littorina obtusata*, showed a rapid intraspecific morphological shift in shell thickness and height, becoming markedly flatter and thicker within a period of 100 years in response to new but intense directional selection by alien green crabs (Seeley 1986). On Japan's Ogasawara Islands, Chiba (2007) provided evidence of ecological and morphological shifts in the land snail *Mandarina anijimana* in areas invaded by ship rats. In just 17–19 years, rat predation pressure selected for snails with small, high, and dark shells. While changes in shell size, thickness, and shape are common in gastropods facing predators, shell darkness may be associated with change in habitat use by snails restricted to refugia.

The great diversity of native island snails is disappearing rapidly (Cowie 2004, Lydeard et al., 2004). Many species are extinct or severely threatened, and often restricted to high-elevation refugia (e.g., Lee et al. 2008). Introduced seabird predators (mainly rats) can affect not only the population dynamics of native snail species, but also cause phenotypic and ecological changes in native snails, and thus may alter interactions among native species.

AMPHIBIANS AND REPTILES (HERPETOFAUNA)

There are few examples where introduced seabird predators were demonstrated agents of decline of amphibians on islands. There are two reasons for this. First, because islands often lack substantial freshwater ecosystems, they can represent harsh environments for aquatic amphibians. Furthermore, the climatic areas occupied by some seabird predators are beyond the range of amphibians (and reptiles). For example, the cool temperate and arctic environments invaded by foxes are not usually inhabited by herpetofauna. Second, some amphibians are able to avoid predation because toxins in the skin make them unpalatable. Nonetheless, some species of salamander are largely terrestrial, and can inhabit relatively dry islands. Examples may be found on islands off the west coast of North America. Some species, such as the slender salamander (*Batrachoseps pacificus*) survived on islands off California invaded by cats, rats, and pigs, but the effect on these amphibians is as yet unknown.

By comparison, reptiles are widespread on temperate and tropical islands. Some reptiles have demonstrated vulnerability to seabird predators. Little is known of the effects of feral pigs, but there is a growing literature on cats and rodents. The most comprehensive studies of the effects of cats are in the Canary Islands, where cats are implicated in the decline and local extinction of several species of large endemic *Gallotia* lizards (Nogales et al. 2006). Cats have also been listed as contributing to declines of large terrestrial species of *Iguana* in the Caribbean (Mitchell et al. 2002). Why such large species are vulnerable remains unclear.

Traits affecting vulnerability to rats and mice can now be inferred through the responses of resident species when the rodents are removed. For example, in New Zealand, tuatara (*Sphenodon punctatus*) populations coexisted with Pacific rats on nine islands. Even though adult tuatara can be five times the weight of Pacific rats, tuatara had declined to near extinction (<20 individuals) on five islands, and

showed consistently impaired recruitment on three other islands. When the rats were removed from three islands, tuatara consistently demonstrated increased juvenile recruitment on those islands, and continued lack of recruitment on a nontreatment island where Pacific rats remained. The results indicated that Pacific rats probably affected recruitment through predation of eggs and juveniles. An unexpected response on some islands was increased body condition (mass relative to length) after the removal of rats. The effects on body condition were likely indirect, through competition for food or interference competition resulting in reduced foraging time by tuatara (Towns et al. 2007).

The list of other reptiles whose responses were measured after rat removal is relatively short (see Towns et al. 2006). For example, three species of geckos and two of skinks responded positively to the removal of Pacific rats (plus rabbits) from islands around New Zealand. Similarly, removals of Norway rats were followed by recovery of one species of skink in New Zealand, plus one species of skink and two of gecko in Mauritius. Ship rats affected one species of whiptail lizard and one of snake in the Caribbean. Coupled with presence and absence data (non-overlapping ranges of predator and native species), rats appear to heavily affect ground-dwelling and nocturnal species with low reproductive output. However, depending on rat species, they are also capable of affecting diurnal species having high annual reproductive output. There are even fewer examples of the responses of reptiles to house mice. In northern New Zealand, tuatara appeared to coexist with mice on one small island until the island was invaded by Norway rats, at which point the mice and tuatara were eliminated (Newman 1987). On Mana Island off central New Zealand, a small diurnal skink, nocturnal geckos, and a large nocturnal skink all increased in abundance after mice were removed (C. Miskelly personal communication). Each of the species was largely or exclusively ground-dwelling.

LAND BIRDS

The introduction of mammalian predators has, perhaps unsurprisingly, had dramatic effects on the land birds of many islands. The overwhelming impact has been to affect populations negatively through predation on some or all life stages. This has led to population declines, extirpation from islands shared with introduced predators and, in an unfortunately large number of cases, the extinction of the birds concerned.

The two key life history traits that increase bird vulnerability to many of the most widely introduced mammalian predators are the lack of antipredator defense mechanisms (often termed “island naivety”) and/or largely terrestrial habits. Thus, the impacts of foxes, cats, and pigs on land birds are often similar to their impacts upon seabirds (Courchamp et al. 2003, Nogales et al. 2004, see also Chapter 3). This is seen not only with endemic island species, but also with widely distributed ground-nesting species such as shorebirds and waterfowl which, like seabirds, often breed in large numbers on small islands because of the limited presence of mammalian predators. A clear example of this is the impact of Arctic foxes in the

Aleutian Islands, where the Aleutian cackling goose (*Branta hutchinsii leucopareia*) was almost driven to extinction through fox predation of all life stages, and other species including shorebirds and ptarmigan (*Lagopus* spp.) have been severely affected (Bailey 1993, Ebbert and Byrd 2002).

Pigs can readily consume nest contents and, while most records of such impacts are for seabirds rather than land birds (Chapter 3), there is no reason to consider the latter group immune; pigs have been suggested as a major predator of long-extinct species such as the flightless birds of Mauritius (Cheke and Hume 2008). Cats are also adept at consuming flightless and ground-foraging birds (Courchamp et al. 2003, Nogales et al. 2004). Indeed, the evolution of flightlessness and other “naïve” traits, such as slower reproduction and smaller clutch sizes, have frequently proven to be fatal for avifauna once mammals were introduced to an island (Fuller 2000). While the list of such species is already long, paleontological and archeological evidence from areas such as the South Pacific islands demonstrate that, prior to European arrival in the islands, many species were eliminated by the combination of people and the Pacific rats, pigs, and dogs that usually accompanied them (Steadman 2006). A good example of the impacts of the Pacific rat is seen with the Stephen’s Island wren (*Traversia lyalli*) in New Zealand. While the last remaining population of this bird was extirpated by cats (Fuller 2000, Galbreath and Brown 2004), archeological evidence has revealed that it had been widespread on mainland New Zealand until the arrival of Pacific rats (Worthy and Holdaway 1994).

Norway rats are also important predators, particularly of more terrestrial species (Atkinson 1985). For example, their removal from Campbell Island (Towns and Broome 2003) has led to the natural recolonization, from an offshore islet, of an undescribed snipe (*Coenocorypha* sp.; Miskelly and Fraser 2006), and enabled the reintroduction of the extirpated flightless Campbell Island teal (*Anas nesiotis*; McClelland and Gummer 2006). In the Falkland Islands, two species—the tussac bird (*Cinclodes antarcticus*) and the endemic Cobb’s wren (*Troglodytes cobb*)—are both restricted to rat-free islands (Hall et al. 2002). However, some of the clearest examples of the impact of rats on land birds have followed the introduction of the ship rat. Lord Howe Island (Tasman Sea) rapidly lost five species after ship rats colonized (Hutton et al. 2007), and nine species were either extirpated or severely reduced in number on Big South Cape Island, New Zealand (Atkinson and Bell 1973, Towns 2009b). This species is significantly more arboreal than the other two *Rattus* species, and is therefore able to affect a wider range of species. They are probably the most frequent predator of New Zealand forest birds, taking eggs, chicks, and even sitting adults of smaller species (Innes 2001). The presence of ship rats was highly correlated with the decline and/or extinction of Polynesian monarch flycatchers of the genus *Pomereia*, while the presence of Pacific rats was not (though birds susceptible to the latter species may have gone extinct much earlier; Thibault et al. 2002). Indeed, this study also revealed variation in the vulnerability of nests based on their position within vegetation, with nests of flycatchers on horizontal branches suffering higher rates of rat predation than those of another native species on more vertical branches.

While the impact of Pacific rats has often been considered to be less than that of the European-introduced species, this has recently been challenged (Towns 2009b); results from pre- and post-eradication monitoring of Pacific rats have revealed increases in a number of native species on Tiritiri Matangi, New Zealand, for example (Graham and Veitch 2002). However, some of these effects may not be a result of direct predation—an alternative possibility is that these mammals act as resource competitors by consuming prey, particularly invertebrates, thus reducing prey availability for insectivorous birds. Nectar and flowers can also be consumed, which not only removes a resource but also potentially disrupts pollination interactions (Chapter 9). Interestingly, the impacts of rats on land birds appear to be lower on tropical islands, perhaps because such species have evolved alongside land crabs, and so have retained their antipredator strategies to a greater extent (Atkinson 1985).

The impact of mice is little known, and so is probably underestimated. There is some evidence that mice prey on the endemic Gough bunting (*Rowettia goughensis*) on Gough Island (Angel et al. 2009), and they also appear to act as competitors for invertebrate prey on other islands (Angel et al. 2009). It is therefore likely that, ecologically, they have similar effects to rats.

Although the vast majority of impacts have been negative, a few land birds have benefited from mammalian introductions. One fascinating example occurred as a result of the introduction of pigs to the Channel Islands, California. Here, piglets formed the basis of an increased food supply that allowed golden eagles (*Aquila chrysaetos*), which were already visiting the islands, to set up breeding territories. However, while this had a positive effect on the eagles, it has had severe negative impacts on the endemic Channel Islands fox (*Urocyon littoralis*; Roemer et al. 2002). Introduced rodents are important components of the diets of island raptors.

MAMMALS

On oceanic islands, the native mammal fauna consists mainly of large marine mammals that use the islands as breeding sites, or bat species that could fly across an oceanic barrier. Many islands closer to continents, however, such as land-bridge islands, contain relictual terrestrial mammal faunas that are often characterized by high rates of endemism, and small rodent species are particularly represented in this category (Amori et al. 2008, Rando et al. 2008, Harris 2009).

Introduced predatory mammals that share a close phylogenetic relationship to native mammals (e.g., belong to the same taxonomic family) may have strong indirect ecological effects on them, because they compete for resources and share predators, parasites, and diseases (Harris 2009). Introduced rodents have been implicated in the declines and extinctions of many native island small mammal species, although evidence is sometimes equivocal and mechanisms unknown (Harris 2009). Harris (2009) comprehensively reviewed the impacts of introduced rodents on native mammals, which we only briefly summarize here, in addition to considering other introduced predators for which data exist. We broadly classify

the impacts upon nonflying native mammals as direct predation, and indirect effects such as competition or infectious agent transmission.

The Australian mainland provides the most compelling evidence of introduced predator impacts on native mammals (Salo et al. 2007). Mammals are the largest component of the diets of introduced foxes and cats (Riseby et al. 1999). Small mammals (<200 g) are most susceptible to cats, and medium-sized mammals (450–5,000 g) to foxes (Dickman 1996), although the fox diet is less diverse than that of cats (Riseby et al. 1999). Small native rodents increase in abundance in the absence of foxes and cats (Moseby et al. 2009). Competition with dingoes (*Canis lupus dingo*) also likely led to many declines, even in larger native mammals (Dickman 1996). The presence of introduced rabbits (Dickman 1996) and rodents (Harris 2009) as alternative prey for predators also contributes to impacts on native mammals. A lack of appropriate antipredator behavior in native mammals also contributed to surplus killing by foxes and dingoes (Short et al. 2002), but for native rats, some mortality by foxes may be merely compensatory (Banks 1999). On Australian islands, large ground-dwelling native mammals were most susceptible to extinction in the presence of foxes and cats, and the impact of cats was greater on arid than on wet islands (Burbidge and Manly 2002).

Islands off California and Mexico also provide much evidence of impacts upon endemic small mammals. Predation by cats is the most likely cause of declines in many native rodent species, but competition with introduced rats (Álvarez-Castañeda and Ortega-Rubio 2003) and habitat degradation by introduced herbivores (Knowlton et al. 2007) also play a role. On San Clemente Island, California, introduced cats and native foxes appeared to have dietary overlap, but partitioned resources, possibly reducing competition (Phillips et al. 2007). On islands off Mexico, extinctions of nonflying native mammals were greater in the presence of cats and ship rats when other factors contributed, such as an absence of alternative prey, presence of native predators, native populations with large carrying capacities, and increased variation in seasonal rainfall patterns (Donlan and Wilcox 2008). Many other examples exist of introduced mammal impacts on native mammals, particularly within assemblages of small mammals (see review in Harris 2009).

Rodents may also affect island mammals indirectly, by acting as vectors for novel diseases. The extinction of the rats native to *Christmas Island* in the Indian Ocean (*Rattus macleari* and *R. nativitatis*) has been attributed to a trypanosome (a type of protozoan parasite) introduced by ship rats (Wyatt et al. 2008, Harris 2009; Box 4.2). Trypanosomes have also been implicated in European *Rattus* species' replacement of the introduced Pacific rat in New Zealand, but competition seems a more likely explanation (Russell and Clout 2004). On Santa Cruz Island in the Galápagos, an experimental population of the Galápagos rice rat (*Aegialomys galapagoensis bauri*) succumbed to a mystery illness when in contact with ship rats (Harris 2009). In contrast, short-tailed mice (*Leggadina lakedownensis*) on Thevenard Island off Australia were not found to be vulnerable to murine virus from introduced house mice (Moro et al. 1999). In Madagascar, introduced ship rats have an impact on native rodents only at high altitudes, where bubonic plague

persists (Harris 2009). At low altitudes, the distribution of native rodents is, instead, better predicted by habitat fragmentation than by interactions with ship rats (Ganzhorn 2003). Impacts of introduced mammals can interact with habitat modification, such as in the Philippines, where habitat degradation facilitates invasion by introduced rodents by reducing the community richness of native small mammals (Harris 2009).

Some evidence exists of cats, stoats, and rats preying on bats (O'Donnell 2000). Competition for roost sites may also contribute to declines in bat populations. Convincing circumstantial evidence exists that introduced rats have played a major role in the decline of some bat species on islands around the world, though the mechanism is unclear (Harris 2009). The brown tree snake contributed to the decline of bats and birds on Guam (Fritts and Rodda 1998).

Marine mammals have been greatly impacted recently by the emergence of novel infectious agents, and it has been suggested that alien species may be one vector for these. Examples include canine distemper virus infecting Caspian seals (*Pusa caspica*), possibly through contact with domestic or wild dogs (Kennedy et al. 2000), *Salmonella* infecting both New Zealand sea lions (*Phocarcos hookeri*) and introduced pigs on the Auckland Islands (Fenwick et al. 2004), and a male-biased *Salmonella* that could have infected subantarctic fur seals (*Arctocephalus tropicalis*) from house mice on Marion Island (de Bruyn et al. 2008).

PLANTS

Island plants have evolved in environments lacking mammalian herbivores and seed eaters, and are therefore widely believed to lack defensive adaptations against herbivorous and granivorous mammals (Carlquist 1974, Bowen and Van Vuren 1997). However, there have been surprisingly few direct tests of this hypothesis. Perhaps the best evidence that island plants are weakly defended comes from an experimental study comparing six plant taxa from the California mainland and their close relatives on Santa Cruz Island, 30 km offshore (Bowen and Van Vuren 1997). The island plants all possessed physical and/or chemical traits that suggested they were more weakly defended than their mainland relatives. In feeding trials, sheep (*Ovis aries*) always preferred eating island plants over their mainland relatives. Elsewhere, on islands in the Haida Gwaii archipelago, where plants were freed from ungulate browsing just 10,000 years ago, relaxed selection apparently resulted in lower concentrations of defensive compounds, and increased susceptibility to herbivory, in *Thuja plicata* trees (Vourc'h et al. 2001). Plants in families known to have chemical defenses against mammalian herbivores are less likely to be consumed by rats (*Rattus* spp.) than are plants in families not known to have such defenses (Grant-Hoffmann and Barboza 2010).

Much of the evidence that island plants are weakly defended against mammalian herbivores comes from the observation that introduced mammals typically prefer to eat island plants, rather than introduced plants that evolved in the presence of continental mammals (Nuñez et al. 2008). For example, house mice (*Mus musculus*) prefer native over alien plants on islands in the southern oceans

(Angel et al. 2009). However, in some cases, it is possible that the introduced plants are not a random sample, but instead are successful invaders because they are exceptionally well defended against herbivores.

Throughout the Indo-Pacific, members of certain plant genera are consistently identified as prone to seed predation by introduced rats, though it is not known what traits make them so vulnerable. Plants include eudicot trees such as *Elaeocarpus* (Elaeocarpaceae), *Ochrosia* (Apocynaceae), *Pittosporum* (Pittosporaceae), *Planchonella* (syn. *Pouteria*; Sapotaceae), and *Santalum* (Santalaceae) and monocot trees such as *Pandanus* (Pandanaceae), and many members of the palm family (Arecaceae; Chimera and Drake 2011, Campbell et al. 1984, McConkey et al. 2003, Yamashita et al. 2003, Kawakami 2008, Meyer and Butaud 2009). Rats are regarded as a major threat to Hawaiian *Pritchardia* palm species, many of which are quite rare (Chapin et al. 2004, Perez et al. 2008). Palaeoecological evidence suggests that a Hawaiian dry lowland forest dominated by *Pritchardia* was devastated by *Rattus exulans* well before it was directly impacted by humans (Athens et al. 2002). Recent evidence suggests that *R. exulans* also played a role in the decline of palm forests on Rapanui (Hunt 2006).

A MULTIVARIATE COMPARISON OF THE PREDATORS

We performed a principal components analysis (PCA) to determine similarities in predator identity among the nine most common seabird predators (see Chapter 3 for a parallel analysis using seabirds as prey). We tested the vulnerability of non-seabird prey to predators based on five groups (plants, land birds, small mammals, reptiles, and insects) preyed upon by the introduced predators. The vulnerability of each prey type to an introduced predator was ordinally ranked in five categories (Table 4.1).

Our first two principal components explained 69% of the variation in predator identity, with Axis 1 explaining 41% of the variation, and the addition of Axis 2 explaining a further 28% (Figure 4.3). The first principal component distinguishes predators based on omnivory and carnivory (prey type). The second principal

TABLE 4.1.
Ordinal Ranking System for Introduced Predator Impacts on Prey.

Island Taxa	Predator Species								
	Fox	Cat	<i>R.n</i>	<i>R.r</i>	<i>R.e</i>	Mouse	Dog	Mongoose	Pig
Plants	0	0	3	3	4	3	0	0	4
Mammals	4	4	3	4	0	0	3	1	0
Reptiles	3	4	4	4	4	3	4	3	2
Land birds	4	4	4	4	4	2	4	4	1
Invertebrates	1	2	3	3	3	3	1	2	3

0 = no recorded predation, 1 = Some predation (documented or assumed), 2 = Evidence of regular predation, 3 = Suppression without local extinction, 4 = Suppression to local or total extinction. See text for justification of rankings. (*R.n* = *Rattus norvegicus*, *R.r* = *R. rattus*, *R.e* = *R. exulans*).

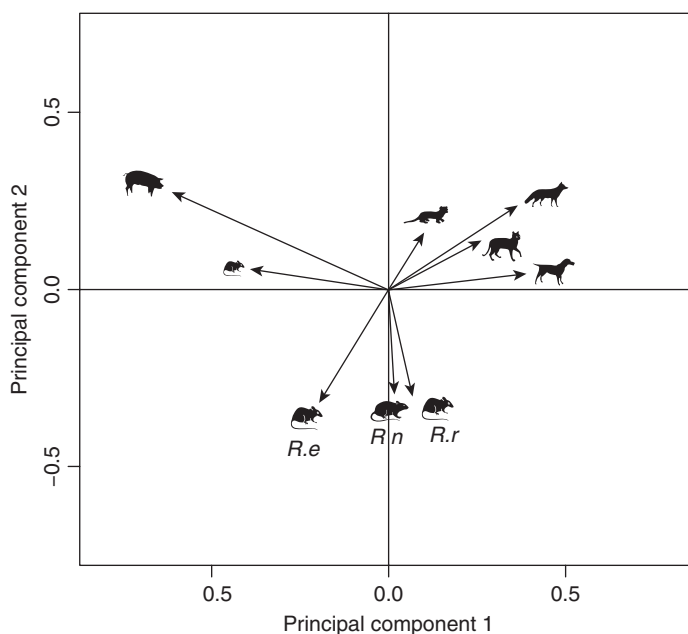


FIGURE 4.3 Principal Components Analysis (PCA) of predator identity as determined by non-seabird prey identity. The length of arrows is proportional to the strength of the relationship with the first two principal coordinate axes. (Predators are identified in Table 1; *R.n* = *Rattus norvegicus*, *R.r* = *R. rattus*, *R.e* = *R. exulans*).

component distinguishes predators on their relative harm (prey breadth), especially separating the generalist introduced rats as a group from all other introduced predators. Pigs and mice stand out as introduced predators with particularly distinct impacts upon prey.

Summary and Directions for Future Research

While much remains to be learned about the mechanisms involved in the ecological interactions between introduced mammalian seabird predators and the biota of islands, we can use the combined results of observational, experimental, and historical studies to draw a number of general conclusions about these interactions (Table 4.2).

All of the seabird predators consume not only seabirds, but also a wide range of other animal species; the non-carnivores additionally consume a wide range of plant species. All of the predators directly or indirectly cause declines and/or local extinctions of many additional island species that are not directly consumed. Pigs are unique among the seabird predators in their ability to cause severe disturbance to the soil. A key question that remains to be addressed is: to what extent and under what conditions are declines in island species attributable to direct

TABLE 4.2.

General Summary of the Seabird Predators' Interactions with Non-Seabird Island Organisms.

Interaction with Native Species	Predator Species				
	Cat	Fox	Rat	Mouse	Pig
Negative Interactions:					
Predation	Strong	Strong	Strong	Strong	Strong
Herbivory	No	No	Strong	Strong	Strong
Disturbance agent	No	No	No	No	Strong
Positive Interactions:					
Prey	No	No	Strong	Strong	Weak
Reproductive mutualist	No	No	Weak	No	Weak

predation, herbivory, or physical damage, as opposed to indirect effects (addressed in Chapters 7 and 9) such as resource competition, trophic cascades, disruption of mutualistic interactions, or disturbance?

The island species for which the effects of seabird predators have been studied most thoroughly are the land birds and, to a lesser extent, terrestrial plants. Much less is known about their effects on other species of island animals, though reptiles and snails have been well studied in some island groups. Given the ecological importance of insects, more attention should be directed to determining how they are affected by seabird predators, and how impacts on insects affect other island species, including insect-eating animals and insect-pollinated plants (St Clair 2011). Furthermore, while all of the seabird predators forage in the intertidal zone (Navarrete and Castilla 1993, Carlton and Hodder 2003), very little is known about the ecological significance of their effects there, though they may be substantial (Kurle et al. 2008). Finally, surprisingly little is known about interactions between introduced rodents and the many threatened or extinct rodents endemic to the world's larger or less remote islands, including the Caribbean Islands, Canary Islands, Solomon Islands, and Galápagos Islands (Amori et al. 2008, Harris 2009).

While seabird predators are associated with the decline of many island plant species, and consequent changes in plant and animal communities, a few plant species may benefit directly from seed dispersal by rodents or pigs, or indirectly through disturbance or reductions in competitors or herbivorous insects. Additional research is needed to determine what traits make plants vulnerable to seabird predators, and whether or not island species are especially vulnerable.

With respect to the ecology of the predators themselves, rodents present a special case. Attempts have been made to understand the ecological interactions among the three introduced rat species (and house mice), but their relations are complex and remain poorly understood (Yom-Tov et al. 1999, Russell and Clout 2004, Harper et al. 2005, Wilson et al. 2007). In some cases, pairs of rat species, such as ship rats and Pacific rats, can coexist on quite small islands (Steadman

et al. 1999) or even in communal cages (Storer 1962), yet they are unable to coexist throughout much of New Zealand. Ship rats occurred throughout Great Britain until Norway rats arrived and displaced them, whereas in New Zealand, the widely established Norway rats were later displaced from most of their range when ship rats were introduced (Long 2003). It is possible that the coexistence of some of these rodents is mediated by the presence or absence of other introduced animals, such as house mice. There is a clear need for research on niche overlap among these species.

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