

Impacts of Introduced Predators on Seabirds

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Introduction

In 1767, Captain Samuel Wallis of HMS *Dolphin* made the first recorded European contact with the people of Tahiti. Much of the crew was ill with scurvy. A high-born Tahitian who assisted with their treatment was later presented with a “cat in litter” as a gesture of thanks (Salmond 2003)—a nice idea, but one in a parade of “introductions” of non-native species. Two years later, Captain James Cook followed on *Endeavour*, which was loaded with “cattle, sheep, goats, chickens, ducks in pens, while dogs and cats ran underfoot and rats and cockroaches swarmed throughout the vessel” (Salmond 2003). Much of the livestock was also donated to locals or released onto islands throughout the Pacific. By 1777, Cook’s ship *Resolution* was likened to a floating menagerie of “cattle, sheep, goats, pigs, rabbits, turkeys, geese, ducks and peafowl,” some of which were destined for deliberate release as alternative food sources for Māori in New Zealand (Salmond 2003). Benjamin Franklin similarly wished to “convey the conveniences of life, as fowls, hogs, goats, cattle, corn, iron, &c., to those remote regions which are destitute of them, by personally delivering such items to the South Seas” (Strauss 1963). These gentlemen scientists could not have dreamed that their benign intentions would ultimately result in widespread damage to native ecosystems. Plants and animals were certainly spread beyond their natural range well before the voyages of eighteenth century explorers, but Cook’s releases were meticulously recorded, largely deliberate, and sanctioned by the Royal Society. This trickle of exotic species released onto islands, and supported by scientific exploration, subsequently became a flood, producing a catastrophe that reached almost all parts of the globe. Over 200 years later, the effects are still being evaluated and remedied.

The species spread by western explorers include several destructive predators of seabirds. In this chapter, we identify the most damaging of these invasive species and assess which species of seabirds are the most vulnerable to them. We begin by reviewing the distribution and effects of introduced predators on seabirds. This older literature is mostly descriptive and based on observations in the wild. In the second section, we outline experimental and more technically advanced methods

for measuring the effects of invasive predators. We emphasize in particular the value of deleting invasive predators from island food webs as a means of determining their impacts on island species and ecosystems (Courchamp and Caut 2005). Finally, we attempt to provide a global assessment of the effects of seabird declines as a result of predation by introduced species.

Predator Effects based on Distribution

THE VULNERABILITY OF SEABIRDS TO INTRODUCED PREDATORS

The habits that make seabirds vulnerable to introduced predators include slow growth to sexual maturity, low rates of egg production, and chicks present for long periods in nests on the ground or in burrows (Chapter 2). For seabirds that rely on productive ocean systems, breeding areas need to be close to food sources, to which adults can commute while raising chicks, and nest sites need to be isolated from terrestrial predators. Some of the most remote, precipitous and windswept places on the planet are thus used for breeding by generations of seabirds. The most inhospitable of these includes the permanent snow and ice used by penguins in the Antarctic, and isolated pockets of glacial scree habitat among snow fields used by murrelets (*Brachyramphus* spp.) in Alaska.

Space for colonies at suitable sites can be limited, so seabirds often form enormous aggregations to mate, nest, and raise chicks. Any terrestrial predator reaching such sites can cause catastrophic effects. For example, sooty terns (*Onychoprion fuscatus*) nested in “great abundance” at Denham Bay on Raoul Island in the Kermadec group (Veitch et al. 2004). Cats (*Felis catus*) reached the island with settlers in the early nineteenth century, followed by Norway rats (*Rattus norvegicus*) after a shipwreck in 1921. In 1967, 80,000 adult terns were still present. In 1994, these had been reduced to 1,300 and carcasses of terns killed by cats littered the beach. By 1997, the entire breeding population at Denham Bay had disappeared (Veitch et al. 2004).

WIDESPREAD AND OBVIOUS PREDATORS

Cook's voyages, and others like Vitus Bering's explorations in the North Pacific, were contemporaneous with the beginning of the Industrial Revolution. The spread of problem species onto islands reflected the spread of people and industry. Deliberate large-scale releases included foxes (e.g., Arctic fox, *Vulpes lagopus*), mink (e.g., American mink, *Neovison vison*) and sable (*Martes americana*) in attempts to establish a fur industry; goats (*Capra hircus*), rabbits (*Oryctolagus cuniculus*) and pigs (*Sus scrofa*) as food for castaways or those involved in fur harvesting; and cats, mongooses (*Herpestes* spp.) and mustelids such as stoats (*Mustela erminea*) for control of other pests. Atkinson (1989) identified 80 species of mammals that have been introduced to islands. At least 40 of these are actual or potential predators of seabirds, although only seven species or species groups make up 92% of the reports (Figure 3.1).

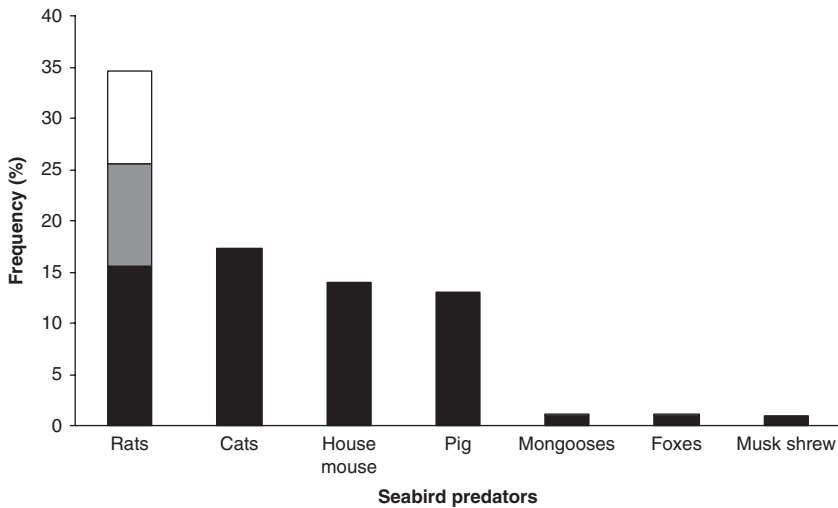


FIGURE 3.1 Frequency of occurrence of the most widespread introduced predatory mammals on 469 islands and archipelagos. The figure is based on data from Atkinson (1989), with rats comprising ship or black rats (*Rattus rattus*) (black shading), Norway rats (*Rattus norvegicus*) (gray shading) and Pacific rats (*Rattus exulans*) (no shading).

Among the predators are six species of monkeys; six species of mustelids; four species of pig, other than feral domestic pigs; three species of rats; four species of canids, including domestic dogs (*Canis familiaris*) and three species of foxes; and at least two species of mongoose (see Appendix C for a list of all seabird predators mentioned in this book). The most widespread species are rats (Figure 3.1), with frequency of occurrence of ship rats (*Rattus rattus*) 15.6%, Norway rats 10%, and Pacific rats (*R. exulans*) 8.9%. These and house mice (*Mus musculus*) are probably the only species accidentally spread to islands.

Evidence for detrimental effects of predators in the early reviews of Atkinson (1989) and Burger and Gochfeld (1994) is largely observational or circumstantial. Also, because of patchy records, these authors treated whole archipelagos as a single unit. Although understandable, archipelago-based accounts minimize the effects of predators that have spread across large numbers of islands in a small number of archipelagos. Furthermore, if islands within archipelagos are large, and once supported significant numbers of seabirds, small numbers of invasions might have extensive effects. For example, in New Zealand, three species of rats have reached the three main islands and at least 142 offshore islands ≥ 5 ha (42% of all islands), yet the data available by archipelago list New Zealand as a single location. Similarly, Arctic foxes and red foxes (*Vulpes vulpes*) make up only 1% of all records for archipelagos, yet they were released onto at least 450 sites in Alaska alone (Bailey 1993), including some very large islands (Ebbert and Byrd 2002).

A more precise indication of the distribution of introduced mammalian predators can be obtained by comparing those archipelagos with detailed distribution data (Table 3.1). The largest fauna of predators is on the offshore islands of Cuba,

TABLE 3.1.

Frequency of Occurrence (percentage) of Seabird Predators on Offshore Islands within Selected Archipelagos before Pest Eradications.

| Predator | New Zealand (238) | Southern Ocean (13) | West Australia (93) | W. Indian Ocean (49) | Canary (7) | Med (43) | Alaska NMWR (84) | Channel/Baja California (52) | Cuba (33) | Hawaii (17) |
|---|----------------------|------------------------|------------------------|-------------------------|---------------|-------------|---------------------|---------------------------------|--------------|----------------|
| Cat (<i>Felis catus</i>) | 11.3 | 61.5 | 18.3 | 75.5 | 100 | 18.6 | | 34 | 36.4 | 5.9 |
| Dog/Dingo (<i>Canis familiaris</i>) | 4.2 | | 4.3 | 12.2 | | | | 17 | 45.5 | |
| Hedgehog (European) (<i>Erinaceus europaeus</i>) | 2.5 | | | | | 4.7 | | | | |
| Mouse (<i>Mus musculus</i>) | 11.8 | 84.6 | 22.5 | 26.5 | 100 | 23.3 | | 1.9 | 30.3 | 11.8 |
| Norway rat (<i>Rattus norvegicus</i>) | 16.4 | 23.1 | | 18.4 | 100 | 4.7 | 19 | 3.9 | 16.7 | |
| Pacific rat (<i>Rattus exulans</i>) | 16.8 | | 2.2 | | | | | | | 29.4 |
| Possum (Australian brush-tailed) (<i>Trichosurus vulpecula</i>) | 5.5 | | | | | | | | | |
| Pig (<i>Sus scrofa</i>) | 4.2 | 30.8 | 1.1 | 8.2 | | | | 25 | 12.1 | |
| <i>Rattus</i> sp. | | | | | | | | 3.9 | | 11.8 |
| Ship rat (<i>Rattus rattus</i>) | 13 | 61.5 | 43 | 81.6 | 100 | 100 | | 13.5 | 60.6 | 17.6 |
| Stoat (<i>Mustela erminea</i>) | 14.3 | | | | | | | | | |
| Argentine grey fox (<i>Pseudalopex griseus</i>) | | 7.7 | | | | | | | | |
| Red fox (<i>Vulpes vulpes</i>) | | | 8.6 | | | | | | | |
| Mongoose (<i>Herspestes</i> sp.) | | | | 4.1 | | | | | 9.1 | |
| Hedgehog (Algerian) (<i>Atelerix algirus</i>) | | | | | | 57 | | | | |
| Weasel (<i>Mustela nivalis</i>) | | | | | | 4.7 | | | | |
| Pine marten (<i>Martes martes</i>) | | | | | | 4.7 | | | | |
| Red fox and arctic fox (<i>Vulpes lagopus</i>) | | | | | | | 57.1 | | | |
| Arctic ground squirrel (<i>Spermophilus parryii</i>) | | | | | | | 20.2 | | | |

(Continued)

Natural History of Seabird Islands

TABLE 3.1. (Contd.)

| Predator | New Zealand (238) | Southern Ocean (13) | West Australia (93) | W. Indian Ocean (49) | Canary (7) | Med (43) | Alaska NMWR (84) | Channel/Baja California (52) | Cuba (33) | Hawaii (17) |
|---|----------------------|------------------------|------------------------|-------------------------|---------------|-------------|---------------------|---------------------------------|--------------|----------------|
| Vole (<i>Microtus</i> sp.) | | | | | | | 2.4 | | | |
| Deer mice (<i>Peromyscus</i> sp.) | | | | | | | 1.2 | | | |
| Grivet (vervet) monkey (<i>Clorocephus</i> sp.) | | | | | | | | | 3 | |
| Pig-tailed macaque (<i>Macaca nemestrina</i>) | | | | | | | | | 3 | |
| Long-tailed macaque (<i>Macaca fascicularis</i>) | | | | | 2 | | | | 3 | |
| Stump-tailed macaque (<i>Macaca arctoides</i>) | | | | | | | | | 3 | |
| Barn owl | | | | | | | | | | 23.5 |

Sample sizes are in parentheses. Data for New Zealand (Atkinson and Taylor 1992), Southern Ocean (Chapuis et al. 1994, Angel et al. 2009, J. Russell unpublished data), West Indian Ocean (Parr et al. 2000, J. Russell unpublished data), Western Australia (Burbidge and Morris 2002), Canary Islands (Nogales et al. 2006), Mediterranean (Med) L. Ruffino (personal communication), Alaska National Maritime Wildlife Refuge (NMWR) (Ebbert and Byrd 2002), Channel and Baja California (McChesney and Tershy 1998), Cuba (Borroto-Páez 2009) and Hawaii (OIRC website).

with 11 species. In New Zealand with the main islands added, and the inclusion of Australian brushtail possums (*Trichosurus vulpecula*), which are now known to prey on eggs and chicks (Brown et al. 1993), this number increases to 12 (Atkinson 1989, Towns et al. 1997). Other heavily invaded archipelagos include the West Indies and Fiji (9 species), and Hawaii, Marianas and Mauritius (8 species; see Towns et al. 1997). However, in Hawaii only four species of predatory mammals appear to have established on offshore islands and islets (Table 3.1).

The sequence of invasions of predators in New Zealand, and the time of arrival, is now well known (Towns and Daugherty 1994, Tennyson and Martinson 2006). The arrival of Polynesians in about 1280 was accompanied by Pacific rats (Wilmshurst et al. 2008) and dogs (Tennyson and Martinson 2006), and the remaining 8 species of mammalian predators arrived with Europeans, beginning in 1769. The cumulative effect of these introductions, and harvesting by people, was the disappearance of almost all species of burrowing seabirds from the main islands (Taylor 2000). Most species now survive on the offshore islands, but at least three species became extinct: a species of penguin (*Megadyptes waitaha*), Scarlett's shearwater (*Puffinus spelaeus*) and the southern merganser (*Mergus australis*). Reasons for the disappearance of the penguin are unclear. The most

likely cause of decline of the shearwater was Pacific rats (Tennyson and Martinson 2006), although harvesting and dogs cannot be discounted as contributing effects. Mergansers also succumbed to introduced predators and harvesting – by museum collectors – and the last bird was seen at the beginning of the twentieth century (Fleming 1982, Tennyson and Martinson 2006). Similar sequences of introductions and extinctions have been recorded in Hawaii, elsewhere in the Pacific, and also in the Caribbean (Milberg and Tyrberg 1993).

New Zealand is unusual among the heavily invaded archipelagos because of its temperate climate. Other archipelagos with numerous invasive predators are all in the tropics, which raises the question of whether invaders may be more successful in warmer climates. Burger and Gochfeld (1994) identified the degree of impact of seabird predators using literature citations divided by climatic region. Of the most widespread species reported to have significant impacts on seabirds, including causing local extinction, the frequency of reported effects was often highest in the tropics, with species such as mongoose only found in the tropics.

THE BIZARRE AND THE INSIDIOUS

Rarer examples of predation by non-native organisms include some that are particularly bizarre. For example, on the island of Rum off Scotland, red deer (*Cervus elaphus*) kill Manx shearwater (*Puffinus puffinus*) chicks by biting off their heads during the month when pre-fledging birds exercise outside their burrows. Similarly, sheep (*Ovis aries*) on Foula, in the Shetland Islands, target unfledged Arctic terns (*Sterna paradisaea*; see Furness 1988). Since deer and sheep are ruminants, they are unable to digest flesh. However, both islands have mineral-deficient soil, and the bones of seabird chicks appear to be the best available source of phosphorus and calcium. The mortality of shearwaters and terns is apparently not high enough to significantly affect their populations on each island (Furness 1988). Similar predatory behavior was observed when attempts were made to intensify domesticated reindeer (*Rangifer tarandus*) herds in the Kamchatka region of Russia. The reindeer trampled nests and ate the eggs and chicks of black-headed (*Chroicocephalus ridibundus*), mew (*Larus canus*), and slaty-backed gulls (*L. schistisagus*). Subsequent declines in the size of bird colonies were reversed when stocking rates of reindeer were reduced (Kondratyev et al. 2000).

Other non-native predators of seabirds include birds and ants, both of which appear to be problems on islands in Hawaii. Introduced barn owls (*Tyto alba*) are regarded as significant predators of seabirds on islets off Niihau, Kauai, and Kahoolawe (Byrd and Telfer 1980, www.hawaiiiorc.org). Similarly, predation by Indian or common mynas (*Acridotheres tristis*) was sufficient to destroy 25% of sooty tern eggs on Ascension Island in the south Atlantic (Hughes et al. 2008), and at least 20% of wedge-tailed shearwater (*Puffinus pacificus*) eggs were taken by mynas at a colony in Hawaii (Byrd 1979). More insidious effects are now being reported for invasive ants. Over 44 species of ants have been introduced into the Hawaiian archipelago. On islands invaded by tropical fire ants (*Solenopsis geminata*),

up to 100% of shearwater chicks showed injuries to their feet. Chicks that lost >20% tissue on their feet weighed significantly less than uninjured chicks, and did not fledge (Plentovich et al. 2009). Four additional species of ants are spreading through tropical islands, and all of them detrimentally affect vertebrates. They include red imported fire ant (*S. invicta*), yellow crazy ant (*Anoplolepis gracilipes*), Argentine ant (*Linepithema humile*), and little fire ant (*Wasmannia auropunctata*; Plentovich et al. 2009).

As with ants, previously unsuspected effects have now been documented for mice on islands where they are the only rodent present. Burger and Gochfeld (1994) listed mice as widely distributed, but a problem on only a few islands, such as the Antipodes Islands and the southeast Farallon Islands, where they fed on eggs of small seabirds such as storm petrels (*Oceanodroma* and *Oceanites* spp.). However, studies on islands off southern Africa indicate that these effects have been underestimated. On Marion Island, mice so heavily reduced invertebrate numbers that the insectivorous lesser sheathbill (*Chionis minor*) population declined due to food competition (Angel and Cooper 2006). On Gough Island, infrared time lapse recordings revealed that Tristan albatross (*Diomedea dabbenena*) succumbed to multiple attacks from mice eating through the body wall of live chicks (Wanless et al. 2007). Mice were responsible for albatross chick mortality of up to 60%, killing birds almost 300 times the body weight of an individual mouse. They were also responsible for up to 95% predation at the nests of Gough buntings (*Rowettia goughensis*), and 64% mortality of the chicks of Atlantic petrels (*Pterodroma incerta*). Mice appear to be the main cause of a 28% decline in the abundance of Tristan albatross on Gough Island, and are likely to cause a decrease in Atlantic petrels because of low chick production (Wanless et al. 2007). In total, mice on these islands affect two species of land birds and four species of seabirds. They probably detrimentally affect another six species of seabirds (Angel and Cooper 2006), and may thus be capable of causing devastating, irreversible, and ecosystem-changing effects on islands (Angel et al. 2009).

SUBTLE EFFECTS AND NATIVE PREDATORS

Natives Out of Range

So far, we have largely described the range and effects of alien species spread far beyond their centers of origin. However, there are some predators released onto islands that are natives out of range, found within the geographic area (such as the adjacent mainland), but historically absent from specified islands. For example, Arctic and red foxes native to North America were released into archipelagos where they have no previous history, and where they caused local extirpations and substantial declines in island bird populations (e.g., Bailey 1993). Another example is raccoons (*Procyon lotor*) released onto islands off western Canada (Harfenist et al. 2000). One described in more detail later (Chapter 12, Box 12.1) is European hedgehogs (*Erinaceus europaeus*), which were released onto the Uist Islands off western Scotland. Burger and Gochfeld (1994) reported hedgehogs as natural predators of gulls and terns. However, as hedgehog numbers increased on the

Uists, populations of at least four species of wading shore birds declined. Enclosures that protected the birds from hedgehogs had over twice the nesting success recorded in areas where hedgehogs were not controlled (Jackson 2001).

Similar effects on ground-nesting birds have been reported from islands off New Zealand, where a native flightless rail, the weka (*Gallirallus australis*), has frequently been released as an alternative food for people harvesting sooty shearwaters (*Puffinus griseus*; Atkinson and Bell 1973). Releases of weka have been followed by declines of fairy prions (*Pachyptila turtur*), diving petrels (*Pelecanoides urinatrix*), mottled petrels (*Pterodroma inexpectata*), and Cook's petrels (*Pterodroma cookii*; Atkinson and Bell 1973, Imber et al. 2003). Direct observations of predation by weka were made by Harper (2006), who saw the birds entering burrows and pulling out 2–3 day old chicks of sooty shearwaters, which were killed with repeated pecks to the back of the head. Weka were also reported stealing and destroying eggs (see Harper 2006) of southern Buller's albatross (*Thalassarche bulleri*), and up to 19% of eggs of Fiordland crested penguins (*Eudyptes pachyrhynchus*). The role of seabirds in the diet of weka was confirmed using stable carbon isotopes (Harper 2007), an approach that we describe in more detail later.

Natives in Range but Out of Control

Some native predators have had major effects on resident seabird populations as a result of subtle changes to the local environment. These have resulted in detrimental effects on seabirds by native species that include gulls, terrestrial birds, and seals. For example, in eastern North America and around the Mediterranean, several gull species have increased in abundance in response to the availability of supplementary food such as organic waste and garbage (reviews in Vidal et al. 1998, Donehower et al. 2007). In North America, increasing populations of large gulls since the late nineteenth century have been linked to declines of terns (see also Chapters 11 and 12). On Country Island off eastern Canada, Whittam and Leonard (1999) found that 77% of the chicks of roseate terns (*Sterna dougallii*) were taken by herring gulls (*Larus argentatus*) and great black-backed gulls (*L. marinus*). Arctic terns (*S. paradisea*) and common terns (*S. hirundo*) also suffered heavy losses, with the number of breeders reduced 48% and 62% respectively between 1996 and 1997. However, the depredation of roseate terns was such that the birds subsequently abandoned the island (Whittam and Leonard 1999). On Eastern Egg Rock, Maine, herring, great black-backed gulls, and laughing gulls (*Leucophaeus atricilla*) were responsible for the loss of eggs and chicks of 23% of common terns, 32% of Arctic terns, and 6% of roseate terns. An intensive cull of gulls by shooting did not reduce predation by gulls, although other methods, such as disturbance and destruction of the gull's eggs and nests, may be more effective (Donehower et al. 2007). As of 1997, almost all colonies of roseate terns in the United States were managed to control predation by native birds, especially gulls (Whittam and Leonard 1999).

Our second example comes from eastern Australia, where pied currawongs (*Strepera graculina*), which are large, predatory crow-like birds, appear to have

become more abundant as a result of forest clearance and urbanization. Currawongs have been implicated in a concurrent decline of native forest birds, but the data in support of this are weak (Bayly and Blumstein 2001). However, currawongs appeared responsible for increased mortality of chicks and adults of the rare Gould's petrel (*Pterodroma leucoptera*) on Cabbage Tree Island. When the currawong population was controlled, mortality of the petrels substantially declined (Priddel and Carlile 1995).

Our third example is a native predator that is itself recovering from overharvest. In southwestern Africa, Cape fur seals (*Arctocephalus pusillus pusillus*) on islands and coastal areas washed by the Benguela Current were harvested to extirpation on at least 23 island sites. The species rebounded after legal protection in 1893, with annual growth of 3.5% between 1971 and 1993. Concurrently with the increase of seals, African penguins (*Spheniscus demersus*) declined by 90% since 1910, bank cormorants (*Phalacrocorax neglectus*) by 44% since 1980, and Cape gannets (*Morus capensis*) by 30% between 1956 and 1996 (David et al. 2003). These three species, as well as Cape cormorants (*P. capensis*) and crowned cormorants (*Microcarbo coronatus*), are known to be killed by seals, and all five species are now regarded as threatened. Around Malagas Island in South Africa, seals attack newly fledged gannets that land on the water. In one fledging season from November 2000 to March 2001, the seals were estimated to have killed over 4,700 young gannets, a number equivalent to at least 7.4% of the annual production (David et al. 2003). A trial cull of seals that were witnessed attacking gannets was eventually effective in reducing the kill rate of young birds. All of the seals that attacked birds were younger males aged 2–10 years. While raising pups, female seals swim to feeding grounds and are not known to take seabirds at this time (David et al. 2003). The reason for this behavior by seals, and whether there is a direct link between the overall declines of seabirds and predation by seals, is unclear. Conceivably, declines of the five species of seabirds could be related to disruptions of marine food webs through harvest of commercially important fish, with predation by seals adding to the decline (e.g., Tasker et al. 2000).

HUMANS AS INCIDENTAL PREDATORS

Humans have long been predators of seabirds for their eggs and chicks as food, and even to render the birds down as a source of oil. The latter activities, which have now ceased, destroyed entire penguin colonies on Macquarie Island. There have also been indirect effects from human activities, such as losses due to pollution, especially those resulting from oil spills. Burger and Gochfeld (1994) provide more detailed accounts of such effects. One indirect effect of human activity not detailed in the earlier reviews of human impacts is loss due to the effects of fisheries. These losses have taken two forms: drift or fixed nets, which may catch seabirds regardless of their feeding method (Ogi 1984, DeGange et al. 1993), and baited long lines, which catch birds attracted to the baits (Brothers et al. 1999). The costs to some seabird populations have been enormous. For example, northern hemisphere drift nets were estimated *annually* to drown 500,000 sooty shearwaters

and short-tailed shearwaters (*Puffinus tenuirostris*) that originated from breeding colonies in the southern hemisphere (Tasker et al. 2000). Following pressure from international conservation agencies, a moratorium on high seas drift netting was enacted in 1992.

Inshore drift nets, or fixed gill nets, were also responsible for enormous mortality of seabirds. Heavily affected species included the endangered Japanese murrelet (*Synthliboramphus wumizusume*) Brunnich's guillemots (*Uria lomvia*) and common guillemots (*U. aalge*), long-tailed ducks (*Clangula hyemalis*) and velvet scoter (*Melanitta fusca*) and marbled murrelets (*Brachyramphus marmoratus*), with localized losses of up to 20% of adults (Carter et al. 1995, Tasker et al. 2000, and references therein).

Pelagic longlines have proved to be equally devastating (Tuck et al. 2003, Lewison et al. 2004). Each year, these hooked and drowned thousands of northern fulmars (*Fulmarus glacialis*; Tasker et al. 2000) and albatrosses (Brothers 1991). The effects on black-footed albatross are likely to be sufficient to cause population declines over the next three generations, or about 60 years (Lewison and Crowder 2003). In the Southern Ocean, harvest of Patagonian toothfish, or Chilean seabass (*Dissostichus eleginoides*), is estimated to have killed 265,000 birds between 1996 and 1999, including white-chinned petrels, wandering albatrosses (*Diomedea exulans*), and giant petrels (*Macronectes* spp.). Unsustainable annual reductions of 1%–16% in breeding populations were recorded for some of these species (Tasker et al. 2000).

In waters around New Zealand, government observers retrieved 4,055 seabirds from longliners and trawlers in 1996–2005 (Anon. 2008). These comprised 44 taxa, of which six formed 83% of the total (Figure 3.2). One of these, sooty shearwaters, was also a casualty of pelagic drift nets, so may have been subjected to high mortality of adults at sea for decades. Perhaps we should not be surprised that population declines are now indicated from falling oceanic counts, reduced burrow density, and declining rates of chick harvest by Rakiura Maori in southern New Zealand (Clucas et al. 2008). Encouragingly, modified fishing practices (e.g., Melvin et al. 2001) and technological innovations have reduced seabird bycatch (Gilman et al. 2005), particularly within fisheries overseen by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), which is the regional fisheries management organization for the southern oceans (Donlan and Wilcox 2008a). Efforts to reduce bycatch included bycatch data collection, observer and research programs, and mitigation requirements such as streamer poles and weighted lines (Small 2005). Impressive results have followed, with longline seabird mortality in the majority of the convention area reduced from 6,589 birds in 1997 to 15 birds in 2003 (excluding Economic Exclusive Zones (EEZ); CCAMLR 2003; Small 2005). Unfortunately, in other regional fisheries management organizations, bycatch rates remain largely unknown due to lack of data collection and transparency (Small 2005). For example, seabird catch rates by French vessels operating around Crozet are still believed to be high (C. Wilcox unpublished data) and Japanese longline vessels alone are estimated to kill 6,000–9,000 birds per year in the area managed by the

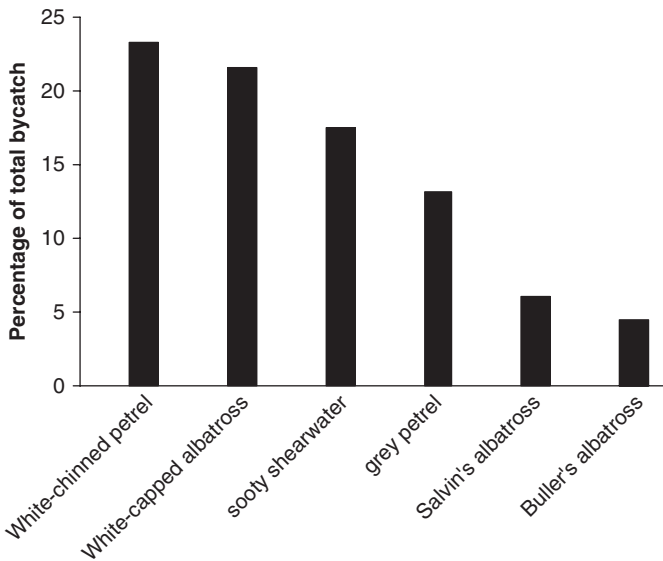


FIGURE 3.2 Species composition of the most commonly encountered seabirds out of 4055 specimens identified from bycatch in fisheries off New Zealand between 1996 and 2005.

Commission for the Conservation of Southern Bluefin Tuna (Kiyota and Takeuchi 2004, cited in Small 2005).

Although mortality of birds at sea has been devastating, the effects of predators at the breeding sites of these birds on land can be even greater (Wilcox and Donlan 2007, but see Pontier et al. 2002 and Peck et al. 2008 for extreme cases). For example, pelagic longlining for tuna and billfish off eastern Australia was estimated to kill 1,800–4,500 flesh-footed shearwaters (*Puffinus carneipes*) annually (Baker and Wise 2005). Based on predation rates for related species, this is equivalent to the annual mortality caused by just 7–18 feral cats preying on one breeding colony. Similarly, when Laysan albatross (*Phoebastria immutabilis*) colonized Guadalupe Island off Mexico in 1983, there was exponential growth of the colony until fewer than 20 feral cats killed half the breeding population. This was equivalent to about 10% of the total longline fishery bycatch of Laysan albatross around the Bering Sea and Aleutian Islands (Wilcox and Donlan 2007). The combination of seabird mortality from interacting with fisheries, and from introduced predators on breeding colonies, can cause serious population declines.

Given the effects recorded on land, the following section examines introduced terrestrial predators from the perspective of the damage they cause.

The Effects of Invasive Predators

Seabirds are referred to as apex predators (e.g., Clucas et al. 2008) because they often feed on smaller predators, such as some species of fish (see Chapter 2).

Courchamp et al. (1999) call some apex predators *superpredators*, which is a useful term when applied to invasive species because it implies runaway consumption. A second group of invasive species is *mesopredators*. These are often the prey of superpredators, but mesopredators themselves may also be responsible for runaway consumption. The following are examples of the effects of superpredators and widespread mesopredators.

SUPERPREDATORS: CATS AND FOXES

Cats were regarded by Moors and Atkinson (1984) as among the most destructive of seabird predators. On Raoul Island (Kermadec Islands), in addition to the sooty terns, seabirds that were eliminated by the combined effects of cats and rats included wedge-tailed shearwater (*Puffinus pacificus*), Kermadec petrel (*Pterodroma neglecta*), and black-winged petrel (*P. nigripennis*; see Veitch et al. 2004). On Jarvis Island in the central Pacific Ocean, cats combined with mice extirpated gray-backed terns (*Onychoprion lunatus*), blue noddies (*Procelsterna cerulea*), brown noddies (*Anous stolidus*), Christmas shearwaters (*Puffinus nativitatis*) and Audubon's shearwaters (*P. lherminieri*), and white-throated storm petrels (*Nesofregatta fuliginosa*; Rauzon 1985). Cats have also destroyed populations of terrestrial species. For example, in Northwest Mexico, cats have been the most likely cause of extinction or local extirpation of island reptiles, plus at least 10 taxa of endemic rodents. Globally, cats are implicated in the total extinction of at least 33 species of land birds (see Nogales et al. 2004).

Rodents play an important role as an alternative food source for cats on islands. Five of the eight species of the world's most endangered species of petrels are threatened by the combined effects of cats and rats (Le Corre 2008). Rabbits can also serve as an alternative food source that assists with the persistence of cats. For example, cats were released onto Grande Terre in the subantarctic Kerguelen Archipelago in 1951, in an attempt to control rodents and rabbits. Rabbits are now a significant part of the diet of cats, which by 1997 had increased to an estimated 3,500 individuals consuming 1.2 million birds per year (Pontier et al. 2002). More detailed discussions of such interactions between introduced species are provided in Chapter 9.

Foxes were introduced to more than 450 islands in Alaska to provide a fur industry (Jones and Byrd 1979, Bailey 1993), with the more valuable blue morph of Arctic foxes placed onto more islands than red foxes (Ebbert and Byrd 2002). The foxes attacked a wide range of terrestrial and marine birds, which nest on the ground on these treeless islands. Eggs, chicks, and adults of waterfowl, shorebirds, seabirds, and ptarmigan (*Lagopus* sp.) were taken (Bailey 1993), and one species, the Aleutian race of cackling goose (*Branta hutchensii leucopareia*), was almost driven to extinction (Byrd 1998, Ebbert and Byrd 2002). This is unsurprising, considering a single Arctic fox on the Yukon River delta was seen taking up to 56 goose eggs per day (Bailey 1993). Colonial seabirds were particularly vulnerable to foxes; crevice nesters were safer, but still taken in some numbers; and cliff nesters such as kittiwakes (*Rissa* spp.) were substantially less affected

(see Byrd et al. 2005). However, surface-nesting birds like loons (*Gavia* spp.), waterfowl such as common eiders (*Somateria mollissima*) and shorebirds were often eliminated as breeders (Bailey 1993). Colonial seabirds largely or totally eliminated on islands inhabited by foxes included Cassin's auklets (*Ptychoramphus aleuticus*), ancient murrelets (*Synthliboramphus antiquus*), storm petrels, northern fulmars, and whiskered auklets (*Aethia pygmaea*). The effects of small numbers of foxes were illustrated when two red foxes reached Shaiak Island across seasonal ice and remained on the island for a season. There was complete breeding failure due to egg predation or nest disturbance of the 100 common eiders, 2,500 glaucous-winged gulls (*Larus glaucescens*) and most of 25,000 common murrelets (*Uria aalge*). Other species that sustained heavy losses included double-crested cormorants (*Phalacrocorax auritus*) and tufted puffins (*Fratercula cirrhata*; see Petersen 1982). Such depredation was apparently known to trappers, who realized that the foxes died out if bird life was seriously depleted. As alternate food, and to help foxes establish, trappers also introduced voles (*Microtus* spp.) and Arctic ground squirrels (especially *Spermophilus parryii albusus*; see Bailey 1993, Ebbert and Byrd 2002). The ground squirrels appear also to take eggs of small burrow-nesting seabirds such as storm petrels (Ebbert and Byrd 2002). Similar introductions with equally devastating effects were reported on Russian and Japanese islands of the northwest Pacific. Here too, red and Arctic foxes devastated colonies of fulmars, crested and least auklets, and tufted puffins, as well as black-tailed gulls (*Larus crassirostris*) and Japanese cormorants (*Phalacrocorax filamentosus*). As in Alaska, the foxes often died out after eliminating seabirds. Again, fur trappers tried to augment prey for foxes by releasing tundra voles (*Microtus oeconomus*). They also released sable, which appeared as destructive as foxes (Kondratyev et al. 2000 and references therein).

Cats and foxes are categorized as superpredators for good reason: both species kill far more prey than they need at the time, and both species have died out on islands when their seabird prey has been eliminated. The behavior of the two species is a little different. Cats seem hardwired as predators, and will simply catch seabirds because they are there, killing the bird but consuming little of them. For example, on Little Barrier Island, cats that killed numerous adult Cook's petrels (*Pterodroma cookii*) in a single night only removed a favored piece such as the brain or liver (C.R. Veitch personal communication). Similarly, on Juan de Nova Island in the Mozambique Channel, Peck et al. (2008) estimated that cats ate 5.94 sooty terns per cat per day, but 22% of the terns were killed without being consumed. In contrast, foxes seem hardwired as hoarders. After the red foxes reached Shaiak Island, eggs and hundreds of dead adult puffins and gulls were cached all over the island (Bailey 1993).

OTHER SUPERPREDATORS: PIGS, MONKEYS AND RACCOONS

Pigs are the third most widely distributed group of introduced predators after rodents and cats (Figure 3.1). They are renowned for their extremely destructive foraging behavior, and such a varied diet—which includes the eggs, chicks, and

adults of ground-dwelling birds such as seabirds (Harper 1983, Cuthbert 2002, McLroy 2005)—that they can be viewed either as superpredators or mesopredators (see Chapter 4 for more details). However, the effects of pigs on island populations of seabirds have been poorly documented (but, see “Predator Removals” later in this chapter). One reason for this may be the difficulties of separating the effects of pigs from those of other introduced species (e.g., Walker and Elliott 1999).

At least six species of monkeys have been released onto islands (Atkinson 1989). The largest number of species is in the West Indies, where green monkeys (*Cercopithecus callitrichus*), rhesus macaques (*Macaca mulatta*) and pale-fronted capuchins (*Cebus albifrons*) have been introduced. Their ecological effects are largely unknown, although Gochfeld et al. (1994) reported that rhesus macaques released onto Desecheo Island off Puerto Rico in 1966, as part of a medical experiment, contributed to the destruction of all remaining colonies of seabirds.

Raccoons were introduced to Graham Island, Haida Gwaii, off western Canada, in the 1940s by the Provincial Game Commission as a source of fur (Golumbia 2000). The raccoons then naturally spread through the archipelago, reaching up to 11 smaller islands that support breeding colonies of seabirds (Harfenist et al. 2000). For example, three raccoons on East Limestone Island during the 1991 breeding season excavated bird burrows and ate the eggs, chicks, and adults of seabirds. Killing more than they could consume, the raccoons destroyed an estimated 6% of approximately 1,200 breeding pairs of ancient murrelets and caused reproductive failure in 10%. On Helgesen Island, 9–12 raccoons were discovered in 1993 after 30,000 burrow-nesting seabirds had been lost since 1986, with declines of rhinoceros auklets (*Cerorhinca monocerata*), ancient murrelets, and Cassin’s auklets, comprising 79%, 83%, and 95% respectively. The loss of 10,000 pairs of rhinoceros auklets represented about 30% of the entire breeding population of the archipelago (Harfenist et al. 2000).

Raccoons have at times also apparently been deliberately released on islands off the northeastern United States. Raccoons were found on the Isles of Shoals in the Gulf of Maine around 2004. Before 11 raccoons were trapped on two islands, there was catastrophic breeding failure of herring and great black-backed gull colonies. On one island, Appledore, where 8 raccoons were present, there were only 0.02 chicks per gull nest, compared with 0.75 chicks per nest in a sample season before raccoons invaded. Furthermore, the year after raccoons were removed, less than 25% of gull nests were empty in June, compared with 60% while raccoons were present (Ellis et al. 2007).

Raccoons were released from pet collections onto the Japanese island of Hokkaido in about 1978 (Abe et al. 2006), and by 1988 were also naturalized on Honshu (Hayama et al. 2006). Raccoons have not yet reached Japanese seabird islands, where their effects are likely to mirror those in North America.

Like cats and foxes, pigs, monkeys, and raccoons can act like superpredators given the speed with which they can eliminate or severely reduce the size of seabird populations. The declines of seabirds are hastened by the nondiscriminate

effects of superpredators, which take eggs (raccoons and foxes), chicks, and adults (all species). However, unlike cats and foxes, pigs, monkeys, and raccoons are omnivores, and perhaps for this reason, there is little evidence that they have eaten themselves to local extinction. Furthermore, the distribution range of monkeys and raccoons is still very narrow. Nonetheless, judging by the effects of raccoons on the auklets of Haida Gwaii, a small number of animals can rapidly cause severe declines of seabirds over a large area.

The last group of predators is distinctive because of their extraordinarily wide distribution. The four commensal species of rodents have effects that are not usually as rapid as those of the superpredators, and they are often part of the diet of superpredators—but they often also survive on islands where superpredators fail.

MESOPREDATORS: COMMENSAL RODENTS

The effects of rats on islands have been reviewed by Towns et al. (2006) and there are also recent reviews of the specific effects of rats (Jones et al. 2008) and mice (Angel and Cooper 2006) on seabirds. Details of these reviews will only be briefly summarized here. The meta-analysis conducted by Jones et al. (2008) identified 115 independent rat–seabird interactions on 61 islands involving 75 affected species of seabirds in 10 families. Storm petrels (Hydrobatidae) and other small burrow-nesting species were the most heavily affected by rats, and the larger surface-nesting seabirds were the least affected. The analysis was not sufficiently sensitive to distinguish severity of predation by rat species. However, the mean seabird population impact was highest for ship rats. This was also the only species that affected seabirds from all four nesting types: trees, ground surface, burrows, and holes and crevices. Although Norway rats are the largest rat species by weight (e.g., Towns et al. 2006), they had a lower average impact than ship rats, but higher impact than Pacific rats (Jones et al. 2008). The range of seabird species affected was also partly related to rat body weight, with Pacific rats and ship rats generally only affecting smaller seabirds <260 g, whereas Norway rats usually affected species of <750g (Towns et al. 2006). This relationship was not confirmed by the meta-analysis (Jones et al. 2008), partly because there are circumstances where some rat species will attack seabirds far larger than expected. One example is the discovery of Pacific rats attacking Laysan albatross, which at 2855 g (supplementary data in Jones 2008), are 30x the average body weight of the rat. The ability of mice to take on prey that is proportionally even larger than that for Pacific rats has already been mentioned.

The potential for mice to have detrimental effects on seabirds can be influenced by other rodents. If other rat species are present, mouse population densities may be suppressed, but, as is noted above, if mice are the only introduced mammal, they can be responsible for predation of seabird eggs and chicks (Angel et al. 2009). This situation points to complications from interactive effects between mesopredators. However, regardless of the mesopredators present, their effects are largely on eggs and chicks, rather than adult seabirds.

Novel Ways of Measuring Predator Effects

Most accounts of the effects of predators have, until recently, relied on direct or indirect observational information, including comparisons between historical and contemporary data to estimate the level of impact as a predator invades, nest failure rates, measured mortality, and even sophisticated infrared surveillance (e.g., Booth et al. 1996, Wanless et al. 2007). However, there is much evidence that even the best observational data may underestimate the effects of predators on seabird populations. Responses of seabirds to the removal of predators have, therefore, been proposed as one useful measure of their effects while present (e.g., Veltman 1996, Courchamp and Caut 2005). In the following section, we examine the effects of predator removal, but first we review other methods of measuring the effects of invasive species. We concentrate on studies of rats, which provide some of the best examples of novel measures of predator impacts.

STABLE ISOTOPES

A commonly used method of determining the impact of introduced predators is the examination of stomach contents or animal remains in feces. Because such remains only reflect waste from the last meal, their use in isolation can provide misleading indications of a predator's effects on populations of prey. This is because the effects of predators are cumulative over a breeding cycle, and for some species over much longer periods. More accurate assessments can be obtained if there is a measure of total prey ingestion over the life of the predator. One measure of this is the ratio of natural stable isotopes of carbon, often expressed as $\delta^{13}\text{C}$, nitrogen as $\delta^{15}\text{N}$, or sulfur as $\delta^{34}\text{S}$. These ratios vary according to the environment of origin. Because seabirds are apex predators in marine systems, they accumulate stable isotopes with a unique marine signature. The value of analysis of isotopes was illustrated for ship rats in the Shiant Islands, off western Scotland, where dietary studies indicated nil effect of rats on seabirds (Key et al. 1998), but analysis of stable isotopes of carbon and nitrogen indicated a high proportion of seabirds in the diet of coastal rats (Stapp 2002). Similarly, Hobson et al. (1999) found that $\delta^{15}\text{N}$ in tissues of some coastal populations of Norway rats on Langara Island, Canada, were consistent with a diet largely comprising ancient murrelet eggs, and probably chicks. The rats have since been eradicated from Langara (Taylor et al. 2000).

Such analyses have also proved useful for discriminating between the effects of more than one introduced predator. For example, on Taukihepa (Big South Cape) Island in southern New Zealand, extinctions and local extirpation of invertebrates, forest birds, and bats were attributed to an invasion of ship rats. However, there had also been out-of-range releases of weka, a predatory rail, and these may have contributed to the declines (Towns 2009). Additional species lost or declining on the island included all smaller species of seabirds, which were absent, and the large sooty shearwater, which were declining. Using a combination of localized

predator removal experiments, analyses of dietary composition, and stable isotopes, Harper (2007) demonstrated that ship rats consumed more passerine birds than did weka, whereas weka consumed chicks and eggs of sooty shearwaters, destroying almost 10% of nests each year. Whether weka or ship rats were responsible for the early loss of the smaller seabird species remains unknown (Towns 2009). Similar approaches using stable isotopes from cat scats on Natividad Island in Mexican Baja California indicated that 90% of the cats' diet was black-vented shearwaters (*Puffinus opisthomelas*; see Keitt et al. 2002).

PREDATOR SUPPRESSION

Localized predator removal or suppression, such as the example above, can be a useful method for testing hypotheses about the effects of introduced predators. However, the method relies on efficient and sustained predator removal, and prey species capable of providing a measurable response. Localized control of ship rats using poison on Lavezzi Island, Corsica, indicated greater predation of the chicks of Cory's shearwaters (*Calonectris diomedea*) when rats were present, accounting for 85% failure of breeding in some years (Thibault 1995). However, the numbers of shearwaters appeared stable, possibly because of wide annual fluctuations in the abundance of rats (Thibault 1995). On Île de la Possession, in the Crozet archipelago (southern Indian Ocean), Jouventin et al. (2003) measured the intensity of localized poisoning of ship rats required to elicit a breeding response in white-chinned petrels. After 8 years, they found that with intensive poisoning of ship rats, petrel breeding success averaged 50% compared with 16% in the preceding 8 years with little or no rat control. In a similar long-term study, Pascal et al. (2008) continued the studies on Lavezzi Island, but compared the cost-effectiveness of rat eradication with control. They found that breeding success of Cory's shearwaters doubled when ship rats were controlled or eradicated. Although the initial costs of eradication of rats were high compared with control, these costs were recovered within six years. Furthermore, other ecological advantages not possible with rat control accrued from eradication. Some of these are subjects of later chapters in Section III.

ARTIFICIAL EGGS AND NESTS

Artificial nests with clay eggs can be a quick and relatively easy means to measure relative predation rates before and after predator eradication or control on islands (e.g., Jones et al. 2005). Artificial nests cannot directly substitute for studies of natural nests, but the artificial nests sometimes provide advantages. Seabirds often nest in places such as steep cliffs and sea caves that are inhospitable or inaccessible areas to humans. For example, on islands with invasive predators, seabirds are often only able to successfully reproduce in areas inaccessible to predators and people. Also, some seabirds are adversely affected by human disturbance to their nest sites (Schreiber and Burger 2001). In such instances, studies using artificial

nests can provide a less intrusive and safer index of predation, as long as the predators take eggs and not chicks.

Issues raised in opposition to artificial nests (Faaborg 2004; Thompson and Burhans 2004; Villard and Pärt 2004) rarely apply on offshore islands, because many island-nesting seabirds are colonial and thus breed at relatively high densities, construct no nests, have long periods with no adult nest attendance, and are threatened by only a few nest predators (Jones et al. 2005). While possibly not reflecting natural predation rates, artificial nests are particularly well suited to measure relative predation rates (Villard and Pärt 2004), which makes them useful on islands before and after predator control or removal. Thus, for many island-breeding seabirds, artificial nest studies can quickly document the impact of introduced predators on both extant and extirpated island-nesting seabirds.

Artificial nests have rarely been used in a predator eradication context, so it is difficult to determine their utility among different kinds of predators. Jones et al. (2005) used artificial nests to study rates of predation by invasive rats, native deer mouse, and gulls on Xantus's murrelets (*Synthliboramphus hypoleucus scrippsi*), by comparing the distinctive marks left by each predator. Artificial nests may be of less use on islands with many predator species, or predators whose teeth marks cannot be distinguished from one another. Data from artificial nests may also provide misleading results for predators such as foxes that cache food, and are likely to remove the clay eggs, so the identity of the predator is unknown. However, even though rats are known to cache food, artificial nest studies have still been used with minimal loss (e.g., Jones et al. 2005), likely because clay eggs are not palatable. Studies using a variety of predators would improve current knowledge about the utility of artificial nests as a measure of predator effects during control or eradication.

PREDATOR REMOVALS

The use of localized control and experiments with artificial nests are confounded by design and reinvasion problems. Unequivocal answers to the effects of predators are provided when they are completely removed, and the recolonization or recovery of seabirds then recorded (Table 3.2). We have treated Table 3.1 in the order of predator distribution given in Figure 3.1, although mongooses and musk shrew (*Crocidura* spp.) have been excluded in the absence of any available post-eradication data.

Positive responses for at least 45 species of seabirds in 11 families have been reported after the removal of mammalian predators (Table 3.2). The largest single group was the petrels and shearwaters (16, 36%), which dominated the southern hemisphere examples. With the exceptions of Cory's shearwaters and Kermadec petrels, which nest on the surface, these are burrow-nesting species. However, there were also 8 (18%) species of alcids from the northern hemisphere, which are also burrow- and crevice-nesting species. For some species, the response was predicted through experiments or observations before the predators were removed, or during predator removal. The example of ship rat predation on Anacapa Island has already been outlined (Jones et al. 2005). Similarly, egg predation of little shearwaters by

TABLE 3.2.
Responses of Seabirds to Removal of Introduced Mammalian Predators
Responses marked with + indicate an increase.

| Island Location | Species | Form of Response | Comments | References |
|---------------------------------|---|---|---|--|
| Ship Rat | | | | |
| Lavezzi, Corsica | Cory's shearwater (<i>Calonectris diomedea</i>) | +breeding success | | Pascal et al. (2008) |
| Hardy, French West Indies | Brown noddy (<i>Anous stolidus</i>), Audubon's shearwater (<i>Puffinus lherminieri</i>), bridled tern (<i>Onychoprion anaethetus</i>) | +breeding success +breeding success, nest distribution | | Lorvelec and Pascal (2005) |
| | Xantus's murrelet (<i>Synthliboramphus hypoleucus</i>); Cassin's auklet (<i>Ptychoramphus aleuticus</i>) | + nest distribution, recolonization | | Whitworth et al (2005) |
| Anacapa, California | | | | |
| Kure and Midway Atolls, Pacific | Bonin petrel (<i>Pterodroma hypoleuca</i>) | +abundance | Mice still present on some islands | Rauzon (2007) |
| Mokoli'i, Hawai'i | Wedge-tailed shearwater (<i>Puffinus pacificus</i>) | +breeding success | | Smith et al. (2006) |
| Norway Rat | | | | |
| Alisa Craig, Scotland | Northern fulmar (<i>Fulmarus glacialis</i>); black guillemot (<i>Cepphus grylle</i>), Atlantic puffin (<i>Fratercula arctica</i>), European shags (<i>Phalacrocorax aristotelis</i>), razorbill (<i>Alca torda</i>) | +breeding success recolonization | | Zonfrillo (2001) |
| | Razorbill, European shags; Manx shearwater (<i>Puffinus puffinus</i>) | +pairs, nest success recolonization recolonization | Herring gull population stable, lesser blacked backed gull declined, but fledging numbers increased | |
| | European storm petrel (<i>Hydrobates pelagicus</i>) | | Feral cats and hedgehogs remain | www.wildlifeextra.com (2008) |
| | Grey-faced petrel (<i>Pterodroma gouldi</i>) | +breeding success | Rabbits also present and eradicated with rats | Lorvelec and Pascal (2005) |
| Malban, Sept-Îles, Atlantic | White-chinned petrel (<i>Procellaria aequinoctialis</i>), grey-backed storm petrel (<i>Garodia nereis</i>) | recolonization | Cats previously present, but died out | Imber et al. (2000) |
| | | | | P. McClelland (personal communication) |

Pacific Rat

| | | | | |
|--|---|--|---|---|
| Midway and Kure Atolls, Pacific Lady Alice and Coppermine, New Zealand | Bonin petrel (<i>Pterodroma hypoleuca</i>) Little shearwater (<i>Puffinus assimilis</i>), Pycroft's petrel (<i>Pterodroma pycrofti</i>) Cook's petrel (<i>Pterodroma cookii</i>), broad-billed prion (<i>Pachyptila vittata</i>) Cook's petrel | +breeding success +breeding success +breeding success +abundance +breeding success recolonization | Mice remain on Midway Cats eradicated 24 y previous Cats eradicated 30 y previous | Rauzon et al. (2008) Pierce (2002) Imber et al. (2003) |
| Hauturu, New Zealand Cuvier, New Zealand | Fluttering shearwater (<i>Puffinus gavia</i>), diving petrel (<i>Pelecanoides urinatrix</i>) Diving petrel Diving petrel | +breeding success +abundance +breeding success recolonization | Rabbits also present and eradicated with rats | Rayner et al. (2007) R. Chappell (personal communication) Townes and Atkinson (2004) A. Cox (personal communication) |

Cat

| | | | | |
|--|--|--|--|---|
| Ascension, Atlantic Natividad, Mexico | Sooty tern (<i>Onychoprion fuscatus</i>) Black-vented shearwater (<i>Puffinus opisthomelas</i>) | +breeding success, recovery +breeding success, recovery | Ship rats, mynas remain | Hughes et al. (2008) |
| Jarvis and Wake Atolls, Pacific | Wedge-tailed shearwater (<i>Puffinus pacificus</i>), great frigatebird (<i>Fregata minor</i>), red-footed booby (<i>Sula sula</i>), masked booby (<i>S. dactylatra</i>), brown booby (<i>S. leucogaster</i>), red-tailed tropic bird (<i>Phaeton rubricauda</i>), black noddy (<i>Anous minutus</i>), brown noddy (<i>A. stolidus</i>), white tern (<i>Gygis alba</i>), sooty tern, gray-backed tern (<i>Onychoprion lunata</i>) | +breeding success and recolonization | Pacific rats and <i>Rattus tanezumi</i> remain on Wake | Keitt and Tershy (2003) Rauzon (2007), Rauzon et al. (2008) |
| Raoul, Kermadecs, New Zealand | Black-winged petrel (<i>Pterodroma nigripennis</i>), Kermadec petrel (<i>P. neglecta</i>) wedge-tailed shearwater, red-tailed tropic bird, sooty tern | recolonization | Norway rat, Pacific rat also present and eradicated with cats | K. Baird (personal communication) |

(Continued)

TABLE 3.2. (Contd.)

| Island Location | Species | Form of Response | Comments | References |
|---|--|--|---|--|
| Mouse | | | | |
| Selvagem Grande, NE Atlantic | Cory's shearwater | +breeding success | Rabbits also eradicated | Zino et al. (2008) |
| Pig | | | | |
| Aorangi, Poor Knights, New Zealand | Buller's shearwater (<i>Puffinus bulleri</i>), fairly prion (<i>Pachyptila turtur</i>), fluttering shearwater (<i>Puffinus gavia</i>), grey-faced petrel, Pycroft's petrel, diving petrel, white-faced storm petrel (<i>Pelagodroma marina</i>) | +abundance and recolonization | Later decline of other species as Buller's shearwaters predominated | Harper (1983) |
| Arctic Fox | | | | |
| Aleutians, Alaska | Whiskered auklet (<i>Aethia pygmaea</i>) | +abundance | | Williams et al. (2003) |
| Ogliuga, Skagul; Aleutians | Horned puffin (<i>Fratercula corniculata</i>), Arctic and Aleutian (<i>Onychoprion aleuticus</i>) terns | recolonization recolonization +abundance | | References in Bailey (1993) References in Bailey (1993) |
| Vsevidof, Kaligagan, Aiktak, Baby; Aleutians | Storm petrels, tufted puffins (<i>F. cirrhata</i>) | | | Byrd et al. (1994), references in Bailey (1993) |
| Nizki-Alaid; Aleutians | Pelagic cormorants (<i>Phalacrocorax pelagicus</i>), glaucous-winged gulls (<i>Larus glaucescens</i>), tufted puffins | | | |

Pacific rats was observed using video surveillance (Booth et al. 1996), with the extent of the mortality caused measured when the rats were removed (Pierce 2002).

The removal of cats from Wake Atoll elicited the typical predator release response. Unlike the Kermadec Islands, where two species of rats were also removed, Pacific rats have not yet been removed from Wake Atoll. Nonetheless, since cat removal began in 1996, at least 11 species of seabirds have responded (Table 3.2) with increased population sizes through recolonization and improved breeding success (Rauzon et al. 2008). Included among these are several species that nest in trees, indicating that the cats were climbing into the colonies (see also Chapter 11).

The single published example of the effects of pig removal on Aorangi Island, New Zealand (Table 3.2), demonstrated the destructive effects of this species on islands and the complex recolonisation patterns of seabirds. Pigs were first taken to Aorangi Island as food by Māori residents near the end of the eighteenth century. The island was abandoned by people in 1823, and the pigs were left to become feral. While present, the pigs rooted out and ate burrowing seabirds, and by the 1920s no living petrels could be found. After the pigs were eradicated in 1936, there was rapid expansion of Buller's shearwaters, which ousted the remaining fairy prions. By 1940, an additional four species of seabirds had recolonized, with fluttering shearwaters (*Puffinus gavia*) and grey-faced petrels (*Pterodroma macroptera*) the most common (Harper 1983 and references therein). Buller's shearwaters appear to be aggressive colonizers, and compete with other seabirds for nest space. From an estimated few hundred birds in 1938, within 50 years Buller's shearwaters were estimated to have reached 200,000 pairs and had largely evicted the grey-faced petrels and fluttering shearwaters (Harper 1983). This is a rare example of recorded recovery of seabirds over many decades, but also an associated change in species dominance. Whether Buller's shearwaters historically dominated the seabird fauna of these islands before disturbance by people is, as yet, unknown.

The only equivalent accounts follow fox removals or natural declines in the Aleutians (Table 3.2), where there are numerous examples of seabird recolonization or recovery (e.g., Bailey 1993, Byrd et al. 1994, Byrd et al. 1997, Williams et al. 2003). For example, within 15 years following removal of introduced foxes from Nizki-Alaid Island, glaucous-winged gull, pigeon guillemot (*Cepphus columba*), and tufted puffin populations increased at least fourfold (Byrd et al. 1994).

Characteristics of Seabird Predators

A combination of observational and experimental data enables us to summarize characteristics of the nine most widespread introduced predators of seabirds. In order to identify specific traits of these predators, we performed two principal components analyses (PCAs). The first analysis focused on predator identity, which was based on a combination of four categories of information: biology (average body length, maximum body weight, average lifespan, and average litter size), behavior (carnivore or omnivore, propensity to climb, diurnal or nocturnal,

super- or mesopredator), climatic preferences (warm, temperate, or cold islands) and archipelago distributions (using data from Table 3.1).

We standardized all data to mean zero and similar variances (“normalization”) and equally weighted the variance contributions of our four categories by dividing each observation by the square root of the number of entries for each category. Our first two principal components explained only 42.9% of the variation in predator identity, indicating that they were not easily distinguishable by strong traits. Much of the remaining variation separates the nine predators further in multivariate space, as a result of historical biases in introductions to specific archipelagos. The four rodent species are grouped together, along with the other relatively small nocturnal predator, the feral cat (Figure 3.3). This probably reflects the wide distribution of these four species, but also the association between cats and rodents on islands. The remaining predators differed in all characteristics considered. In particular, foxes stood out as a large diurnal predator found only in high-latitude cold environments (e.g., Alaska and the Falklands), whereas mongooses stood out as a medium sized predator confined to the tropics. Although our results are based on those archipelagos for which we obtained precise distributional data, the picture changes little when other archipelagos with poorer data are added.

We then tested the vulnerability of seabirds to the nine predators, based on the different sizes and life stages used (whether seabirds were large, medium, or small;

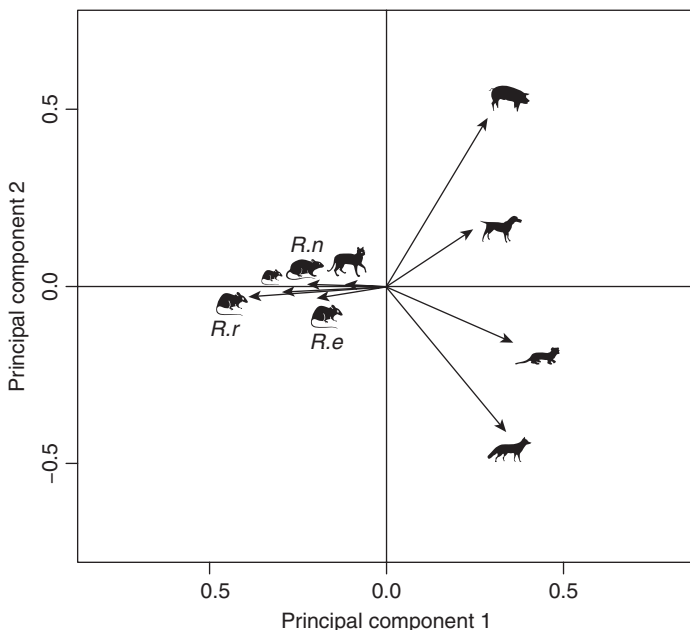


FIGURE 3.3 Principal Component Analysis (PCA) of predator identity as a combination of biology, behavior, climate and historical introductions to archipelagos. The length of arrows is proportional to the strength of the relationship with the first two principal coordinate axes.

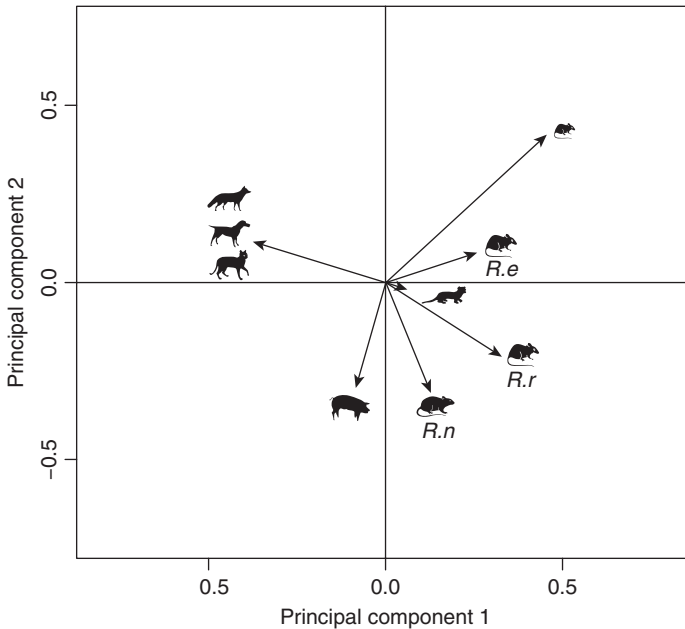


FIGURE 3.4 Principal Component Analysis (PCA) of predator identity as determined by seabirds as prey. The length of arrows is proportional to the strength of the relationship with the first two principal coordinate axes.

adults, chicks or eggs). Here, the associations were far stronger. The first two principal components explained 62% of the variation in predator identity with respect to seabird prey types. This suggests that introduced predators are distinguishable by a simple combination of the traits of seabirds they prey upon (Figure 3.4).

Superpredators, which are able to prey upon almost any life stage and most size stages, all cluster identically together on the left of axis one, whereas the smaller mesopredators (or omnivorous opportunistic pig) each fall out as distinctive in the various sizes and age classes upon which they can prey. Mesopredators all fall on the right of axis one. Mice, in particular, stand out as being highly selective seabird predators.

Discussion

The spread of alien predators to islands inhabited by seabirds probably began when people started to cross marine boundaries and accidentally dispersed rats and mice (Atkinson 1985, Ruffino et al. 2009). In the Pacific, other species were deliberately spread, over many centuries, including pigs and dogs (Anderson 2009). The range of introduced predators greatly increased 250–300 years ago with the coincidence of global exploration, the Western industrial revolution, and associated deliberate release of animals for fur, or to control earlier introductions of

rodents. Early contact with European explorers must have devastated once-robust seabird colonies. We now know that the explorations by Cook alone led to widespread releases of pigs, and probably the accidental spread of cats and Norway rats. These are three of the five most widespread predators of seabirds. The earlier literature contains many examples of direct observations of the effects of these predators on seabirds (e.g., Burger and Gochfeld 1994). Over the last 10–15 years, there have been increasingly intensive and innovative analyses of the effects of the more widespread invasive species. These have included recent global analyses of the effects of rats (e.g., Towns et al. 2006, Jones et al. 2008), tests of the predicted outcomes of eradication of cats (Keitt and Tershy 2003), and accounts of the recovery of seabird populations after eradications of cats (Rauzon et al. 2008) and foxes (Ebbert and Byrd 2002). These are also now being coupled with technological advances in video surveillance (Wanless et al. 2007) and the use of stable isotopes (e.g., Stapp 2002).

We are therefore strongly placed to identify the worst predators of seabirds within the two groups that we have identified: mesopredators, such as rats and mice that prey on eggs and chicks, and superpredators, such as cats and canids (dogs and foxes) that prey on all life stages. Because of their destructiveness and indiscriminate effects, pigs may also be regarded as superpredators, although their omnivorous habits set them aside from cats and foxes. If effects are overlaid with distribution, the most damaging of the mesopredators appears to be ship rats, which have at least 15% frequency of occurrence on islands. Ship rats are responsible for the largest number of recent local extinctions of seabirds, and total extinctions of other terrestrial species (Towns et al. 2006). However, the very early dispersal of Pacific rats with Polynesian migration produced a significant wave of avian extinctions that are only now being unraveled (e.g., Tennyson and Martinson 2006). Furthermore, earlier analyses pointed to Norway rats as the most destructive of the rat species for seabirds (e.g., Atkinson 1985), which indicates that all three rat species can have devastating effects, depending on circumstances and the data available. With over 35% occurrence on islands, the three species in combination are also the most widespread seabird predators. A similar overlay of effect and distribution for superpredators identifies cats as the most widespread of the most destructive seabird predators. Cats have at least 17% frequency of occurrence, and their threats to seabirds were well known to earlier workers (e.g., Moors and Atkinson 1984, Rauzon 1985, Atkinson 1989). Other superpredators, such as foxes, raccoons, and monkeys, can be incredibly destructive over short periods, but are more restricted in distribution. There are similarly restricted distributions for mongooses and mustelids such as mink. For these, the effects are much less well documented.

The corollary to questions about the most damaging of predators is whether there are seabirds that are particularly prone to predation. In their meta-analysis of the effects of rats on seabirds, Jones et al. (2008) confirmed earlier studies that identified crevice and burrow-nesting seabirds as the most vulnerable. These included hydrobatids and alcids, but not procellariids. However, the latter family has a great range of body mass, which confounds analysis, with the larger species

the least susceptible to rats (Towns et al. 2006). As a measure of the susceptibility of this group, there has been a strong response by these burrowing species when rats have been eradicated (Table 3.2). Nonetheless, if we restrict consideration of effects to rats, there is still a large discrepancy between the 75 seabird species affected according to Jones et al. (2008), and the 21 identified in Table 3.2 as responsive to eradications of rats. One reason for this difference is a history of poor monitoring of the outcomes of island management. Many of the examples provided here are from personal communications, rather than accessible reports. A second reason is that the history of the eradications is brief, and the recolonization rates of many seabirds are low and may vary by species and location. Finally, the behavior of some seabirds constrains their ability to enter new habitats (see Chapter 11); for these species, natural recolonization may be unlikely. However, there are other influences that may be at play. Despite intensive monitoring, on some islands there has been no response by seabirds after pest removals, even though relict resident populations remained. Examples include sooty and flesh-footed shearwaters on Titi Island in New Zealand (Gaze 2000).

The answer to these discrepancies may lie in the behavior of the birds, and events far from the nesting island may have major effects on recolonization rates. Because of the enormous range traveled by species such as sooty shearwaters (see also Chapter 2), they are extremely vulnerable to incidental fisheries bycatch a hemisphere away from their nesting areas. For example, Uhlmann et al. (2005) estimated that bycatch of sooty shearwaters and short-tailed shearwaters, in North Pacific driftnet fisheries between 1952 and 2001, killed 1.0–12.8 million (95% CI) sooty shearwaters and between 4.6–21.2 million (95% CI) short-tailed shearwaters. To these must be added losses due to longlines, the use of which overlapped and then superseded pelagic driftnets. The effects of fishing were illustrated for New Zealand by over 4000 individual birds of more than 40 species of seabirds reported to fisheries observers during 1996–2005. These losses at sea are the most likely cause of a decline in the density of sooty shearwaters nesting on islands in New Zealand untouched by human harvest (Fletcher et al. 2010). Nesting frequency and chick survivorship may also be affected by climate change and the frequency of El Niño Southern Oscillation (ENSO) events (e.g., Mills et al. 2008). Unfortunately for sooty shearwaters, two destructive forms of fishing, climate change, plus expanding populations of introduced predators such as cats and weka on southern New Zealand islands, have combined to heavily affect the species (Fletcher et al. 2010). Introduced predators are being removed, and bycatch can be controlled. But the likelihood of a measurable response depends on the lag effect of bycatch on the adult population and the frequency of ENSO events.

While seabirds may have been affected by complex influences away from nesting islands, the effects of predators on the islands may not be simple, either. Frequently, more than one species has invaded island systems. These can have additive effects. One example we used was an introduced rail (weka) and ship rats that prey on seabirds on islands off southern New Zealand. Other examples have demonstrated how introduced predatory and nonpredatory species can interact

(see Chapter 9). For example, populations of cats can be elevated by the presence of rabbits as alternative food, which, through this hyperpredation, increases threats to indigenous vertebrates (Courchamp et al. 2000).

Within groups of introduced predators, there are geographic and temporal relationships that are as yet poorly understood. For example, models of the probability of extinction of native taxa for islands off Western Australia indicated that cats were associated with extinctions of native mammals only on the more arid islands (Burbidge and Manly 2002). These authors concluded that cats are particularly well adapted to persist in arid environments. Given these results, it is not surprising that cats have such a prominent place on islands in the tropical Pacific and off Mexico (Table 3.1). Burbidge and Manly (2002) found no relationship between ship rats and mammal extinctions in Western Australia, although they did not undertake a similar analysis for birds. On the other hand, Donlan and Wilcox (2008b) found an interplay between autecological, synecological and geographic traits that lead to extinction through predation by feral cats. In western Mexico, rainfall was a strong predictor of increased extinction rates of small mammals on islands with feral cats, presumably through a link with primary productivity (Donlan and Wilcox 2008b).

There has been no analysis of frequency of occurrence of species of *Rattus* relative to climate on a wider scale, although there is much evidence of species replacement within the genus. For example, ship rats have been replaced by Norway rats in the United Kingdom, and are now confined to a few islands (McDonald et al. 1997, Symes and Yalden 2002). In contrast, ship rats have replaced Norway rats throughout much of the mainland of New Zealand (Innes 2005). At present, data on the distribution of introduced mammals is complete for a small selection of archipelagos, so developing patterns are difficult to analyze in detail. Similarly, the global effects of predation on seabird populations are difficult to estimate, although they must have been exceedingly high. For example, Wilcox and Donlan (2007) believed that mortality rates of seabirds due to introduced predators on land can exceed that due to incidental catch at sea. This may now be true for species where incidental catch has declined (e.g., Melvin et al. 2001), and is certainly true for those seabirds that are not susceptible to the fishing industry. However, it is difficult to estimate the proportion of nonsusceptible species, and probably varies by location and fishing method. Of the 84 species of seabirds breeding in the New Zealand region (Taylor 2000), 44 (52%) were taken at sea between 1996 and 2005 (Anon. 2008), and six of these (7%) formed the bulk of the sample. We may gain some reassurance from such figures, at least for New Zealand. However, there is good reason to be concerned that of the six highly affected species near New Zealand, three are albatrosses, which may take decades to recover from such losses. Furthermore, the incidental take from the southern bluefin tuna fishery by longlines will never be known, because the fishery is largely unregulated. Nonetheless, for those that have suffered high incidental take, the time involved (up to 50 years) is far less than the 250–300 years of losses on land due to cats, and even longer periods from invasions of rats.

There is good evidence of significant recovery of seabirds on islands in Alaska after declines and eradications of foxes (Byrd et al. 1994, Byrd et al. 1997, Williams et al. 2003). There are also increasing numbers of successful eradications of cats (Nogales et al. 2004), rats (Howald et al. 2007), and other introduced predators of seabirds (Donlan and Wilcox 2008a). At present, it is difficult to determine the extent to which the declines still being recorded as a result of the combined effects of fisheries bycatch and climatic variability might be outweighed by recovery at those sites where pest eradication has been successful. There are additional questions that arise from our review. If predators are successfully removed, which seabird populations will recover without direct management intervention? Even if there is natural recovery, what are the indirect effects of predators on ecosystem function, and can these effects be reversed? The remaining chapters will investigate many aspects of these questions.

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