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Effects of kiore (*Rattus exulans* Peale) on recruitment of indigenous coastal trees on northern offshore islands of New Zealand

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Possible effects of kiore (*Rattus exulans*) on selected indigenous tree species in coastal forests of northern New Zealand are surveyed from recent field sampling and a literature review. Recruitment rates are compared on islands with and without kiore (i) on the same island before or at the time of rat eradication compared with recruitment some years later, and (ii) on geographically separated islands with and without kiore. In addition, kiore-proof exclosures enabled some comparisons to be made of seed germination and survival in the presence and absence of kiore. There is evidence that kiore have substantially reduced recruitment of *Pittosporum crassifolium*, *Pouteria costata*, *Streblus banksii*, and *Nestegis apetala* by eating the seed. Seed consumption and/or depressed recruitment is demonstrated for *Rhopalostylis sapida*, *Vitex lucens* and *Pisonia brunoniana*, but the extent of recruitment reduction is not yet clear. No depressive effect by kiore on the recruitment of some species, including *Dysoxylum spectabile*, *Beilschmiedia tawa*, *B. tarairi*, *Corynocarpus laevigatus*, *Melicytus ramiflorus*, *Pseudopanax arboreus*, *P. lessonii* and *Coprosma macrocarpa*, has yet been demonstrated; juveniles remain abundant in the presence of kiore. Some tree species most affected by kiore are now rare in coastal forest of the northern islands and mainland. Evidence from recruitment reduction in these species suggests that the composition of northern coastal forest before kiore arrived was significantly different from that of the present. It also suggests that if rats are present, current successional pathways following burning or other disturbance of coastal forest will not restore the forest to its pre-human composition.

Keywords: seed predation; *Pittosporum crassifolium*; *Pouteria costata*; *Streblus banksii*; *Nestegis apetala*; *Rhopalostylis sapida*; *Pisonia brunoniana*; *Vitex lucens*; forest composition; island-recovery model

INTRODUCTION

Early Polynesians brought two mammal species to New Zealand, the Polynesian dog or kuri (*Canis familiaris* L.) and the Pacific rat or kiore (*Rattus exulans* Peale 1848). It is generally thought that kiore arrived about 1000 AD (McGlone et al. 1994), but an arrival time of 2000 yr BP has been suggested from recent controversial C^{14} dates, as yet uncorroborated by archaeological evidence (Holdaway 1996). Either way, the first kiore encountered a flora whose constituent plants evolved in the absence of browsing mammals: some 90% of the trees and shrubs possess fleshy fruit, but most fruit are < 8 mm diameter (Burrows 1994).

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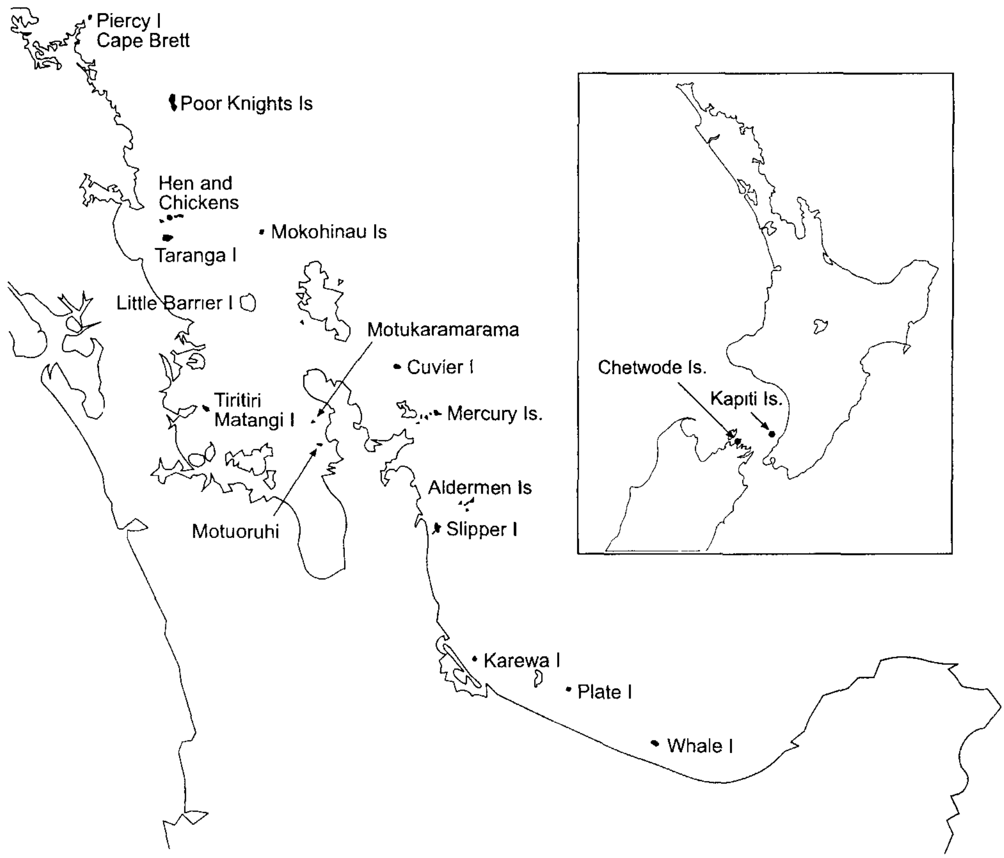

Fig. 1 Locations of island groups referred to in the text.

Kiore became widespread on the three main islands, and reached many of the offshore islands (Atkinson & Moller 1990).

That kiore eat seed of native trees and shrubs was recognized last century, and they were then described as "vegetarian" and "harmless" (e.g., Colenso 1891, White 1895). The view that kiore were harmless to the native biota had not changed fifty years later (Wodzicki 1950), although evidence of kiore eating carrion and their possible predation on birds and their eggs had been documented by Stead (1936). More recently, kiore have been increasingly implicated in the declines of small indigenous animals (e.g., Thoresen 1967; Crook 1973; Whitaker 1973, 1978; Imber 1975, 1978; Atkinson 1978; Ramsay 1978; Watt 1986; Newman 1988; Booth 1995). The Pacific rat is now regarded as one of the nine most widespread species responsible for species extinctions on islands (Atkinson 1996). In contrast, studies of the possible effects by kiore on indigenous plants are limited in number and scope (Campbell 1978; Campbell et al. 1984; Bunn 1979; Dick 1985; Atkinson 1986).

During the last two decades, second-generation anticoagulants such as brodifacoum have become available, and rodents have been eradicated from progressively larger islands (Veitch & Bell 1990, Taylor & Thomas 1993) including Kapiti Island (1965 ha) Comparisons of plant and animal populations before and after rat eradication can provide indirect evidence of the depressive effects of rats on the numbers or age (size) classes of vulnerable species including plants, but these data need to be checked with more rigorous direct methods

Kiore eat a wide range of plant items, including flower buds, flowers, leaf laminae, petioles, rhizomes, bark, and shoot apices as well as fleshy fruit, seeds, seed capsules and seedlings (Campbell 1978, Campbell et al 1984) Although the range of items eaten by kiore is wide, few plants are affected in more than one way However, even if two or more parts of a plant or more than one stage of the plant's life cycle are affected, such information does not by itself demonstrate that kiore suppress the recruitment of that species

This paper follows up previously published and unpublished reports with further sampling, and examines kiore effects on recruitment of some common coastal trees that they are known to eat, as well as others where the population structure of the trees suggests failed recruitment in the presence of kiore It concentrates on changes in population structure after kiore eradication, together with evidence such as comparisons of plant population dynamics and forest composition between islands with and without kiore

Table 1 The kiore status of selected offshore islands of northern New Zealand

Kiore still present		Island Area (ha)
Little Barrier Island		2817
Hen Island		476
Fanal Island Mokohinau group		75
Mauitaha (West Chicken), Chickens group		22
Kiore have never been present		**Area (ha)**
Poor Knights group (4)		271
Hongiora and 8 others (excluding Middle Chain), Aldermen group		74
Middle Island, Mercury group		13
Karewa Island		5
Ohinauiti		5
Muriwhenua, Chickens group		4
Motunau (Plate)		3 6
Piercy Island		3
Green Island Mercury group		2 5
Sail Rock		1 8
Kiore were present but now exterminated	**Area (ha)**	**Date of extermination**
Red Mercury Mercury group	225	1992
Tiritiri Matangi	196	1993
Cuvier Island	170	1993
Lady Alice Island, Chickens group	137	1995
Whatupuke Island, Chickens group	102	1993
Stanley Island, Mercury group	100	1991
Coppermine Island, Chickens group	80	1994
Burgess Island, Mokohinau group	56	1990
Double Island, Mercury group	32	1989
Middle Chain, Aldermen group	23	1992
Korapuki Island, Mercury group	18	1986

STUDY SITES

Kiore were introduced to most of the larger (>5 ha) northern offshore islands by Maori in pre-European times, but a few islands have remained free of them Kiore apparently disappeared from the North Island mainland during the first half of last century (Atkinson 1973, Taylor 1975) and have a very restricted distribution in the South Island mainland (Atkinson & Moller 1990) The major study sites therefore, were confined to northern islands which share many native tree species (Fig 1) They extend from the Cavalli Islands in the north to islands in the Bay of Plenty, but our sampling concentrated on Double Island, Mercury group (two small islands connected at low tide) and Cuvier Island where kiore have been eradicated in the past decade The area and kiore status of the islands selected are given in Table 1

The small islands (Table 1) are dry and have no permanent water (e g , Piercy, Muriwhenua (Chickens group), Sail Rock (south of Hen Island), Motunau or Plate (Bay of Plenty), Korapuki (Mercury group), Ohinauiti (East Coromandel), and Middle Chain (Aldermen group)) Most of these islands appear not to have been permanently occupied by Maori, but some have been greatly modified by them A second group of small islands (e g , Green, Middle (Mercury group), and Karewa (Bay of Plenty)) do not have kiore but are densely burrowed by large populations of petrels and shearwaters They are highly modified and have few seedlings or saplings of the canopy trees The remaining islands are larger, most have permanent water and were permanently occupied by Maori, some have since been farmed A majority of the listed islands have been burnt, and the larger islands have regenerating forest still dominated by pohutukawa (*Metrosideros excelsa*) or kanuka (*Kunzea ericoides*)

Kiore have also been eradicated from Inner Chetwode Island and both kiore and Norway rats (*Rattus norvegicus*) from Kapiti Island, Cook Strait region Most of the tree species found on the northern offshore islands are also found in the Cook Strait region, but some distinctive species such as *Beilschmiedia tarairi*, *Nestegis apetala*, *Pisonia brunoniana*, *Pouteria costata*, and *Vitex lucens* are absent *Pittosporum crassifolium* has been introduced to Kapiti Island

METHODS

Among tree species selected for study, we gave particular attention to those with large or aggregated fruit that could provide kiore with an easy meal (Table 2) Tooth marks on seed, or on the remains of seedlings, were used to determine items eaten by kiore and distinguish them from feeding sign left by parakeets (*Cyanoramphus* spp), kaka (*Nestor meridionalis*), or wetas (Orthoptera)

Replicated experiments to test hypotheses relating to kiore effects on plant populations and their recruitment are generally precluded by differences between islands and site differences within islands For these reasons we derived hypotheses using systematic comparisons of islands in a search for repeating patterns of depressed recruitment Annual variation in kiore numbers from year to year may sometimes affect the magnitude of differences in seedling establishment in exclosure trials In this part of the study we have examined changes in tree recruitment before and after rat eradication on the same island or on recruitment differences between islands with and without kiore These comparisons integrate kiore effects on recruitment over several to many years

We assigned size classes as a surrogate for age classes of woody species Two kinds of comparison were possible

(i) comparison of size-class distributions (or sometimes qualitative abundance of seedlings) of tree populations on an island before and after eradication of kiore from the island (Table 3)

(ii) comparison of size-class counts (or sometimes relative abundance assessed qualitatively) of tree populations on islands with and without kiore (Table 4–7) Kiore status of the island refers to the time of the cited reference Relative abundance ratings given by different authors are not always exactly comparable, when different ratings are given, both are listed Islands that had herbivores, such as pigs or rabbits, up to the time of the cited references have been excluded

Accounts of island floras usually do not record size classes of trees or the presence of seedlings and saplings, so it is difficult to determine from the literature whether an island population is self-replacing or represented by mature trees with only occasional juveniles Size classes used in this study are given in Table 3 To compare size-class distributions between populations, we excluded seedlings < 0 3 m and then calculated the ratio of juveniles (0 3 < 2 m ht) to the remainder of the population This ratio can be conveniently expressed as a percentage of juveniles (0 3 < 2 m) in the population (Table 3)

A third kind of comparison on islands inhabited by kiore makes use of exclosures that exclude kiore Kiore effects on germination and seedling survival can then be compared with adjacent control areas accessible to them (Campbell 1978) However, in this part of the study, exclosures on Little Barrier and Cuvier Islands were used only for a preliminary testing of kiore effects on seeds (or seedlings) of parapara (*Pisonia brunoniania*), puriri (*Vitex lucens*) and nikau (*Rhopalostylis sapida*)

We collected size-class data using two sampling methods

(i) counting and measuring seedlings and saplings in 2 × 2 m or 10 × 0 5 m quadrats, or in circular plots centred on trees that could be easily relocated The circular plots were demarcated by rotating a 5 m length of cord around the circumference of the tree at its base, the exact area of the plot was unimportant as there was no particular interest in estimating seedling/sapling density, the area of each plot was the same for each of the seedling counts at different times Plot positions were selected as places where habitat conditions appeared suitable for seedling establishment of the species under study

(ii) counting and size-classing all individuals of a particular species encountered within a fixed distance (2 m) of a pre-determined traverse (cf Atkinson 1962a) Traverse routes

Table 2 Grouping of tree species according to fruit size

Fruit > 15 mm length			
Beilschmiedia tarairi	taraire	Lauraceae	25–35 mm
Beilschmiedia tawa	tawa	Lauraceae	20–30 mm
Corynocarpus laevigatus	karaka	Corynocarpaceae	25–40 mm
Dysoxylum spectabile	kohekohe	Meliaceae	c 25 mm, (6–8 seeds)
Pittosporum crassifolium	karo	Pittosporaceae	20–30 mm, (c 16–30 seeds)
Pouteria costata	tawapou	Sapotaceae	c 25 mm, (1–4 seeds)
Pisonia brunoniana	parapara	Nyctaginaceae	c 30 mm
Vitex lucens	puriri	Verbenaceae	20 mm, (3–4 seeds)
Fruit 8–15 mm length			
Coprosma macrocarpa	coastal karamu	Rubiaceae	10–25 mm, (2 seeds)
Hedycarya arborea	pigeonwood	Monimiaceae	± 15 mm
Nestegis apetala	broad-leaved maire	Oleaceae	8–9 mm
Rhopalostylis sapida	nikau	Arecaceae	10 mm
Fruit 4–8 mm length			
Pseudopanax arboreus	fivefinger	Araliaceae	5–8 mm, (2 seeds)
Pseudopanax lessonii	houpara	Araliaceae	7 × 5 mm, (2 seeds)
Streblus banksii	milk tree	Moraceae	6 5 mm diam
Melicytus ramiflorus	mahoe	Violaceae	4–5 mm, (3–6 seeds)

Table 3 Frequency distribution of size-classes of trees mentioned in the text. Offset columns represent the two adjacent size classes.

<table>
<tr><th>Species</th><th>Island</th><th>Date</th><th>1†</th><th>2</th><th>3</th><th>4</th><th>5</th><th>6</th><th>7</th><th>8</th><th>9</th><th>10</th><th>11</th><th>12</th><th>13</th><th>14</th><th>15</th><th>16</th><th>17</th><th>Total</th><th>% juv.</th></tr>
<tr><td>Beilschmiedia tawa</td><td>Cuvier</td><td>1994</td><td></td><td>58</td><td>9</td><td>8</td><td>2</td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td></td><td>77</td><td>87</td></tr>
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† **Size classes**: **1** = seedlings <30 cm tall; **2** = short saplings 30 cm < 1 m tall; **3** = short saplings 1 m <2 m tall; **4** = tall saplings 2 m tall < 5 cm dbh; **5** = small trees 5 cm dbh < 10 cm dbh; **6** = trees 10 < 15 cm dbh; **7** = 15 < 20 cm dbh; **8** = 20 < 25 cm dbh; **9** = 25 < 30 cm dbh; **10** = 30 < 35 cm dbh; **11** = 35 < 40 cm dbh; **12** = 40 < 50 cm dbh; **13** = 50 < 60 cm dbh; **14** = 60 < 70 cm dbh; **15** = 70 < 80 cm dbh; **16** = 80 < 90 cm dbh; **17** = 90 < 100 cm dbh.

followed tracks, contours on seaward or valley slopes, ran parallel with ridge-lines when ridges were sampled, or followed compass lines where the land was flat or of gentle slope Methods (i) and (ii) were used on Cuvier and Double Islands, but only method (ii) was applied to Green, Little Barrier, Sail Rock and the Poor Knights Islands We collected data during the following visits to particular islands Cuvier Island (January 1964, May 1966, October 1993, December 1996), Double Island (January 1990, October 1990, December 1996, December 1997), Green Island (December 1997), Little Barrier Island (April 1998), Sail Rock (March 1971), Poor Knights Islands (1980, 1984)

RESULTS

All the species chosen, except parapara (*Pisonia brunoniana*), have been listed as eaten by kiore (Campbell 1978 or Campbell et al 1984) Most have fruits > 8 mm in size, and the few with smaller-sized fruit have their fruit aggregated (Table 2) Evidence for kiore effects on the trees listed in Table 2 is as follows

Tawa (*Beilschmiedia tawa*) and taraire (*B. tarairi*)

Because nibbled tawa fruit were sometimes found in husking stations (dry and protected sites to which kiore take food items to eat, Campbell et al 1984), tawa was listed by these authors as a species whose fruit was eaten by kiore, with the comment that there was little evidence that kiore ate the kernels Tawa and taraire are represented on several smaller islands by only a few small-sized individuals, suggesting either recent dispersal by pigeons (*Hemiphaga novaeseelandiae*) or an inability to survive severe drought Therefore we did not attempt an analysis of the distribution of tawa and taraire on islands with and without kiore Kiore are known to eat the flesh from the fruit of both species (Stead 1936, Campbell 1978) On Hen Island and Lady Alice Island (Chickens group), seedlings, saplings and poles of tawa and taraire were regenerating in suitable sites, and taraire seedlings were especially common (Court 1978, Bellingham 1984) Population size-class data from Cuvier Island in 1994 and 1996 suggested that although tawa was regenerating in the presence of kiore, there may have been some depression of seedling numbers

Karaka (*Corynocarpus laevigatus*)

Kiore had often nibbled karaka endocarps at husking stations but usually had not eaten them, suggesting that they eat karaka flesh without destroying the kernels (Campbell 1978, Campbell et al 1984) Intact karaka endocarps that remain after the flesh has rotted or been eaten by kiore were abundant beneath parent trees on Little Barrier Island, but there were few signs of gnawed endocarps Moreover, Norway rats and ship rats (*Rattus rattus*) do not appear to like karaka kernels, but do eat the flesh (Beveridge & Daniel 1965, Daniel 1973) However, on Whale Island in 1984, all karaka fruit found by Ogle (1990) "had been gnawed open, probably by rats [Norway rats], although a few intact seeds were found " Palatability of karaka kernels may vary with time, so that fruit that has lain on the forest floor for months may be less toxic than freshly fallen fruit Connor (1977) cites references which found old karaka kernels to be less toxic, but Bell (1974) showed that fruits stored for up to 20 years were still toxic, a one-year-old aqueous extract remained toxic despite having grown mould

Evidence for a kiore effect on karaka regeneration is conflicting (Table 4) Karaka has become an abundant tree in the presence of kiore on many of the larger islands that were cleared during Maori occupation On both Lady Alice Island and Hen Island, karaka regeneration is abundant in moister sites in the presence of kiore (Court 1978, Bellingham 1984) In contrast, two years after kiore had been eradicated from Inner Chetwode Island, numbers of karaka seedlings had risen by eleven times on four out of ten quadrats, and after

Table 4 Status of karaka (*Corynocarpus laevigatus*) on selected northern offshore islands in relation to distribution of kiore or other rats at the time of the cited reference.

Island	Status of karaka	Presence/absence of kiore	Source of information
Cavalli Is			
Nukutaunga I.	Few	?	Wright 1979a
Haraweka I.	Not recorded	+	Wright 1979a
Motukawanui I.	Few (heavily modified by farming)	+	Wright 1979b; Court 1979
Te Anaputa I.	Not recorded	?	Wright 1979a
Motuharakeke I.	Not recorded	–	Wright 1979a
Piercy I.	Frequent as seedlings to small trees in forest; Saplings common	–	Cameron & Taylor 1991; Atkinson (unpub.)
Unnamed I. (C. Brett)	Occasional	Rr?	Cameron 1982
Poor Knights Is			
Tawhiti Rahi I.	Abundant	–	Atkinson (unpub.)
Aorangi I.	Abundant	–	Atkinson (unpub.)
Chickens Is			
Muriwhenua I. and Wareware I.	Many	–	Atkinson 1971
Pupuha I.	Rare	–	Atkinson 1971
Mauitaha I.	Rare	+	Atkinson 1971
Lady Alice I.	Common; Regenerating in most communities	(+)	Cameron 1984; Bellingham 1984
Whatupuke I.	Common	(+)	Cameron 1984
Coppermine I.	Abundant; Common	(+)	Atkinson 1968; Cameron 1984
Hen I.	Common; Abundant regeneration	+	Wright 1978; Court 1978
Sail Rock	Locally abundant, numerous seedlings and saplings	–	Atkinson 1972
Mokohinau Is			
Fanal I.	Occasional in more mature stands, dense patches of seedlings	+	Wright 1980
Burgess I.	Not recorded (forest virtually gone)	(+)	Esler 1978b
Little Barrier I.	Abundant	+	Hamilton & Atkinson 1961
Tiritiri I.	Rare	(+)	Esler 1978c
Motukaramarama I.	Occasional; Seedlings abundant	Rn	Newhook et al. 1971; Esler 1978b
Motuoruhi I.	Frequent, many seedlings	–	Newhook et al. 1971
Cuvier I.	Common; Abundant	(+)	Beever et al. 1969; Atkinson (in prep.)
Mercury Is			
Red Mercury I.	Occasional, forest and stream side	(+)	Lynch et al. 1972
Double I.	Abundant	(+)	Atkinson (unpub.)
Middle I.	Local	–	Atkinson 1964
Green I.	Not recorded	–	Atkinson 1964
Ohinauiti I.	Not recorded	–	Atkinson (unpub.)
Old Man Rock	Not recorded	–	Atkinson1962(b)
Aldermen Is			
Hongiora I.	Not recorded	–	Court et al. 1973
Middle Chain I.	Locally abundant	(+)	Court et al. 1973
Ruamahuaiti I.	Not recorded	–	Court et al. 1973
Ruamahuanui I.	Not recorded	–	Court et al. 1973
Slipper Island group			
Rabbit I.	Not recorded	+	Court 1974
Karewa I.	Present	–	Sladden 1924
Motunau (Plate) I.	Not recorded	–	Taylor 1991

Key: Islands with kiore +; Islands without kiore –; Islands from which kiore have since been removed (+); Islands with *Rattus rattus* Rr; Islands with *Rattus norvegicus* Rn

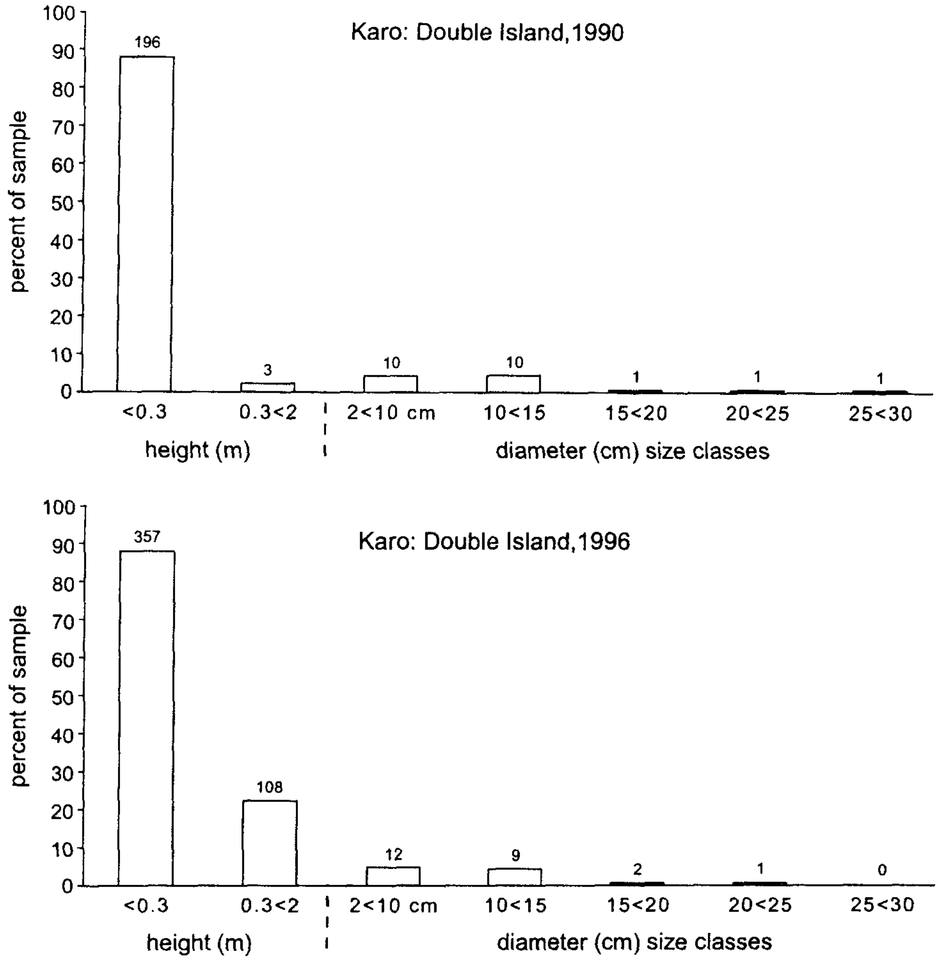

Fig. 2 Change in the size class distribution of a karo (*Pittosporum crassifolium*) population on Double Island, Mercury Island group, sampled at the same site: (a) 12 months after kiore eradication (n=222) and (b) 6 years after kiore eradication (n=489). Size classes as in Table 3.

four years the numbers of seedlings had increased on all ten quadrats (Avis 1997; Brown 1997). Similarly, the numbers of karaka seedlings in the exclosure on Cuvier Island increased after two years from five to 40 compared with an increase from seven to 21 seedlings in the adjacent control area (Campbell 1978).

Although these results may not be significant statistically, at all sites where kiore were removed, more karaka seedlings established subsequently. Karaka is absent from many small dry islands that lack drought-free sites, making comparisons with kiore-free islands difficult.

Comparison of size-class data (Table 3) from Cuvier Island (1996) and Double Island (1996), both recorded after kiore eradication, and from Little Barrier Island which still (1999) has kiore, and Sail Rock (1971), where kiore have never been present, do not show any consistent effect on karaka by kiore.

Table 5 Status of kohekohe (*Dysoxylum spectabile*) on selected northern offshore islands in relation to distribution of kiore or other rats at the time of the cited reference.

Island	Status of kohekohe	Presence/absence of kiore	Source of information
Cavalli Is			
Nukutaunga I.	Not recorded	?	Wright 1979a
Haraweka I.	Not recorded	+	Wright 1979a
Motukawanui I.	Common (heavily modified by farming)	+	Wright 1979b; Court 1979
Te Anaputa I.	Not recorded	?	Wright 1979a
Motuharakeke I.	Not recorded	–	Wright 1979a
Piercy I.	Locally common as seedlings/ saplings to trees	–	Cameron & Taylor 1991; Atkinson (unpub.)
Unnamed I. (C. Brett)	Not recorded	Rr?	Cameron 1982
Poor Knights Is			
Tawhiti Rahi I.	Abundant	–	Atkinson (unpub.)
Aorangi I.	Abundant	–	Atkinson (unpub.)
Chickens Is			
Muriwhenua I. and Wareware I.	Not recorded	–	Atkinson 1971
Pupuha I.	Not recorded	–	Atkinson 1971
Mauitaha I.	Locally abundant	+	Atkinson 1971
Lady Alice I.	Abundant, common in all size classes; Establishing or regenerating in all communities	(+)	Cameron 1984; Bellingham 1984
Whatupuke I.	Common in all size classes	(+)	Cameron 1984
Coppermine I.	Abundant; Common	(+)	Atkinson 1968; Cameron 1984
Hen I.	Important and common; Smaller size classes well represented	+	Wright 1978; Court 1978
Sail Rock	Not recorded	–	Atkinson 1972
Mokohinau Is			
Fanal I.	Major constituent of canopy, seedlings and saplings numerous	+	Wright 1980
Burgess I.	Not recorded (forest virtually gone)	(+)	Esler 1978b
Little Barrier I.	Abundant	+	Hamilton & Atkinson 1961
Tiritiri I.	Locally abundant	(+)	Esler 1978c
Motukaramarama I.	Abundant	Rn	Newhook et al. 1971; Esler 1978b
Motuoruhi I.	Abundant	–	Newhook et al. 1971
Cuvier I.	Abundant	(+)	Beever et al. 1969; Atkinson (in prep.)
Mercury Is			
Red Mercury I.	Occasional, forest	(+)	Lynch et al. 1972
Double I.	Many	(+)	Atkinson (unpub.)
Middle I.	Few	–	Atkinson 1964
Green I.	Not recorded	–	Atkinson 1964
Ohinauiti I.	Not recorded	–	Atkinson (unpub.)
Old Man Rock	Not recorded	–	Atkinson 1962(b)
Aldermen Is			
Hongiora I.	Not recorded	–	Court et al. 1973
Middle Chain I.	Not recorded	(+)	Court et al. 1973
Ruamahuaiti I.	Not recorded	–	Court et al. 1973
Ruamahuanui I.	Not recorded	–	Court et al. 1973
Slipper Island group			
Rabbit I.	Not recorded	+	Court 1974
Karewa I.	Not recorded	–	Sladden 1924
Motunau (Plate) I.	Not recorded	–	Taylor 1991

Key: Islands with kiore +; Islands without kiore –, Islands from which kiore have since been removed (+); Islands with *Rattus rattus* Rr; Islands with *Rattus norvegicus* Rn

Table 6 Status of karo (*Pittosporum crassifolium*) on selected northern offshore islands in relation to distribution of kiore or other rats at the time of the cited reference

Island	Status of karo	Presence/absence of kiore	Source of information
Cavalli Is			
Nukutaunga I	Not recorded	?	Wright 1979a
Haraweka I	Not recorded	+	Wright 1979a
Motukawanui I	Few (heavily modified by farming)	+	Wright 1979b, Court 1979
Te Anaputa I	Not recorded	?	Wright 1979a
Motuharakeke I	Few	–	Wright 1979a
Piercy I	Frequent on cliff ledges and forest margins, Saplings present	–	Cameron & Taylor 1991, Atkinson (unpub)
Unnamed I (C Brett)	Occasional	Rr?	Cameron 1982
Poor Knights Is			
Tawhiti Rahi I	Abundant	–	Atkinson (unpub)
Aorangi I	Abundant	–	Atkinson (unpub)
Chickens Is			
Muriwhenua I and Wareware I	Abundant	–	Atkinson 1971
Pupuha I	Abundant	–	Atkinson 1971
Mauitaha I	Rare	+	Atkinson 1971
Lady Alice I	Frequent, Three adults, some seedlings since rat eradication	(+)	Cameron 1984, D Towns pers comm
Whatupuke I	Common	(+)	Cameron 1984
Coppermine I	Local, Frequent	(+)	Atkinson 1968, Cameron 1984
Hen I	Locally abundant	+	Wright 1978
Sail Rock	Locally abundant, numerous seedlings and saplings	–	Atkinson 1972
Mokohinau Is			
Fanal I	Scattered small trees, Occasional larger trees, no seedlings	+	Wright 1980, de Lange et al 1995
Burgess I	Not recorded (forest virtually gone)	(+)	Esler 1978b
Little Barrier I	Uncommon	+	Authors
Tiritiri I	Common	(+)	Esler 1978c
Motukaramarama I	Not recorded	Rn	Newhook et al 1971, Esler 1978b
Motuoruhi I	Present	–	Newhook et al 1971
Cuvier I	Occasional, Few to many	(+)	Beever et al 1969, Atkinson (in prep)
Mercury Is			
Red Mercury I	Common, local, coastal	(+)	Lynch et al 1972
Double I	Abundant, seedlings rare	(+)	Atkinson (unpub)
Middle I	Many	–	Atkinson 1964
Green I	Many	–	Atkinson 1964
Ohinauiti I	Abundant	–	Atkinson (unpub)
Old Man Rock	Abundant	–	Atkinson 1962(b)
Aldermen Is			
Hongiora I	Abundant	–	Court et al 1973
Middle Chain I	Abundant	(+)	Court et al 1973
Ruamahuaiti I	Abundant	–	Court et al 1973
Ruamahuanui I	Abundant	–	Court et al 1973
Slipper Island group			
Rabbit I	Present, no record of regeneration	+	Court 1974
Karewa I	Not recorded	–	Sladden 1924
Motunau (Plate) I	Abundant, regeneration abundant	–	Taylor 1991

Key Islands with kiore +, Islands without kiore – Islands from which kiore have since been removed (+), Islands with *Rattus rattus* Rr, Islands with *Rattus norvegicus* Rn

Kohekohe (*Dysoxylum spectabile*)

Remains of kohekohe fruit were often found in kiore husking stations (Campbell 1978, Campbell et al 1984) Kohekohe is similar to karaka in its distribution, abundance and site requirements on the northern islands (Table 5) Again, evidence for a kiore effect on recruitment is conflicting Matthews (1980) reported kiore feeding sign on kohekohe fruit on Fanal Island, where kiore appeared to prefer the flesh In a postscript to this note (p 82), he commented that on Cuvier Island "the intensity of attack [by kiore] on some trees was remarkable Fruit at all heights in these trees had been eaten out, and a widespread litter of skin fragments and seeds lay beneath " It is not clear whether the kernels had been eaten or how the feeding evidence had been separated from that of parakeets Results from the 1960s exclosure on Cuvier Island were inconclusive, as there were large numbers of kohekohe seedlings in both exclosure and control samples at the start of the experiment, and kohekohe seedling numbers declined in both during the experiment (Campbell 1978) However, after kiore were eradicated from Inner Chetwode Island, numbers of kohekohe seedlings on six quadrats rose from none in 1994, to 38 in 1995, and to 175 in 1996, suggesting that recruitment of kohekohe seedlings on that island had been strongly depressed by kiore (Brown 1997)

Kohekohe continued to regenerate on the ridges of Cuvier Island even when goats were present, but seedlings were scarce on the seaward slopes and none were found in the valleys in 1960 (Atkinson, unpub) Since kiore have been eradicated, numbers of seedlings on the ridges have greatly increased Kohekohe was establishing or regenerating strongly on Hen Island (Court 1978), and Lady Alice Island (Bellingham 1984) Size-class histograms from Cuvier Island and Double Island (Table 3), do not show a kiore effect

Karo (*Pittosporum crassifolium*)

Karo capsules, from which seeds had been eaten, were found lying on the ground on Lady Alice Island, sometimes with kiore droppings in the capsules (Atkinson, unpub) The apparently self-replacing karo population that Atkinson (1972) found on kiore-free Sail Rock contrasted with the poor regeneration of karo on adjacent Hen Island and other islands that have kiore He attributed poor recruitment on kiore islands to kiore eating karo seed

Karo was one of the foods most commonly eaten by Norway rats on the Noises Islands (Moors 1985) He found a cache of fresh capsules which had been harvested from nearby karo shrubs up to 2 m high by rats biting cleanly through the stalks at the tips of branches Kiore have been observed on Kapiti Island feeding from karo capsules in the tree crowns (P Daniel pers comm) Vigorous regeneration of karo saplings has been reported from islands that have karo yet lack kiore such as Motunau (Plate) Island (Taylor 1991), or the small islands in the Mercury Island group (Taylor et al 1990) Data on distribution and abundance of karo in relation to kiore status on an island are summarized in Table 6 No small-sized stems were recorded by Bellingham (1984) in the only plot in which karo was encountered on Lady Alice Island

No seedlings were seen under a ridge stand of karo on West Double Island which was examined in January 1990, soon after kiore eradication Karo germinates in winter, by October 1990 there were 196 seedlings By December 1996 a count of the same strip of ridge gave 465 plants < 2 m tall, compared with only three plants in this size class in 1990 Of these, 357 were seedlings and 108 were saplings between 0 3 m and <2 m Changes in the size-class histogram are shown in Fig 2a and 2b In contrast, size-class histograms from Little Barrier Island, that still has kiore, and from Green Island in the Mercury group (that has never had kiore, but where regeneration is inhibited by a dense population of burrowing

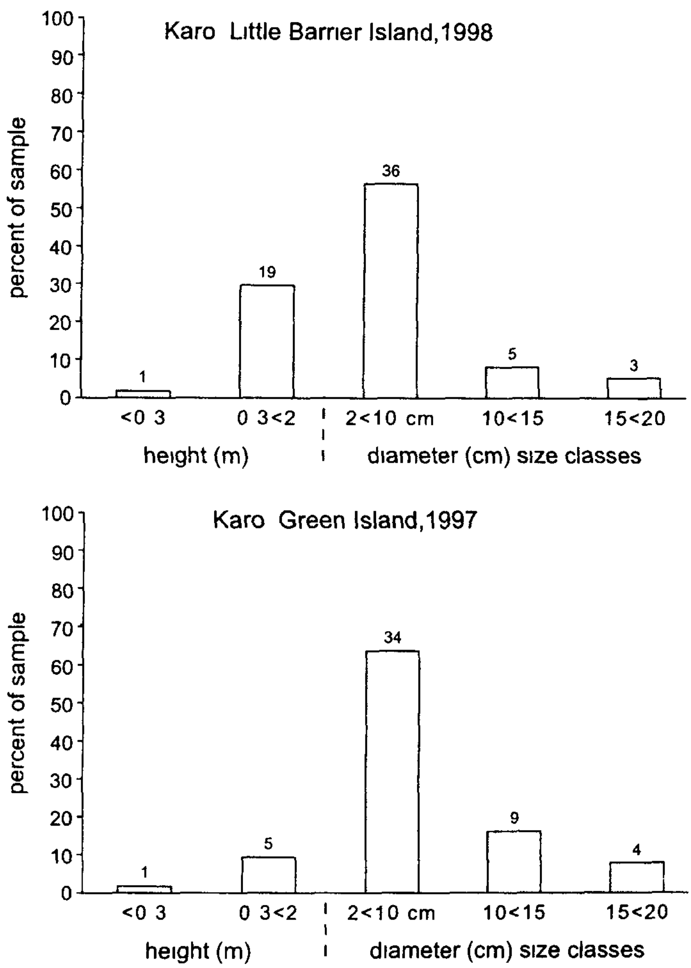

Fig. 3 Low recruitment of karo (*P crassifolium*) populations (a) in the presence of kiore on Little Barrier Island (n=64) and (b) on kiore-free Green Island, Mercury Island group, in the presence of a dense population of burrowing seabirds (n=54) Size classes as in Table 3

petrels), are shown in Fig 3a and 3b These contrast with the histogram from Sail Rock (Atkinson 1972), where kiore are absent and there are few petrels

The establishment of many karo seedlings after kiore eradication on Double Island and their subsequent growth into short saplings, provides clear evidence that kiore severely reduce germination by eating karo seed It is not known if they also eat seedlings

Tawapou (*Pouteria costata*)

It is rare to encounter tawapou seeds that have not had their kernels removed (Campbell 1978, Court 1978 Esler 1978b) The woody endocarps can last for many years, and often are found in dry sites such as husking stations, as many as 1400 can accumulate outside a single site (Campbell 1978, Campbell et al 1984) Kiore eat the flesh from freshly-fallen tawapou fruit but the kernel may not be extracted until later in the season (Campbell et al 1984) Tawapou is found on many of the northern offshore islands, but its seedlings and saplings are uncommon to rare on islands with rats (Table 7) Mature tawapou trees were rare on Lady

Table 7 Status of tawapou (*Pouteria costata*) on selected northern offshore islands in relation to distribution of kiore or other rats at the time of the cited reference

Island	Status of tawapou	Presence/absence of kiore	Source of information
Cavalli Is			
Nukutaunga I	Locally abundant after goat removal	?	Wright 1979a
Haraweka I	Not recorded	+	Wright 1979a
Motukawanui I	Few (heavily modified by farming)	+	Wright 1979b, Court 1979
Te Anaputa I	Not recorded	?	Wright 1979a
Motuharakeke I	Not recorded	–	Wright 1979a
Piercy I	Commonest tree on the island, Saplings present	–	Cameron & Taylor 1991, Atkinson (unpub)
Unnamed I (C Brett)	Occasional	Rr?	Cameron 1982
Poor Knights Is			
Tawhiti Rahi I	Abundant	–	Atkinson (unpub)
Aorangi I	Abundant	–	Atkinson (unpub)
Chickens Is			
Muriwhenua I and Wareware I	Rare	–	Atkinson 1971
Pupuha I	Not recorded	–	Atkinson 1971
Mauitaha I	Rare	+	Atkinson 1971
Lady Alice I	Common, Mature trees rare, regeneration infrequent	(+)	Cameron 1984, Bellingham 1984
Whatupuke I	Frequent	(+)	Cameron 1984
Coppermine I	Many, Common	(+)	Atkinson 1968, Cameron 1984
Hen I	Common to frequent, Seedlings and adults uncommon	+	Wright 1978, Court 1978
Sail Rock	Not recorded	–	Atkinson 1972
Mokohinau Is			
Fanal I	Common tree, Few seedlings	+	Wright 1980, de Lange et al 1995
Burgess I	Not recorded (Forest virtually gone)	(+)	Esler 1978b
Little Barrier I	Uncommon, localized	+	Authors
Tiritiri I	Rare	(+)	Esler 1978c
Motukaramarama I	Abundant	Rn	Newhook et al 1971
Motuoruhi I	Common, seedlings abundant	–	Newhook et al 1971
Cuvier I	Occasional Many, seedlings rare to few	(+)	Beever et al 1969, Atkinson (in prep)
Mercury Is			
Red Mercury I	Common, local	(+)	Lynch et al 1972
Double I	Locally abundant	(+)	Atkinson (unpub)
Middle I	Frequent	–	Atkinson 1964
Green I	Local	–	Atkinson 1964
Ohinauiti I	Many	–	Atkinson (unpub)
Old Man Rock	Many	–	Atkinson 1962(b)
Aldermen Is			
Hongiora I	Not recorded	–	Court et al 1973
Middle Chain I	Few	(+)	Court et al 1973
Ruamahuaiti I	Not recorded	–	Court et al 1973
Ruamahuanui I	Not recorded	–	Court et al 1973
Slipper Island group			
Rabbit I	Rare Several seedlings and regeneration reported	+	Court 1974
Karewa I	Present	–	Sladden 1924
Motunau (Plate) I	Not recorded	–	Taylor 1991

Key Islands with kiore +, Islands without kiore , Islands from which kiore have since been removed (+), Islands with *Rattus rattus* Rr, Islands with *Rattus norvegicus* Rn

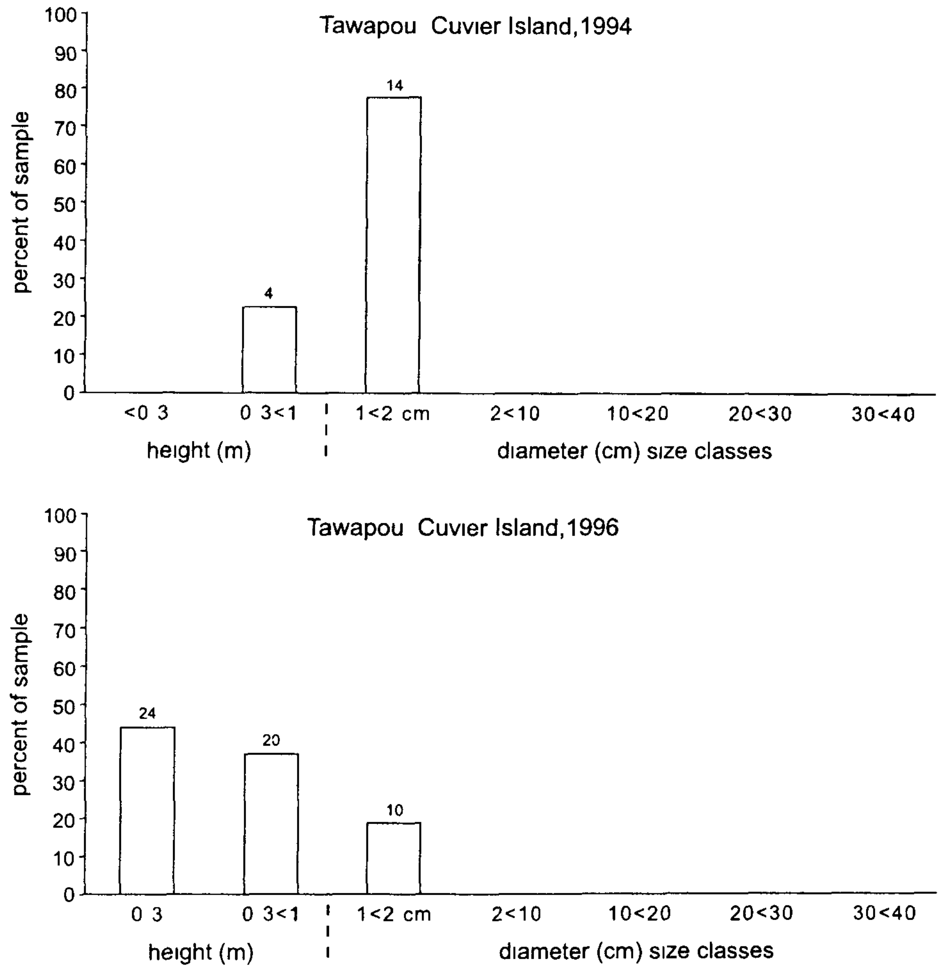

Fig. 4 Change in the size class distribution of a tawapou (*Pouteria costata*) population on Cuvier Island sampled at the same site (a) 6 months after kiore eradication (n=18) and (b) 3 years after kiore eradication (n=54). Size classes as in Table 3.

Alice Island and regeneration was infrequent in most vegetation types (Bellingham 1984). Seedlings and adult trees were both uncommon on Hen Island (Court 1978).

Juveniles have become more common on islands from which kiore have been removed, in contrast to their scarcity on Little Barrier Island where kiore are still present. When goats were eradicated from Nukutaunga Island in the Cavalli group (the rat status of the island was unknown but considered to be rat-free) tawapou seedlings became locally abundant (Wright 1979a). Tawapou size-class data were collected from Double Island (1990, 1996), Cuvier Island (1994, 1996), and Little Barrier Island (1998). Circular plots for seedlings were established on Cuvier Island in 1994 shortly after kiore were eradicated. With the exception of eastern Double Island, tawapou is uncommon on these islands, and all populations have few juveniles.

On Cuvier Island the numbers of seedlings <10 cm tall recorded in nine circular plots (2.5 m radius), and in six 2 × 2 m or 2 × 3 m plots, increased from none in 1994 to 24 in 1996. Tawapou were counted on Cuvier Island in a 550 m traverse along the ridge track to

Northwest Bay in 1994 and 1996 Few mature tawapou grow on the ridge and numbers were very low compared with other fast-growing species previously suppressed by goats (such as houpara) Numbers of tawapou juveniles (< 2 m ht) encountered along this traverse rose from 18 in 1994, shortly after kiore eradication, to 54 in 1996 The proportion of < 30 cm-sized individuals rose by a factor of 1 5 (Fig 4a & 4b)

Population counts were made in the talus forest on eastern Double Island and on western Double Island A count in 1996 of tawapou growing in the talus forest on the eastern island showed that although there were relatively few individuals in the largest size classes, there had been recent strong recruitment of < 30 cm-sized individuals, representing 61% of the total population (Fig 5a) In contrast, on the NW bench of the western island, although the forest included only two mature tawapou (not sampled), 30 individuals were counted in the 0 3 < 2 m size-class This suggests that significant regeneration had taken place on this site prior to 1990, when kiore were still present (Fig 5b)

During a brief visit to Red Mercury Island in December 1996, we found juvenile tawapou < 30 cm height were common but not saplings, whereas both seedlings and small saplings were rare in 1971 (Lynch et al 1972) On Little Barrier Island, where kiore are still present, only 13 tawapou were encountered along a 472 m traverse along a beach terrace of mixed talus and boulders, of which only two were juveniles < 30 cm tall and one was between 30 cm and 2 m The apparent thoroughness with which kiore find and eat the kernels before the seed germinates shows that kiore can substantially reduce seedling numbers Population size-class histograms show few tawapou seedlings on islands that have kiore seedlings soon appear after kiore have been eradicated Numbers of tawapou, and the proportion of tawapou trees in forest vegetation, will increase after rat eradication on any island that still retains tawapou trees

Parapara (*Pisonia brunoniana*)

On Fanal Island in the Mokohinau group, parapara was listed by de Lange et al (1995) as a species affected by kiore They commented on the absence of seedlings, and on "caches of gnawed seed" beneath the trees

Parapara is susceptible to summer drought, so is found mainly on moister sites on larger islands, when present on smaller islands its distribution depends largely on the availability of suitable sites On larger rat-free islands parapara is usually recorded as regenerating For example, all age classes were abundant on the Poor Knights Islands, seedlings and saplings were locally abundant on Motuoruhi, west of Coromandel Peninsula and all age classes are locally abundant on Little Barrier Island (author references to islands as in Table 4) By contrast, few adult parapara trees were found on Hen Island, and regeneration is quite poor (Court 1978), on Lady Alice Island both mature trees and seedlings were infrequent (Bellingham 1984)

Numerous parapara seedlings (average $417/m^2$ of cotyledon stage seedlings) were reported from beneath a large parapara tree on Motuoruhi Island (Newhook et al 1971) This island appears not to have any species of rodent, and pigs and goats have both been eradicated (Atkinson & Taylor 1992) In contrast, on Little Barrier Island where kiore numbers can be high, over 150 vigorous parapara seedlings were growing beneath an isolated tree that had seeded prolifically and on an old boulder beach and talus slope on the south coast, 30% of the stems in a stand of 140 parapara were 30 cm 1 m high although there were no seedlings <15 cm tall

In 1990 on Double Island just after kiore eradication, only one seedling was present beneath one of the adult trees in a plot of 5 m radius, but by 1996, there were 316 seedlings <10 cm, suggesting that kiore had previously had a strongly depressive effect on seedling

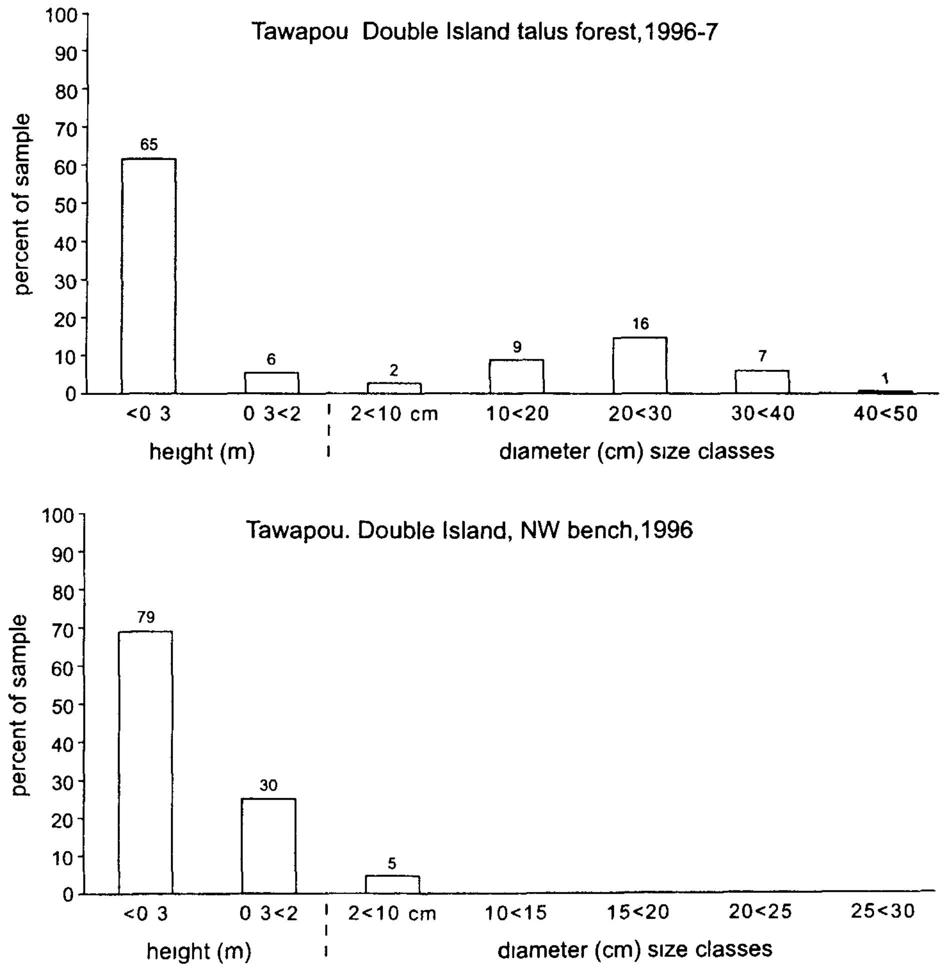

Fig. 5 Differences in size class distributions of tawapou (*P costata*) on Double Island seven years after kiore eradication (a) recruitment within an established population on East Double (n=106) and (b) recruitment within a population on West Double which was expanding in the presence of kiore (n=114) Size classes as in Table 3

germination By 1997, nine seedlings had grown to 35 cm tall and smaller seedlings were still very abundant Size-class data from Cuvier Island do not show a clear kiore effect Cuvier Island has few parapara, a legacy of the effects on the vegetation of the formerly large population of goats However, even before the goats were shot out in 1960, parapara seedlings were locally abundant beneath parent trees, after that, and while kiore were still present, many parapara seedlings established near mature trees Whether kiore will eat seedlings at the cotyledon stage is not known but an exclosure trial on Little Barrier Island indicated that kiore do not eat older parapara seedlings

Puriri (*Vitex lucens*)

Woody endocarps from puriri fruit often have been found in husking stations (Stead 1936, Campbell 1978, Campbell et al 1984) Kiore eat flesh from ripe drupes, and often leave tooth marks on the endocarps Each bony endocarp has two to four locules, and each can contain a viable kernel Thus up to four seedlings can establish from a single fruit, although Godley (1971) found usually only one or two live kernels in each fruit The depressive effect by kiore on the germination of a single puriri drupe can range from 25% (loss of one kernel) to 100% Only 3% of a sample of 128 endocarps collected from a cavity below a boulder on Cuvier Island had not been gnawed by kiore Assuming that each endocarp contained four locules, kiore had destroyed all kernels in 10% of endocarps, and two or three kernels in a further 50% of the endocarps Kiore can certainly reduce germination rates, but if some kernels remain, a seedling may still germinate from a chewed endocarp Kiore also eat the basal nectar disc of puriri flowers (Campbell 1978), but this would not prevent the development of fruit unless flowers are eaten in the tree crown, as with pohutukawa (Campbell et al 1984)

Regeneration of puriri on Hen Island was sometimes present under kanuka or young pohutukawa but, as has been observed elsewhere, was poor beneath parent trees or in mature forest (Court 1978) On Hen Island, puriri-rewarewa forest can follow kanuka forest in a vegetation succession (Court 1978) Puriri was not regenerating on Lady Alice Island (Bellingham 1984), and seedlings have not been found on Double Island, although the solitary very large tree produces viable seed

Analysis of size classes of puriri stems at two forest sites on Little Barrier Island suggests that kiore may have inhibited the establishment of puriri seedlings (Table 3) However, further data are needed, because puriri seedlings often establish in strong light, suggesting that the species is adapted to exploit canopy gaps Preliminary results from exclosures on Little Barrier Island suggest depressed germination in the presence of kiore

Pigeonwood (*Hedycarya arborea*)

Kiore eat the flesh from pigeonwood fruit, but initial observations suggest that they not favour the kernel (Campbell et al 1984) Pigeonwood can regenerate on islands that have kiore, e g , on Lady Alice Island, seedlings and saplings were not abundant but can establish on moister sites (Bellingham 1984) Pigeonwood established strongly after goats were eliminated from Cuvier Island, even while kiore were present Small seedlings of pigeonwood are now establishing on Double Island, presumably from fruit recently dispersed by pigeons, but it is still too early to predict survival rates

Broad-leaved maire (*Nestegis apetala*)

Broad-leaved maire seed was often encountered in husking stations on Cuvier Island and Hen Island, seedlings or saplings were uncommon in the vegetation (Campbell 1978) Regeneration is infrequent to poor on any islands that have kiore Court (1978) found few juveniles of tall sapling size on Hen Island, and regeneration on Lady Alice Island was infrequent (Bellingham 1984) Broad leaved maire is not found on Double Island, where kiore were present until recently, or on Little Barrier Island that still has them Broad-leaved maire is abundant on Tawhiti Rahi and Aorangi Island (Poor Knights group), both of which are rat-free, and is frequent and regenerating on rat-free Piercy Island (references to authors as in Table 4) Even when goats were on Cuvier Island, some sapling and pole-sized broad-leaved maire juveniles survived, but smaller juveniles were uncommon (Atkinson in prep) Three years after kiore eradication, broad-leaved maire seedlings were common near mature trees, and the total number of seedlings recorded on circular plots had risen from none in 1994 to 39 in 1996

Nikau (*Rhopalostylis sapida*)

Husks from nikau fruit are among the most common items left at husking stations (Campbell et al 1984) Kiore eat the leaves of first-year seedlings, and dig them up to eat the bulbous root base (Campbell 1978) An exclosure built in 1964 near a grove of mature nikau palms on Cuvier Island demonstrated that kiore can reduce seedling survival (Campbell 1978) After kiore were eradicated from Inner Chetwode Island, the total numbers of nikau seedlings on six quadrats increased from 25 in 1994 (a year after eradication), to 66 in 1995, and to 348 in 1996 (Brown 1997)

Furthermore, exclosures on Little Barrier Island have demonstrated that kiore strongly depress the survival of nikau seedlings Mature nikau palms were growing between the exclosure and control areas, and seed could fall naturally onto both sites In September 1997, 48 seeds were added to the exclosure and 84 to the larger control area By April 1998, only three seedlings were in the control area, compared with 86 in the exclosure Thirteen seedlings had established naturally in an area surrounding the exclosure and double the size of it, but over a period of two weeks kiore had eaten ten of them A second exclosure, constructed in September 1997, without added seed but with nikau palms nearby, was examined in April 1998 Inside the exclosure 13 seedlings had established, whereas in an area of twice the size surrounding the exclosure there were no nikau seedlings

Even so, nikau palms do establish on islands with kiore There was spectacular nikau regeneration on Cuvier Island after goats were removed and while kiore remained (Atkinson in prep) In 1996, two years after kiore had been eradicated, nikau seedlings had become very abundant beneath a stand of mature palms, in contrast to their rarity there in the 1960s Despite kiore, nikau is locally common to locally abundant on Little Barrier Island It is also locally abundant on Hen Island, but regeneration there is infrequent (Court 1978)

Mahoe (*Melicytus ramiflorus*)

Kiore are known to eat the leaf lamina, seedlings, fruit and bark of mahoe (Campbell et al 1984) Mahoe is abundant on most of the northern offshore islands, forming a major component of forest It appears in most early successions that follow burning or clearing, although on moister sites is often later replaced by kohekohe and karaka On Hen Island, mahoe is a major part of early successions (Court 1978), and on Lady Alice mahoe is regenerating in all forest types, especially in pohutukawa-taraire-karaka forest It has regenerated in the presence of kiore on Cuvier Island since the removal of goats Size classes on Double Island show no obvious kiore effect (Table 3)

Fivefinger (*Pseudopanax arboreus*), and houpara (*P. lessonii*)

Leaves and bark of both fivefinger and houpara are eaten by kiore (Campbell 1978, Campbell et al 1984), but no evidence has yet been found of kiore having eaten the fruit of either species On Kapiti Island when kiore and Norway rats were present, fivefinger became a major component of early successions following nineteenth century burning and clearing Fivefinger features in early successions on both Lady Alice Island and Hen Island (Bellingham 1984, Court 1978)

In contrast, Cameron (1984) listed houpara as frequent on Lady Alice Island, although it was not recorded in quadrats (Bellingham 1984) It appears in early successions on Hen Island (Court 1978) Both fivefinger and houpara have regenerated strongly on Cuvier Island since the eradication of goats, while kiore were still on the island (Table 3) Both species are common and regenerating on Double Island, especially West Double Island

Milk tree (*Streblus banksii*)

Fruit of milk tree is avidly eaten by kiore (Campbell 1978) Atkinson (1986) summarized information concerning the distribution of milk tree in relation to the presence of kiore on the northern offshore islands He found that on kiore-inhabited islands, this tree was either uncommon or absent. Where the species was common on an island, kiore had never been present. Abundant milk tree seedlings, such as the dense carpets of seedlings on Middle Island, Mercury group (Atkinson 1964), or those recorded by Wright (1979a) on Nukutaunga Island, Cavalli group, after goat eradication (estimated 1375 seedlings/m^2), have never been found on a kiore-inhabited island. Milk tree has not been found on Little Barrier Island, even though at least some of the stable coastal cliffs appear suitable.

Coastal karamu (*Coprosma macrocarpa*)

Kiore eat fruit, bark, twigs and seedlings of coastal karamu (Campbell 1978; Campbell et al. 1984). Seedlings up to 30 cm tall on Lady Alice Island had had their leaves stripped when kiore ate the petioles, and they were expected to die (I. McFadden, pers. comm. 1990). Esler (1978a) observed that on Trig Island (Mokohinau group), "it seems that most seeds of *Coprosma macrocarpa* are eaten by kiore as soon as they ripen."

Regeneration of coastal karamu on Lady Alice Island was abundant in the early stages of succession, but became less common as the vegetation matured (Bellingham 1984). There is a similar pattern of regeneration of coastal karamu on Hen Island (Court 1978). Coastal karamu was abundant on Cuvier Island even when goats were present, and regenerated strongly in the presence of kiore after goats were removed: it was not recorded in a 240 sq m plot in 1960, but by 1993 there were 1208 stems/ha, and seedlings were abundant (Atkinson in prep.).

DISCUSSION

Effects of kiore on individual plant species

These initial results show that seed predation by kiore severely reduces the regeneration of a small group of coastal trees. They are tawapou, karo, milk tree, and broad-leaved maire whose numbers are greatly depressed on islands that have or have had kiore. Some tree species appear to have been so severely affected by kiore over successive generations that it is difficult to find a suitable sample for population analysis. Moreover, comparisons with islands that lack kiore are not always satisfactory, as often these islands are small and have a limited range of site types, do not have the species of interest, have only a few individuals of these species, or have dense populations of breeding seabirds that inhibit seedling establishment (Campbell 1967). On islands that have kiore, depressed recruitment allows only occasional trees to establish in specialized sites such as a bouldery foreshore, on blocky talus, or in thick leaf litter where seed can escape detection by kiore. Neither milk tree nor broad-leaved maire have been recorded from Little Barrier Island. Much of this large island is bounded by steep coastal cliffs, so it is difficult to believe that these species will not eventually be found on sites that kiore find hard to search. Tawapou, milk tree and broad-leaved maire are all uncommon on islands that previously had kiore but now that kiore have been eradicated, seedlings are becoming more widespread. However, the scarcity of fruiting trees on modified islands slows seed dispersal and population recovery. Where species are dioecious such as milk tree, the problem of scarce fruiting trees is increased.

Exclosure experiments on both Cuvier and Little Barrier Island have demonstrated that nikau seedling establishment is greatly inhibited by kiore. Nevertheless, nikau is still common on islands that have kiore. Kiore eat both seed and first-year nikau seedlings, but after the vulnerable stage has passed, older seedlings appear to be no longer palatable. With species whose seed and seedlings are both eaten by kiore, annual fluctuations in the amount of fruit may enable a few seedlings to establish in years with a heavier crop and/or fewer kiore. If a vulnerable species can escape the effects of kiore eating seed or small seedlings, survival of juveniles may then be more assured.

Kiore may partially depress seedling recruitment of a somewhat larger group of common species including mahoe, coastal karamu, fivefinger and houpara, and perhaps karaka and kohekohe However, the evidence for a depressive effect is inconclusive and sometimes differs between islands Puriri is affected by kiore, but measurement of the extent of seedling reduction awaits further exclosure trials Parapara is uncommon on many islands, and although restricted mainly to drought-free islands, our results suggest its numbers may be limited by kiore

A third group of trees that includes mapou, (*Myrsine australis*) appears not to be affected by kiore Both mapou and houpara are abundant on islands in early stages of regeneration even when kiore are present Thus a gradient of depressive effects ranges from a major effect on germination success of some species to an unmeasurable effect on the seed crop of others

This study has concentrated on the consequences of seed predation, but kiore can also affect seed output by eating flowers, flower buds or developing fruit in the tree crown or depress juvenile recruitment by eating seedlings There is ample evidence that kiore are expert climbers For example, case moths (*Liothula omnivora*) and pohutukawa flowers have been taken to husking stations on the ground, (Campbell et al 1984) Kiore obtain some of their food such as karo capsules from tree crowns, but it is not known how much seed is eaten in tree crowns before birds can disperse it

Even though the range of foods that kiore eat may differ between islands, the strong suppressive effects on their preferred species (Group 1 species listed above), appear to be consistent on all islands where these trees and kiore are found together This suggests that in these cases the availability of alternative foods for kiore has little influence on their impact Nonetheless, the abundance and availability of alternative foods may determine the size of their impact on less preferred species especially when their seeds are hard to locate Infrequent heavy crops of fruit ("masting"), allows a plant to maximise establishment

The species most affected are those with large seeds that are easy for kiore to locate and eat (Table 2) These are not necessarily the species that produce the largest seeds because their kernels often contain toxins that deter all but specialist, usually invertebrate, seed predators (Smith 1975) Species that appear earlier in a vegetation succession have abundant smaller seeds, and usually escape severe predation simply because seed predators cannot find all the seeds

Kiore have been gone from Double Island and Cuvier Island for < 10 years, so it is too early to estimate the proportions of the woody floras of these islands affected by kiore, or the magnitude of effects on particular species Several trees and shrubs have more than one part of the life cycle affected by kiore, but evidence that kiore exert a depressive effect on the population has yet to be established Moreover, any depressive effect attributed to kiore has to be distinguished from other background changes that have followed clearing or burning and, on Cuvier Island, selective browsing by goats On parts of Cuvier Island there has been a strong recovery of seedling and sapling houpara that partly coincides with the period following kiore eradication, but much of this enhanced regeneration can be attributed to increased fruit output from trees that established after goats were exterminated

Annual variation in food availability on an island is likely to be the major factor determining the differences in kiore numbers from year to year Such differences may sometimes affect the magnitude of differences in seedling establishment in exclosure trials However the major conclusions in this part of the study are based on changes in tree recruitment before and after rat eradication on the same island or on recruitment differences between islands with and without kiore These comparisons encompass several to many years of kiore effects, and thus integrate the total effect of kiore on recruitment over these time periods

Recovery of vegetation after rat eradication

Ongoing changes to vegetation as a result of rat eradication are difficult to predict because of flow-on effects on recovery of birds, lizards, and invertebrates, some of which disperse fruit, and some of which destroy it. These animals may be pollinators, consume flowers, or eat developing seed or seedlings. There will be substantial increases in tree species that previously were rare or uncommon because of seed predation, and smaller increases in the numbers of trees on which kiore have had a lesser impact. This implies that the proportion of small-fruited species in the vegetation (e.g., mahoe, mapou, and coastal karamu), on which kiore appear to have had little effect, may decline. However, as these species are prominent in early stages of forest succession, their abundance usually declines as forest matures. Eventually the proportions of species in the vegetation that were affected by kiore and those not affected will move towards a new balance.

A generalized model of island recovery following modification can explain many of the distribution patterns of uncommon and rare trees on the northern offshore islands. On smaller, dry islands that were not permanently occupied by Maori, e.g., Double and Korapuki Islands, the presence or absence of karo, tawapou, milk tree, puriri, broad-leaved maire, parapara, karaka, and kohekohe depends on the availability of suitable sites, especially for the last three species which are drought-sensitive. Many smaller islands have been burnt, and many have had kiore. But the numbers of kiore-sensitive trees have either been static or their post-burn population recovery has been very slow. A common pattern of vegetation recovery is for successions to proceed through kanuka and/or pohutukawa, and sometimes through mapou. Small-fruited species spread by birds, especially tuis (*Prosthemadera novaeseelandiae*) and bellbirds (*Anthornis melanura*), become abundant in the understorey on most islands. These include mahoe and houpara, as well as mapou. Larger islands that have permanent water, and were once permanently occupied by Maori, e.g., Red Mercury and Cuvier Island, were more extensively modified by burning and cultivation. Some of these islands, e.g., Great Mercury Island, have since been farmed and converted to pastures of exotic grasses, with native forest persisting as small remnants in gullies. Drought-tolerant trees have survived on these islands on dry coastal cliffs. Most larger islands except the Poor Knights Islands have had kiore. Larger islands progress slowly towards forest, through the same stages as for smaller modified islands, but eventually kohekohe and karaka gain dominance on moister sites, together with puriri, tawa, taraire, and nikau. Hinau (*Elaeocarpus dentatus*) and pigeonwood are frequent minor species. Rates of change in the abundance of these larger-fruited species depend on pigeon numbers within the island group, and on their patterns of movement and fruit dispersal. Pigeons would have become scarce on most island groups during the period of habitat modification and loss of large-fruited trees; recovery of their numbers largely depends on the return of forest habitat. On islands that have a sward of exotic grasses, kiore can become very numerous (Moller & Craig 1987), which leads to severe predation on seed from the trees that survive in forest remnants. This slows the recovery and spread of forest. In general, kiore densities appear to be lowest in mature forest that contains kohekohe, karaka, tawa and taraire (Campbell, unpub.).

Court (1978) concluded, from trends in forest composition on Hen Island, that what he termed a mixed species forest type containing karaka, parapara, tawapou, milk tree, and broad-leaved maire will develop just inland from coastal karaka forest, but this could not happen in the presence of kiore. Bellingham (1984) noted that there are possible remnants of the mixed-species forest type on Motuoruhi Island west of Coromandel Peninsula. Data from Piercy Island, (3 ha) off Cape Brett, which has never had rats, suggest that puriri may also form part of the mixed-forest type, despite the inability of puriri to regenerate beneath its own canopy. Puriri is long lived, grows very rapidly as a seedling, and can exploit canopy gaps.

Tawapou is the commonest canopy tree on Piercy Island (18.5% crown cover), followed by puriri (13%), milk tree (9%), parapara, pohutukawa, and *Melicytus novae-zelandiae* (all 6%) and broad-leaved maire (5.5%) (Atkinson, unpub.).

The mixed species forest type is absent from most of the modified islands that have had kiore, because although the species are found in small numbers on most islands, seed predation by kiore continues to suppress their regeneration. Furthermore other seed eaters, especially parakeets and kaka, influence the amount of seed available for other birds that disperse fruit. Parakeets and kakas feed on a wide range of flower buds, flowers and fruit, reducing the seed crop of many trees. Eradication of kiore may remove nest predation on parrots, but if parrot numbers then rise, their seed consumption can partially replace the effects of kiore on the size of the seed crop of several tree species, e.g., parapara, puriri, and hinau.

Implications for mainland forest since kiore were introduced

The arrival of kiore in New Zealand initiated fundamental changes to the biota. Predation on invertebrates, (especially weta, the larger beetles and moths), lizards, tuatara (*Sphenodon punctata*), and birds is now well documented. This study demonstrates that kiore have also affected the direction of forest succession on offshore islands, and similar effects must have been initiated on the mainland. Changes in the abundance of trees important as food for some birds, together with direct competition by kiore for food, is likely to have had an immediate and ongoing effect on some bird populations. For example, Reid & Williams (1975) state that the North Island brown kiwi (*Apteryx australis mantelli*) has "... a significant vegetable component in the diet." Fruits include those of *Elaeocarpus*, *Mida*, *Nestegis*, *Podocarpus*, *Rhopalostylis*, *Coprosma*, *Cordyline*, *Cyathodes*, *Dacrydium*, *Geniostoma*, *Pseudopanax*, *Rubus*, and *Solanum*. Invertebrate foods include crickets, wetas, ants, cicada nymphs, caterpillars and pupae of moths, and adults and larvae of various beetles. There is a substantial dietary overlap between kiore and kiwi, as kiore are known to eat most of the invertebrate items recorded in kiwi diet (including earthworms), as well as many of the fruits that kiwis eat. A similar overlap between the diet of kiore and at least parts of the diet of weka (*Gallirallus australis*), takahe (*Porphyrio mantelli*) other rails, and kakapo (*Strigops habroptilus*) could be demonstrated.

It is tempting but unwise to assume that all species of rodent eat the same plant foods and affect plant regeneration to the same extent. For example, although kiore appear to inhibit milk tree regeneration (Atkinson 1986), milk tree was regenerating on Motukaramarama (Bush) Island, western Coromandel (Newhook et al. 1971), where Norway rats are present (Atkinson & Taylor 1992). Similarly, abundant karo regeneration has been reported from Rimariki Island in the presence of mice (Cameron 1986). Nevertheless, many items eaten by kiore appear to be similar to those eaten by other rat species (Campbell et al. 1984), so our findings should assist the understanding of the effects of other combinations of rodents in mainland forests.

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