

Eradications as reverse invasions: lessons from Pacific rat (*Rattus exulans*) removals on New Zealand islands

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Abstract Eradications of kiore or Pacific rats (*Rattus exulans*) from islands around New Zealand have been followed by responses from resident species of coastal plants, invertebrates, reptiles and seabirds. These responses are compared with an invasion by ship rats (*Rattus rattus*), which devastated populations of invertebrates, birds and bats. Post-eradication responses only approximate the effects of invasions because recovery is limited to the residual pool of native species. Greater effects of kiore are indicated by adding incompatible species confined to rat-free locations. The extended list includes at least 15 species of invertebrates, two species of frogs, tuatara (*Sphenodon punctatus*), 11 species of lizards and 9 species of seabirds. The analyses indicate direct and indirect effects of kiore similar to those reported after ship rat invasions. This is despite indications from the literature that kiore are the least damaging of the three commensal rat species.

Keywords Invasion · Ship rats (*Rattus rattus*) · Direct and indirect effects · Fruit and seed predation · Honey dew scale · Tuatara (*Sphenodon punctatus*) · Burrowing seabirds

Introduction

Invasive species are those exotic organisms that establish in new locations and threaten native biodiversity, ecosystem functioning, animal and plant health, and human economies (Myers et al. 2000). Such species have been particularly damaging on islands, where two thirds of recorded animal extinctions have been attributed to introduced species (Cole et al. 2005). Rats are quintessential invaders that have been spread to at least 80% of the world's island groups (Atkinson 1985), but information about their effects is surprisingly weak, patchy, geographically scattered and biased towards vertebrates, especially birds (Towns et al. 2006).

Differences between the fauna of islands invaded by rats and those that are rat free were noted in New Zealand early in the twentieth century. The naturalist Herbert Guthrie-Smith lamented differences between the birdlife of the rat-free islands in the Muttonbird (Titi) Islands in 1913, and those elsewhere that had been invaded by rats introduced from Europe (Guthrie-Smith 1925). More commonly, the link between rats and declines of indigenous biota was never made. Had the link been known, Joseph Banks would perhaps have been less prosaic in his description of the song of bellbirds (*Anthornis melanura*) at Ship Cove at the northern end of the South Island, New Zealand. On the morning of 17 January 1770 he wrote from the ship *Endeavour*: "...the numbers of them were certainly very great who seemed to strain

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their throats with emulation perhaps; their voices were certainly the most melodious wild music I have ever heard, almost imitating small bells but with the most tuneable silver sound imaginable..." (Begg and Begg 1969). The day previously, expedition leader James Cook had careened *Endeavour*. The ship was aground or moored to the shore for 3 weeks (Reed and Reed 1969) providing a perfect opportunity for some of its cargo of "vermin" or Norway rats (*Rattus norvegicus*) to jump ship. The loss of "wild music" may well have begun at that point. Subsequently, for 3 weeks in March 1773, Cook tied the *Resolution* so close to shore in the south-western South Island, that "the vermin could walk ashore over the bridge" (Beaglehole 1961). If the first invasion failed, the second most likely succeeded.

The impacts of these early invasions remained unclear because the locations visited by early explorers were already inhabited by kiore or Pacific rats (*Rattus exulans*). These south-east Asian rats were spread by Polynesian voyagers throughout the Pacific and had reached New Zealand at least 500 years before European contact (Atkinson and Towns 2005; Wilmshurst et al. 2008). Furthermore, with European settlement, mice (*Mus musculus*), ship rats (*Rattus rattus*), mustelids, domestic cats and other mobile predators were added to the main islands. It was not until ship rats invaded Big South Cape Island off southern New Zealand that the devastating effects of rats on some naive indigenous species were demonstrated (Atkinson and Bell 1973; Ballance 2007).

Invasions are uncontrolled experiments, and because of their unpredictable occurrence, are rarely documented in detail. As an alternative to using invasions, the impacts of rats may be revealed when rats are removed and the response of resident species is measured (Campbell et al. 1984; Veltman 1996). Since 1960, three species of rats have been removed at least once from about 80 islands around New Zealand and on 34 of these rats were the only introduced mammal (Towns and Broome 2003; Clout and Russell 2006). Here, I review the information gained about the invasive effects of rats from these eradications.

I focus on kiore, partly because the history of eradications is longest for this species, but also because its effects have been intensively studied in New Zealand. Kiore are widespread elsewhere in the Pacific, but I have been unable to find published

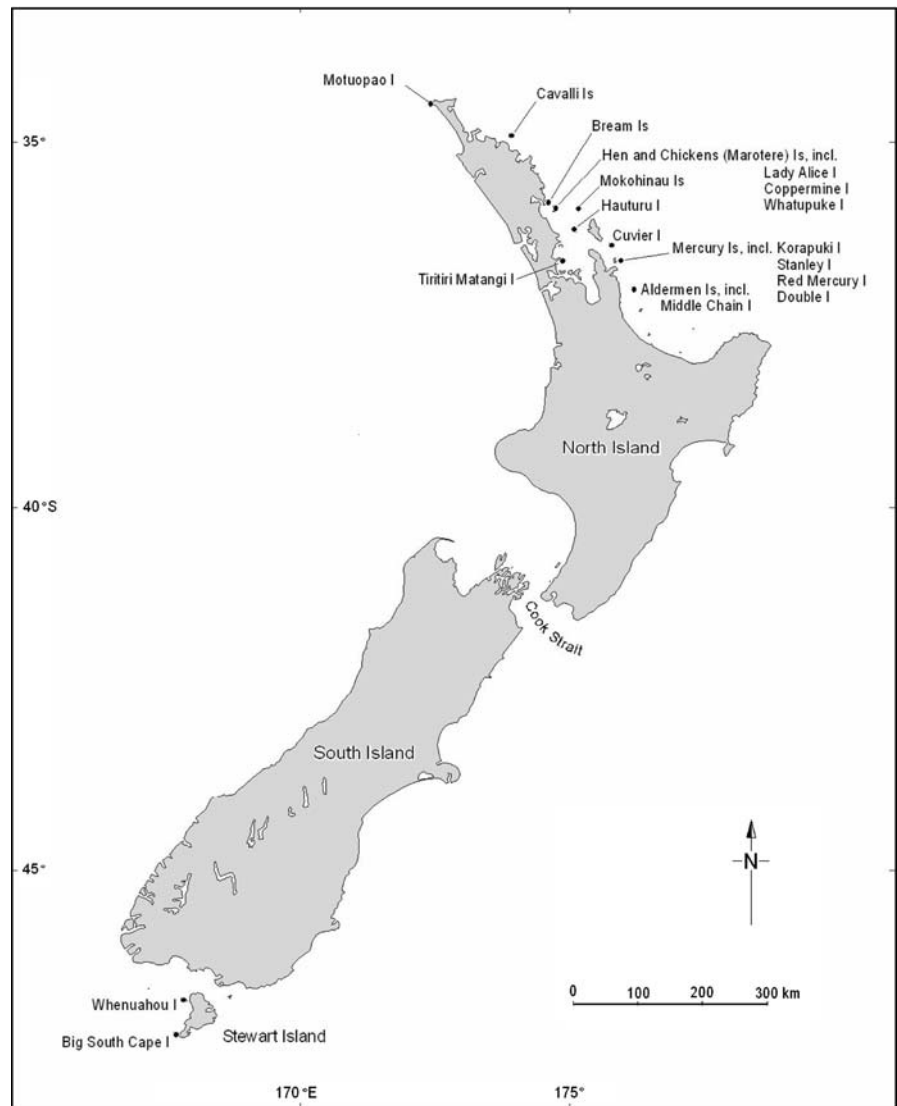
accounts of post eradication responses by native species in the Pacific islands.

To answer whether rat eradications are in effect reversed invasions, it is necessary first to describe a rat invasion. There are few accounts of the effects of a kiore invasion into complex island systems. The one exception is the invasion of 1 ha Lizard Island in 1977, but the kiore were eradicated within 12 months (McCallum 1986). I therefore begin with the ship rat invasion of the Big South Cape archipelago, because it provides insights into likely general effects of rat invasions (e.g. Courchamp and Caut 2005). I then illustrate the range of effects of kiore demonstrated after eradications using selected island case studies and discuss the validity of using eradications as a means of determining the effects of invasions.

The invasion of Big South Cape and neighbouring islands

Big South Cape Island (Taukihepa)—hereafter referred to as Big South Cape Island—is the largest of the Muttonbird (Titi) Islands which are privately owned and used for traditional harvesting of sooty shearwaters (*Puffinus griseus*). The islands, which are off southwestern Stewart Island/Rakiura (Fig. 1), include Big South Cape Island (939 ha), Rerewhakaupopo (Solomon) Island (26 ha) and Pukeweka Island (1.5 ha). In about 1962 ship rats invaded the three islands, presumably over stern lines from fishing boats (Atkinson and Bell 1973; Bell 1978; Atkinson 1989) which, based on analyses of mtDNA, were carrying rats from outside the Stewart Island archipelago (R. Fewster, pers. comm., 2006). Following the invasion, two groups of plants showed the effects of severe browsing, some to ground level; one species of weevil was extirpated, flightless crickets were all but eliminated and nine species of birds and both resident species of bats were either greatly reduced in numbers or extirpated. Of the extirpated birds and bats, one species of bird and bat were total extinctions, as were two subspecies of bird (Table 1). There was no immediate evidence of detrimental effects on burrowing seabirds (Bell 1978), and some native passerines including tui (*Prothemadera novaeseelandiae*), silvereyes (*Zosterops lateralis*), grey warblers (*Gerygone igata*),

Fig. 1 Locations in New Zealand mentioned in the text



tomtits (*Petroica m. macrocephala*) and at least three species of introduced passerines appeared to be more abundant after the invasion (Atkinson and Bell 1973; Bell 1978).

The invasion has many implications. First, the spread of rats and loss of sensitive species was extremely rapid. The time between the earliest recorded rat presence in August 1962 and the peak of the irruption in February 1965, when all 939 ha of the island were occupied, was only 2.5 years (Atkinson and Bell 1973). Within 5 years, five species of birds were extirpated or functionally so (reduced to one sex) and three had shown substantial declines.

Second, damage to some native species was greatest during the invasion phase, which implies that the spreading rats overshot their food supply. For example, megaherbs were initially gnawed to near ground level, but were recovering within 5 years (Atkinson and Bell 1973).

Third, the recorded effects were wide-ranging and included plants, invertebrates, birds and mammals. However, with the exception of bats, the effects were also selective within each group. Large flightless invertebrates were heavily affected. Furthermore, ten of the eleven species of affected vertebrates nest or roost either on or near the ground and in tree, ground

Table 1 Species affected by the invasion of ship rats onto Big South Cape and neighbouring islands, with extirpation referring to local loss and extinction total loss

Species	Size (mm)/wt (g)	Vulnerability	Fate
<i>Plants</i>			
Tree <i>Pseudopanax arboreum</i>		Sensitive to bark stripping	Local extirpation
Megaherb <i>Stilbocarpa lyallii</i>		Fleshy leaves and stems	Heavily browsed
<i>Invertebrates</i>			
Flightless crickets (weta)		Large, nocturnal, flightless	All but eliminated
Knobbed weevil <i>Hadramphus stilbocarpae</i>	20–25 mm	Large, obligate host, flightless	Extirpated
<i>Birds</i>			
Bellbird <i>Anthornis melanura</i>	26–34 g	Nests in tree forks, rock or tree cavities	Suppressed
Yellow-crowned parakeet <i>Cyanoramphus a. auriceps</i>	40–50 g	Tree hole nesting	Suppressed
Red-crowned parakeet <i>C. n. novaezelandiae</i>	70–80 g	Tree-hole nesting	Suppressed
Banded rail <i>Rallus philippensis</i>	170 g	Ground-nesting	Extirpated
Bush wren <i>Xenicus longipes variabilis</i>	16 g	Nests near ground level or in holes	Extinct
Fernbird <i>Bowdleria punctata stewartiana</i>	35 g	Nests near ground level	Extirpated
Robin <i>Petroica australis rakiura</i>	35 g	Tree forks	Extirpated
Snipe <i>Coenocorypha aucklandica iredalei</i>	105 g	Ground-nesting	Extinct
Saddleback <i>Philesternus c. carunculatus</i>	70–80 g	Tree-hole roosting and nesting	Extinct in wild
<i>Mammals</i>			
Greater short-tailed bat <i>Mystacina robusta</i>	70–85 mm	Roost in tree cavities, seabird burrows	Extinct
Lesser short-tailed bat <i>Mystacina tuberculata</i>	60–70 mm (14 g)	Roost in tree cavities, caves, seabird burrows	Extirpated

Data on species declines from Atkinson and Bell (1973), Bell (1978), Atkinson (1989), Kuschel and Worthy (1996), Ballance (2007); data for invertebrates from Meads (1990), bird habits from Heather and Robertson (2000) and bats from Lloyd (2005a, b)

and rock cavities. All of them were within or less than the body weight (100–180 g) of ship rats (Innes 2005). Other species appeared unaffected and some apparently became more abundant.

Fourth, the effects were apparently direct and indirect. The loss of the large flightless weevil may have been direct through predation and indirect due to loss of its host plant during the period of extensive browsing. However, the increase of some species of birds is likely to have been an indirect response to the loss of others. This implies that invasions can have unpredictable knock-on effects.

Fifth, for most species the mechanism for decline is unknown. However, at least some species were directly affected by predation of roosting females, as revealed by a sex bias to males in the last of the surviving saddlebacks (Blackburn 1965). Subsequent video camera studies indicate that ship rats frequently feed on eggs and chicks in the nest (Brown 1997).

Finally, although heralded as the best account of an invasion in New Zealand, there are complicating effects. A native flightless rail, the Stewart Island weka (*Gallirallus australis scotti*) is present on Big South Cape Island. Weka were introduced to many southern islands (probably including Big South Cape), most likely as an alternative food supply for mutton-birders (Atkinson and Bell 1973). Weka are omnivores that eat fruit, carrion, invertebrates, lizards, eggs, chicks and adults of burrowing seabirds and ground-dwelling terrestrial birds (Beauchamp et al. 1999). Releases of weka elsewhere onto islands in the Stewart Island archipelago were 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). The first three of these species were present on Big South Cape Island (Blackburn 1965). Weka were

reported on Solomon Island in 1913, as were banded rails (Guthrie-Smith 1925, p. 118). However, Bell (1978) considered weka to be responsible for the later absence of banded rails from Rerewhakaupopo Island and the restricted range of wren and snipe on Big South Cape Island. Recent analyses of δC^{13} isotope signatures in rats and weka on these islands indicate a stronger marine component in the diet of weka than for ship rats. This evidence, and the experimental local removal of rats and weka, indicates that weka feed more frequently on seabirds than do rats, whereas ship rats feed more frequently on terrestrial passerines than do weka (Harper 2007). Comments by Bell (1978) that seabirds did not appear to have been detrimentally affected by the ship rat invasion are therefore probably correct, because weka may have already severely depleted the more vulnerable species. However, there are local reports of the loss of prions and diving petrels since the rat invasion (G. Harper, pers. comm., 2006). Whether there were additive or synergistic effects between weka and ship rats is unknown but cannot be discounted.

Such complications bedevil most studies of the effects of invasive rodents, including those based on responses after rats were eradicated. Accordingly, most of the examples used below are from locations where the effects of kiore are unlikely to be complicated by synergistic effects of other introduced predatory birds or mammals.

The eradication of rats from islands provides an opportunity to investigate three of the above effects indicated for Big South Cape and neighbouring islands: the range and life history of the species most likely to be affected; the extent to which the effects are direct or indirect; and, at least for some species, the likely mechanisms for decline. Below, I use four sets of examples to illustrate these for kiore.

Selective and successional effects of kiore on plants

The possible effects of kiore on island-inhabiting plants were reviewed by Atkinson (1986), who identified the nikau palm and the trees karo and milktree (Table 2) as vulnerable to the effects of kiore based on distributional evidence. This hypothesis was tested when kiore were removed from several islands off northeastern New Zealand.

Increased seedling recruitment in the absence of kiore confirmed the hypotheses for all three species, but revealed that the effects had been under-estimated. In fact, at least 11 plant species showed significant increases in seedling recruitment when kiore were removed (Table 2), when compared with locations still with kiore and those never invaded. Additional species with large fruit showed patchy responses or tended to be most common on the larger islands, thereby restricting the range of sites for comparison. For example, karaka (*Corynocarpus laevigatus*) showed consistent seedling responses on some islands following removal of kiore but gave conflicting data on others (Campbell and Atkinson 1999). Furthermore, some of the effects of kiore were underestimated for resident populations. For example, Campbell and Atkinson (2002) found dioecious species that showed hitherto unrecognised sex imbalances, species that survived only where seeds lodged in rock falls, and species that were propagating vegetatively by layering.

The species of plants suppressed by kiore have a range of fruit sizes and reproductive modes. Studies of seedling recruitment imply that kiore are seed predators. However, impaired seedling recruitment may also reflect destruction of flowers, flower buds or developing fruit on the tree (Campbell and Atkinson 1999). Increased recruitment of seedlings after kiore are removed therefore represents the sum of these effects. For example, of two species with large fruit (Table 2), tawapou appears heavily affected by kiore, which eat the flesh and seeds, whereas kohekohe is less obviously affected, probably because kiore often only eat the fruit (Campbell and Atkinson 1999). Nonetheless, the strong response by kohekohe after kiore are removed suggests other effects of kiore, perhaps on the flowers, which are formed into large panicles that protrude from the trunk.

At least 6 additional species of plants have been identified as sensitive to kiore using experimental cages and exclosures (Campbell and Atkinson 2002; Towns et al. 2006), but whether they similarly respond when kiore are removed is yet to be determined.

Many of the species detrimentally affected by kiore produce copious fruit and four of the 11 species in Table 2 produce very large fruit. Some of these are favoured food species of the native fruit pigeon or kereru (*Hemiphaga novaeseelandiae*), which is the

Table 2 Plants responsive to removal of kiore from New Zealand islands (Campbell and Atkinson 1999, 2002), with data on tree biology from Poole and Adams (1990)

Species	Form (max height, m)	Reproduction	Fruit (max length, mm)	Response location (island)
<i>Fruit > 15 mm</i>				
Kohekohe <i>Dysoxylum spectabile</i>	Tree (17)	Bisexual	Globose capsule (25)	Double, Cuvier, Red Mercury
Parapara <i>Pisonia brunoniana</i>	Small tree (10)	Bisexual	Viscid perianth (20–30)	Cuvier, Double, Middle Chain
Karo <i>Pittosporum crassifolium</i>	Shrub or small tree (10)	Usually bisexual	3-Valved capsule (20–30)	Double, Red Merc. Mid. Chain
Tawapou <i>Pouteria costata</i>	Tree (15)	Bisexual	Berry (25–40)	Double, Red Merc. Mid. Chain
<i>Fruit 8–15 mm</i>				
Karumu <i>Coprosma macrocarpa</i>	Shrub (4)	Dioecious	Drupe (10–25)	Double, Red Mercury
Taupata <i>C. repens</i>	Prostrate to small tree (8)	Dioecious	Drupe (6–8)	Red Mercury
Coastal maire <i>Nestegis apetela</i>	Small tree (7)	Dioecious	Drupe (8–9)	Cuvier
Nikau <i>Rhopalostylus sapida</i>	Palm (10)	Monococious	Drupe (10)	Cuvier
<i>Fruit 4–8 mm</i>				
Houpara <i>Pseudopanax lessonii</i>	Shrub or small tree (7)	Dioecious	Globose (6)	Double, Cuvier, Middle Chain
Milktree <i>Streblus banksii</i>	Small tree (8)	Dioecious	Drupe (6)	Middle Chain
Hymenanthera <i>Meliccytus novae-zelandiae</i>	Shrub (3)	Dioecious	Berry (6)	Red Mercury

only species capable of transporting the ingested seeds in their gut. Furthermore, trees such as kohekohe, tawapou and milktree are canopy species which, on some islands without rats, dominate the mixed coastal forest. Campbell and Atkinson (2002) suggest that historic forest clearance on islands, coupled with the presence of kiore, has limited the recruitment pool of species into coastal forest. Without kiore, kereru are attracted to numerous fruiting trees, the forest may become dominated by species vulnerable to kiore, and these often bear the large fruit dispersed by kereru. Where kiore are present, kereru are less likely to visit the few fruiting trees, the forest is more likely to be dominated by species resistant to kiore, and species vulnerable to rats become rare or locally extinct. Such effects can be modified by site differences but, overall, the recovery of a wide range of species after removal of kiore indicates that, while present, these rats can fundamentally change successional pathways (Campbell and Atkinson 2002).

Indirect effects of kiore on an invertebrate

The honey dew scale insect *Coelostomidia zealandica* (Hemiptera: Margarodidae) inhabits northeastern islands. Immature scale insects or crawlers settle in cracks or on the branches of its host plants, which include karo and ngaio (*Myoporum laetum*). The larvae insert their mouthparts and produce a long tube to exude sugary waste. Infested trees have distinctive black trunks caused by sooty moulds growing on the secretions. The honeydew is highly sought after by nectivorous birds and geckos (Towns 2002a) and can be a major energy source in some forest ecosystems (Beggs 2001).

Since karo often becomes rare on islands inhabited by kiore (Campbell and Atkinson 1999), the scale insects decline as well. Invaded islands usually lack honey dew scale on the remaining karo but also ngaio, even though the latter species does not appear to be negatively affected by kiore. Towns (2002a) found that the scale insects occasionally recover and slowly reinfest karo and ngaio trees after rats (and other browsing mammals) are removed. Karo appears to be a vital component of the life cycle of the scale insects because it is a shade-tolerant species. Without karo, ngaio that die lose their scale populations and

new plants are not reinfested because there is no mechanism for transfer between the scattered light-hungry ngaio trees. Furthermore, because female scale insects are flightless, the rate of re-infestation is very slow, and may cease altogether if source populations are lost. Consequently, honeydew scale in some archipelagos can be confined to tiny rat-free islets, and be absent from their larger, forested but kiore-inhabited neighbours (Towns 2002a). In this example, loss of one host species has resulted in the collapse of a parasite transfer pathway that, in turn, can destroy an energy transfer source.

More direct effects of kiore have been reported for three species each of terrestrial snails, cockroaches, flightless crickets and beetles, a species of earwig and a species of large spider (Table 3).

Direct and indirect effects of kiore on a large reptile

The endemic tuatara (*Sphenodon punctatus*) is a large iguana-like sphenodontid reptile that can weigh up to 1,300 g (Gill and Whitaker 1996). By comparison, kiore are unusually large if they reach 120 g (Atkinson and Towns 2005). Tuatara were unknown to eighteenth century European explorers, when kiore were the only rats on the mainland, and were not revealed until about 1840 when populations were discovered on offshore islands (Robb 1986). Nonetheless, that tuatara had previously been present on the mainland is demonstrated by extensive Holocene deposits throughout the North and South Islands (Worthy and Holdaway 2002). Today, tuatara have a disjunctive distribution on islands off the northeastern North Island and in Cook Strait between the North and South Islands (Gaze 2001).

The potential role of kiore in the range contraction of tuatara was identified by Crook (1973) and Whitaker (1978). They found lower densities of tuatara and populations with little juvenile recruitment on islands where kiore were present. These findings were confirmed by Cree et al. (1995), who concluded that juvenile recruitment was impaired on 8 of the 9 islands where kiore and tuatara co-existed and, of these, the tuatara populations were near extinction on five. Cree et al. (1995) proposed possible direct and indirect effects of kiore. Direct effects were likely to be predation of eggs and young,

which would explain low or failed recruitment. Indirect effects could include competition for food, as a result of dietary overlap between the two species (e.g. Ussher 1999).

Removal of kiore was proposed as one way to test hypotheses about their effects on tuatara (Cree et al. 1995; Veltman 1996), with the appearance of hitherto missing cohorts of juvenile tuatara as the predicted outcome. These predictions were tested on three islands in the Marotere group, with neighbouring Taranga Island retaining kiore as control (Towns et al. 2007). The removal of kiore was followed by significant increases in juvenile recruitment on the three treatment islands. However, the proportional increase varied by island and by sites within islands, indicating location-specific responses. These may be a response to localised tuatara nesting sites from which juveniles gradually disperse to other locations.

An unpredicted response was increased body condition of tuatara on two of the three islands after kiore were removed. This indicated location-specific indirect effects of kiore, either through interference competition or competition for food.

Other species of herpetofauna with detrimental effects attributed to kiore include two species of frogs (now extinct), three species of geckos, and seven species of nocturnal or presumed nocturnal skinks (one now extinct). Two species of diurnal skinks have showed variable responses to kiore removal, with measurable effects at some (but not all) sites (Table 4).

Effects of kiore on ecosystem drivers

Coastal ecosystems around New Zealand were almost certainly influenced by the nutrients imported and activities of vast numbers of burrowing seabirds now largely confined to offshore islands (Worthy and Holdaway 2002). On islands, seabirds can form extremely dense colonies with burrow of densities at least $1/m^2$. As a result, soil geochemical properties can be strongly modified, with low pH but high nutrient concentrations (Mulder and Keall 2001). The burrows are also used as retreats for lizards and tuatara (e.g. Newman 1987). Burrowing seabirds are therefore viewed as ecosystem drivers because their activity has a multitude of direct and indirect effects. These effects can be measured in below-ground food

Table 3 Invertebrates responsive to removals of kiore from northern New Zealand islands, or showing incompatible distributions with kiore, with data on body dimensions and habit from McGuinness (2001), Meads (1990) and Crowe (2002)

Species	Length (mm)	Habits	Island/island group (Islands) location	Evidence
Gastropoda (terrestrial snails)				
<i>Amborhyda tarangaensis</i>	23–25 (width)	Carnivorous	Lady Alice, Taranga	Rat-gnawed shells and extirpation (Campbell et al. 1984; Brook 1999; R. Parrish pers. comm.)
<i>Placosystylus hongii</i> , <i>P. a. ambagiosus</i>	85	Herbivorous	Lady Alice, Coppermine, Motuopao	Total or near extirpation and rat-gnawed shells (Parrish and Shirley 1993; Brook 1999); post eradication recruitment (R. Parrish, pers. comm. 2007)
Blattoidea (cockroaches)				
<i>Platysoxterea novaeseelandiae</i>	27	Nocturnal, flightless	Mokohinau, Mercury Islands	Remains in kiore husking stations (Campbell et al. 1984); post eradication reappearance (Towns et al. 1997)
<i>Celatoblatta</i> sp.	12	Nocturnal, flightless	Mokohinau, Mercury Islands	Remains in kiore husking stations (Campbell et al. 1984); post eradication reappearance (Towns et al. 1997)
<i>Parallipstidion latipennis</i>	15	Nocturnal, near flightless	Mercury Islands	Post eradication reappearance (Towns et al. 1997)
Hemiptera (parasitic scale)				
<i>Coelostomidia zealandica</i>	6–15 (female)	Flightless female	Marotere, Mercury Islands	Local extirpation; post eradication recovery (Towns 2002a)
Orthoptera (weta crickets)				
<i>Hemianandrus</i> sp.	26	Nocturnal, flightless, burrow-inhabiting	Lady Alice, Tiritiri Matangi	Post eradication recovery (Green 2002; D.R. Towns and G.R. Parrish, unpublished data)
<i>Motuweta isolata</i>	85	Nocturnal, flightless, burrow-inhabiting	Mercury Islands	Incompatible distribution with kiore in archipelago (McIntyre 2001)
<i>Neonetus</i> sp.	15	Nocturnal, flightless, litter inhabiting	Mercury Islands	Post eradication re-appearance (Towns et al. 1997)
Coleoptera (beetles)				
<i>Mimopeus opaculus</i>	23	Nocturnal, flightless tenebrionid	Northeastern Islands	Incompatible distributions with kiore in most archipelagos (Watt 1986)
<i>Anagotus turbotti</i>	24	Nocturnal, flightless weevil	Marotere Islands	Incompatible distribution with kiore within archipelago (Watt 1986)
<i>Geodorcus ithaginus</i>	22	Nocturnal flightless stag beetle	Mokohinau Islands	Incompatible distribution with kiore in archipelago, extirpation following invasion by kiore (Watt 1986)
Dermaptera (earwigs)				
<i>Anisolabis littorea</i>	25	Nocturnal, flightless	Hen and Chickens Islands, Tiritiri Matangi, Mercury Islands	Remains in kiore husking stations (Campbell et al. 1984); post-eradication reappearance (Towns et al. 1997; Towns unpublished data)
Arachnida (spiders)				
<i>Ulitodon</i> sp.	20	Nocturnal, ground-dwelling	Tiritiri Matangi	Post eradication recovery (Green 2002; C. Green, pers. comm. 2007)

Table 4 Amphibians and reptiles responsive to removal of kiore from New Zealand islands or showing incompatible distribution with kiore with data on body dimensions from Department of Conservation (2002), with extinct species (*)

Species	Length (mm)	Habits	Location	Evidence
Leiopelmatidae (endemic frogs)				
<i>Leiopelma markhami</i> *	50–60	Probably terrestrial	Northern North Island	Extinction following arrival of kiore (Worthy 1987; Worthy and Holdaway 2002)
<i>Leiopelma waitomoensis</i> *	100			
Sphenodontidae (endemic tuatara)				
<i>Sphenodon punctatus</i>	600	Nocturnal, burrow inhabitant	Marotere Islands	Juvenile recruitment post kiore eradication (Townes et al. 2007)
Gekkonidae				
<i>Hoplodactylus duvauceli</i>	230	Nocturnal, forest and coastal	Marotere, Mercury Islands	Post eradication habitat shifts (Atkinson and Townes 2005; Hoare et al. 2007)
<i>Hoplodactylus pacificus</i>	170	Nocturnal, mainly forest	Marotere Islands	Post eradication re-appearance (R. Parrish, pers. comm.).
<i>Hoplodactylus maculatus</i>	155	Nocturnal, mainly coastal	Mercury Islands, Tiritiri Matangi	Post eradication recovery (Townes 2002a) and reappearance (G. Ussher, pers. comm.).
Scincidae				
<i>Cyclodina alani</i>	240	Nocturnal, burrow inhabitant	Mercury Islands	Incompatible distribution with kiore in archipelago (Townes and Daugherty 1994)
<i>Cyclodina northlandi</i> *	c. 340	Unknown	Northern North Island	Extinction following arrival of kiore (Worthy 1991; Worthy and Holdaway 2002)
<i>Cyclodina oliveri</i>	150–190	Nocturnal	Mercury, Aldermen Islands	Incompatible distribution with kiore in archipelagos (Townes and Daugherty 1994)
<i>Cyclodina macgregori</i>	200	Nocturnal	Cavalli, Bream and Hen and Chicken Islands	Incompatible distribution with kiore (Townes and Daugherty 1994; Townes 1999)
<i>Cyclodina townsi</i>	180	Nocturnal	Mokohinau, Marotere Islands, Hauturu	Incompatible distribution with kiore (Townes 1999) except on Little Barrier Island, with post-kiore response (R. Griffiths, pers. comm.)
<i>Cyclodina whitakeri</i>	200	Nocturnal, burrow inhabitant	Mercury Islands	Incompatible distribution with kiore (Townes 1999)
<i>Oligosoma moco</i>	180	Diurnal	Mercury Islands	Variable, with post eradication responses on some islands (G. Ussher and D.R. Townes, unpublished data)
<i>Oligosoma smithi</i>	150	Diurnal, coastal	Marotere, Mercury Islands	Variable, with post kiore responses on some islands (Townes 1991, 1996; Townes et al. 2003)
<i>Oligosoma suteri</i>	180	Nocturnal, coastal	Marotere Islands	Post eradication response (Townes et al. 2003)

webs, above-ground vegetation composition and structure (Fukami et al. 2006; Mulder et al. 2008), and in biomass of other dependent groups such as lizards and tuatara (Markwell and Daugherty 2002; Towns 2002b).

Following the eradication of kiore from islands, at least four species of burrowing seabirds <300 g in weight have shown positive responses either through increased fledging success or increased colony size (Table 5). One such example is Cook's petrel (*Pterodroma cookii*). Only two island populations of this species remain although evidence indicates that it was previously widespread on the mainland (Imber et al. 2003). The smallest population is on Whenuahou (Codfish) Island, off Stewart Island/Rakiura where, over the 10 years before 1998, there was periodic heavy predation of chicks by kiore at a ridge-top site. The percentage of chicks successfully fledging at this site ranged from 8 to 69%. However, when kiore were removed in 1998, fledging success increased from 8% (immediately before the eradication) to 54% the following breeding season, and by 2003 reached 88%. The control for this was the second population on Hauturu (Little Barrier Island) which, where predation by kiore was high, had fledging success $\leq 22\%$ (Imber et al. 2003). Immediately before kiore were removed from Hauturu in 2004, fledging success was as low as 5%, but this increased to an average 60% when kiore were removed (Rayner et al. 2007).

The effects of such declines following invasions by kiore were summarised by Holdaway (1999). At least 10 species of seabirds have become locally or totally extinct in New Zealand following invasions by kiore, and most of them were less than 200 g and with an egg length ≤ 60 mm. In addition, at least 13 species or subspecies of terrestrial birds declined to extinction soon after the arrival of kiore in New Zealand (Tennyson and Martinson 2006).

Discussion

Rats have been eradicated from New Zealand islands at the behest of government conservation agencies in order to: (i) develop new eradication technologies (Towns and Broome 2003); (ii) protect resident species under threat, such as tuatara (see earlier); (iii) enable the ex situ management of threatened

species such as the flightless parrot or kakapo *Strigops habroptilus* (Elliot et al. 2001); (iv) enable recolonisation by extirpated species (natural or assisted); and to (v) increase the ecological integrity of nature reserves penetrated by exotic species (Reserves Act 1977). None of the eradications were undertaken as experiments to measure the effects of rats on native species, which is understandable given the expense and infrastructure needed as support (Cromarty et al. 2002; Towns and Broome 2003). Nonetheless, considerable data have been gathered as species respond to rat removals, and these provide a useful basis for comparison with invasions.

Post eradication responses confirmed that the effects of rats can be direct or indirect. In response to direct effects, there were rapid responses such as increased fledging success of seabirds, and the appearance of new cohorts of juveniles, such as those measured for tuatara. By comparison, indirect effects can be difficult to detect and may involve long term and subtle responses. The impacts of kiore on karo trees and suppression of the plants as hosts of honeydew scale is such an example.

However, the effects identified after eradications of kiore only partly reflect those revealed from the ship rat invasion of Big South Cape and neighbouring islands; eradications should be seen as invasions in reverse only within limits. The first problem is that invasion can result in local extirpation or total extinctions, which cannot be revealed from responses to rodent eradications. Many extirpated species cannot recolonise and it becomes necessary to use circumstantial evidence within archipelagos to indicate the likely effects of rats while present. For example, if invertebrates apparently incompatible with kiore are included in the list of vulnerable species, the number increases from 11 to 15, all of which are ground-dwelling, nocturnal and have body lengths >12 mm. Furthermore, extinctions or dramatic range declines that coincide with the arrival of kiore on the main islands of New Zealand are reported for an additional six species of large invertebrates (Gibbs 2008). Consequently, the total number of invertebrates incompatible with kiore as revealed from eradications is only 52% of the total revealed from total or local extinctions.

In addition to invertebrates, lists that include detrimentally affected and incompatible species of vertebrates include two species of frogs, tuatara, and

Table 5 Seabirds responsive to removal of kiore from New Zealand islands or showing incompatible distribution with kiore with data on body dimensions and habits from Heather and Robertson (2000)

Species	Weight (g)	Habits	Range	Evidence
Procelleriidae (shearwaters, petrels and prions)				
<i>Pachyptila turtur</i>	125	Spring–summer breeding in burrows or crevices	Some northeastern islands, more commonly Cook Strait south	Incompatible distribution with kiore (Holdaway 1999)
<i>Pterodroma cookii</i>	200	Spring through autumn breeding in burrows	Hauturu, Codfish Islands	Predation during kiore presence and post eradication response (Imber et al. 2003)
<i>Pterodroma pycroftii</i>	160	Spring through autumn in burrows	Northeastern Islands	Post eradication response (Pierce 2002)
<i>Puffinus assimilis</i>	200	Autumn–winter breeding in burrows	Northeastern Islands	Post eradication response (Pierce 2002)
<i>Puffinus gavia</i>	300	Spring through summer breeding in burrows	Northeastern Islands	Historic declines and range contractions in presence of kiore (McCallum et al. 1984; Holdaway 1999)
Hydrobatidae (Storm petrels)				
<i>Garrodia nereis</i>	35	Spring through autumn breeding in hollows under vegetation	North and South Islands; Chatham and subantarctic Islands	Now confined to outer and subantarctic Islands, extinction on main islands following arrival of kiore (Worthy and Holdaway 2002)
<i>Pedeornis maoriana</i> (species identity to be confirmed)	?	Unknown	North and South Islands, probably islands around north-eastern North Island	Extinction on main islands following arrival of kiore (Worthy and Holdaway 2002); reappearance after kiore removal from islands but nesting sites unknown (Gaskin and Baird 2005)
<i>Pelagodroma marina</i>	45	Spring and summer breeding in burrows	Mokohinau, Mercury, Aldermen; also islands around southern North and South Islands	Incompatible distribution within archipelagos with kiore (Holdaway 1999)
Pelecanoididae				
<i>Pelecanoides urinatrix</i>	130	Late winter and spring breeding in burrows	Northeastern Islands	Often rare on islands with kiore, post eradication response (G. Taylor, pers. comm.)

11 species of lizards. Almost all of these species are nocturnal and the tuatara and nine species of affected skinks are ground dwelling. The latter include six species of *Cyclodina*, representing all of the larger members of the genus. The avifauna includes nine species of small-bodied seabirds of less than 300 g. However, kiore were identified as the most likely cause of extinction for one additional species of seabird and 13 species of terrestrial birds from the New Zealand archipelago (Holdaway 1999; Tennyson and Martinson 2006). Whether rats were the sole cause either directly or indirectly is difficult to assess for all of these species because some, such as seabirds and ducks, may also have been harvested by people. Furthermore, predation by feral dogs cannot be discounted as a contributing factor (Towns and Daugherty 1994), something dismissed by others (e.g. Tennyson and Martinson 2006).

A second problem is that resident species need to have residual populations that are sufficiently large and reproductively viable for responses to be measured when rats are eradicated. For example, plants may be present but represented by reproductively constrained populations (Campbell and Atkinson 2002), in which case, a lack of a response may not necessarily indicate a lack of sensitivity to rats.

How ever they are revealed, the effects of kiore discussed to this point are largely at species level. Furthermore, published records of vertebrate declines indicate that kiore are probably the least-damaging of the three commensal rat species (Towns et al. 2006). Nonetheless, when plants and invertebrates are added to vertebrates, the effects of kiore can likely accumulate into pervasive impacts on whole ecosystems. On seabird islands around New Zealand, kiore have been demonstrated to directly affect all four components of the islands' unique seabird-reptile-invertebrate-plant communities (Fig. 2). These effects are probably greatest in coastal forest where there are three pathways of interaction: direct predation of seeds, seedlings and flowers; indirect effects through suppression of seabirds; and the modification of successional pathways. Invertebrates may also be affected directly and indirectly. Indirect effects may stem from interruption of host-parasite pathways, but also, presumably, through modification of forest vegetation. Because of the loss of honeydew sources, geckos can also be indirectly affected by kiore. The fact that tuatara showed shifts in body condition on

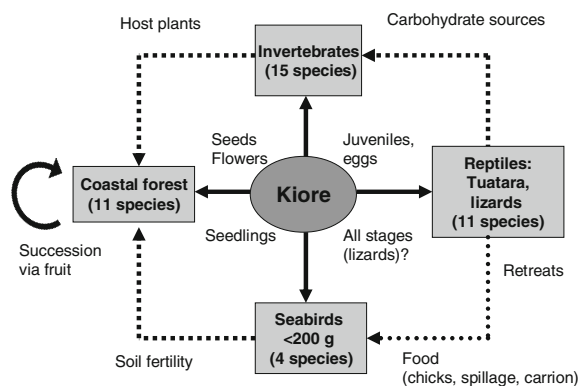


Fig. 2 Diagrammatic representation of the effects of kiore on islands around New Zealand dominated by small seabirds. Based on examples from post-eradication recovery, with *solid lines* showing direct effects and *broken lines* showing indirect effects. Additional data for affected species and those with exclusive ranges are given in Towns et al. (2006)

some islands after removal of kiore indicates that there are site-specific indirect effects on these species as well. Finally, since burrowing seabirds provide refuges and food for tuatara and lizards, the loss of seabirds must inevitably affect reptiles. Although for most species of lizards, the direct effects of kiore on reptiles are probably sufficiently strong to mask most indirect effects through the loss of seabirds. Therefore, it would not be surprising if kiore have effects on marine derived nutrients and below ground organisms similar to those described on islands invaded by ship and Norway rats (Fukami et al. 2006).

It is unclear to what extent lessons from temperate New Zealand can be transferred to kiore populations in the tropical Pacific. Suggestions that kiore were responsible for major forest transformations in the Hawaiian islands (Athen et al. 2002) and loss of palms from Easter Island (Hunt 2007) at present have little contemporary data in support from the region. There is some evidence that at least four species of seabirds responded to kiore eradication from Kure Atoll (Alton 2000), and there are anecdotal reports of rapid responses of lizards after recent eradications of kiore in Fiji (C. Morley and R. Chappell, pers. comm., 2007). Much could be revealed about the past effects of kiore from intensive studies at such sites.

The final lesson from New Zealand eradications is that the interactive and indirect effects of rats can be exceedingly complex, are very difficult to disentangle, and as a result, may be underestimated. This does not

mean that our lessons from eradications are of dubious value. It may mean that the hypotheses and models proposed have to be quite general and perhaps site-specific (e.g. Towns and Atkinson 2004). It also means that we will need to be patient and prepared for the unpredicted. Of course, if these long-running experiments are to be of use, they will need regular and long-term measurement. Most of all, they will need constant vigilance to ensure that rats do not recolonise.

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