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Te Whare Wananga o te Upoko o te Ika a Maui

**Keystone species on New Zealand offshore islands:
Ecological relationships of seabirds, rats, reptiles and
invertebrates on Cook Strait islands**

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of the requirements for the degree of
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Abstract

The influence of seabirds and rats on island ecosystems was measured to assess the applicability of the keystone species concept for ecology and conservation. Pitfall trapping for lizards and small invertebrates, soil sampling and stable isotope analysis was used to assess the roles played by seabirds and rats on six islands in the Marlborough Sounds.

Both abundance and ordinal richness of invertebrates were found to be greater on islands with seabirds than on seabird-free islands. Although lizard distribution was strongly influenced by species-specific habitat requirements, the greatest numbers of lizards recorded in this study were found on seabird-inhabited islands. Although significant differences were not found, the C:N ratio of soils in seabird colonies in this study and at other sites was lower than that at seabird-free sites. Nitrogen stable isotope analysis showed that a proportion of the diet of animals at a range of different levels throughout the island foodweb was derived from seabirds.

Rats were found to negate many of the positive effects of seabirds. As well as significantly lower numbers of seabirds, islands with rats had lower abundance of lizards and lower abundance and diversity of small invertebrates than rat-free islands.

Although both seabirds and rats play important roles in island ecosystems, neither conformed to a definition of a keystone species. Theoretical and practical problems were found with the calculation of keystone status for different taxa. Given that important species cannot be shown to be keystones, and that calculation is technically difficult (and maybe impossible) the classification of seabirds, rats, or any other species as keystone is not likely to advance theoretical ecology or assist with conservation management. Attempts to define keystone species were found to be unsuccessful and abandonment of the term was advised.

Chapter 1: Pitfalls in the quest for keystones

Groups of organisms that are important in maintaining organisation and diversity of ecological communities have been labelled keystone species (Paine 1969, Mills et al. 1993). Since its inception, the keystone species concept has proved popular and appealing for ecology and conservation purposes (e.g. Simberloff 1990, Bond 1994). However, the applicability and validity of the concept is now in doubt (Mills et al. 1993, Hurlburt 1997).

Seabirds (order Procellariiformes) and rats (*Rattus* spp.) play significant roles in determining structure and function of New Zealand offshore island ecosystems (Atkinson and Bell 1973, Whitaker 1973, Daugherty et al. 1990). In this thesis I quantify some of the effects of seabirds and rats on offshore islands and use the results to assess the applicability of the keystone species concept for ecological studies.

KEYSTONE SPECIES

The concept of keystone species, as introduced by Paine (1966, 1969), appeared to identify species crucial in maintaining the organisation and diversity of ecological communities (Mills et al. 1993). Paine (1969) found that the activities of *Pisaster ochraceus*, a predatory starfish, greatly modified the species composition and physical appearance of the rocky intertidal zone. He defined *Pisaster* as a "keystone of the community's structure" because the "integrity of the community and its unaltered persistence through time ... are determined by [*Pisaster's*] activities and abundance" (Paine 1969). If *Pisaster* were removed, the community would be fundamentally different.

The keystone species concept has since been expanded beyond this relatively narrow focus to encompass a range of different species, from tsetse flies (*Glossina* spp.) to elephants (*Loxodonta africana*) (Bond 1994). The concept has proved attractive for conservation and particularly restoration projects (Simberloff 1990, Mills et al. 1993) because attention could be placed on keystone species, thereby preserving the whole community in one fell swoop.

Definition of keystone

The keystone concept was originally intended as a metaphor “to convey a sense of nature’s dynamic fragility and the unexpected consequences of removing (or adding) species” (Paine 1995). Many cases of keystones cited in the literature do, in effect, only use the term keystone in this metaphorical sense. In these cases keystone has come to mean little more than ‘important for something’ (e.g. examples in Bond 1994). Attempts have also been made to more explicitly define keystone species. Significant difficulties are associated with such attempts.

Problems with definitions of keystone species

Types of keystones - Although Paine (1969) identified only one type of keystone species, keystone predators such as *Pisaster*, the relatively narrow focus has subsequently been vastly expanded. Mills et al. (1993) found five major types of keystone species in the literature, while Bond (1994) identified eight different types of keystones. Marked differences exist in interpretation of what defines a keystone species.

Within the published description of keystones there are significant differences in the scale at which keystone interactions are measured. Brown and Heske (1990) termed three species of kangaroo rats a “keystone rodent guild” because their removal led to changes in animal and plant diversity in a Chihuahuan desert ecosystem. At a larger scale, Owen-Smith (1987) has attributed the loss of mammalian genera during the Pleistocene to a keystone group of megaherbivores (animals exceeding 1000 kg body mass). At the most extreme, Bond (1994) has described the entire angiosperm division as “keystone competitors” responsible for the transformation of Mesozoic gymnosperm/pteridophyte dominated landscapes to more modern vegetation patterns.

The broadness of the range of taxa that have been classed as keystones in the literature makes classification of other species (or guilds or orders or divisions) difficult. If species are to be defined as keystone in the future, it will not be clear what level of precision is being applied, and the utility of the classification is significantly reduced.

Level of effect - Another theoretical anomaly is the level at which any keystone effect is found to take place. If keystone effects are brought about by the suppression of one species by another (by predatory or competitive effects), decisions as to which species is the keystone may be purely subjective. For example Bond (1994) cites both rabbits (*Oryctolagus cuniculus*) and the *Myxoma* virus as keystones. Rabbits prevent transition of grassland to woodland while the virus kills rabbits and leads to the vegetation change (Bond 1994). Even in Paine's classic example of the rocky intertidal, it is not clear why *Pisaster* was picked out for special attention. If *Mytilus* did not have the ability to competitively dominate available space, the predatory effects of the starfish would not be special. Classification of a species as a keystone in situations such as these may be purely subjective, or based on the particular interests of a researcher.

Is an unambiguous definition of keystonehood possible?

An implied dichotomy - Implicit in the concept of keystone species is that a distinct dichotomy exists in nature between keystone species and non-keystone species. Yet evidence or theoretical support for this dichotomy has not been forthcoming (Hurlbert 1997). Paine (1992) calculated an index of per capita interaction strength for a group of species in the rocky intertidal. Interaction strength is thought to be positively correlated with keystone status in most cases (Power et al. 1996). Paine (1992) concluded that the index revealed "a few strong interactions embedded in a majority of negligible effects". This result was thought by Mills et al. (1993) to support an assumption of highly skewed interaction strengths, i.e. that some species had strong effects and others did not. Hurlbert (1997) points out that this study, and others in which a dichotomy of interaction effects is assumed, do not show skewed interaction strengths because they are plotted on incorrect axes. If interaction strength values are plotted on a log scale, the distributions tend to become symmetrical and continuous (Hurlbert 1997). Although the effects that different species have on other components of their ecosystem vary, a continuum between strong and weak interactors seems a more plausible description than a dichotomy between keystone and non-keystone species.

Density effects - Keystone species are thought to be species with impacts disproportionate to their abundance (Power et al. 1996). Hurlbert (1997) noted that incorporation of the abundance factor into the formalisation of a definition of keystone species makes analysis more difficult and can detract from the usefulness of the calculation. Consider for example a parasitic soil fungus. The number of individual parasitic organisms is irrelevant to the importance of the disease. Differences in abundance of the fungus due to minor factors such as soil conditions could lead to different values at the two sites, and not provide a meaningful indication of the importance of the disease (Hurlbert 1997).

There are also practical implications of a density restriction on a definition of keystone. Dominant species are often crucial for the maintenance of their communities because they provide the major energy flow and three-dimensional structure that supports and shelters other organisms (Power et al. 1996). A definition of keystone species that calculates importance in relation to abundance will not include these abundant, dominant species. Because of a supposed potential for keystone species to influence communities, management of keystone species has been suggested as a method of resolving conservation problems (Mills et al. 1993). Misguided management could lead to removal of focus from dominant abundant species and on to proposed keystone species. Management of important species could be ignored.

Can keystones be found in nature?

Difficulties in testing for keystones - Assuming that a definition of keystone could be agreed upon, practical difficulties hinder the application of the concept. In order to definitively determine if a species in an ecosystem is a keystone, one would need to measure the desired keystone trait for all of the species in a system for a number of generations in order to establish baseline values. All individuals of the target species must then be removed. One must then wait a period of time equal to a large multiple of the generation time of the longest lived organisms in the system until a new equilibrium is reached. One then would have to measure the trait again in all of the remaining species to determine if change has taken place. The process must be replicated to give statistically meaningful results, and repeated with a range of different species in order to enable

comparison of the data. Any extraneous factors such as invasion of new species or climate change would bias any conclusions. The difficulty in carrying out this procedure make measurement or accurate estimation of keystone status practically impossible (Hurlbert 1997).

Variability in reported keystones - A number of species have consistently been accepted as keystones in the communities in which they live. *Pisaster ochraceus*, the starfish and *Enhydra lutris*, the sea otter, are often cited examples (Paine 1969, Menge and Sutherland 1976, Estes et al. 1978, Duggins 1980, Estes et al. 1982, Krebs 1985, Menge et al. 1994, Estes and Duggins 1995, Power et al. 1996). Yet these species show considerable variation in their keystone status at different times or places.

Sea otters on the North American coast prey on sea urchins (*Strongylocentrotus* spp.), which in turn can control the abundance of the kelp upon which they feed. In the presence of otters, subtidal reefs were found to be forested in kelp with few large urchins. In the absence of predation by otters, urchin populations overgrazed their algal food source and prevented kelp establishment (Estes and Duggins 1995). Differences in near-shore fish abundance were also hypothesised as being related to otter density (Estes et al. 1982) although no evidence was provided. These effects were such that sea otters have been classed as "a keystone species that determines the structure of near-shore marine communities" (Krebs 1985).

In spite of the conclusions about the importance of the otters to the Californian subtidal communities, further observations revealed that the effects are spatially and temporally variable. Kelp community structure at sites outside the range of sea otters could vary independently of urchin control. It was influenced by factors such as light, wave motion, nutrient availability and substratum type (Foster and Schiel 1988, Estes and Duggins 1995). The abundance of drift kelp reduces urchin impact on communities, even when they are abundant. Depletion of drift kelp will not alter permanent habitat structure (Power et al. 1996). Hence predation by otters will have differing effects depending on the type of algae available. Temporal variation is also recorded in kelp community dynamics. Estes and Duggins (1995) recorded 62 fold differences in abundance of kelp at one site over the space of a year. No significant difference in urchin or otter abundance was recorded in this time.

Variation is also recorded in *Pisaster's* effects on its community. Paine (1966) suggested that the trend for mussels (*Mytilus* spp.) to dominate the available space and competitively displace other sessile plants and animals was a general phenomenon on the open coast of north-eastern North America. *Pisaster* feeds on *Mytilus*, controls its density, and thereby maintains the density of other species in the habitat. However the keystone effect is not realised at all locations. At a range of different sites on the Washington coast, the total amount of rock unoccupied by attached organisms was variable, and reached up to 44% of the land area (Foster 1990). Hence space is not consistently a limiting factor in these areas and domination by mussels would not necessarily lead to a reduction in other species. By carrying out transplant experiments, Menge et al. (1994) tested the importance of *Pisaster* under a range of environmental conditions. They found that the effects of predation by *Pisaster* varied significantly depending on wave exposure, prey recruitment and growth, and extent of sand burial of mussels. The importance of *Pisaster* depends on the environmental conditions of the site at which it is found. Even in the supposedly archetypal example of a keystone species, no clear predictions can be made, and each individual case must be investigated separately.

"Density vague" interactions - Keystone effects, especially those involved with predation or competition, are likely to be density dependent. Increases in abundance of one species (e.g. a predator) lead to decreases in abundance of another species (e.g. prey). When densities of either of the interacting organisms are low, no significant interactions are likely to occur. When numbers increase to a certain level, the species can start to have an effect on each other's birth or death rates. Until this level of abundance is reached keystone effects will not be evident. There is a threshold density where keystone effects begin to take place. For example, any keystone effects of *Pisaster* will not be apparent until its numbers drop to a level where *Mytilus* can competitively dominate available space. Even when threshold abundances have been reached, there is still likely to be some stochastic variation, and a "density vague" region in which interactions may or may not take place (Strong, 1986).

The inherent variation in species abundance and distribution mean that the conditions under which a species is granted keystone status do not occur throughout the range of that species. Even in species that are defined (by whatever definition) as

keystones, one can still expect variation in keystone-ness depending on time, place or abundance of the species concerned.

The applicability of the keystone species concept for conservation

The keystone species concept has been cited as providing optimism for conservation projects (Simberloff 1990). However the theoretical and practical difficulties involved with identifying keystone species make hopes for a conservationists' panacea somewhat premature. Even assuming that the tests are theoretically possible (see above), a research project to identify a keystone species will necessarily be a formidable task. A large team of researchers and a project spanning many field seasons is necessary to detect any trends (see for example Menge et al. 1994). In conservation projects time and money are not always available. Species may become extinct while waiting the many years necessary to define keystone species.

Even if resources to carry out the research are available, practical problems still occur. The experiments needed to identify keystone species usually involve removal or perturbation of species in an ecosystem (Power et al. 1996). Removal experiments involving endangered species or restricted habitat are often ethically or practically unfeasible (Mills et al. 1993).

If the practical difficulties could be overcome and the traits to be measured defined, difficulties still remain. Even in some of the supposedly clearest examples of keystone species, variation occurs. If a species plays a keystone role at one site, there is no guarantee that the species will carry out the same role at others (Menge et al. 1994, Estes and Duggins 1995). The best one can hope for, even after an extensive research project, is identification of species that might be keystones at different sites or times. There is no point specifically targeting an identified keystone in a conservation project, because it may not continue to be keystone at different times or places from those at which it was initially measured. The inherent variability in the keystone status of a given species significantly detracts from the value of the concept as a quick-fix for conservation or restoration projects.

Basing conservation plans on the keystone concept can have other management implications. Acceptance of the validity of the concept by scientists is likely to lead to incorporation of the idea by managers and policy formulators. Inclusion of the term keystone species in legislation implies that keystone species actually exist in nature and that the concept is unambiguously defined (Mills et al. 1993). Both of these factors are in doubt (Hurlbert 1997). Focussing conservation attention on supposed keystone species can lead to waste of scarce conservation funds on possibly fruitless searches for keystone species, or ignorance of potentially significant species in conservation projects. Species critical for ecosystem function could escape protection, while less important species, arbitrarily assigned keystone species status, are protected by legislation.

Species are given conservation attention for a number of different reasons. Their importance in the ecosystem is not necessarily one of them. Tuatara (*Sphenodon* spp.) are an important focus for conservation in New Zealand not because of their strong effects on their ecosystem, but because they represent an order found nowhere else in the world (Daugherty et al. 1990). Protection for keystone species will not provide protection for species that have conservation importance but are not necessarily strong interactors in their ecosystem.

Conservation projects often focus upon endangered species. Numbers of individuals are limited, available space is scarce, and time is short. Given these considerations, an ill-defined and inherently variable concept such as the keystone appears a somewhat risky premise upon which to base conservation plans.

The future for keystones

Mills et al. (1993) noted that the term keystone species is "broadly applied, poorly defined and non-specific in meaning". They advocated abandonment of the term. Instead of abandonment, attempts have subsequently been made to resuscitate the keystone species concept, and define it for use in management processes (Power and Mills 1995, Power et al. 1996). Such attempts to redefine keystones may be adding precision to an inherently vague concept. In Chapter 3 I use a practical example to outline some of the difficulties with the application of the keystone species concept.

A practical test of the applicability of the keystone species concept

Power et al. (1996) provide a formula to test if a species is a keystone. If species that can be shown to be crucial in maintaining the organisation and diversity of an ecosystem do not fit into this description, the paradigm would seem to be of little use for practical purposes. Seabirds and rats both play significant roles in maintaining organisation and diversity in New Zealand offshore island ecosystems. In this thesis I use these two taxa to carry out a practical test of the applicability of the keystone species concept on island ecosystems.

To confirm that differences in ecosystem properties on seabird-inhabited and seabird-free islands are related to seabirds, it is important to show that the animals are directly affected by seabirds. I use stable isotopes to determine the extent to which diets of animals of different taxa on seabird islands contain nutrients brought to land by seabirds. I also determine carbon and nitrogen levels in soils on Cook Strait islands to see if the activities of seabirds can be implicated in increasing productivity at seabird-dominated sites.

Chapter 2: New Zealand islands, scale and habitat heterogeneity

NEW ZEALAND ISLANDS

Seabirds

New Zealand offshore islands contain a set of features that make them unique (Daugherty et al 1990). Some of the most predominant features of New Zealand offshore islands are the high densities and diversities of seabirds. Although seabirds may return to their colonies at different times of the year, they are usually present in large numbers only during their breeding seasons. All of the birds studied in this thesis are commonly burrow dwellers. Burrows provide protection from predators and shelter the birds in the often inhospitable climates in which they live (Furness 1991).

At the beginning of their breeding season, birds return to their colonies (Ovenden et al. 1991) and clear out an existing burrow or dig a new one (Richdale 1944b). Burrows are dug with the beak and feet, and can reach up to 3 m underground, depending on the size of the bird and the terrain. In dense colonies, many burrows anastomose to form a complex lattice under the fragile soil.

On Takapourewa in Cook Strait, fairy prion (*Pachyptila turtur*) begin to return about July, and pairing and burrow excavation reach a peak in mid-September (Walls 1978). During the hours of darkness on a seabird island at this time, colonies are alive with seabird activity. Incoming birds swoop above the canopy, or crash through the trees to land in a tangled heap on the forest floor. Birds scuttle around finding burrows and roosting on the ground. The raucous calls made during altercations over burrows mingle with the more peaceful, although not often melodic calls of paired birds. A high pitched peeping of mating birds punctuates the cacophony.

Eggs are laid, and adult birds alternate incubation duties (Richdale 1944b). The chicks are fed regularly, often daily. Large amounts of food are brought by the parents to feed the hungry chick, and much is excreted. Given that the number of birds fledged each

year amounts to thousands, a significant amount of marine resources are added to the terrestrial island system each breeding season.

Effects of seabirds on their environment - The significance of burrow dwelling seabirds as a dominant force modifying and maintaining faunal, floral and edaphic dynamics of island ecosystems has been recognised in the past. Ward (1961) noted that seabirds played an important part in soil formation on Takapourewa by introducing new material to the island and by the homogenisation of soil horizons. The soils on Takapourewa differ markedly from those developed in similar environments on the mainland where seabirds are absent (Ward 1961). They are heavily burrowed and dark reddish brown. They show very little trace of horizons and structures present before burrowing. Seabird soils are extremely acid, and contain high amounts of phosphorus, nitrogen and potassium. The amount of N and P added to a seabird colony can be up to 500 times that added by rain (Furness 1991). Soils in seabird colonies are aerated, but dry and friable. In the absence of vegetation cover they are very prone to erosion (Ward 1961, Atkinson 1964).

Seabirds also have a significant effect on the vegetation of the islands on which they live. For example *Senecio sterquilinus* grows only in the high nutrient conditions created by seabirds (Campbell 1967). In high densities, seabirds crush and uproot small plants. Undergrowth and ground cover is sparse on many seabird islands. The friable soils can lead to down-slope soil movement, exposing the roots of trees at the top of the hills and burying the stems of trees at the bottom. Burrows can undermine trees, which become more susceptible to wind-throw.

Rats

Kiore (Polynesian rat, *Rattus exulans*), Norway rats (*R. norvegicus*), and ship rats (*R. rattus*) have a dramatic impact on the flora and fauna of New Zealand offshore islands (Atkinson and Bell 1973, Gibb and Flux 1973) and may be crucial in determining the organisation and diversity of island ecosystems. Kiore were the first of the troika of rodents to arrive in New Zealand (Holdaway 1996), and their effects are well documented. The extinction of a range of different bird species can be directly or indirectly attributed to kiore (Holdaway 1989). Tuatara density and recruitment rates are lower on islands with kiore

than islands without (Cree et al. 1995). Small prions are often rare on kiore-inhabited islands (Crook 1975). On Raoul Island, in the Kermadec group, kiore contributed to the decline of a population of Kermadec petrels (*Petrodroma neglecta*) and scavenged the eggs and chicks of the birds (Merton 1970). The average number of lizard species found on an island is reduced by the presence of kiore (Whitaker 1973). Nocturnal predation by kiore can lead to a reduction in numbers of nocturnal lizards and a change in lizard habitat range (Towns 1991, Towns et al. 1985). Historically, the extinction of a number of vertebrate and invertebrate species is correlated with the arrival of rats. For example, the greater short-tailed bat (*Mystacina robusta*) and three species of leiopelmatid frogs disappeared from the North, South and Stewart Islands at the time of the introduction of kiore (Daniel and Williams 1984, Worthy 1987). Large invertebrates are preyed upon by kiore, and the viability of many populations is threatened by their presence (Atkinson and Bell 1973, Gibb and Flux 1973, Hicks et al. 1975, Meads et al. 1984, Campbell et al. 1984).

Plants

New Zealand offshore islands have, in general, a flora dominated by low-growing, salt and wind tolerant plants. Coastal trees such as pohutukawa (*Metrosideros* spp.), taupata (*Coprosma repens*), ngaio (*Myoporum laetum*) and mahoe (*Melicytus ramiflorus*) are common on many offshore islands (Atkinson and Bell 1973). The trees often form a complete canopy over a forest floor kept open by the seabirds (Campbell 1967).

Reptiles

High densities of reptiles occur on New Zealand offshore islands (Daugherty et al. 1990). New Zealand's terrestrial reptile fauna consists of two orders and three different families. Two species of tuatara (*Sphenodon punctatus* and *S. guntheri*) are the sole extant members of the Sphenodontidae, the sole family in the order Sphenodontida (Gill and Whitaker 1996). They are restricted to islands around the New Zealand coast (Newman 1982).

For its size, New Zealand has a very diverse lizard fauna (Daugherty et al. 1990). Native New Zealand lizards belong to family Scincidae (skinks) (genera *Oligosoma* and *Cyclodina*) or family Gekkonidae (geckos) (genera *Hoplodactylus* and *Naultinus*) (Gill and Whitaker 1996). The latest published data records at least 60 species of lizards in New Zealand, 22 of which are limited solely to islands (Daugherty et al. 1994, Patterson and Daugherty 1995). This leads to high local diversity. For example, Middle Island, a 13 ha island in the Mercury group off the north-eastern coast of New Zealand, supports ten species of lizard, plus tuatara (Towns et al. 1990). Offshore islands also support high abundance of reptiles. Up to 0.33 spotted skinks (*Oligosoma lineoocellatum*) per m² have been reported in Takapourewa grassland, as well as lower numbers of another three species of skink, two species of gecko and one species of tuatara (East et al. 1995).

Invertebrates

Large populations of invertebrates are another common feature of New Zealand offshore islands. Although most invertebrate species are found on the mainland, 48% of all arthropods designated as protected species occur only on offshore islands (Gibbs 1990). The invertebrates that are known and listed as endangered tend to be large, charismatic species that are easy to see, such as giant weta (*Deinacrida* spp.), Stephens Island weevil (*Anagotis stephensis*), snails (*Rhytida* spp.; *Powelliphanta* spp.), slugs (e.g. *Pseudaneitea* spp.) and giant centipedes (*Cormocephalus rubriceps*). If thorough studies are carried out and smaller species counted, numbers of invertebrate species and levels of island endemism would probably rise. As well as the rare and endangered species, islands also contain very high abundance of other more common species. For example, on Nuku-waiata and Takapourewa in Cook Strait, the Wellington tree weta (*Hemideina crassidens*) reaches densities up to 6 animals/m², while at nearby Cable Bay on the mainland, only about 1 animal/m² is recorded (Rufaut 1995). Similarly, large beetles such as darkling beetles (e.g. *Mimopeus* spp.) and ground beetles (e.g. *Mecodema* spp.) are rarely seen on the mainland, but are very common on Takapourewa (Walls 1981).

ISLANDS INCLUDED IN THIS STUDY

In my study, islands in the same geographic area were used to measure the effects of rats and seabirds. The area studied was the Cook Strait/Marlborough Sounds region in central New Zealand (Fig. 2.1A). The islands studied were chosen from over 200 islands, islets and rock stacks in this area (Miller and Gaze 1997). Study islands had to be habitable and accessible by helicopter or (preferably) by boat. Therefore, a minimum island size was required. From the somewhat reduced pool of acceptable islands, a subset of six islands was chosen upon which to base my study (Fig. 2.1B). The predominant plants at each site are presented in Appendix 3.

Islands with and without rats and islands with and without seabirds were included in the study. Vegetation type, island size, seabird species present, and presence or absence of tuatara vary between sites (Table 2.1).

FIG. 2.1. A) New Zealand, showing the Marlborough Sounds region at the top of South Island. B) The Marlborough Sounds with the six study islands indicated.

Takapourewa (Stephens Island) - The majority of my field work was carried out on Takapourewa (40°40'S, 174°00'E). Takapourewa supports an estimated 1×10^6 fairy prion (Harper 1985). Small numbers of sooty shearwater (*Puffinus griseus*), fluttering shearwater (*P. gavia*) and diving petrel (*Pelicanoides urinatrix urinatrix*) also nest on the island (Newman 1987). Although farmed since the establishment of a lighthouse in 1894, over 80% of the island has been fenced off to stock since the 1950s (East et al. 1995). Low growing forest, native grassland and *Muehlenbeckia* scrub now cover much of the island. For this study, Takapourewa represented an island with high densities of seabirds upon which to collect baseline data on seabird effects and their interactions with other members of the community.

TABLE 2.1 Features of sites in the Marlborough Sounds. A "p" indicates species present but in low densities. An "ex" indicates exterminated at date shown. Island sizes from Miller and Gaze (1997). Data from North Brother from Gaston and Scofield (1995) and N. Nelson *pers. comm.* 1997. Data from Titi Island from Gaze (1982). Data from Nuku-waiata from Walls (1984) and Rufaut (1995).

* Soil sampling was not carried out on North Brother.

Site	Island size (ha)	Vegetation type	Species present (densities in individuals/m ² where available)		
			Seabirds ¹	Tuatara	Rats
Takapourewa	150	grasses, tussocks, vines, shrubs, forest	fairy prion, sooty shearwater, fluttering shearwater, diving petrel (0.46 - 1.14)	tuatara (0.03-0.11)	absent
North Brother*	4	tussocks, shrubs, bare ground	fairy prion, diving petrel (0.36)	Günther's tuatara (0.03)	absent
Titi	32	forest	sooty shearwater, flesh footed shearwater (0.005)	absent	Norway rat (ex. 1975)
Maud	309	forest	absent	absent	absent
Whakatere-papanui	61	grasses, shrubs	absent	absent	Norway rat, kiore
Nuku-waiata	194	forest	Sooty shearwater (p)	absent	kiore (ex.1993)

¹Little blue penguins (*Eudyptula minor*) are present on all islands.

North Brother - An estimated 8500 fairy prion and 6800 diving petrels nest on North Brother Island (41°07'S, 174°26'E) (Gaston and Scofield 1995). At 4 ha, North Brother was the smallest island studied. Because of its exposed location, North Brother experiences strong winds and salt spray. Vegetation is correspondingly sparse (Gillham 1960). A lighthouse is situated at the top of the island. The light and the associated infrastructure dominate much of the available land. Nevertheless, North Brother represented a second site with high seabird density, although any seabird effects were moderated by the small island size and severe environmental conditions.

Titi - The third island with seabirds was Titi Island (40°57'S, 174°08'E). Flesh-footed (*Puffinus carneipes*) and sooty shearwater nest on Titi Island in densities of up to 15 pairs per hectare (Gaze 1982). Norway rats were recorded on Titi Island in 1955, but were eliminated by poisoning campaigns from 1970 to 1975 (Gaze 1982). Titi Island was included in my study because it represented a seabird island where the effects of rats could also be measured. Because Titi Island has been rat-free for at least 20 years, it could also be used to determine how (if at all) an island can recover from the ravages of rodents.

Maud - Maud Island (41°01'S, 173°54'E) was included in my study as an island with no seabirds and no rats. Maud is a relatively sheltered island in Pelorus Sound. It is highly modified after a century of farming, but 16 ha of remnant forest remains. Sampling was carried out within this forest. Although the New Zealand Ornithological Society is attempting to establish a colony of fluttering shearwater on the western extremity of the island (Bell 1994), no seabirds naturally occur on Maud Island.

Nuku-waiata - Nuku-waiata (40°54'S, 174°05'E) is the innermost island of the Chetwodes group. Very small numbers of sooty shearwater nest at the eastern and western extremes of the island (D. Brown *pers. comm.* 1995). No seabirds are found in the area of the island where sampling was carried out. Kiores were present on Nuku-waiata until eradicated by a poisoning campaign initiated in 1993 (Rufaut 1995). Nuku-waiata is a seabird-free island from which rats have only relatively recently been removed. Comparison with Titi Island can be used to show the speed of recovery from rat effects.

Whakatere-papanui - The outermost island of the Rangitoto group, Whakatere-papanui (40°45'S, 174°00'E) is the closest island to Takapourewa included in this study. Whakatere-papanui is inhabited by Norway rats and, apart from low densities of little blue

penguins, has no resident seabirds. There is practically no flat land on Whakatere-papanui, no habitation and no running water. Sampling on the island was limited. It did however give another seabird-free island, and, because rats are currently extant on the island, showed the immediate impact of rats.

POTENTIAL DIFFERENCES BETWEEN ISLANDS

Island biogeography

The island biogeographical theory of Macarthur and Wilson (1963) highlights many factors important for life on islands. Although direct application of this theory is sometimes contentious (Kelly et al. 1989) especially when applied to reserve design, the general theory of island biogeography contains important information that is relevant to the analysis of island ecosystems.

There is a strong correlation between island area and the number of different species it can support. Different reasons have been suggested for the trend. Macarthur and Wilson (1963) contend that "all things being equal" the number of species on an island is controlled by a dynamic equilibrium between immigration onto an island (which is related to the degree of isolation of that island) and extinction caused by stochastic processes. The further an island is from a source of animals and plants (i.e. the mainland), the lower the rate of immigration. The smaller an island is, the fewer organisms it can support, so the fewer individuals of each species it can support, and the greater the potential for stochastic processes to drive a population extinct. Hence smaller, more isolated islands have a lower number of species than do closer larger islands. This theory was supported by studies of island bird faunas in the Pacific.

Although popular following its publication, the direct applicability of the Macarthur-Wilson model has faced increasing reservation (Bengtson and Enckell 1983). The main alternative hypothesis explaining the empirical data of depauperate island biotas was that of habitat diversity (Conner and McCoy 1979). Protagonists of this theory maintain that the number of species is related to the amount and heterogeneity of ecological resources (i.e. the number of habitats) in an area. A larger area can physically

hold a greater number of different habitats than a smaller area. There is room for forests and lakes and grassland etc. on a large island, while a small island may only have room for say, a forest and a lake. If an island has only a subset of the possible habitats, it can only possibly hold a subset of the potential species (Haila 1983, Haila and Järvinen 1983).

As well as direct size and space considerations, some habitats cannot occur on small islands. For example, one would expect to find neither alpine species nor animals whose natural habitat is savannah on an island. However, the geography of islands does mean that habitats can occur on small islands that are not found on the mainland. For example, some species may be able to exist only on islands free from larger competitors or predators (Polis and Hurd 1995) and so are restricted to predator/competitor free island habitats.

Geometrical relationships of islands can also have an affect. Because edge length increases linearly while area increases as a squared function, small islands have more edge per unit area than large islands. If environmental effects are more severe at edges than in more sheltered interior sites, productivity per unit area of a small island could be less than that on a larger island. Overall abundance, and hence diversity on the island would then be lower than on the mainland (Kelly et al. 1989). However, the opposite can also occur on islands where terrestrial based productivity is very low and allocthanous resources provide the main energy input (Polis and Hurd 1995). Small islands, with more coast per unit land area than large islands can receive proportionally more marine detrital input, and have greater productivity and hence the potential for greater diversity (Bengtson and Bloch 1983, Polis and Hurd 1995).

Impact of species-area relationships in this study

The islands in my study encompassed a range of sizes, from 4 ha North Brother to 309 ha Maud (Table 2.1). Diversity and abundance of the lizard and invertebrate taxa measured in this study can be expected to vary between the islands studied, independently of the effects of seabirds or of rats. The influence of island size is included in the analyses carried out in subsequent chapters.

Habitat variation

As well as differences in size, the islands studied have a range of different histories, climates and vegetation. On one island in this study, Takapourewa, sampling was carried out separately in four different locations, each with a different vegetation type (Table 2.1). Analysis of data from these sites can reveal how microhabitat differences can affect the results found.

Habitat type can have significant influence on the abundance of small invertebrates and lizards caught in pitfall traps (McColl 1974, East et al. 1995, Gill and Whitaker 1996). I used pitfall trapping to measure diversity and abundance of small invertebrates and lizards in different habitats on Takapourewa. Full methodology is given in Chapter 3. Although no significant difference was found between the overall abundance of invertebrates in the different sites (ANOVA, $F_{[3,4]} = 4.00$, $P > 0.05$) (Table 2.2), significant differences were found between the number of invertebrate orders captured in different habitats on Takapourewa ($F_{[3,4]} = 29.583$, $P < 0.05$). Significantly more orders were measured in samples taken in scrub and grassland habitats than in those taken in pasture. Samples from forest had intermediate values.

TABLE 2.2. Mean (± 1 SE) ordinal diversity and abundance per trap of small invertebrates in different habitats on Takapourewa. See chapter 3 for further details on methods.

Site	Diversity		Abundance	
	Mean	SE	Mean	SE
Pasture	10.1 $\pm$ 0.5		179.9 $\pm$ 29.2	
Grassland	14.0 $\pm$ 0.7		357.9 $\pm$ 53.2	
Scrub	14.1 $\pm$ 0.4		332.0 $\pm$ 41.3	
Forest	11.8 $\pm$ 0.6		446.1 $\pm$ 48.9	

The numbers of lizards of the different species varied between habitats (Table 2.3). Spotted skinks are the most common lizard on Takapourewa (East et al. 1995). Significant differences were found between the numbers of spotted skinks caught in each habitat type ($F_{[3,4]} = 25.80$, $P < 0.05$).

TABLE 2.3. Mean (± 1 SE) abundance per trap-night of lizards in different habitats on Takapourewa. See chapter 3 for further details on methods.

Site	<i>H. maculatus</i>		<i>O. infrapunctatum</i>		<i>O. lineoocellatum</i>		<i>O. nigriplantare</i>	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Pasture	-		-		0.17 $\pm$ 0.03		-	
Grassland	0.01 $\pm$ 0.005		0.020 $\pm$ 0.007		0.53 $\pm$ 0.08		0.04 $\pm$ 0.01	
Scrub	0.03 $\pm$ 0.010		0.059 $\pm$ 0.013		1.06 $\pm$ 0.16		0.08 $\pm$ 0.02	
Forest	-		0.005 $\pm$ 0.003		-		-	

These samples were taken at locations separated by less than 1 km on the same rat-free island. Although the number of seabirds differs between the four sites (Appendix 1), all have a significant seabird presence. The differences in invertebrate diversity and lizard abundance can be attributed to the different history, vegetation type, climate, geology etc. at each site. These examples illustrate some of the variation that can be seen within one island, and highlight the potential differences that could be present between the different islands measured in this study.

Replication and pseudoreplication

My study includes two islands on which seabird effects can be measured (Takapourewa and North Brother), two islands on which the effects of rats have been experienced (Nuku-waiata and Whakatere-papanui), one island upon which both rats and seabirds have been present (Titi), and one island with neither rats nor seabirds (Maud). Although geographically close and superficially similar, these islands cannot be viewed as differing only in the treatment effects of this study (i.e. seabirds and rats). The density and species of seabirds differs between the seabird islands, as does the rat inhabitation status of the rat islands (Table 2.1). Climate, geology, vegetation cover, history and island size also differ between the islands. These differences may lead to variation in measured variables independently of the presence or absence of seabirds or rats. These islands are not true replicates, but pseudoreplicates, where the differences in measured variables can be caused by pre-existing site variation rather than the treatments themselves (Hurlbert 1984).

Sets of identical islands large enough to have complete functioning ecosystems do not exist. The islands chosen were thought to be the best alternative. Inferential statistics on the, in effect, unreplicated data will need to be approached with some circumspection (Hurlbert 1984). Comparisons between the different islands should still show gross effects of the treatments. Although not describing all of the processes that take place on offshore islands, the approach taken will shed light on the largely unknown interactions that take place on New Zealand offshore islands, and provide information on the roles played by seabirds and rats.

Chapter 3: A practical test of the keystone status of seabirds and rats on New Zealand offshore islands

INTRODUCTION

Groups of organisms that are important in maintaining the organisation and diversity of ecological communities have been labelled keystone species (Paine 1969, Mills et al. 1993). The concept of keystone species has proved attractive for ecological study, conservation and particularly restoration projects (Simberloff 1990, Mills et al. 1993). Special conservation attention could be placed on keystone species, thereby preserving the whole community in one fell swoop. Seabirds that form large colonies on New Zealand offshore islands have been called keystones (Daugherty et al. 1990). Similarly, introduced rats have been shown to have important effects on New Zealand islands (Merton 1970, Atkinson and Bell 1973, Gibb and Flux 1973, Whitaker 1973, Hicks et al. 1975, Ramsay 1978, Whitaker 1978, Campbell et al. 1984, Meads et al. 1984, Towns 1991, Cree et al. 1995) and may also fit a definition of keystone.

Although widely used, the keystone species concept is ambiguous and lacks a clear operational definition. Mills et al. (1993) noted that the term keystone species was "broadly applied, poorly defined and non-specific in meaning". They advocated abandonment of the term. Instead of abandonment, attempts were subsequently made to resuscitate the keystone species concept, and define it for use in management programmes (Power and Mills 1995, Power et al. 1996). A keystone species was defined as "one whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance" (Power et al. 1996). To enable determination of whether or not a species has disproportionately large effects in its community, Power et al. (1996) use the concept of "*Community Importance*" introduced by Mills et al. (1993). *Community Importance* (CI) for a given species is defined as the "change in a community or ecosystem trait per unit change in the abundance of the species". If a species is a keystone, the absolute value of CI will be "much greater than 1" (Power et al. 1996).

A practical test of the applicability of the keystone species concept

If species that can be shown to be crucial in maintaining the organisation and diversity of an ecosystem do not conform to the definition of keystones as described by Power et al. (1996), the paradigm would seem to be of little use for practical purposes. Seabirds and rats both play significant roles in maintaining organisation and diversity in New Zealand offshore island ecosystems (*see above references*). I use these two taxa to carry out a practical test of the applicability of the keystone species concept.

Invertebrates and lizards are dominant and functionally important components of the ecosystems of New Zealand offshore islands (Daugherty et al. 1990). Power et al. (1996) state that species richness or abundance of functionally important species can be used as traits with which to calculate CI of a species in an ecosystem. I test the hypotheses that invertebrate abundance, invertebrate diversity and lizard diversity are not significantly different on a) seabird-inhabited and seabird-free islands, and b) rat-affected and rat-free islands. Then, to measure if seabirds or rats can be classified as keystone species, I use the method suggested by Power et al. (1996) for measuring the keystone status of a taxon, that is, I test the hypotheses that CI_{seabirds} and CI_{rats} are not significantly greater than 1,

$$\text{where: } CI_i = \left(\frac{[T_N - T_D]}{T_N} \right) \left(\frac{1}{p_i} \right)$$

t_N is invertebrate abundance, invertebrate diversity or lizard diversity on a) a seabird-inhabited island, and b) a rat-affected island; t_D is invertebrate abundance, invertebrate diversity or lizard diversity on a) a seabird-free island, and b) a rat-free island; and p is the proportional biomass of a) seabirds, and b) rats.

Rejection of the first hypothesis and failure to reject the second will indicate that the keystone concept is not a useful measure of the importance of seabirds or rats in an island system.

METHODS

Study areas

Sampling was carried out on six islands in Cook Strait, New Zealand that exhibit different combinations of rat abundance, seabird abundance and habitat quality (Fig. 2.1, Table 2.1).

Islands with seabird effects and without rat effects - Fairy prion (*Pachyptila turtur*) nest on Takapourewa (40°40'S, 174°00'E; 150 ha) at densities up to 6000 pairs/ha (Appendix 1). Small numbers of sooty shearwater (*Puffinus griseus*), fluttering shearwater (*P. gavia*) and diving petrels (*Pelicanoides urinatrix urinatrix*) also nest on the island (Newman 1987). An estimated 8500 fairy prion (density 2000 pairs/ha) and 6800 diving petrels (density 1600 pairs/ha) nest on North Brother Island (41°07'S, 174°26'E; 4 ha) (Gaston and Scofield 1995).

Islands with rat effects and without seabird effects - Kioore (*Rattus exulans*) were present on Nuku-waiata (40°54'S, 174°05'E; 194 ha) until eradicated by a poisoning campaign initiated in 1993. Although rats have been exterminated from this island, the fauna may be still recovering from their effects (Rufaut 1995). Only very low numbers of sooty shearwater nest at the extremities of Nuku-waiata (D. Brown *pers comm.* 1995). As well as a dense population of Norway rats (*R. norvegicus*), weka (*Gallirallus australis*), a predatory rail, live on Whakatere-papanui (40°45'S, 174°00'E; 61 ha) and may prey upon lizards and invertebrates. Apart from low densities of little blue penguins (*Eudyptula minor*), no seabirds nest on Whakatere-papanui.

An island with both rat effects and seabird effects - Norway rats were present on Titi Island (40°57'S, 174°08'E; 32 ha) until exterminated some time before 1981 (Gaze 1982). Sooty shearwater and flesh-footed shearwater (*Puffinus carneipes*) now nest on Titi Island at densities of at least 15 pairs/ha (Gaze 1982).

An island with neither rat effects nor seabird effects - No rats are known to have ever been present on Maud Island (41°01'S, 173°54'E; 309 ha). In spite of freedom from mammalian predators, no seabirds naturally nest on Maud Island. An introduction programme for fluttering shearwater is presently taking place on the island (Bell 1994). Sampling was not carried out in the vicinity of the reintroduction site.

Lizard sampling regime

I sampled for lizards on Takapourewa during the austral summer of 1994-1995 and on all islands (including Takapourewa) during summer 1995-1996 (Table 3.1). During the 1994-1995 sampling on Takapourewa five pitfall traps were randomly located within each of eight 10 m $\times$ 10 m quadrats. Sampling effort was increased in the later studies, and three traps in each of 24 quadrats were used in the 1995-1996 studies on Takapourewa. Three traps in each of six quadrats were used on all other islands (Table 3.1).

During capture periods, I checked every trap every morning. All captives were removed, weighed and had their day of capture marked on their backs with white correcting fluid. Although not permanent, the marking lasted the length of a sampling trip. The number of lizards caught in each habitat is presented as number of lizards per trap-night, i.e. at each Takapourewa quadrat in 1994-1995 there were five cans, so one night at one quadrat represents five trap-nights.

TABLE 3.1. Dates, temperature and number of traps used during lizard and invertebrate trapping.

Site	Date	Nights lizard traps open	No. lizard traps	Nights invertebrate traps open	No. invertebrate traps	Mean minimum temperature	SE
Takapourewa	Jun-94	9	40	-	-	8.47	0.43
Takapourewa	Aug-94	10	40	-	-	7.29	0.40
Takapourewa	Nov-94	9	40	6	40	10.10	0.50
Takapourewa	Jan-95	6	40	6	40	11.66	0.58
Takapourewa	Jun-95	2	72	-	-	7.75	0.39
Takapourewa	Nov-95	6	72	7	72	8.52	0.99
Takapourewa	Oct-96	-	-	5	72	9.43	0.69
Titi	Feb-95	6	18	5	18	15.36	0.46
Whakatere- papanui	Nov-95	4	18	4	10	10.30	0.69
North Brother	Mar-96	5	18	5	18	11.64	1.25
Maud	Apr-96	5	18	5	18	12.89	0.34
Nuku-waiata	Apr-96	5	18	5	18	13.71	0.49

Lizard trap design

Lizard traps were constructed from 4 l paint cans, with the inside lacquered to retard rusting. Holes were drilled in the bottom of the traps to allow drainage. Wire supports held can lids approximately 25 mm above the trap opening to shelter captives from the sun, keep debris out of the trap, and make it difficult for captives to escape. Traps were baited with canned pear (Whitaker 1967).

Geckos have wide digital pads that allow them to climb smooth surfaces (Gill and Whitaker 1996) and many may escape from pitfall traps. Pitfall trapping will give an index of relative gecko numbers on different islands, but results will not necessarily represent actual densities and cannot be used to compare between different habitats. Skinks do not have the wide digital pads of geckos, and so are much less likely to be able to escape from pitfall traps. Consequentially, skink samples form a more quantitative representation of actual abundance.

In addition to pitfall trapping, searches for lizards were made, by day and by night, in all of the different habitats. Potential lizard refugia were investigated (trees, logs, rocks, sheets of iron etc.) to determine if lizards were present in an area but not being captured.

Invertebrate sampling regime

I collected invertebrate samples from all islands throughout the austral summer of 1995-1996. In addition, samples were collected on Takapourewa on three occasions in summer 1994-1995 and in summer 1996 (Table 3.1). Three pitfall traps were randomly located within each of six replicate study sites on each island except Takapourewa. On Takapourewa five traps were installed in each of eight study sites for the 1994-1995 season. The number of sites on Takapourewa was increased in the 1995-1996 season and three pitfall traps were randomly located within each of twenty four replicate study sites. All traps were left in the ground for five nights, except for Whakatere-papanui, where they were in place for four nights, and Takapourewa, where samples of six and seven nights were taken (Table 3.1).

Invertebrate trap design

Invertebrate traps were made from polystyrene cups, with an external diameter at the rim of 75 mm. Each cup was embedded in soil until the rim was flush with ground level (Fig. 3.1). Approximately 50 ml of sodium benzoate solution was added to each cup to preserve captives. I added a few drops of Decon 90 detergent to break surface tension and ensure any animals that fell into the trap were drowned. The detergent was not perfumed, and should have neither attracted nor repelled potential captives. Skinks, geckos, tuatara, *Leiopelma* frogs, large spiders and large predatory carabid beetles occur on the islands studied. Some of these animals are endangered and all will eat small invertebrates. To avoid catching non-target animals, or biasing samples by allowing captives to be eaten, an aluminium mesh (10 mm²) was placed over the traps. The only invertebrates that could be caught were less than the size of the mesh. A 100 mm² ridged metal roof was placed over each trap (Fig. 3.1). The roof kept rain out of the preservative/killing solution, and stopped leaves or debris falling into the cups and blocking them or allowing captives to escape from the traps.

Invertebrate sorting

At the completion of the sampling period, all traps were collected and samples washed into plastic jars. On return to the laboratory, the sodium benzoate solution was replaced with 70% isopropanol to allow long-term preservation of the samples. Captives

FIG. 3.1. Pitfall trap covered with aluminium mesh and used to trap invertebrates on Marlborough Sounds islands.

from each site were sorted into orders. This coarse grained analysis masked much variation in the invertebrate diversity found in the samples, but served to highlight the effects of the treatments under investigation. Effects of seabirds or rats that can be measured at ordinal level are likely to be great enough to play a significant role in determining the structure of the ecosystem.

To enable more detailed analysis of the invertebrate diversity sampled, I further subdivided members of order coleoptera. Because of the likelihood of large numbers of undescribed species, no effort was made to identify the actual species involved. I sorted beetles into "RTU"s (Recognisable Taxonomic Units) based on characters such as size, colour, antennae length and structure and morphology of the head, notum, elytra and legs. RTUs have been found to be an acceptable method of assessing species richness in biodiversity surveys (Oliver and Beattie 1993).

Species area relationships

Islands with different land areas were included in this study (Table 2.1). Due to species/area relationships, lizard or invertebrate diversity and abundance could vary independently of seabird or rat presence (Chapter 2). Lizard abundance, invertebrate abundance, invertebrate richness, beetle RTU abundance and beetle RTU richness were regressed against island size to measure the influence of island size on the results found.

Temperature

Level of animal activity influences the effectiveness of pitfall traps and can change the number of animals caught (Greenslade 1964). The maximum and minimum temperatures at a weather station on the northern end of Takapourewa were recorded for each day that sampling took place on all islands. The maximum and minimum values were highly correlated ($r = 0.91$), and so only minimum temperatures were included in statistical tests.

Calculation of Community Importance of seabirds and rats

To calculate the CI (*Community Importance*) and hence keystone status (Power et al. 1996) of a species, three variables are required: t_N , t_D , and p_i . To calculate CI_{seabirds} , t_N was calculated using data from Takapourewa, an island on which seabirds are present, and t_D was calculated using data from Maud Island, where seabirds are absent. To calculate

CI_{rats} , t_N was calculated using data from Nuku-waiata and Whakatere-papanui, islands on which rats are present, and t_D was calculated using data from Titi Island, from where rats have been removed.

Invertebrate abundance and diversity, beetle RTU abundance and diversity, and lizard abundance were used for t_N and t_D from the respective islands. The proportional biomass of seabirds and rats on each island (p_i) was estimated using results from this study, unpublished data and values from the literature. Invertebrate density was not directly measured in this study, but large invertebrates were caught in the same traps as the lizards. Invertebrate biomass was estimated using the relationship between the biomass of lizards and the biomass of invertebrates.

Separate values of CI were calculated using invertebrate abundance, invertebrate diversity, beetle RTU abundance, beetle RTU diversity, and lizard abundance for t_N and t_D from the respective islands. The mean of these five values was then taken to give overall CI values for both seabirds and for rats.

RESULTS

Lizards caught in different habitats

Common geckos (*Hoplodactylus maculatus*), spotted skinks (*Oligosoma lineoocellatum*), speckled skinks (*O. infrapunctatum*), common skinks (*O. nigriplantare polychroma*) and brown skinks (*O. zelandicum*) were trapped during the sample periods (Table 3.2). By far the majority of lizards caught were spotted skinks.

Significant differences were found between the number of lizards in the different habitats (Kruskal-Wallis $H_{[5,608]} = 57.89$, $P < 0.05$). Comparison of means ($\alpha = 0.05$) showed that significantly more lizards were found on Takapourewa and North Brother than on Maud, Nuku-waiata and Whakatere-papanui (Table 3.2). Takapourewa lizard abundance was significantly greater than that on Titi Island. Due to the high variation, lizard counts from North Brother and Titi were not significantly different from each other.

TABLE 3.2. Mean (± 1 SE) abundance of lizards caught per trap per night (trap-night) in pitfall traps, 1994-1996.

Site	Lizards per trap per night (± 1 SE)				
	<i>H. maculatus</i>	<i>O. infrapunctatum</i>	<i>O. lineocellatum</i>	<i>O. nigriplantare</i>	<i>O. zelandicum</i>
Takapourewa	0.01 (0.003)	0.02 (0.004)	0.44 (0.049)	0.03 (0.005)	-
North Brother	0.02 (0.015)	-	0.48 (0.115)	0.07 (0.037)	0.01 (0.010)
Nuku-waiata	-	-	-	-	-
Maud	-	-	-	-	-
Titi	0.02 (0.013)	-	0.09 (0.052)	-	-
Whakaterere-papanui	-	-	-	0.01 (0.010)	-

Lizards seen in different habitats

Geckos - In the forest on Takapourewa, Maud and Titi Island, *Hoplodactylus maculatus* geckos were frequently encountered on trees at night and under rocks and pieces of wood or iron during the day. Many of the forest traps showed signs that lizards had been in and out of the traps (i.e. the pear had been eaten), but no geckos were caught.

H. maculatus were found on the ground in the grassland and scrub habitat, especially in piles of rocks. As distinct from Takapourewa forest, geckos in grassland and scrub were caught in pitfall traps. Many geckos in the traps were wet and cold to the touch. It is possible that geckos in open habitats were chilled by settling dew as they foraged at night. Marlborough green geckos, *Naultinus manukanus* were commonly seen basking and feeding on low shrubs on Takapourewa. They were infrequently encountered on the ground and none were caught in pitfall traps.

On North Brother Island, two species of geckos were seen on the ground and vegetation by night, and under rocks and shelter by day. In addition to the ubiquitous *H. maculatus*, Duvaucel's gecko (*H. duvaucelii*) were also frequently encountered on the island.

Skinks - *Oligosoma zelandicum* were positively identified in this study only on North Brother Island. *O. nigriplantare polychroma* were seen in Takapourewa grassland and scrub, North Brother and on Whakaterere-papanui. They were not seen in forested habitats on any islands. *O. infrapunctatum* were only encountered on Takapourewa. As well as being found in grassland and scrub, they were often seen basking in sunny gaps in the forest.

Spotted skinks were found in all open habitats. High densities of *O. lineoocellatum* were commonly seen basking and feeding in pasture, grassland and scrub on Takapourewa, and on North Brother. One *O. lineoocellatum* was found under a rock on Whakaterapapanui. Although not seen in the tree covered Maud Island or Takapourewa forest habitats, *O. lineoocellatum* were caught in forest on Titi.

Temperature effects on lizards

Temperatures ranged from a low of 4.9°C, recorded during sampling on Takapourewa (2/9/94) to 22.1°C recorded during sampling on Titi Island (1/2/96). Mean temperatures at each site are presented in Table 3.1. There was a significant relationship between minimum temperature each trapping night and the number of lizards caught (regression, $F_{[1,612]} = 0.19$, $P < 0.05$).

Although statistically related to lizard abundance, temperatures were never cold enough to completely limit lizard activity. Sixteen lizards were caught on Takapourewa on 2 September 1994, the date at which the coldest minimum temperature (4.9°C) was recorded. If temperature were playing a significant role, mean lizard counts would be lower on Takapourewa (with relatively low average temperatures) than on the other islands. As the opposite is occurring, one can assume that temperature has not affected conclusions.

Invertebrates caught

Although a 10 mm grid was used on the invertebrate traps, the animals caught were almost exclusively smaller than this. Apart from three carabid beetles (approximately 20 mm in length) all captives were less than 5 mm long. The majority of captives were between 1 and 3 mm. Hence the sampling regime was not exhaustive, and represents only a subset of the invertebrate species present on the islands studied.

In total, over 79 000 individual animals were counted, of which 63 000 were Collembola. At all sites the number of Collembola caught in the samples was significantly greater than the combined number of all other groups. Collembolan numbers per sample reached an (estimated) maximum of 4000. Mean Collembola abundance was 215 ± 33.6

(mean $\pm$ 1 SE). Collembolla also showed a very clumped distribution (variance : mean ratio = 1548). The maximum abundance recorded for any other taxon was 600, and the mean considerably lower (8.6 ± 0.49) (appendix 3.1). Although still exhibiting a clumped distribution, the variance : mean ratio of all other taxa was less than 4% of that for Collembolla (55). The distribution patterns shown by the Collembolla appeared to differ from those for the other invertebrate species. No model that suitably described Collembolla and other species could be formed. Hence, Collembolla were not included in analysis of invertebrate abundance. Because invertebrate richness is calculated on a presence/absence basis, the skewed distribution does not affect richness values (a "1" was scored regardless of how many individuals were present in a sample). Collembolla were still included in analyses of invertebrate richness.

Twenty-four different taxonomic groups were recorded in total (appendix 3.1). Beetles made up 4% of the invertebrates caught. They were among the 10 most abundant taxa caught at all sites. The 649 beetles caught included representatives of 88 different RTUs.

Significant differences were seen between the abundance of invertebrates at the different sites ($H_{[5,298]} = 90.10$, $P < 0.05$) (Table 3.3). Invertebrate abundance on Takapourewa was significantly greater than that on all islands except Maud. No significant difference was seen between invertebrate abundance on Maud and North Brother and between North Brother and Whakatere-papanui, Titi and Nuku-waiata (Fig. 3.2a).

TABLE 3.3. Mean ($\pm$ 1 SE) diversity and abundance of small invertebrates captured in pitfall traps on Marlborough Sounds islands.

Site	n	Invertebrate ordinal richness		Invertebrate abundance/trap-night		Beetle RTU richness		Beetle abundance/trap-night	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
Takapourewa	222	10.74 ± 0.66		0.88 ± 0.07		2.67 ± 0.16		7.36 ± 0.12	
North Brother	18	4.67 ± 1.62		0.11 ± 0.04		0.44 ± 0.17		5.06 ± 0.41	
Nuku-waiata	18	2.10 ± 0.43		0.12 ± 0.05		0.44 ± 0.17		4.94 ± 0.36	
Maud	18	8.00 ± 1.50		0.16 ± 0.04		0.72 ± 0.19		4.94 ± 0.40	
Titi	18	2.28 ± 0.33		1.28 ± 0.30		1.33 ± 0.18		5.33 ± 0.38	
Whakatere-papanui	10	3.45 ± 0.89		0.13 ± 0.08		0.40 ± 0.22		4.20 ± 0.55

FIG. 3.2. Invertebrates caught on different islands in the Marlborough Sounds. Islands on which rats are or have been present are shaded. a) Mean abundance of invertebrates caught per trap-night. b) Mean abundance of beetles caught per trap-night. c) Mean ordinal richness and d) Mean beetle RTU richness.

The greatest mean beetle abundance was recorded on Titi Island. Beetle abundance on Takapourewa was not significantly different from that on Titi, ($H_{[5,298]} = 56.48$, $P < 0.05$) (Table 3.3), while all other islands had significantly lower beetle abundance, by a factor of up to 10 times (Fig. 3.2b).

Ordinal richness on Takapourewa was significantly greater than that at all other sites ($H_{[5,298]} = 80.97$, $P < 0.05$) (Table 3.3). No difference was seen between ordinal richness on the remaining islands (Fig. 3.2c). Similarly, beetle RTU richness on Takapourewa was significantly greater than that at all other sites ($H_{[5,298]} = 60.16$, $P < 0.05$) (Table 3.3). Although mean beetle RTU richness on Titi Island was almost twice as high as that on other islands, no significant difference was seen between Titi, Maud, Nuku-waiata and Whakatere-papanui (Fig. 3.2d).

Temperature effects on invertebrates

The temperatures at which all samples in this study were recorded were relatively mild and did not differ significantly (Table 3.1). They were also all within the range of temperatures favourable for invertebrate activity (McColl 1975). No relationship was found between the abundance of beetles caught each night, and the temperature in that time ($F_{[1,302]} = 2.69$, $P > 0.05$). However, temperature was a significant predictor of beetle RTU richness ($F_{[1,302]} = 5.12$, $P < 0.05$). More beetle RTUs were caught when the temperature was lower ($y = -1.4x$). Invertebrate abundance per trap-night was not related to minimum temperature ($F_{[1,302]} = 0.496$, $P > 0.05$), but temperature was a significant predictor of ordinal richness ($F_{[1,302]} = 9.942$, $P < 0.05$). Again, the relationship was negative ($y = -0.48x$). No relationship was seen between Collembola abundance and temperature.

Although temperature and richness were statistically related, it seems unlikely that temperature was a causative factor determining richness. Mean minimum temperatures on Takapourewa were colder than those on other islands (Table 3.1). Greater richness was recorded at Takapourewa sites than other islands (Fig. 3.2). Hence sites with low mean temperatures were also sites with high richness.

Species area relationships

A significant positive relationship was found between island size and (log transformed) abundance of invertebrates caught per trap night ($F_{[1,302]} = 15.6$, $P < 0.05$) but

only a small amount of the variance in invertebrate abundance was explained by island size ($r^2 = 0.05$). No relationship was seen between island size and (log transformed) beetle abundance ($F_{[1,302]} = 0.89, P > 0.05$), beetle richness ($F_{[1,302]} = 0.70, P > 0.05$), invertebrate richness ($F_{[1,302]} = 2.01, P > 0.05$) or lizard abundance ($F_{[1,612]} = 2.05, P > 0.05$).

Calculation of Community Importance of seabirds and rats

CI variables - Invertebrate abundance and diversity, beetle RTU abundance and diversity, and lizard abundance are used for t_N and t_D from the respective islands. A number of assumptions need to be made to estimate the third factor, p_i - the proportional biomass of seabirds and rats on each island. Firstly one must calculate of what the potential keystone's biomass is a proportion. The sampling in this study involved measuring the terrestrial dwelling fauna on different islands, and so this group is used in calculation of p_i .

Mean abundance of prions on Takapourewa was estimated as 0.66 ± 0.12 occupied burrows/m² (mean $\pm$ SE) (appendix 1). Given that there are two prions/burrow, there are $13\,240 \pm 2400$ prions per hectare. Prions on Takapourewa weigh on average 121 ± 1 g (Markwell *unpublished data*), therefore there are between 1 300 800 and 1 908 080 g of prion tissue/ha.

Fifty-three per cent of the reptiles on Takapourewa are *Oligosoma lineoocellatum* skinks (East et al. 1995). They reach densities of up to 3333 lizards/ha (East et al. 1995). Given these values, the estimated densities of different lizard species on Takapourewa can be calculated (appendix 3.2). Mean biomass of skinks and geckos (Markwell *unpublished data*) multiplied by density gives lizard biomass per hectare of between 36 812 and 41 062 g lizard tissue/ha (appendix 3.2).

Adult tuatara (*Sphenodon punctatus*) on Takapourewa have a mean density per hectare in different habitats of 1132 ± 403 (references in Thompson et al. 1992). Mean biomass of adult tuatara on Takapourewa is 399 ± 15 g (Markwell *unpublished data*), therefore there are between 279 936 and 635 490 g of tuatara tissue/ha.

Large invertebrate biomass was estimated from the biomass of lizards caught in the same traps. Four main groups of invertebrates were caught: darkling beetles (*Mimopeus*

spp), weta (ground weta *Hemidrus furcifer* complex and cave weta, family Rhaphiphoridae), ground beetles (family Carabidae) and spiders. For every gram of lizards caught on Takapourewa, 0.18 ± 0.06 g of invertebrates were caught in the traps (Markwell unpublished data). Given the estimated lizard biomass (appendix 3.2), between 4159 and 9876 g/ha invertebrate biomass is assumed to be caught on Takapourewa. Because only a subset of the invertebrates present on an island were caught in the lizard traps, total invertebrates per hectare could be twice the initial estimate, or between 8318 and 19 752 g/ha.

Combining these variables, the total biomass of the species measured is between 1 625 878 and 2 604 358 grams per hectare. Of this, between 1 300 800 and 1 908 080 grams is fairy prion tissue. Hence, p_{seabirds} is between 0.73 and 0.80.

A similar process was used to calculate p_i for rats. Rat biomass or abundance was not measured on any of the islands studied. Norway rats on Whale Island reach 10.9 rats/ha (Imber 1978) and the mean biomass of a wild Norway rat on a New Zealand island is 234.38 ± 8.6 g (Moors 1985). Hence one can estimate that there are between 2461 and 2649 grams of rat tissue per hectare on a rat-inhabited island.

Lizard abundance on Nuku-waiata and Whakatere-papanui was 0.14 times that on Takapourewa. Using this relationship, lizard biomass per hectare on the rat-inhabited islands was estimated as 0.14 times that on Takapourewa. Hence between 507 and 565 grams of lizard mass are estimated per hectare on Nuku-waiata and Whakatere-papanui.

Invertebrate biomass on Nuku-waiata and Whakatere-papanui was estimated from the relationship between lizards and invertebrates caught. On the rat-inhabited islands, 1.62 invertebrates were caught for every lizard. When doubled to account for the invertebrates not caught in the traps, between 1641 and 1829 grams of invertebrate tissue can be estimated per hectare on Nuku-waiata and Whakatere-papanui.

Combining all of these variables, the total biomass of the species measured is between 4609 and 5043 grams per hectare. Of this, between 2461 and 2649 grams is rat tissue. Hence, p_{rats} is between 0.534 and 0.525.

Calculation of CI - Separate values of CI were calculated using invertebrate abundance, invertebrate diversity, beetle RTU abundance, beetle RTU diversity, and lizard abundance for t_N and t_D from the respective islands. The mean of these five values was then

taken to give an overall CI value for both seabirds and for rats. Mean CI_{seabirds} was calculated as between 0.77 and 0.89, while mean CI_{rats} was between -15.81 and -8.43.

DISCUSSION

The largest values of invertebrate abundance and diversity, beetle RTU abundance and diversity and lizard abundance were recorded on seabird-inhabited islands. In contrast, diversity and abundance of lizards and invertebrates was lower on rat-inhabited islands than on rat-free islands. Ecosystems on islands with seabirds and especially on islands with rats are significantly different from those on islands where these species are absent. In testing the keystone status of seabirds and rats, CI_{seabirds} was found not to be greater than the value of 1 noted by Power et al. (1996) as defining a keystone species. CI_{rats} was greater than 1, but only by one order of magnitude.

Effects of seabirds

Seabirds discard guano and food matter, shed feathers, and leave eggshells and carcasses (Burger et al. 1978, Williams and Berruti 1978, Williams et al. 1978). This input provides a direct food source that can support a range of detritivores and scavenging invertebrates (Polis and Hurd 1996). Burrowing by the subterranean petrels homogenises soil horizons, aerates soil and increases the friability and fertility of an island (Ward 1961). Homogenisation and the fertilisation with guano can significantly increase the plant productivity in an area (Williams et al. 1978, Furness 1991). Hence seabirds can add energy to the system directly, by food addition, and indirectly, by increasing plant production.

In this study, the greatest abundance of lizards was measured on seabird-inhabited Takapourewa, North Brother and Titi Island. Significantly more beetles and greater ordinal and beetle RTU diversity was found on seabird-inhabited, rat-free Takapourewa than on seabird-free, rat-free Maud Island. This provides evidence that the energy provided, the environmental modification and the extra niches created by seabirds can be important in maintaining the organisation and diversity of island communities.

Further indication of the effect of seabirds is given by comparison of Maud Island and North Brother. Neither abundance nor richness (for beetles or for invertebrates) was significantly greater on Maud Island than on North Brother. North Brother is more than 70 times smaller than Maud. Because of species/area relationships alone, one expects fewer species to be found on the smaller island (See Chapter 2). Maud is a relatively sheltered island and does not experience the strong winds and salt spray common on North Brother. Maud Island is well vegetated (Cannington 1982) whereas North Brother has only low scrubby vegetation and a significant proportion of the island is bare rock (Gillham 1960). One would expect higher diversity and abundance on a large, sheltered island. Because greater invertebrate diversity and abundance was not found on Maud Island than on North Brother, it can be concluded that some factor is maintaining invertebrate numbers on North Brother. One hypothesis is that the energy and niches provided by the seabirds on North Brother enhance the invertebrate population.

Effects of rats

The most dominant environmental effect measured in this study was the presence or absence of rats. Introduced rodents are clearly important in maintaining the organisation and diversity of Marlborough Sounds island communities.

Whitaker (1973) has shown that islands with rats have on average one species of lizard fewer than rat-free islands. My work shows that there is also an abundance effect. Islands with rats had significantly lower numbers of lizards than rat-free islands. This was shown most clearly on Whakatere-papanui where, based on the results of sampling on nearby Takapourewa, one would have expected the grassland/scrub habitat to be ideal for skinks. Although individuals of both *O. lineocellatum* and *O. nigriplantare polychroma* were found on the island, the abundances were orders of magnitude lower than those on Takapourewa (Table 3.2).

On New Zealand islands the negative effects of rats on large invertebrate diversity and abundance are well documented (Hicks et al. 1975, Ramsay 1978, Campbell et al. 1984). The results of this study demonstrate that rats can also have a measurable effect on small invertebrate diversity and abundance. Although most of the animals sampled in this

study were below the optimal prey size for rats (Ramsay 1978), significantly more invertebrates were caught per trap-night on rat-free islands than on rat-inhabited islands. Bremner et al. (1984) similarly found a reduction in the abundance of invertebrates below optimal rat prey size on rat-inhabited islands. Animals do not always forage optimally (Markwell et al. 1993). It may be that rats feed on invertebrates smaller than the optimum when large prey becomes scarce. It is also possible that reductions in the number of large invertebrates (within the prey size for rats) could cause other predators on the islands to shift their prey targets lower and thus influence small invertebrate densities.

Both ordinal and beetle RTU richness were found to be greater on rat-free than rat-inhabited islands. Rats may remove especially palatable or easy to catch members of different orders from an ecosystem. Invertebrate richness may also be reduced on rat-inhabited islands as an effect of rarity. Invertebrate abundance is lower on rat-inhabited than rat-free islands, and so richness is consequently also lower.

Combined effects of seabirds and rats

Because the seabird-inhabited islands are also rat-free and vice-versa, it is difficult to disentangle the effects of seabirds from the effects of rats. Because Titi Island has had rats in the past and currently has a population of seabirds, it can provide indications of the relative effects of both taxa. Because seabird numbers are low, and rats were eliminated 20 years ago, neither rat effects nor seabird effects are likely to be as strong as they are on other islands. However, residual effects of a rat presence in the past are still shown in invertebrate richness, and the density of seabirds is enough to modify the habitat in some places (Mazey 1982). The richness of invertebrates and beetles and abundance of invertebrates was significantly lower on Titi Island than on Takapourewa (Fig. 3.2), but no significant difference was seen between beetle abundance at the two sites. Of the 115 beetles measured on Titi Island, 107 (93%) belonged to one RTU. Lizard abundance on Titi, although lower than that on Takapourewa, was significantly higher than on rat-inhabited Nuku-waiata or Whakatere-papanui.

The low invertebrate diversity measured on rat-inhabited islands shows that species can be driven to extinction by rats. The removal of rats and subsequent re-establishment of

seabirds (Gaze 1982) can not lead to a replacement of invertebrate diversity. The relatively high abundance of beetles and of lizards on Titi Island (in relation to that on other rat-inhabited islands) shows that, following removal of rats, species that had not been driven extinct are able to take advantage of the release from competition and the nutrients brought by seabirds, and increase in numbers.

Habitat variation

The differences between islands with and without seabirds and with and without rats give indications of the effects of these two factors. Because the islands sampled are not true replicates, it is not justified to carry out inferential statistical tests assuming that they were. Some of the variation between the different islands could be caused by inter-island habitat differences (see Chapter 2). A major difference between the islands was their size. The more than 70-fold variation in size could lead to differences in lizard or invertebrate abundance or diversity between islands (Macarthur and Wilson 1963). Species/area effects may have had an influence on invertebrate abundance on the islands in this study. The positive relationship between island size and invertebrate abundance could have masked effects of seabirds or rats. No other variables showed significant relationships with island size, indicating that island-biogeographic considerations are unlikely to have significantly influenced the results found.

Habitat requirements of the lizard species had a significant influence on the lizard distributions found. Skinks are avid baskers (Gill and Whitaker 1996) and were most common in open habitats with ample basking sites. Few skinks were caught from under forest cover. Geckos are commonly arboreal (Gill and Whitaker 1996) and were often seen on trees and shrubs on Takapourewa, North Brother, Maud and Titi Islands. Pitfall traps on the ground are unlikely to catch these tree-dwelling animals. Also, the climbing ability of the geckos means that they can easily escape any traps into which they fall. For this reason, samples taken in forested habitats (Takapourewa forest, Maud, Nuku-waiata, Titi) where geckos predominate, will have not provide accurate indications of overall lizard abundance. Samples taken at more open sites, where skinks were more prevalent, will be more accurate.

Although *Oligosoma zelandicum* is reportedly present on several Marlborough Sounds islands (Gill and Whitaker 1996), it was positively identified in this study only on North Brother Island. *O. zelandicum* has quite distinct habitat requirements. It is not found in dense forest, but prefers shady moist habitats (Gill 1976). East et al. (1995) only found *O. zelandicum* in *Muehlenbeckia* vine-land on Takapourewa. My pitfall traps were not located under the *Muehlenbeckia*, and so an absence of *O. zelandicum* is not surprising.

Keystone status of seabirds and rats on Marlborough Sounds islands

Calculation of *Community Importance* reveals that, under the criteria described by Power et al. (1996) seabirds cannot be classified as keystones on the islands they inhabit. The maximum mean CI_{seabirds} of 0.89 is not "much greater than 1" and so seabirds are not keystones. Maximum absolute mean CI_{rats} was 15.83. This value is greater than 1, but only by one order of magnitude. An arbitrary decision needs to be made as to whether this fits the keystone paradigm. Under the definition of Power et al. (1996), rats may be keystone species on Marlborough Sounds islands, but until a definition of "much greater" is developed, ambiguity will remain. Power et al. (1996) note that it is premature to prescribe numeric thresholds for applying the keystone designation until more data are collected and theory developed. This however leaves a somewhat circular argument. The keystone concept cannot be properly studied until a workable definition of keystone is formulated, yet we cannot define keystone species in a useful manner until data is collected describing keystones in nature. Faced with this argument it seems unlikely that the numerical bounds of CI that describe keystone status are likely to be found any time soon.

The calculation of CI for seabirds and rats highlights further problems with the proposed definition of keystones (Power et al. 1996). Not least among these are the problems associated with calculating p_i , the proportional biomass of the proposed keystone. Putting aside the logistic difficulties associated with calculating the biomass of every organism in an ecosystem (which could in theory be overcome with an extensive research programme), arbitrary decisions must be made as to the bounds of the system to be measured. The physical bounds of an ecosystem are not always clearly defined. Many, if not most, ecosystems are subsidised by nutrients from adjacent habitats (Polis and Strong

1996). Animals may move between adjacent physical habitats (Bormann and Likens 1967) transferring nutrients, as well as their own biomass from one ecosystem to another. Even in physically constrained ecosystems such as islands, many nutrients are transferred between adjacent habitats by biotic and abiotic processes (Polis and Hurd 1995, 1996, Anderson and Polis 1998).

Within the physical bounds of an ecosystem, further decisions must be made as to the species included in the calculation of total biomass. If large structurally dominant organisms (for example trees or kelps) are included in calculations of total biomass, the proportional biomass of species i will be lower, and CI_i will be higher than if they are not included. If only animals are being measured, should the more than 20t/ha of worms and micro-organisms that live in soil (McLaren and Cameron 1996) be ignored? Soil micro- and meso-faunal biomass is at least as great as the estimated biomass of seabirds, lizards, tuatara and invertebrates per hectare on Takapourewa. Inclusion of soil fauna biomass could change the conclusions of the CI calculation. Decisions as to which individuals belong to an ecosystem are likely to be made on an *ad hoc* basis and hence calculation of keystone status can depend on the interests and skills of individual researchers.

There is also debate as to whether the dichotomy between functionally important species that are abundant or structural dominant and those that are equally important but less abundant is useful (Hurlbert 1997). Creation of this arbitrary distinction can lead to artificial distinctions between effects of different species. A virus population may have a negligible biomass in the ecosystem it inhabits, and yet can have dramatic population effects. If the proportional biomass of a virus in one ecosystem has two (or ten or ten thousand) times the biomass of that in another system, it is not necessarily any more important, and may be just responding to stochastic changes in host populations. By the same token, why should the virus be classified as a keystone when an elephant in the same system is not? Both may significantly alter the organisation and diversity of their community (Krebs 1985, Bond 1994) yet, because of its greater biomass, the elephant will not be classed as keystone under the definition of Power et al. (1996) but the virus will.

Although proportional biomass of seabirds and rats on the island systems in this study was calculated using representatives of their ecological communities, other taxa could equally validly have been included. The conclusion that seabirds are not keystone and

that rats may be is contingent upon the choice of taxa with which to estimate proportional biomass. Ambiguity in the conclusions remain.

Choice of the trait (or traits) measured in the calculation of CI also adds ambiguity to any definition of a keystone. Power et al. (1996) suggested "productivity, nutrient cycling, species richness, or the abundance of one or more functional groups of species or dominant species" as possible traits, but no single factor was identified. In this study, abundance and richness of functional groups of species were analysed and conclusions as to the keystone status of seabirds and rats made using this data. It is possible that if another trait, e.g. productivity, had been studied, different conclusions would have been reached. Allocation of keystone status is therefore contingent on the particular trait measured. Decisions as to whether or not a species is keystone will still vary in an *ad hoc* way depending on the trait chosen by researchers.

Conclusions

Significant differences were seen between invertebrate and lizard diversity and abundance on some (but not all) seabird-inhabited and seabird-free islands. Clear differences were found between the fauna on rat-inhabited and rat-free islands. These findings indicate that seabirds and, more especially, rats are important in maintaining the organisation and diversity of Marlborough Sounds island communities.

Calculation of *Community Importance* to evaluate keystone status, as proposed by Power et al. (1996), showed that seabirds have a CI value not greater than one, and so are not keystone species. Rats have a CI greater than one, and so may be keystone species. Seabirds and rats can be shown to be important in maintaining their ecosystem function, and yet cannot be unambiguously shown to be keystones (or in the case of rats, to be non-keystones either). The keystone concept as elucidated by Power et al. (1996) does not seem to have great practical use for ecology or conservation.

The calculations revealed a number of difficulties with the application of Power et al.'s (1996) definition of keystone. The threshold beyond which keystone status can be attributed is not defined. The traits with which to calculate CI are not defined and could vary depending on the choice of the researcher. The boundaries of the ecosystem to be

studied are not easily defined, and so the calculation of proportional biomass could vary depending on the choices made by the researcher. These factors mean that allocation of keystone status to different species can vary depending on choices made in the research and calculations. Ambiguity in the definition of keystones remains.

Although purporting to add clarity to the keystone concept, the definition proposed by Power et al. (1996) is still not clear and is open to different interpretations. Instead of attempts to resuscitate the concept, I conclude that the advice of Mills et al. (1993) should be taken, and the keystone concept should be abandoned.

APPENDIX 3.1. Number of invertebrates of different taxa caught per trap-night at different sites.

		Invertebrates per trap per night			
Common name	Taxa	Takapourewa pasture	Takapourewa grassland	Takapourewa scrub	Takapourewa forest
Springtails	Collembola	1.111	0.448	0.986	0.620
Mites	Acari	0.049	0.127	0.105	0.115
Flies	Diptera	0.017	0.035	0.023	0.039
Land hoppers	Amphipoda	<0.001	0.004	0.012	0.065
Bugs	Hemiptera	0.018	0.011	0.005	0.010
Wasps	Hymenoptera (not ants)	0.006	0.010	0.011	0.015
Ants	Formicidae	0.002	0.015	0.016	0.001
Beetles	Coleoptera	0.003	0.011	0.007	0.011
Spiders	Araneae	0.004	<0.001	0.002	0.001
Slaters	Isopoda	0	0.002	0.004	<0.001
Thrips	Thysanoptera	<0.001	<0.001	0.001	0.004
Pseudoscorpions	Pseudoscorpiones	0	0.001	<0.001	<0.001
Millipedes	Diplopoda	0	0.002	<0.001	<0.001
Centipedes	Chilopoda	0	0.002	<0.001	<0.001
Moths	Lepidoptera	<0.001	<0.001	<0.001	<0.001
Fleas	Siphonaptera	<0.001	<0.001	<0.001	<0.001
Snails	Gastropoda	0	<0.001	<0.001	0
Barklice	Psocoptera	<0.001	0	0	<0.001
Worms	Annelida	<0.001	0	<0.001	<0.001
Weta	Orthoptera	<0.001	<0.001	<0.001	<0.001
Lacewings	Neuroptera	<0.001	0	<0.001	0
Harvestmen	Opiliones	0	<0.001	<0.001	0
Bristletails	Archeognatha	0	0	<0.001	0
Earwigs	Dermaptera	0	0	<0.001	0

		Invertebrates per trap per night				
Common name	Taxa	North Brother	Titi	Nuku-waiata	Whakatere- papanui	Maud
Springtails	Collembola	1.016	0.604	0.529	0.335	0.807
Mites	Acari	0.183	0.060	0.050	0.133	0.374
Flies	Diptera	0.010	0.018	0.012	0.145	0.007
Land hoppers	Amphipoda	0	<0.001	0.006	0.025	0.005
Bugs	Hemiptera	0.009	0.002	0	0.010	0.004
Wasps	Hymenoptera (not ants)	0.006	0.015	0.002	0.008	0.014
Ants	Formicidae	0.023	0.004	0.020	0.005	0.009
Beetles	Coleoptera	0.005	0.015	0.005	0.010	0.008
Spiders	Araneae	0.014	0.005	0.002	0.005	0.002
Slaters	Isopoda	0.006	0.003	0.001	0	0.009
Thrips	Thysanoptera	0.001	0.001	<0.001	0	0.010
Pseudoscorpions	Pseudoscorpiones	<0.001	0.001	0.001	0	<0.001
Millipedes	Diplopoda	0	0	<0.001	0	0
Centipedes	Chilopoda	<0.001	0	0	0.003	0
Moths	Lepidoptera	0	<0.001	0	0.003	0
Fleas	Siphonaptera	0	0	0	0	0
Snails	Gastropoda	0	0	0.009	0	0.002
Barklice	Psocoptera	<0.001	0	0.007	0	<0.001

APPENDIX 3.2. Abundance, density and biomass of lizards and tuatara on Takapourewa.

¹Data from East et al. (1995). ²Data from Markwell (*Unpublished*).

Species	Proportional abundance ¹	Density (animals/ha)	Mean biomass (g) $\pm$ 1 SE ²	Minimum mass (g/ha)	Maximum mass (g/ha)
<i>O. infrapunctatum</i>	0.08	503	12.72 $\pm$ 1.66	5564.2	7234.5
<i>O. lineoocellatum</i>	0.53	3333 ¹	6.40 $\pm$ 0.20	20664.6	21997.8
<i>O. nigriplantare</i>	0.04	252	3.29 $\pm$ 0.10	802.4	852.7
<i>O. zelandicum</i>	0.02	126	3.29 $\pm$ 0.10	401.2	426.4
<i>H. maculatus</i>	0.15	943	8.34 $\pm$ 0.49	7404.9	8329.4
<i>H. stephensi</i>	0.01	63	8.34 $\pm$ 0.49	493.7	555.3
<i>N. manukanus</i>	0.03	189	8.34 $\pm$ 0.49	1481.0	1665.9
Total lizards		6289		36 812.0	41 061.9
<i>S. punctatus</i>	0.14	1132 $\pm$ 403	399 $\pm$ 15	279 936	635 490

Chapter 4: Seabird input into island communities in the Marlborough Sounds: evidence from stable carbon and nitrogen isotopes

INTRODUCTION

Burrow-dwelling seabirds play an important role in determining edaphic and floral dynamics of island ecosystems. While at their breeding colonies, they dig burrows, deposit guano and food matter, shed feathers, leave unhatched eggs and eggshells, and in some cases die (Ward 1961, Burger et al. 1978, Williams and Berruti 1978, Williams et al. 1978). In other chapters of this thesis, I attempt to quantify the abundance and diversity of reptiles and invertebrates on seabird-inhabited islands in the Marlborough Sounds, New Zealand. To confirm that any differences in abundance or diversity between seabird and seabird-free islands are related to seabirds and not another factor of the islands, it is necessary to show that the animals are directly affected by seabirds. In this study, I use stable isotope analysis to determine if the diets of animals of different taxa on seabird islands contain nutrients brought to land by seabirds.

Stable isotope analysis is a relatively new field. As far as is known, this is the first time that it has been used to study marine input onto New Zealand offshore islands (but see Anderson and Polis 1998). This study is not definitive, but will be explorative in nature. I hope to investigate the possibilities of the technique and the nature of the system and so determine areas where further study is warranted.

Stable isotopes

The isotope signature of a consumer will reflect that of its prey in a predictable manner (Peterson and Fry 1987). When the nature of this variation is known, one can infer trophic relationships between different species. By convention isotope ratios are presented

in δ notation, as deviations from a standard, in thousandths (‰), as defined by the equation:

$$\delta^{13}\text{C}\text{‰ or } \delta^{15}\text{N}\text{‰} = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad \text{equation 1}$$

where R denotes the ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Carbon from PeeDee belemnite (PDB) limestone and atmospheric nitrogen are used as standards for carbon and nitrogen respectively (Peterson and Fry 1987).

Carbon - Carbon isotope values provide information about the source of nutrients. A common usage of this is in determining if a carbon source is aquatic or terrestrial in origin. Atmospheric CO_2 has a $\delta^{13}\text{C}$ of approximately -7‰. During chemical reactions the ratio of the heavy (^{13}C) to the light (^{12}C) isotope changes or fractionates. Fractionation during photosynthesis leads to a net $\delta^{13}\text{C}$ depletion of about 21‰ to approximately -28‰ for most terrestrial plant tissue. At the interface between air and water, fractionation also occurs as CO_2 ($\delta^{13}\text{C}$ -7‰) dissolves to HCO_3^- ($\delta^{13}\text{C}$ 0‰) (Peterson and Fry 1987). Underwater, fractionation during planktonic photosynthesis leads to algal $\delta^{13}\text{C}$ values of approximately -19‰ (Mizutani and Wada 1988).

An enrichment in $\delta^{13}\text{C}$ of approximately 1‰ is expected between most animals and their diets (DeNiro and Epstein 1978). Animals with a $\delta^{13}\text{C}$ close to -19‰ are likely to have diets based on aquatic autotrophs, while animals with a $\delta^{13}\text{C}$ of approximately -28‰ or below are likely to have diets based on terrestrial dwelling autotrophs. Intermediate values suggest that an animal has a diet deriving from a combination of terrestrial and aquatic sources (Ramsay and Hobson 1991).

Seabirds usually feed at sea (Croxall and Prince 1987). The primary producers at the base of their food-web are photosynthetic phytoplankton. The variation in $\delta^{13}\text{C}$ between seabirds and their diet is sometimes greater than that for other taxa, and differences of up to 3‰ have been recorded (Mizutani and Wada 1988), but these are not universal (Hobson et al. 1994) and $\delta^{13}\text{C}$ values have been used to measure marine input into terrestrial systems (Anderson and Polis 1998).

Nitrogen - There are two stable isotopes of nitrogen, ^{14}N and ^{15}N . The lighter isotope, ^{14}N is preferentially volatilised from ammonium in seabird guano to such an extent that the remaining ammonium is enriched in ^{15}N (Mizutani et al. 1985). Because of this,

$\delta^{15}\text{N}$ of samples taken from seabird colonies is considerably higher than that from other areas (Mizutani and Wada 1988, Mizutani et al. 1991). Delta ^{15}N values can be used to give a measure of a marine influence in the nitrogen component of a sample.

Nitrogen isotope values also provide information about relative trophic status of different samples. Because the light isotope (^{14}N) is preferentially excreted, an animal's $\delta^{15}\text{N}$ is enriched relative to that of its prey (DeNiro and Epstein 1981). The $\delta^{15}\text{N}$ of an animal's tissues therefore indicate the number of feeding steps below it (Cabana and Rasmussen 1994) and can be used to estimate relative trophic levels of different taxa (Sydeman et al. 1997).

Dual-isotope models - The use of two or more different isotopes provides a better segregation of individuals than the use of a single isotope signature (e.g. Ben-David et al. 1997, Kline et al. 1993, Hesslein et al. 1991). In this study, both carbon and nitrogen stable isotope signatures will be used to measure the marine input in samples taken from different islands in the Marlborough Sounds.

METHODS

Study islands

Sampling was carried out on six islands in Cook Strait, New Zealand (Fig. 2.1, Table 2.1). The islands chosen exhibited different combinations of rat abundance, seabird abundance and habitat type (see Chapter 2). The predominant plants at each site are presented in Appendix 3. Little blue penguins nest in relatively low abundance on all islands, including those classified as "seabird-free". Therefore a residual and probably small seabird effect is expected at all sites.

In spite of freedom from mammalian predators, no seabirds naturally nest on Maud Island (41°01'S, 173°54'E; 309 ha). An introduction programme for fluttering shearwater (*P. gavia*) is presently taking place on the island (Bell 1994), but sampling was not carried out in the vicinity of the reintroduction site. Because of the current and presumed historical absence of seabirds from Maud Island, it is used as a baseline with which to compare other sites.

Fairy prion (*Pachyptila turtur*) nest on Takapourewa (40°40'S, 174°00'E; 150 ha) at densities up to 6000 pairs/ha (Appendix 1). Small numbers of sooty shearwater (*Puffinus griseus*), fluttering shearwater and diving petrel (*Pelicanoides urinatrix*) also nest on the island (Newman 1987). An estimated 8500 fairy prion (density 2000 pairs/ha) and 6800 diving petrels (density 1600 pairs/ha) nest on North Brother Island (41°07'S, 174°26'E; 4 ha) (Gaston and Scofield 1995). Norway rats (*Rattus norvegicus*) were present on Titi Island (40°57'S, 174°08'E; 32 ha) until exterminated by 1981 (Gaze 1982). Since that time seabird numbers have increased and flesh-footed shearwater (*Puffinus carneipes*), and sooty shearwater now nest on Titi Island at densities of at least 15 pairs/ha (Gaze 1982). Samples were collected on these three seabird-inhabited islands to determine the extent of the seabird effect that can be measured in the tissues of plants and animals.

Kiore (*R. exulans*) were present on Nuku-waiata until eradicated by poisoning in 1993 (Rufaut 1995). Norway rats are currently found on Whakatere-papanui (*pers. obs.*). Presumably because of the presence of rats, seabirds are not found in any numbers on Nuku-waiata or Whakatere-papanui (D. Brown *pers comm.* 1995). Samples were collected on these seabird-free islands to provide comparison with the seabird-inhabited islands.

Although relatively pristine in relation to the mainland, all islands in this study have been influenced to some extent by humans. The original cover of Takapourewa (East et al. 1995) and probably the other islands, with the exception of North Brother, was forest. Burning and clearing of vegetation took place on all islands during Maori and early European times (Cannington 1982, Gaze 1982, Walls 1983, East et al. 1995). Since then, forests have been left to regenerate. Scrub or forest now predominates at all study sites except Takapourewa grassland and pasture. Sheep are grazed at the Takapourewa pasture site. The removal of vegetation and the addition of nutrients in the form of ovine faeces and urine could influence nutrient relationships in this habitat.

Replication

On all islands except Takapourewa, six subsites were chosen at random distances and directions from established tracks. On Takapourewa, 24 subsites were included. Each

subsite was an area approximately 10 m × 10 m. Within these subsites, samples were collected for isotope analysis. The number of individual specimens that made up each replicate varied depending on the taxa (Table 4.1). Although attempts were made to sample the same taxa on all islands, the final sample set was not balanced because some specimens could not be found on all islands. Nevertheless, soil, plants and at least one animal taxon were sampled at all sites.

Sampling was carried out over two seasons. Preliminary sampling was carried out during summer 1995. More thorough sampling, incorporating a greater number of sites and taxa, was carried out over summer 1996.

Materials sampled for isotopic analysis

Seabirds - Samples of seabird tissues were collected to determine the isotope values that form the base of the marine food webs. Shed feathers were chosen as a measure of seabird isotope values because they were relatively plentiful and could be sampled without capturing or harming the birds. Feathers were collected from a wide area in an attempt to ensure each feather came from a different bird. Approximately 20 feathers were combined to make up each replicate.

All of an animal's tissues carry an isotopic signature, but differences exist in the degree of fractionation by different tissues (Peterson and Fry 1987). To compare feather

TABLE 4.1. Total number of samples collected at different sites in the Marlborough Sounds in 1995 and 1996. Seabird-free sites are shaded.

Island	Number of replicates collected								
	Seabirds	<i>Coprosma</i>	<i>Macropiper</i>	<i>Lolium</i>	Soil	Amphipods	Beetles	Geckos	Spiders
Takapourewa	25	29	15	30	24	7	25	17	10
North Brother	2	6	0	4	6	0	5	6	0
Titi	6	12	5	1	6	0	13	9	6
Maud	0	2	12	0	6	15	9	11	5
Nuku-waiata	0	2	12	0	5	17	0	0	6
Whakatere-papamui	0	10	10	4	6	12	0	0	0

isotope signatures with those of other tissues, three fairy prion that died after flying into the lighthouse on Takapourewa were dissected. Samples of breast muscle and liver tissue as well as feathers were removed and analysed. The average difference in isotope ratio between feathers and tissues of the birds was determined.

Plants - Leaves of plants common on the study islands were collected to measure the isotope values that form the base of the terrestrial system. *Coprosma repens*, a shrub common on Marlborough Sounds islands, was collected from all sites where it was found. At sites with dense forest (Maud Island and Nuku-waiata), few *Coprosma* were present and another common shrub, *Macropiper excelsum*, was collected (Table 4.1). In non-forest habitats (Takapourewa pasture and grassland) shrub samples were not available, and rye grass (*Lolium perenne*) samples were collected instead. At sites where more than one species (*C. repens*, *M. excelsum* or *L. perenne*) was available, as many of the three as possible were collected (Table 4.1). At each subsite, three leaves, each leaf from a separate tree or grass tussock, were collected for each replicate.

Soil - Marine-derived nutrients entering the terrestrial ecosystem via seabirds go first to the detritus component of the food-web. Similarly, much terrestrial plant biomass is cycled directly into the detrital component of the system (Polis 1994). To gain a measure of the isotope values of these nutrients as they enter the ecosystem, samples of soils were taken at all sites. By comparing soil isotope ratios with those of seabirds and of plants, one can determine whether autochthonous or allochthonous input has the greatest impact on soil formation.

Soil samples were collected from approximately 5-10 cm depth. This level was below the top layer of recently fallen leaf litter, but still above soil largely composed of parent material. The soil samples therefore contained detrital material, but were not dominated by recently fallen leaves. At each subsite three collections of approximately 50 g of soil were collected to make up each replicate.

Animals - Four groups of animals were analysed. The taxa chosen were expected to increase in trophic level in the following order : amphipods, beetles, lizards and spiders.

Amphipods (*Orchestia*, *Transorchestia* spp.) live in leaf litter and are detritivores (Forster and Forster 1970). At all subsites, samples of leaf litter were collected haphazardly and searched in the field for amphipods. All amphipods found were manually removed from

the litter. Each replicate contained a minimum of six and up to 20 individual amphipods, depending on the size of the animals. Litter at all sites was searched, but only areas with a layer of moist litter were found to contain amphipods. Amphipods were not collected at sites where only dry litter was found, but were collected from Whakatere-papanui and Nuku-waiata where beetles were not seen (Table 4.1).

Darkling beetles (*Mimopeus opaculus*, *M. elongatus* and *M. buchanani*) eat mainly detritus. Three pitfall traps were installed in each subsite to capture *Mimopeus* beetles. The traps were constructed from 4 l paint cans, with the insides lacquered to retard rusting. Holes were made in the bottom of the traps to allow drainage. Wire supports held can lids approximately 25 mm above the trap opening, to shelter captives from the sun, keep out debris, and make it difficult for captives to escape. If insufficient numbers were caught in traps, beetles were collected by hand from vegetation, or under rocks and debris in each study site. At least three individual beetles were combined to make each replicate. Large *Mimopeus* beetles were scarce on North Brother. To avoid having too great an impact on the relatively fragile ecosystem of the island by moving around rocks to find large beetles, only individuals of the relatively common smaller beetle species (*M. elongatus*) were collected on North Brother. No darkling beetles were found on Whakatere-papanui or Nuku-waiata.

Lizards on New Zealand islands have a diet of carrion, small invertebrates and fruit (Gill and Whitaker 1996). Common geckos (*Hoplodactylus maculatus*) were chosen as representatives of the lizard trophic level in this study. Common geckos are the most abundant lizard in forest habitats on Marlborough Sounds islands (East et al. 1995). Pitfall traps were set for lizards in all habitats, but very few geckos were caught this way. Geckos were caught by hand from tree trunks and under debris in each subsite. Once caught, tissue was collected from each gecko by holding the animal until its tail was autotomised. At least three individual tails made up each replicate. No geckos were seen on Nuku-waiata or Whakatere-papanui, and no samples were collected (Table 4.1).

Spiders (Order Araneae) are almost solely predatory (Evans 1984) and were expected to be the top trophic level measured. Spiders were caught in pitfall traps or by hand in each subsite. No attempt was made to identify the species involved, but the majority were relatively large, ground dwelling, cursorial spiders. Three whole spiders

made up each replicate. Few spiders were seen on Whakatere-papanui, and none were caught. No spiders were found in Takapourewa grassland. Spiders were found on North Brother, but in very low abundance. I thought that removal of carnivores would have a disproportionately large impact on the ecosystem, and collected no spiders from this site.

Sample preparation

After collection, all vegetation samples were sealed into plastic bags containing silica crystals. On return to the laboratory, samples were frozen at -80°C until processed. Soil samples were packed in the field into plastic jars that were then filled with ethanol. The ethanol prevented rapid decomposition of organic matter and does not affect isotope analysis of soils (Mizutani and Wada 1988).

Spiders from Titi Island and Takapourewa were brought back to the laboratory alive, where they were killed in liquid nitrogen and frozen at -80°C . All other animal specimens were placed in liquid nitrogen in the field, within one hour of capture, then frozen at -80°C on return to the laboratory. As isotopic analysis of whole animals gives a more complete picture of an animal's diet than analysis of separate tissues (DeNiro and Epstein 1978), no attempt was made to separate the different tissue types of any of the invertebrates.

All frozen samples were placed directly into a drying oven, and dried at 45°C for at least 72 hours, or until dry masses stabilised. The dried samples were then ground in a Wiley mill. The resulting powder was sieved through a $250\text{ }\mu\text{m}$ Endicott sieve to remove any large fibrous particles that remained. The powders were sealed in airtight plastic jars until analysed.

Chemical analysis

Samples were analysed at the Waikato Stable Isotope Unit, Hamilton, New Zealand. Using a combustion reactor maintained at around 1020°C , solid samples were vaporised to N_2 or CO_2 in a temporarily enriched atmosphere of oxygen. The resulting combustion gases were swept through a reduction reactor, a water filter and onto a gas

chromatograph column by a carrier gas, helium. In the gas chromatograph column the N_2 or CO_2 gases were separated from any other gases in the sample. A subsample of each separated gas was transferred into a Europa Scientific Tracermass isotope mass spectrometer ion source for the measurement of ^{13}C and ^{15}N abundance. The spectrometer ionised the gas, and the area under the curves produced by the ion beams was measured to determine isotope abundance. Nitrogen and carbon samples were analysed against laboratory standard urea ($\delta^{15}N = -0.45\text{‰}$) and sucrose ($\delta^{13}C = -10.80\text{‰}$) respectively. The laboratory standards had been calibrated against certified standards of atmospheric nitrogen and PDB. When analysing samples, standards were analysed after every 12 samples. The instrument automatically corrected the set of 12 data each time it recalibrated itself against the standard. Instrument error was about $\pm 1\text{‰}$ for $\delta^{15}N$ and $\pm 0.3\text{‰}$ for $\delta^{13}C$ (A. Rajendram *pers. comm.* 1996).

Calculation of marine component of an animal's diet

To determine the difference between the isotopic signature of an animal and the extreme of a completely terrestrial diet, I compared isotope signatures of a sample with those recorded for the same taxon from seabird-free Maud Island. I used a dual-isotope model, consisting of both the carbon and nitrogen isotope ratios of each taxon. The differences between the mean isotopic values for each taxon on each island and the mean isotopic values of the same taxon on Maud were calculated. Using a graph with $\delta^{15}N$ as ordinate and $\delta^{13}C$ as abscissa, the length of the line connecting *a* (Maud) and *b* (test site) (Fig. 4.1) was calculated by: $z = \sqrt{x^2 + y^2}$ equation 2

where *z* is the length of the line between *a* and *b*, and *x* and *y* are the differences between *a* and *b* on the X and Y axes respectively (after Ben-David et al. 1997). Although degree of enrichment in different isotopes may vary

Fig. 4.1. Calculation of *Marine effect*. i.e. Euclidean distance between the isotope values of a sample on a) Maud Island and b) test sites.

between taxa (DeNiro and Epstein 1978, 1981), the isotopic signature of each taxon from each island was always compared with the isotopic signature of the same taxon from Maud. Hence no correction factor was needed. I refer to the calculated difference between the isotope signatures of a sample and that for the same taxon from Maud as the *marine effect* for that sample.

Calculation of trophic levels

Average enrichment in $\delta^{15}\text{N}$ is approximately 3.3‰ per trophic level (DeNiro and Epstein 1981, Mizutani and Wada 1988). I assumed that terrestrial plants were the first trophic level on Marlborough Sounds islands. From this, the *relative trophic level* of different consumers can be determined from the equation:

$$\text{TL}_a = 1 + \left(\frac{D_a - D_p}{3.3\text{‰}} \right) \quad \text{equation 3}$$

where TL_a is the *relative trophic level* of an animal, D_a is the $\delta^{15}\text{N}$ of the animal's tissues, and D_p is the $\delta^{15}\text{N}$ of plant tissue at the site of capture (after Hobson et al. 1994).

Statistical analysis

Mean isotope ratios of seabirds, plants and soil were calculated for each site. The mean value of the carbon and nitrogen ratios of soil at each site was compared with those of plants and seabirds to determine the most likely origin of the soil organic matter. ANOVA and (if data were heteroscedastic) Kruskal-Wallis tests were used to test for differences between isotopic ratios of the three different plant taxa sampled. Seabird density (number of birds per m^2) was determined for each site (Gaze 1982, Gaston and Scofield 1995, Appendix 1). Regression analyses of isotope ratio against seabird density were used to determine if differences between isotope ratios of plants at different sites were related to seabirds.

Isotope ratios for animals from each site were determined and used to calculate *marine effect* and *relative trophic level* for the four groups of animals measured. ANOVA

was used to compare between sites and determine if values differed between seabird-inhabited and seabird-free islands.

RESULTS

Comparison between years

No significant difference was found between data collected in the two different years for plant $\delta^{15}\text{N}$ ($t_{[114]} = 1.83$, $P = 0.069$), animal $\delta^{15}\text{N}$ ($t_{[95]} = 0.900$, $P = 0.370$), plant $\delta^{13}\text{C}$ ($t_{[105]} = 1.63$, $P = 0.106$) or animal $\delta^{13}\text{C}$ ($t_{[58]} = 1.36$, $P = 0.178$). Data from the two sampling periods were therefore pooled.

Seabird isotope ratios

Mean carbon isotope ratio of seabird feathers was -18.57 ± 0.14 (mean $\pm$ SE). Seabird feather $\delta^{15}\text{N}$ was 10.36 ± 0.20 . For the three prion from which tissue samples were collected, $\delta^{13}\text{C}$ of feathers was enriched by 1.93‰ in relation to that of body tissues and $\delta^{15}\text{N}$ of feathers were on average 2.20‰ less enriched than those of tissues.

Plant isotope ratios

Carbon - Significant differences were found between $\delta^{13}\text{C}$ values for *Coprosma*, *Lolium* and *Macropiper* (ANOVA, $F_{[2,152]} = 64.93$, $P < 0.05$). *Lolium* and *Coprosma* $\delta^{13}\text{C}$ were not significantly different from the -28‰ expected from previous studies (Peterson and Fry 1987, Mizutani and Wada 1988, Martinelli et al. 1991, Ramsay and Hobson 1991, Cormie and Schwarcz 1994, Koch et al. 1995) (Table 4.2). *Macropiper* values were significantly less enriched in ^{13}C than the other two taxa (Mean = -32.42‰). To determine if the differences between species were related to seabirds, the analysis was repeated with only those sites inhabited by seabirds. The data were heteroscedastic, and non-parametric analyses were used (Kruskal-Wallis $H_{[2,101]} = 31.09$, $P < 0.05$). Again, *Macropiper* values were significantly less enriched in ^{13}C than the other two taxa when only seabird-inhabited islands were analysed.

Differences were found between carbon isotope values at different sites for *Coprosma* ($F_{[5,55]} = 5.26$, $P < 0.05$). Greatest (least negative) $\delta^{13}\text{C}$ values were recorded on North Brother and Maud Island (Table 4.2). Significant differences were also found between *Macropiper* $\delta^{13}\text{C}$ values ($F_{[4,49]} = 23.65$, $P < 0.05$). Takapourewa had the greatest value and Nuku-waiata and Maud $\delta^{13}\text{C}$ were significantly lower than other sites (Table 4.2). No significant difference was seen between *Lolium* $\delta^{13}\text{C}$ values from different islands ($F_{[3,35]} = 1.84$, $P > 0.05$).

No relationship was found between (log transformed) *Coprosma* and *Lolium* $\delta^{13}\text{C}$ values and seabird density (regression, $F_{[1,99]} = 0.58$, $P = 0.45$), but seabird density was a significant negative predictor of *Macropiper* $\delta^{13}\text{C}$ values ($F_{[1,53]} = 19.04$, $P < 0.05$).

TABLE 4.2. Isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, ‰) of plants and soil at different sites. Seabird-free sites are shaded

	Isotope ratio ($\delta^{15}\text{N}$, ‰)							
	<i>Coprosma</i>		<i>Macropiper</i>		<i>Lolium</i>		Soil	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Takapourewa	15.34 ± 0.53		15.70 ± 0.41		14.75 ± 0.50		15.66 ± 0.24	
North Brother	16.81 ± 1.36		-		16.06 ± 2.61		18.24 ± 0.79	
Titi	17.80 ± 1.46		14.38 ± 0.45		12.54 ± 0.00		17.67 ± 0.54	
Maud	7.52 ± 1.20		3.59 ± 0.83		-		6.46 ± 0.39	
Nuku-waiata	11.18 ± 1.28		10.71 ± 0.68		-		14.92 ± 0.62	
Whakare-papanui	3.33 ± 1.45		5.21 ± 1.29		6.79 ± 1.26		9.80 ± 1.04	
All islands	13.60 ± 0.79		9.83 ± 0.76		14.01 ± 0.62		14.41 ± 0.53	
Seabird-inhabited islands	16.15 ± 0.54		15.37 ± 0.35		14.83 ± 0.51		16.43 ± 0.29	
Seabird-free islands	5.05 ± 1.31		6.58 ± 0.75		6.79 ± 1.26		10.39 ± 0.93	

	Isotope ratio ($\delta^{13}\text{C}$, ‰)							
	<i>Coprosma</i>		<i>Macropiper</i>		<i>Lolium</i>		Soil	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Takapourewa	-27.39 ± 0.37		-30.54 ± 0.30		-28.67 ± 0.47		-26.77 ± 0.19	
North Brother	-25.57 ± 0.31		-		-25.97 ± 0.93		-24.74 ± 0.06	
Titi	-29.23 ± 0.41		-32.08 ± 0.35		-30.71 ± 0.00		-25.84 ± 0.67	
Maud	-26.68 ± 1.37		-34.36 ± 0.43		-		-27.53 ± 0.15	
Nuku-waiata	-28.44 ± 1.68		-34.08 ± 0.30		-		-26.57 ± 0.31	
Whakare-papanui	-29.57 ± 0.73		-31.10 ± 0.46		-29.16 ± 0.67		-27.43 ± 0.36	
All islands	-27.94 ± 0.28		-32.42 ± 0.28		-28.49 ± 0.40		-26.58 ± 0.16	
Seabird-inhabited islands	-27.62 ± 0.30		-30.92 ± 0.28		-28.42 ± 0.44		-26.28 ± 0.21	
Seabird-free islands	-28.99 ± 0.63		-33.30 ± 0.33		-29.16 ± 0.67		-27.18 ± 0.19	

Nitrogen - Significant differences were found between nitrogen isotope ratios for the different plant species ($F_{[2,153]} = 9.19$, $P < 0.05$). *Macropiper* nitrogen isotope ratios on each island were significantly lower than those for the other plant types at the same sites (Table 4.2). No significant difference was found between the $\delta^{15}\text{N}$ values of each plant species when only those islands with high densities of seabirds were included in the analysis ($H_{[2,101]} = 2.004$, $P = 0.367$), indicating that this relationship is seabird related.

Intersite comparison shows that there are significant differences between the $\delta^{15}\text{N}$ values for each of *Coprosma* ($F_{[5,55]} = 21.66$, $P < 0.05$), *Lolium* ($F_{[3,35]} = 8.94$, $P < 0.05$) and *Macropiper* ($H_{[4,49]} = 43.9$, $P < 0.05$), on different islands. Seabird-free islands (Maud, Nuku-waiata and Whakatere-papanui) had consistently lower ratios than the remaining islands (Table 4.2). A significant positive relationship between seabird density and plant nitrogen isotope ratio was found for pooled *Coprosma* and *Lolium* (regression $F_{[1,97]} = 15.11$, $P < 0.05$) and for *Macropiper* ($F_{[1,51]} = 8.93$, $P < 0.05$).

Soil isotope ratios

I compared isotope ratios of seabirds, plants and soil to measure if soil carbon and/or nitrogen was likely to have originated primarily from autochthonous sources (terrestrial plants) or seabird-derived nutrients. The mean $\delta^{13}\text{C}$ value calculated for soil was -26.58‰ , closer to the mean value for plants (pooled *Coprosma* and *Lolium*, -28.16‰ , *Macropiper*, -32.42‰) than that of seabirds (-18.57‰), even when the potential $\sim 2\text{‰}$ variation between different tissues is included (Table 4.2). In contrast, soil nitrogen isotope ratios were all relatively similar to those of both seabirds and of plants. The mean $\delta^{15}\text{N}$ value for soil was 14.14‰ , pooled *Coprosma* and *Lolium*, 13.76‰ , *Macropiper*, 9.83‰ and seabirds 10.36‰ ($\pm \sim 2\text{‰}$) (Table 4.2).

Animal isotope ratios

Carbon - Significant differences were found between the carbon isotope ratios measured for animals on each island (amphipods, $H_{[3,47]} = 10.65$, $P < 0.05$; beetles, $H_{[3,48]} = 17.90$, $P < 0.05$; geckos $F_{[3,39]} = 8.90$, $P < 0.05$ and spiders $H_{[3,23]} = 17.73$, $P < 0.05$). The

highest (least negative) $\delta^{13}\text{C}$ values for beetles, geckos and spiders came from Titi Island. Amphipods were not collected on Titi and the highest values were measured on Takapourewa (Table 4.3). Maud Island $\delta^{13}\text{C}$ values were consistently the lowest. Nuku-waiata and Whakaterere-papanui had lower $\delta^{13}\text{C}$ values than North Brother and Takapourewa, but differences were not significant (Table 4.3).

Nitrogen - Significant differences were found between the nitrogen isotope ratios measured for animals on each island (amphipods, $F_{[3,47]} = 89.7$, $P < 0.05$; beetles, $F_{[3,48]} = 72.7$, $P < 0.05$; geckos $H_{[3,39]} = 26.3$, $P < 0.05$ and spiders $H_{[3,23]} = 21.25$, $P < 0.05$). For all taxa measured, North Brother or Takapourewa (for spiders and amphipods) had the greatest $\delta^{15}\text{N}$. In all cases, islands with seabirds had significantly higher $\delta^{15}\text{N}$ than seabird-free islands (Table 4.3).

TABLE 4.3. Isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, ‰) of animals at different sites in the Marlborough Sounds. Seabird-free sites are shaded.

	Isotope ratio ($\delta^{15}\text{N}$, ‰)							
	Amphipods		Beetles		Geckos		Spiders	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Takapourewa	16.48 ± 0.71		17.87 ± 0.47		18.07 ± 0.30		20.76 ± 0.22	
North Brother	-		20.58 ± 1.66		20.37 ± 1.08		-	
Titi	-		18.58 ± 0.55		18.63 ± 0.51		19.41 ± 0.67	
Maud	6.13 ± 0.28		6.14 ± 0.48		7.82 ± 0.24		8.82 ± 0.23	
Nuku-waiata	11.97 ± 0.38		-		-		14.85 ± 0.26	
Whakaterere-papanui	5.73 ± 0.67		-		-		-	
All islands	9.42 ± 0.60		16.28 ± 0.73		15.89 ± 0.77		16.93 ± 0.89	
Seabird-inhabited islands	16.48 ± 0.71		18.40 ± 0.39		18.66 ± 0.32		20.25 ± 0.32	
Seabird-free islands	8.29 ± 0.31		6.14 ± 0.48		7.82 ± 0.24		12.11 ± 0.28	

	Isotope ratio ($\delta^{13}\text{C}$, ‰)							
	Coprosma		Macropiper		Lolium		Soil	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Takapourewa	-23.92 ± 0.35		-25.07 ± 0.24		-24.35 ± 0.23		-24.35 ± 0.26	
North Brother	-		-24.73 ± 0.08		-23.56 ± 0.22		-	
Titi	-		-24.14 ± 0.24		-23.13 ± 0.29		-23.46 ± 0.15	
Maud	-25.74 ± 0.58		-26.09 ± 0.10		-24.89 ± 0.20		-25.55 ± 0.12	
Nuku-waiata	-25.20 ± 0.17		-		-		-24.67 ± 0.14	
Whakaterere-papanui	-25.01 ± 0.25		-		-		-	
All islands	-25.14 ± 0.21		-24.98 ± 0.16		-24.13 ± 0.16		-24.44 ± 0.17	
Seabird-inhabited islands	-23.92 ± 0.35		-24.75 ± 0.17		-23.86 ± 0.18		-24.01 ± 0.20	
Seabird-free islands	-25.33 ± 0.22		-26.09 ± 0.10		-24.89 ± 0.20		-25.07 ± 0.16	

Marine effect - Greatest *marine effects* were recorded on North Brother Island. Slightly (but not significantly) lower values were measured on Takapourewa and Titi Island (Table 4.4). The *marine effect* calculated for amphipods and spiders on seabird-free Nuku-waiata and Whakaterere-papanui were significantly lower than those from the seabird-inhabited islands (Table 4.4).

Relative trophic level - The *relative trophic level* of each animal taxa was calculated for each site. The mean of the *Coprosma*, *Lolium* and *Macropiper* $\delta^{15}\text{N}$ values for each site was used as D_p for that site. Overall a steady increase in mean *relative trophic level* was seen through the four different taxonomic groups studied on seabird islands, confirming the *a priori* assumptions that the animals chosen for study represented a range of trophic levels. Amphipods were the lowest at $1.40 (\pm 0.22)$, followed by beetles (1.80 ± 0.11) then geckos (1.86 ± 0.09). Spiders were the top *relative trophic level* studied (2.38 ± 0.13) (Table 4.5). The *relative trophic levels* occupied by the different taxa on seabird-free islands were lower than on islands with seabirds for all taxa except geckos (amphipods, 1.45 ± 0.08 ; beetles, 1.60 ± 0.15 ; geckos, 2.11 ± 0.07 ; spiders 2.32 ± 0.06) (Table 4.5).

TABLE 4.4. *Marine effect*, i.e. mean (± 1 SE) Euclidean distance between isotope value ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, ‰) on Maud Island and at test site. Seabird-free sites are shaded.

	<i>Marine effect</i>							
	Amphipods		Beetles		Geckos		Spiders	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Takapourewa	10.46 $\pm$ 1.36		11.77 $\pm$ 1.01		10.26 $\pm$ 0.69		12.00 $\pm$ 0.59	
North Brother	-		14.50 $\pm$ 2.15		12.62 $\pm$ 1.39			
Titi	-		12.59 $\pm$ 1.08		10.95 $\pm$ 0.90		10.79 $\pm$ 0.94	
Nuku-waiata	5.82 $\pm$ 1.00		-		-		6.09 $\pm$ 0.95	
Whakaterere-papanui	0.86 $\pm$ 1.26		-		-		-	

TABLE 4.5. *Relative trophic level*, calculated using $\delta^{15}\text{N}$ of invertebrates and reptiles at different sites in the Marlborough Sounds. Seabird-free sites are shaded.

	<i>Relative trophic level</i>							
	Amphipods		Beetles		Geckos		Spiders	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Takapourewa	1.40 $\pm$ 0.22		1.82 $\pm$ 0.14		1.88 $\pm$ 0.09		2.69 $\pm$ 0.07	
North Brother	-		2.24 $\pm$ 0.50		2.17 $\pm$ 0.33		-	
Titi	-		1.61 $\pm$ 0.16		1.63 $\pm$ 0.16		1.86 $\pm$ 0.20	
Maud	1.61 $\pm$ 0.09		1.60 $\pm$ 0.15		2.11 $\pm$ 0.07		2.41 $\pm$ 0.07	
Nuku-waiata	1.39 $\pm$ 0.12		-		-		2.24 $\pm$ 0.08	
Whakaterere-papanui	1.32 $\pm$ 0.20		-		-		-	

DISCUSSION

Marine effect

The stable isotope analysis revealed measurable effects of seabirds in Marlborough Sounds island ecosystems. Greater *marine effect* was measured on seabird-inhabited islands than on seabird-free islands. Finding marine-derived nutrients in the tissues of animals from a range of trophic levels provides evidence that the high numbers of lizards and invertebrates found on seabird-inhabited islands (see Chapter 3) could be supported by the seabird's nutrient input.

Terrestrial plants obtain their carbon from the atmosphere. On well-vegetated islands the greatest input of carbon into the detrital food-web is likely to come from terrestrial plants. In this study soil $\delta^{13}\text{C}$ was much closer to that of plants than that of seabirds (Table 4.2), and one can conclude that marine-derived carbon has relatively little importance in making up soil detritus. Because the animals in this study are likely to be reliant on the detrital food-web, much of their carbon input will be terrestrial based.

Terrestrial plants obtain nitrogen from soil. Delta ^{15}N values of soils and of plants appeared to vary in relation to seabird density (Table 4.2) and one can conclude that a significant proportion of the nitrogen entering the detrital food-web is likely to be derived from marine sources. Animals consuming this marine-derived detritus will show a marine effect in their tissues. Carnivores such as spiders will have very little direct input from terrestrial plants or of detritus. The isotope ratio of their tissues reflects that of the small animals that are their prey.

Much greater differences were seen between $\delta^{15}\text{N}$ of animals on seabird-inhabited and seabird-free islands than between $\delta^{13}\text{C}$ of animals on the same islands (Table 4.3). The importance of marine-derived carbon in the calculation of *marine effect* is likely to be relatively small. The nitrogen isotope signature provides the greatest degree of differentiation between seabird-inhabited and seabird-free islands.

The calculated *marine effect* values indicate that a proportion of the diet of animals from a range of trophic levels is derived from seabirds. Some of this input may be direct, with animals feeding on marine detritus such as guano, eggshells or carcasses. Other species may be consuming seabird-dependent species, such as ectoparasites. Others may

ingest marine-derived nutrients by less direct routes such as consuming plant detrital matter that has a marine isotopic signature.

The highest *marine effects* were measured on North Brother Island. Vegetation is considerably sparser on this island than on other, more sheltered sites in the Marlborough Sounds (Wilson et al. 1993). Marine-derived nutrients are likely to have greater importance on a poorly vegetated island than on one with adequate *in situ* productivity (Anderson and Polis 1998).

Although the lowest *marine effects* were measured on seabird-free Nuku-waiata and Whakatere-papanui, they were not zero. Nitrogen isotope signatures of past seabird colonies remain in the soil for many years after they have been vacated by the birds (Mizutani et al. 1991). Finding a *marine effect* on Nuku-waiata and Whakatere-papanui provides evidence that seabirds were once more widespread on both of these islands. It is likely that they were removed when rats became established on the islands.

Trophic levels

Plants are the base of food chains. Although *Coprosma*, *Lolium* and *Macropiper* are common plants in the areas studied, they only represent a portion of the vegetation at each site. Herbivores and detritivores are likely to be feeding on plant matter from a range of different plants and not just the three studied. Values of $\delta^{15}\text{N}$ for different species of plants show considerable variation (Peterson and Fry 1987). Although the species chosen are common on Marlborough Sounds islands, they only represent a fraction of the total

seabird-inhabited islands had *relative trophic level* greater than those of amphipods on the same islands. This may indicate an increased use of seabird-derived detritus in the beetles' diets. The difference was not seen on seabird-free islands where detritus from seabirds is not directly available.

Gecko *relative trophic levels* on seabird-inhabited islands were not greater than that of *Mimopeus* beetles, but the *relative trophic level* of geckos on seabird-free islands was significantly higher than that of beetles and of geckos on seabird-inhabited islands (Table 4.5). The apparent difference between the *relative trophic levels* of geckos on the two categories of islands may be caused by different diets on the two islands (e.g. fruit may be more common on seabird-inhabited islands and so is eaten in preference to insects or carrion) or may be an artefact caused by differences in the isotope ratios of plants at the base of the food-webs. More detailed study is required to investigate this finding.

Spiders are carnivorous, and held the highest *relative trophic level* recorded in this study. No significant difference was found between *relative trophic level* of spiders on seabird-inhabited and seabird-free islands. They had $\delta^{15}\text{N}$ values that reflect that of their likely prey and are approximately one *relative trophic level* above soil-dwelling detritivorous amphipods on both seabird and seabird-free islands (Table 4.5).

Rat effects

Although some species were not able to be sampled on islands with rats, rodent presence *per se* did not appear to have a significant impact on the isotope ratios measured on seabird-free islands. The isotope values measured for animals on Whakatere-papanui and Nuku-waiata were broadly similar to those on rat-free Maud Island (Table 4.3). Although the *relative trophic level* on Whakatere-papanui and Nuku-waiata was lower than that on Maud Island (Table 4.5), it is more likely that this is caused by differences in vegetative structure on the islands (see below) than by a rodent effect.

Habitat variation and effects of seabirds on soil and plants

Habitat heterogeneity may explain some of the variation in plant isotope ratios. *Macropiper* $\delta^{13}\text{C}$ values were significantly lower than those of *Coprosma* and *Lolium*

(Table 4.2). Although within the range recorded in other studies (DaSilveira et al. 1989, Martinelli et al. 1991), *Macropiper* $\delta^{13}\text{C}$ values were significantly less than the -28‰ expected from the majority of previous studies (e.g. Peterson and Fry 1987, Mizutani and Wada 1988, Martinelli et al. 1991, Ramsay and Hobson 1991, Cormie and Schwarcz 1994, Koch et al. 1995).

Although not tested in this study, a potential cause of this difference can be postulated. Plant respiration and soil bacteria acting on detrital matter release CO_2 into the air with a carbon isotope ratio similar to that of their substrate (i.e., that of plant tissue, ~ -28‰) (DaSilveira et al. 1989). The CO_2 of forest air otherwise has a $\delta^{13}\text{C}$ value close to that of the atmosphere as a whole (~7‰). Because air mixing is slow near the ground, stratification of CO_2 is more pronounced low in the canopy than at the tree-tops and respired CO_2 with low $\delta^{13}\text{C}$ values accumulates near the ground (DaSilveira et al. 1989). Therefore, plants in the understorey assimilate recycled CO_2 with a low $\delta^{13}\text{C}$ value and have tissues more depleted in ^{13}C than plants higher in the canopy (Martinelli et al. 1991). *Macropiper* is an understorey plant and the majority of *Macropiper* samples were collected in forest habitats (Table 4.1). Although the low stature, high wind environment of forest on New Zealand islands may reduce the effects, the low $\delta^{13}\text{C}$ values of all *Macropiper* samples could be explained by the position of *Macropiper* under forest canopy and recycling of bacterially respired CO_2 with low $\delta^{13}\text{C}$ values.

Macropiper was collected more frequently on seabird-free islands than on those with seabirds (Table 4.1). The underlying difference in $\delta^{15}\text{N}$ values at sites with seabirds (where *Macropiper* was relatively infrequently sampled) probably caused the difference seen between *Macropiper* $\delta^{15}\text{N}$ values and those of the other plants. On seabird-free islands *Macropiper* $\delta^{15}\text{N}$ values were not significantly different from those of *Coprosma* and *Lolium*.

Conclusion

The data support the principal hypothesis of this work that a seabird effect is measurable in the diets of invertebrates and reptiles on seabird islands. The tissues of the amphipods, geckos, beetles and spiders measured on seabird islands had isotope signatures

further from a terrestrial extreme than did the tissues of the amphipods, geckos, beetles and spiders on seabird-free islands. The isotope analysis revealed a link between the marine ecosystem and the animals of the terrestrial island ecosystem.

The *relative trophic level* calculations provide evidence that animals of a range of trophic levels within the food-web are influenced by marine-derived nutrients. Addition of nutrients by seabirds increases the relative amount of animal matter in the forest floor detritus. Animals feeding on detritus on seabird islands will have higher $\delta^{15}\text{N}$ than detritivores on seabird-free islands. Differences will flow through the food-web so that *marine effect* and *relative trophic level* of animals throughout the food-web will be affected.

Future study

The stable isotope analysis carried out in this study proved an effective and relatively efficient method to study nutrient flow through island food-webs. In particular, nitrogen isotope analysis revealed clear differences between seabird-inhabited and seabird-free islands. Although future work should concentrate on $\delta^{15}\text{N}$ values, the use of two or potentially three different isotope signatures may still provide more accurate differentiation in some cases (see e.g. Hesslein et al. 1991).

Although differences were seen between isotope ratios on different islands, further work is necessary to confirm any conclusions. The range of different taxa measured, and especially different plant species, needs to be increased before firm conclusions about trophic levels can be reached.

More detailed study of the diets of animals on the different islands are necessary to confirm the results. The *relative trophic levels* calculated provided an indication that the diets of the different animals may vary between different islands, but more data are needed to confirm this. Although seabird-derived products are available on seabird-inhabited islands, there are no data as to the extent to which they are consumed.

It also remains to be shown that any differences found can be directly attributed to the nutrients brought to an island by seabirds. Other factors, such as the presence or absence of rats could be causing dietary differences between the different islands. The

presence of rats may lead to removal of certain taxonomic groups from an island, forcing their initial predators to change their diets. Detailed dietary studies on the different islands should further describe the causes of any variation.

Significant differences were found between the carbon isotope ratios of different taxa of plants on the different islands. A possible cause of this difference was the gas dynamics under forest canopy and in the open. Sampling of the isotope ratios of air at the different sites and at different strata within forest would help answer this question (attempts were made to sample air during this study, but were unsuccessful for technical reasons). Sampling a greater number of plant taxa could also increase the accuracy of any conclusions.

Stable isotope analysis can reveal that conditions on seabird-inhabited islands are different from those on seabird-free islands. Other methods are necessary to measure the mechanisms bringing about changes to the ecosystem. A key to many of the differences between seabird-inhabited and seabird-free islands may be variation in productivity. Changes to ecosystem dynamics may be brought about by increases in overall system productivity due to fertilisation of primary producers by seabird-derived-nutrients and by soil perturbation. Measurement of primary productivity on different islands could reveal a possible mechanism whereby seabirds have a direct impact on the island ecosystems in which they live.

Chapter 5: Soil nitrogen and carbon:nitrogen ratios on seabird-inhabited islands

INTRODUCTION

Groups of organisms that are important in maintaining the organisation and diversity of ecological communities have been labelled keystone species (Paine 1969, Mills et al. 1993, Power et al. 1996). If species that can be shown to be crucial in maintaining the organisation and diversity of an ecosystem do not fit into the accepted definition of keystone, the paradigm would seem to be of little practical use. Seabirds on New Zealand offshore islands were found not to conform to the definition of keystone proposed by Power et al. (1996) (Chapter 3). Despite this, I contend that seabirds have a significant impact on island ecosystems. In this chapter I test this assumption, and so test the validity of the current definition of keystone species.

Seabirds may cause changes to the islands on which they occur by influencing primary productivity. I measure two determinants of primary productivity: total soil nitrogen and the soil C:N ratio, to determine if significant variation is seen between sites with and without seabirds and so measure the importance of seabirds to island systems.

Seabird guano and soil nitrogen

Plant growth throughout the world is often restricted by the supply of available nitrogen (Lee et al. 1981). Addition of nitrogen (as fertiliser) will often increase plant productivity (Pastor et al. 1984). Large volumes of nitrogen-rich seabird guano are deposited onto seabird colonies (Burger et al. 1978). Some simple calculations can estimate the quantity of guano brought to Takapourewa in the Marlborough Sounds by fairy prion (*Pachyptila turtur*) adults feeding their chicks. By their nature, these calculations can only be approximate, but they can give an indication of the magnitude of the nutrient input.

Approximately 43 days pass between hatching and fledging of fairy prion (Richdale 1944a, Harper 1976). The chicks hatch at between 10-20 g in weight, and increase steadily

until about 160 g 30 days after hatching. From that point, chick weight declines to the average fledging weight of approximately 100 g 43 - 44 days after hatching (Harper 1976). An approximate average chick mass throughout the whole period is 93 g. Surface nesting seabirds on Marion Island excrete on average 10.7 ± 3.9 g dry guano per kg body mass per 24 hour period (mean $\pm$ 1SE) (Burger et al. 1978). Therefore I estimate that a fairy prion chick on average excretes 0.99 ± 0.36 g dry guano per day or 43 ± 16 g dry guano in the 43 days between hatching and fledging.

To calculate total chick guano input it is necessary to determine the total number of chicks on the island. By multiplying the land area of different habitat types (Grant et al. 1992), fairy prion burrow density in each habitat (Appendix 1) and the fledging success of chicks in each habitat (Appendix 2), the total number of chicks fledged on Takapourewa can be calculated. I thus estimate that the total number of fairy prion chicks successfully reared on Takapourewa in one season is 686 860.

Given that each chick excretes on average 43 ± 16 g dry guano, and there are 686 860 fairy prion chicks, $29\,534\,980 \pm 10\,989\,760$ g or between 18 500 and 40 500 t of dry guano is excreted onto Takapourewa every season. On 150 ha Takapourewa, I estimate that between 123 t and 270 t of chick guano are added per hectare. On the New Zealand mainland in 1996, 3 273 059 t of solid fertiliser were added to the approximately 5 000 000 ha of arable land (N.Z. Meat and Wool Boards 1997), or 0.65 t/ha. Hence 200 times more fertiliser is added to Takapourewa soil per hectare than that used to enhance plant growth on the mainland.

These calculations include only one, albeit substantial, route of nutrient input to Takapourewa. Adults also excrete on land, although they spend time at sea, and so quantities will be lower than that produced by chicks. A significant mass of nutrients are also added to seabird colonies in the form of unhatched eggs, egg shells, shed feathers and carcasses of chicks and adults that die on land (Williams et al. 1978, Williams and Berruti 1978).

In this study I compare the soil nitrogen levels on islands with and without seabirds and test the hypothesis that there is no significant difference between the levels of soil nitrogen on seabird-inhabited and seabird free-islands.

Seabird burrowing and soil C:N ratios

Nitrogen turnover rate, and thereby the potential for its recycling to plants, increases with decomposition rate (Bosatta and Staaf 1982). The C:N ratio of litter at a site is an important predictor of the decomposition rate (Taylor et al. 1989). In general, sites with low C:N ratios have high resource quality and rapid rates of decomposition (Killham 1994). Sites with rapid decomposition will have a relatively rapid rate of nitrogen-mineralisation, hence high available nitrogen and a concomitant increase in above-ground productivity (Pastor et al. 1984).

As well as adding nutrients, seabirds have considerable physical impact on the islands on which they live, most obviously by digging burrows. Soils on seabird islands are friable and homogenous, without clear soil horizons (Ward 1961, Atkinson 1964). Mixing may ensure that large amounts of humus do not build up on the soil surface and relative amounts of soil carbon are relatively low. Soil C:N ratios at seabird-inhabited sites may be lower than those at seabird-free sites, thereby increasing available nitrogen and plant productivity.

The level of organic carbon in soils from Cook Strait islands will be measured, and compared to the nitrogen content to get a measure of the resource quality at the different sites. I test the hypothesis that no significant difference is seen between the C:N ratios on seabird-inhabited islands and seabird-free islands.

METHODS

Soil sampling

Two islands on which seabirds currently nest were selected, Takapourewa (Stephens Island) and Titi Island in Cook Strait, New Zealand (Fig. 2.1, Table 2.1). As comparison, soils from Maud Island, Nuku-waiata and Whakatere-papanui (with no or very low numbers of seabirds) were also analysed (Table 2.1).

Soil properties of a site may be influenced by the surrounding vegetation. Sampling was carried out in superficially similar regenerated forest on Titi Island and Nuku-waiata and in scrub and regenerating forest on Whakatere-papanui. Sampling on Maud Island was carried out in mature virgin forest. Soil samples were collected in four different habitat

types on Takapourewa (pasture, grassland, scrub and forest) to measure the effect of habitat type on soil carbon and nitrogen percentages (Chapter 2).

On Takapourewa samples were collected in 24 subsites (six in each habitat type). On all other islands six subsites were selected. I randomly collected three soil samples in each of the 48 subsites during the austral summer of 1995-1996. A sample of approximately 200 grams was collected from between 5 and 10 cm depth. Soil was sealed in plastic bags and returned to the laboratory within 48 hours. Samples were chilled at 4°C until analysed. They were oven dried at 50°C then finely crushed and sieved to remove large particles and vegetable matter before analysis.

Nitrogen measurement

Samples were powdered with a mortar and pestle. The soil was digested with concentrated sulphuric acid which converted the nitrogen-containing substances into ammonia. Ammonia was then fixed by the excess acid as ammonium sulphate. Ammonia was released by adding an excess of sodium hydroxide to the solution. The ammonia concentration was determined with an ammonia sensitive electrode and an Orion Microprocessor Ionalyzer. N content is directly proportional to ammonia concentration.

Carbon measurement

Samples were powdered with a mortar and pestle, then heated in the presence of potassium dichromate and a concentrated sulphuric-phosphoric acid mixture. Organic matter in the soil was oxidised to CO₂ and passed through an open ended tube containing soda lime. Increase in weight of the soda lime after 20 minutes is proportional to the amount of carbon in the sample.

RESULTS

Significant differences were found between the percentage nitrogen in soils at the different sites (Kruskal-Wallis $H_{[4,43]} = 26.24$, $P < 0.05$). The greatest values were recorded on Titi Island, and Maud Island (Table 5.1). Soil nitrogen levels recorded on Takapourewa

were not significantly greater than those on Nuku-waiata. Soil nitrogen values from Whakatere-papanui were not significantly different from those on Nuku-waiata.

The highest levels of soil carbon were found on Maud and Titi Island. Soil carbon values did not differ significantly among the remaining sites (Table 5.1). Significant differences were found between the C:N ratios at the different sites ($F_{[4,43]} = 16.53$, $P < 0.05$). Whakatere-papanui had the highest ratio, and Takapourewa the lowest. Titi, Maud and Nuku-waiata were intermediate between these extremes (Table 5.1).

Soil nitrogen percentages did not differ significantly between the different habitat types on Takapourewa ($F_{[3,20]} = 2.76$, $P > 0.05$). Because of differences between carbon percentages in the different habitat types, significant differences were found between the C:N ratios in different vegetation types on Takapourewa ($H_{[4,43]} = 13.09$, $P < 0.05$). Mean C:N ratio in pasture and in forest were significantly lower than those in scrub and grassland.

DISCUSSION

Nitrogen

The hypothesis that soil nitrogen levels are not significantly different on seabird-inhabited and seabird-free islands was not able to be rejected in this study. Although soil nitrogen levels on seabird-free Nuku-waiata and Whakatere-papanui were lower than those on (seabird-inhabited) Titi Island and Takapourewa, nitrogen levels on (seabird-free) Maud Island were as great as those on the seabird-inhabited islands.

TABLE 5.1. Mean percentage carbon and nitrogen, and mean C:N ratio (± 1 SE) in soils on islands in the Marlborough Sounds. Seabird-free sites are shaded.

	Carbon		Nitrogen		C:N Ratio	
	Mean	SE	Mean	SE	Mean	SE
All Takapourewa	4.97 $\pm$ 0.68		0.89 $\pm$ 0.07		5.35 $\pm$ 0.48	
Titi	13.86 $\pm$ 0.60		1.54 $\pm$ 0.15		9.38 $\pm$ 0.82	
Whakatere-papanui	3.71 $\pm$ 0.38		0.28 $\pm$ 0.04		13.48 $\pm$ 0.94	
Nuku-waiata	4.81 $\pm$ 0.94		0.57 $\pm$ 0.06		8.39 $\pm$ 1.24	
Maud	13.57 $\pm$ 4.03		1.43 $\pm$ 0.35		8.77 $\pm$ 0.72	
Takapourewa forest	2.46 $\pm$ 0.42		0.70 $\pm$ 0.07		3.58 $\pm$ 0.50	
Takapourewa pasture	2.93 $\pm$ 0.60		0.80 $\pm$ 0.18		3.74 $\pm$ 0.16	
Takapourewa grassland	7.95 $\pm$ 1.23		1.19 $\pm$ 0.11		6.90 $\pm$ 1.08	
Takapourewa scrub	6.55 $\pm$ 1.45		0.87 $\pm$ 0.13		7.20 $\pm$ 0.65	

The %N found in soils on all islands investigated during this study was as great as that found on other seabird influenced sites around the New Zealand coast (Leamy and Blakemore 1960, Atkinson 1964) but not as high as those found around nests in a gannet colony (Blakemore and Gibbs 1968). Although greater than most grassland soils (e.g. Brevedan et al. 1996), the nitrogen level of soils from Marlborough Sounds islands was well within the range of %N in forest soils from around the world (Vitousek et al. 1982, Pastor et al. 1984).

In spite of the high guano input onto seabird-inhabited islands, nitrogen levels were not significantly different from those in other sites. Differences in vegetation or parent material may lead to changes in soil nitrogen greater than those caused by seabirds. Although differences were not seen between the nitrogen levels in different habitats on Takapourewa, it is possible that inter-island variation has occurred. Seabird-free Maud Island had relatively high nitrogen levels. The forest patch in which sampling was carried out on Maud Island is a remnant of virgin forest (Cannington 1982) and has not suffered burning. The original forest cover on Takapourewa, Titi, Nuku-waiata and Whakatere-papanui has been cleared, probably by fire, at sometime during the past (Gaze 1982, Walls 1984, East et al. 1993). Nitrogen can be volatilised from the soil by fire (Barbour et al. 1980). This may be affecting the results found. Further work is necessary to confirm this hypothesis. The nature of the nitrogen added by seabirds could also affect the results. Ammonium from seabird guano may be readily volatilised from soil (Mizutani and Wada 1988, Mizutani et al. 1991).

Carbon : nitrogen ratio

The C:N ratio of soils on seabird-inhabited Takapourewa was significantly lower than that at all other sites. On Titi Island, the other seabird-inhabited site, a high nitrogen content was found and the ratio of C:N was not significantly different from that on Maud Island or Nuku-waiata. Overall, the hypothesis that there is no significant difference between the C:N ratios of soils on seabird-inhabited and seabird-free islands was not able to be rejected.

In spite of the similar seabird densities in all of the four habitats sampled (appendix 1) significant variation was seen in the soil C:N ratios on Takapourewa. Habitat variation on the other islands in this study may be influencing the results found. Slightly different vegetation and history on each island could have lead to variation in the C:N ratios independently of seabird density. This may explain why no effect of seabirds was seen in the C:N ratios on different islands.

The carbon : nitrogen ratios measured on Marlborough Sounds islands are comparable with those from other studies. Seabird-influenced soils on Mercury Island have a C:N ratio of between 9 and 11 (Atkinson 1964), while a value of 6 was recorded on Enderby Island, 13 on Ocean Island and 13-18 on Bream Island (Leamy and Blakemore 1960). Soils around gannet nests at Cape Kidnappers had C:N significantly lower than those found in this study (mean 2.025) (Blakemore and Gibbs 1968). The C:N ratios of soils on Marlborough Sounds islands were significantly lower than those measured at sites without a seabird influence, although the data are variable. C:N ratios of between 20 and 68 were recorded for peat soils on Auckland Island away from seabird colonies (Leamy and Blakemore 1960). Values of between 19 and 52 were recorded for C:N in a range of different North American forest types (Vitousek et al. 1982).

Conclusions

Seabird effects were seen in this study. Nitrogen levels on Takapourewa and Titi Island were greater than those on Nuku-waiata and Whakaterere-papanui. Similarly, C:N ratios on Takapourewa (where seabird density is significantly higher than any other site) were significantly lower than those on other islands. C:N ratios from other seabird-influenced sites are also much lower than those in seabird-free areas. Overall, because of the limitations of the study, more specifically because of the variation between the islands studied, statistically significant effects could not be shown. To increase the rigour of the analysis, and to be able to make more conclusions, it is necessary to increase the scope of the study. Different islands should be included so as to eliminate potentially confounding variables. Although it was not attempted in this study, confirmation of the effect of homogenising soils on productivity could be achieved by artificially homogenising soils in

sites without seabirds. Measures of plant productivity, such as increase in trunk girth or litter-fall, could be measured over time.

Because unequivocal effects were not found, it is not possible to make firm conclusions as to the keystone status of seabirds based on the data from this study. Seabirds may have important effects on soil nitrogen levels and hence on productivity, but it was not shown that they are crucial to ecosystem function. Data on seabird-influences on soil nitrogen and soil C:N ratios alone cannot be used to reject the applicability of the keystone species concept.

Chapter 6: Keystone species on New Zealand offshore islands

Seabirds and rats both play significant roles in determining structure and function of New Zealand offshore island ecosystems (Atkinson and Bell 1973, Whitaker 1973, Daugherty et al. 1990, Cree et al. 1995). Groups of organisms that are important in maintaining organisation and diversity of ecological communities have been labelled keystone species (Paine 1969, Mills et al. 1993). In this chapter I collate and summarise details of the significant effects of seabirds and rats elucidated during my work on Marlborough Sounds Islands. I use this information to appraise the keystone species concept, and more specifically to demonstrate the inapplicability of the definition of keystone species as proposed by Power et al.(1996) for ecology and conservation purposes.

SEABIRDS AS KEYSTONE SPECIES

Seabird influences on their environment

Seabirds add significant amounts of nutrients to the island systems on which they nest. Marine-derived resources are transferred to islands in the form of guano, unhatched eggs, egg shells, shed feathers and carcasses of chicks and adults that die whilst on land (Burger et al. 1978, Williams et al. 1978, Williams and Berruti 1978, Chapter 5). As well as adding nutrients, seabirds also have considerable physical impact on the islands on which they live, most obviously by digging burrows. Substantial amounts of soil are moved by the seabirds in the construction and maintenance of burrows. The earth moving activities further enhance the effects of nutrient addition by seabirds. Soils on seabird islands are dry and friable (Atkinson 1964). They are also very homogenous, and the burrowing activities of the birds remove visible soil horizons (Ward 1961). Guano deposited by burrow nesting seabirds on New Zealand offshore islands does not build up on the surface as it does on "phosphate" islands such as Nauru (Manner and Morrison 1991). Instead it is constantly mixed through the soil and can enhance plant growth rates (Furness 1991).

Effects of seabirds on Marlborough Sounds islands

Fertilisation and nutrient addition by seabirds on Marlborough Sounds islands has quantifiable effects on the island ecosystems. The effects identified in this study and some of the methods used to relate these effects to seabirds are outlined below.

Seabird effects on small invertebrates - Significantly more beetles and greater ordinal and beetle RTU diversity were found on seabird-inhabited, rat-free Takapourewa than on seabird-free, rat-free Maud Island (Chapter 3). This provides evidence that the energy provided, the environmental modification and the extra niches created by seabirds can be important in maintaining the organisation and diversity of island communities. Some species are directly dependent on seabirds. Scavenger, detritivore and avian ectoparasite numbers will increase in proportion to the number of seabirds at a site (Polis and Hurd 1996). The homogenisation and the fertilisation due to guano and other nutrient addition can significantly increase the plant productivity in an area (Williams et al. 1978, Furness 1991). Increases in plant productivity increase the amount of energy available and therefore increase the absolute number of organisms that can be supported at a site. Increases in plant productivity allow increased numbers of consumer invertebrates to survive. Abundance and diversity of predators of the animals directly and indirectly supplemented by seabirds can also be increased by increases in seabird energy input.

Seabird effects on lizards - In this study, the greatest abundance of lizards was measured on seabird-inhabited Takapourewa, North Brother and Titi Island. Skinks and geckos have a diet that includes carrion and small invertebrates (Gill and Whitaker 1996). The food available in seabird colonies, as well as the increased numbers of small invertebrates (see above), may provide the resources necessary to maintain increased numbers of reptiles.

Carbon and nitrogen isotope analysis - Stable isotopes can be used to trace the paths taken by nutrients through an ecosystem. Using stable isotopes I calculated the *marine effect*, i.e. the importance of seabird-derived nutrients in the diet of animals on different islands. Amphipods, geckos, beetles and spiders on seabird islands showed significantly greater *marine effects* than did amphipods, geckos, beetles and spiders on seabird-free islands (Chapter 4). Because there is a link between seabirds and the animals of the terrestrial island ecosystem, differences in invertebrate and reptile abundance or diversity between seabird-inhabited and seabird-free islands can be attributed to seabirds.

Seabird effects on soil - Soil carbon and nitrogen levels are influenced by the presence of seabirds. Although no significant differences were found, the C:N ratio of soils in seabird colonies in this study and at other sites was lower than that at seabird-free sites (Atkinson 1964, Blakemore and Gibbs 1968, Leamy and Blakemore 1960, Vitousek et al. 1982, Chapter 5). It is likely that nutrient addition, coupled with the effects of burrowing and the resulting homogenisation of soil horizons, mixed decomposing vegetative matter through the soil and decreased the relative amount of available carbon. The low C:N ratio indicates high decomposition rates and rapid release of nutrients into the soil. Hence the burrowing activity of seabirds can increase the productivity of seabird sites.

RATS AS KEYSTONE SPECIES

While seabirds support higher biodiversity at a site, rats in general have the opposite effect. Kiore (Polynesian rat, *Rattus exulans*), Norway rats (*R. norvegicus*), and ship rats (*R. rattus*) have a dramatic impact on the flora and fauna of New Zealand offshore islands (Atkinson and Bell 1973, Gibb and Flux 1973). The extinction of a range of different bird species can be directly or indirectly attributed to kiore (Holdaway 1989). Tuatara density and recruitment rates are lower on islands with kiore than islands without (Cree et al. 1995). Small prions are often rare on kiore inhabited islands (Merton. 1970, Crook 1975). The average number of lizard species found on an island is reduced by the presence of rats (Whitaker 1973, Towns 1991, Towns et al. 1985). The viability of many invertebrate populations is threatened by rodent presence (Atkinson and Bell 1973, Gibb and Flux 1973, Hicks et al. 1975, Meads et al. 1984, Campbell et al. 1984).

Effects of rats on Marlborough Sounds islands

Rat effect on small invertebrates - Islands with rats had lower average number of beetle RTUs per trap than did rat-free islands (Chapter 3). Rat-free Takapourewa had the greatest diversity and rat-inhabited Whakatere-papanui had the lowest. Significant differences were also seen between the abundance of invertebrates caught per trap-night on rat-free and rat-inhabited islands. Lower overall numbers of small invertebrates were caught on the rat-inhabited islands than on the rat-free.

Rat effects on lizards - Lower numbers of lizards were found on islands with rats than on those without (Chapter 3). In spite of intensive searching, no lizards were found on Nuku-waiata, from where rats have only recently been eliminated. Although individuals of both *Oligosoma lineocellatum* and *O. nigriplantare polychroma* were found on rat-inhabited Whakatere-papanui, abundances were orders of magnitude lower than those in similar habitats on rat-free Takapourewa.

RELATIVE IMPORTANCE OF SEABIRDS AND RATS

The islands chosen in this study allow comparison of different effects with other factors held constant. Islands were chosen to allow comparisons of the effects of 1) seabirds in the absence of rats, 2) rats in the absence of seabirds, 3) seabirds in the presence of rats. The diversity at sites exhibiting the specific features was compared to determine the relative importance of the different affects.

The difficulty of predicting the identity of the next individual collected from a community, and hence a measure of diversity at a site, is given by the Shannon-Wiener function (Krebs 1985):

$$H = -\sum_{i=1}^s (p_i)(\log_2 p_i)$$

where H = Shannon-Wiener index of diversity and p_i = proportion of total sample belonging to the i th species. I calculated H for the animals caught at different sites to make comparisons of diversity under different conditions.

I calculated a Shannon-Wiener index for small insects (H_i), another for small beetles (H_b) and a third for lizards (H_l). In order to weight vertebrates and invertebrates equally, I divided H_i and H_b by two. I added:

$$\frac{H_i}{2} + \frac{H_b}{2} + H_l$$

to give one combined index for small insects, small beetles and lizards. The resulting statistic (H_T), henceforth known as *total diversity*, was calculated for each site (Table 6.1).

The highest *total diversity* recorded was 3.61, calculated for Takapourewa (Table 6.1). *Total diversity* for North Brother was next lowest, followed by Maud Island (Table 6.1). The lowest values were from sites where rats were or had been present (Titi Island, Nuku-waiata and Whakatere-papanui) (Table 6.1).

Seabirds, rats and total diversity

Factors other than seabird abundance and rat presence/absence differ between the islands in this study. Another significant difference between the islands is their size. Although there is a more than 70-fold difference in size between the islands, there was no correlation between island size and *total diversity* ($r = -0.003$). In contrast, there was a high correlation between rat presence/absence and *total diversity* ($r = -0.78$) and between seabird density and *total diversity* ($r = 0.96$). Although species-area relationships may be having an effect on the diversity found at the different sites, the effects of seabirds and rats are greater.

Total diversity was consistently greater in seabird-inhabited sites than at seabird-free sites (Table 6.1). Seabirds have a consistent effect on invertebrate and lizard biodiversity. Lizards and invertebrates are distinctive and important members of the biota of New Zealand offshore islands (Daugherty et al. 1990), and so one can conclude that seabirds do play a significant role in maintaining island ecosystem structure and function. *Total diversity* was consistently lower on rat-inhabited sites than on rat-free sites (Table 6.1). Maud Island H_T was greater than that on both of the rat-inhabited islands, Nukunui and Whakarewa (Table 6.1).

In most cases, the presence or absence of seabirds is not independent of the presence or absence of rats. As well as reducing the numbers of lizards and invertebrates on an island, rats also reduce seabird numbers (Merton 1970). Although seabirds are present on Titi Island, the historical presence of rats means that seabird density is a fraction of that found on Takapourewa (Chapter 2). Comparisons with Titi Island show the indirect effect of rats due to reduction in seabird numbers as well as direct predatory effects on

TABLE 6.1. Shannon-Wiener (H) values for small invertebrates, small beetles and lizards and combined index of the three. Small invertebrate and small beetle indices are divided by two in calculating Total H . Seabird-free sites are shaded.

	H values			
	Small invertebrates	Small beetles	Lizards	Total H
Takapourewa	1.23	4.59	0.70	3.61
North Brother	1.08	2.52	0.88	2.68
Titi	1.31	0.54	0.65	1.58
Maud	1.35	2.61	0.00	1.98
Nukunui	1.18	2.12	0.00	1.65
Whakarewa	2.12	0.07	0.00	1.54

lizards and invertebrates. *Total diversity* from Titi Island was lower than that from rat-free Maud Island, and was not significantly greater than that on rat-influenced Nuku-waiata and Whakatere-papanui (Table 6.1). Although low numbers of seabirds are present on Titi, their effect cannot compensate for the historical effect of rats, and the *total diversity* is closer to that of a rat-influenced island than a rat-free one.

The difference in *total diversity* between Titi Island (with relatively low numbers of seabirds) and Takapourewa (with relatively high numbers of seabirds) was 2.03 (Table 6.1), the greatest of any of the comparisons made. The comparison between Titi Island and Takapourewa shows how the reduction in seabird numbers intensifies the effects of rats on invertebrate and lizard diversity. Although seabirds may ameliorate the negative effect of rats to some extent, *total diversity* on Titi Island is still considerably lower than that in other seabird-inhabited sites. The positive effects of the relatively low density of seabirds are not great enough to overcome the negative effects of rat predation.

Keystone species?

To be useful, a definition of keystone should encompass species that are crucial in maintaining organisation and diversity in their ecological communities. The presence or absence of seabirds or rats materially alters the nature of an island ecosystem. Reptile and invertebrate numbers on an island are enhanced by seabird presence. When rats are introduced to an island, seabirds as well as a range of lizard and invertebrate species are likely to be eliminated or dramatically reduced in numbers. Hence both taxa play significant roles determining the composition of island ecosystems. The formula proposed by Power et al. (1996) did not support seabirds as keystone species. Similarly, rats were not conclusively shown to be keystone species, although they could not be classified as being non-keystones either (Chapter 3). Both seabirds and rats are crucial in determining the structure and function of island ecosystems, yet neither are defined as keystones. Based on the evidence from this study, the definition of keystone proposed by Power et al. (1996) is not useful for conservation or ecological purposes.

Conclusion: the future for keystones

The keystone species concept is ill-defined and imprecise in meaning (Mills et al. 1993). In spite of attempts to redress these flaws (Power et al. 1996), the overall situation

has not changed. Power et al.'s (1996) definition of keystone species is theoretically and practically difficult to calculate. What is actually being measured and the numerical thresholds required to achieve keystone status are yet to be elucidated (Chapter 3). Furthermore, doubt exists as to whether it is technically possible to ever define keystone species (Hurlbert 1997, Chapter 1).

Given these difficulties, it seems clear that continued attempts to define keystone species, and more especially the proposed usage of the keystone species concept by conservation managers, is fraught with pitfalls. Consequently, abandonment of the term seems the most appropriate course of action. In its place, the equally unmeasurable, but more clearly defined variables of *Functional Importance* or *Community Importance* (Hurlbert 1997, Mills et al. 1993) can be investigated for theoretical purposes. For conservation management purposes, no "silver bullets" are likely to ever be found. However concentration on functionally important species, be they abundant or scarce, is likely to provide at least some positive effects for conservation projects.

Seabirds and rats as keystone species

The significant roles played by both seabirds and rats in determining structure and function of New Zealand offshore island ecosystems were illustrated in this study. Although effects varied with habitat types, seabirds and especially rats were shown to have measurable effects on small animal diversity and abundance on islands, and they are functionally important members of their ecosystem. Power et al. (1996) proposed a definition of keystone in order to redress the flaws prevailing in the concept. Under this definition, neither seabirds nor rats were unambiguously shown to be keystone species. The definition remains flawed. Further attempts to define rats, seabirds, or any other species, as keystones will not help future study and management of island ecosystems.

Chapter 7: Conservation management implications

In this chapter I address six questions relating to conservation and management of island biotas.

1) What contributions do seabirds make to the ecology of New Zealand offshore islands that are important for conservation?

In this study, evidence was found that islands with seabirds were significantly more productive than islands without seabirds. The nutrients brought to islands by seabirds can permeate the entire ecosystem and have the potential to supplement the diets of a range of different species. Evidence of this was given by finding seabird derived nutrients in soil, plants and animals of a range of trophic levels on seabird islands (Chapter 4).

The physical activity of seabirds can also have significant effects on island ecosystem dynamics. The C/N ratio of soils on seabird islands were lower on seabird islands than on seabird-free islands (Chapter 5). Burrowing by seabirds mixes vegetable matter through the soil, lowering the C/N ratio and potentially increasing plant productivity.

Both the abundance and ordinal richness of small invertebrates were found to be significantly greater on islands with seabirds than on seabird-free islands (Chapter 3). The presence of seabirds creates niches that would not be present on islands without seabirds. The number of ectoparasitic or obligate scavenger species will increase in proportion to the number of seabirds at a site. The guano, food matter, feathers, eggshells and carcasses discarded by seabirds provide a source of food that can support detritivorous invertebrates (Polis and Hurd 1996) while increases in plant productivity caused by fertilisation and soil homogenisation by seabirds increase the food available for phytophagous invertebrates. Increases in the number of consumer invertebrates can increase the food available for predatory invertebrates.

Although lizard distribution was strongly influenced by species-specific habitat requirements, the greatest numbers of lizards recorded in this study were found on seabird-inhabited islands (Chapter 3). Seabird derived nutrients can provide a food source for lizards, and increases in small invertebrate abundance due to seabirds can further supplement lizard diets on seabird-inhabited islands.

Because of the importance of seabirds to other members of the island ecosystem, translocation of seabirds to islands from which they have been eliminated should be a key component of New Zealand island restoration projects. Energy brought to islands by seabirds has been gained at sea (Furness and Monaghan 1987). It is therefore a supplement to any *in situ* production on an island. Seabird-derived energy is transferred throughout the whole island foodweb (Chapter 4). Because of the interconnectedness of island foodwebs it would be very difficult to artificially supply the energy and nutrients required by an island biota.

Many species may rely on seabirds to provide specific habitat requirements. Ornithocoprophilic plants such as *Senecio sterquilinus* grow only in the high nutrient conditions created by seabirds (Campbell 1967). Seabird chicks provide food for tuatara over the summer months when invertebrate prey is scarce (Walls 1981).

If the energy provided and the unique niches created by seabirds were unavailable it is unlikely that the high abundance and diversity of invertebrates and reptiles found on seabird-inhabited islands (Daugherty et al. 1990) could be sustained in an island restoration programme.

When seabirds are translocated between islands, the means of establishment may be important. Some of the ecosystem effects of seabirds (e.g. decreases in C:N ratios) are caused by the birds' burrowing and soil homogenisation. Artificial burrows to provide temporary homes for new seabirds should not be completely sealed from the soil and should allow birds to dig their own passages. At sites with very hard soil it may be necessary to artificially perturb soil around burrow sites so that the birds are able to commence digging for themselves.

2) What changes to ecosystem processes arise from (a) the introduction and (b) the eradication of rats from New Zealand offshore islands?

I found that islands with rats had lower abundance of lizards than rat-free islands (Chapter 3). The abundance and diversity of small invertebrates was also significantly lower on rat-inhabited islands than on rat-free islands (Chapter 3). These findings support the conclusions of other studies of rat effects on offshore islands (Atkinson and Bell 1973,

Crook 1973, Gibb and Flux 1973, Hicks et al. 1975, Whitaker 1973, 1978, Ramsay 1978, Bremner et al. 1984, Meads et al. 1984, Campbell et al. 1984, Towns 1991, Cree et al. 1995).

The extinction of species from rat-inhabited islands was not universal. Well-defended species such as carabid beetles appeared resistant to rat predation and were relatively abundant on Nuku-waiata where other common island species such as *Mimopeus* beetles were not seen (Markwell *unpublished data*). Because rats appear to selectively avoid some species, the balance of the foodweb is changed. Predation by rats may affect prey species that are not part of their diet (Chapter 3).

As well as depleting lizard and invertebrate numbers, rats can also eliminate seabirds from an island (Merton 1970). In this study, seabird numbers on islands on which rats live or have lived were significantly lower than those on rat-free islands (Chapter 2). Seabirds have significant positive effects on the abundance and diversity of invertebrates and reptiles on islands (see above). As well as directly reducing abundance and diversity of reptiles and invertebrates, rats reduce seabird numbers and thereby negate the positive effects of seabirds on island biotas. These indirect effects may be further reaching than the direct effects of rat predation. Removal of seabirds also removes all of the seabird derived niches on an island. Hence predation by rats can reduce the abundance of species with which they have no trophic links.

Rats can now be successfully removed from offshore islands and quantifiable changes in reptile and invertebrate numbers measured (Towns 1991, Rufaut 1995). Attempts can therefore be made to restore islands to their pre-rat state. In the course of restoration projects, it is likely that seabirds and large reptiles will be translocation targets. Invertebrates may be left to establish themselves as seabirds change conditions.

My data from Titi Island showed that removal of rats and the gradual (natural) reintroduction of seabirds did not lead to a natural re-establishment of invertebrate diversity (Chapter 3). Although invertebrate abundance on Titi was no lower than on Takapourewa, diversity was less. Dispersal over sea was presumably not possible for many of the small terrestrial invertebrates studied. If the aim of a conservation project is to restore an ecosystem to something resembling its pre-rat state, invertebrates need to be actively transferred. Identification and movement of individual small invertebrate species is

not a practical proposition, but samples of soil and leaf litter could be moved from island to island along with the birds and reptiles being actively managed. Because of the high levels of endemism found in New Zealand island invertebrate faunas (Watt 1986), transfers of unidentified small invertebrates should be between islands as geographically close as possible. Isolated islands (such as North Brother) should be avoided as target or source localities because endemism levels are likely to be particularly high and genetic diversity could be lost.

3) Is the keystone species concept useful for conservation?

The keystone species concept has been proposed as a useful tool for conservation (Simberloff 1990, Power et al. 1996). If species that greatly modify the structure and function of entire systems can be identified, scarce conservation resources can be concentrated on those species and system integrity maintained with a minimum of effort. However, keystone species are not readily identified in nature. Mills et al. (1993) found that the term keystone species was ill-defined and non-specific in meaning. In spite of attempts to redress these flaws (Power et al. 1996), the overall situation has not changed. Definitions of the keystone concept are still ambiguous, and what is actually being measured is yet to be elucidated. Furthermore, doubt exists as to whether it is technically possible to ever define a keystone species (Hurlbert 1997). For these reasons I do not think the keystone species concept is useful for conservation.

A management focus on species that are prominent members of a system will provide useful conservation outcomes. However, more will be gained by clearly defining a species' role in a system than by attempting to fit it into an arbitrarily defined pigeonhole. The significant roles played by seabirds and rats in determining structure and function of New Zealand offshore island ecosystems were quantified in my study. Rats and seabirds were shown to have measurable effects on small animal diversity and abundance on islands. Both taxa need to be included in any conservation plan for offshore islands. But defining either seabirds or rats as keystones could lead to ambiguous conclusions as to their role in an ecosystem and would not help achieve conservation goals.

4) How useful is stable isotope analysis for studying energy flow through New Zealand offshore island ecosystems?

I used stable isotope analysis to measure the extent of marine-derived (i.e. seabird-transferred) nutrients in island ecosystems. I found isotope analysis to be an efficient method of gaining information on nutrient and energy flows through an island foodweb.

Isotope analysis is a relatively quick means of determining general trends in an animal's diet. Although some samples must be preserved relatively soon after collection to avoid decomposition, little experimental work needs to be carried out in the field. For this reason, isotope analysis should prove particularly useful on isolated offshore islands where field time is often short and access limited.

Depending on the samples chosen and analysis carried out, stable isotope analysis can be used to gain insights into a range of biological problems. For example, historical vegetation patterns (McPherson et al. 1993), marine pollution (Van Dover et al. 1992), fish migration patterns (Hesslein et al. 1991), seasonal dietary variation by seabirds (Thompson and Furness 1995) and the arrival of rodents in New Zealand (Holdaway 1996) have all been investigated using stable isotopes.

Isotope analysis does have limitations. Significant variation can occur within the isotope signatures of individuals of one species. For example, the $\delta^{13}\text{C}$ values of *Macropiper excelsum* from different sites varied significantly, although all were absorbing atmospheric CO_2 (Chapter 4). The differences were probably caused by the specific environmental conditions in which the plants grew. A degree of temporal variation can also occur in plant isotope signatures (Bunn and Boon 1993). Because of the variation, isotope data cannot be transferred from one study to another. Isotope ratios of plants at the base of a foodweb need to be measured anew for each study.

Isotope analysis can be used to provide evidence that an animal is consuming plant matter from one of a set of known choices. It cannot be used to determine an unknown food source. To determine if an animal is eating something, one must compare the isotope ratio of the animal's tissues with those of the food. Finding that an animal's tissues have isotopic signatures significantly different from those of the supposed available foods will

only provide evidence that it is eating something else, and will not reveal exactly what that something else is (Bunn and Boon 1993). If an animal has a diet made up from two different sources the proportion of each potential food source can be calculated. If more than two food sources make up the diet, calculation of the proportion of each potential food source can be complicated.

Because of the inherent variation in the isotope ratios of plants and because of the difficulties in determining individual diets, detailed dietary studies using solely isotope ratios are difficult to carry out (although not impossible). Isotope ratios are best suited to investigation of coarse differences between the diets of different animals, such as determining if a carbon source is aquatic or terrestrial (e.g. Rounik et al. 1992).

The ease of interpretation of the results of isotope analysis depends on the situation in which the samples are taken. For example, on New Zealand islands where *in situ* productivity is relatively high even in the absence of seabirds and nutrient inputs come from a variety of sources, isotope analysis cannot provide evidence of an animal's exact diet. At other locations, such as the high temperature/low rainfall islands of Baja California, terrestrial plant biomass is very low (Polis and Hurd 1995, 1996). Nutrient input into the foodweb comes almost solely from a marine source (Due and Polis 1985, Polis and Hurd 1995, 1996) and animals in Baja California are highly enriched in ^{13}C . A marine effect is clear in the tissues of Baja California animals (Anderson and Polis 1998). Hence the conclusions that can be drawn from an isotope analysis depend on the site where the sampling was carried out. Methods that are successful in one area may not yield meaningful results in another.

5) How useful are miniature video cameras for studying subterranean species on New Zealand offshore islands?

I used a miniature video camera to study the inside of fairy prion burrows (Appendices 1 and 2). The camera enabled me to see inside seabird burrows and assess the breeding status of the birds inside. The study showed that miniature cameras are useful tools for study of subterranean animals such as seabirds and tuatara. For conservation purposes, cameras allow monitoring of population numbers and assessment of breeding by animals without resorting to potentially destructive or disruptive methods.

There were however some drawbacks to the use of the miniature video camera. Although faster than digging observation chambers, video camera monitoring of the small prion burrows was still a relatively slow process. Although suitable for monitoring a limited number of burrows, a large scale census of a seabird colony using a burrow camera could be a very time-consuming process.

The disturbance caused to burrow inhabitants by the intrusion of a camera was likely to be less than that caused by digging observation burrows. However the intrusion of any foreign object into an animal's nesting chamber is likely to cause some disturbance. Some of the adult and chick prions on Takapourewa pecked at the remote camera head in their burrows, presumably in an attempt to repulse it. In cases where breeding animals are very sensitive to disturbance, portable video camera monitoring should be approached with caution.

A final problem with video cameras is a reliance on electrical power to run the video camera, and the infra-red lighting necessary to see the images. During extended stays on isolated islands, the number of batteries needed for continued monitoring may be prohibitive. Solar panels that can be used to recharge batteries may get around this problem.

6) How should revegetation plans for Takapourewa be carried out?

In my study, and in similar work by East et al. (1995), significant differences were found between the abundance of lizard species in different habitats on Takapourewa. In particular, skinks were very common in grassland and scrub but rare in forest. These findings raise questions for potential conservation options on Takapourewa.

Restoration towards a pre-human condition is planned for Takapourewa (Miller and Gaze 1997). Revegetation will lead to increased forest cover on the island. In the short term this will increase abundance and diversity of lizards as open pasture is converted to scrub and longer grassland. In the longer term the high densities of lizards currently found on Takapourewa are likely to decline as forest cover increases.

Takapourewa is a highly modified island and, for a number of reasons, is never likely to return to a pre-human state. A lighthouse is situated at the north of Takapourewa,

and a certain degree of infrastructure will continue to be necessary for the maintenance of the light. There is a full-time conservation officer present on Takapourewa and the island is often used by research scientists. Facilities for support of humans such as houses with adequate sun-light, water supplies, generators, a helicopter pad and tracks will be required as long as people have a presence on the island. There are also a number of structures on the island, such as the lighthouse and some defence installations, that have "significant historic values" and will continue to be actively managed (Miller and Gaze 1997). Takapourewa is the home of a considerable portion of the world tuatara (*Sphenodon punctatus*) population. Some of the open areas required for successful hatching of tuatara eggs (Thompson 1990) are likely to be maintained throughout any revegetation programme.

Given that Takapourewa is never likely to be returned to a fully pre-human state and is already modified, an extensive revegetation programme may not be the ideal option. Greater value may be gained from the island by acknowledging that it is not pristine, and utilising the current conditions to enhance the range of species that live there. Maintenance of the current mosaic of forest, grassland and scrub should preserve the current abundance of lizards on the island without sacrificing any of the current biological diversity.

Although Takapourewa may not be able to be accurately restored, there are other islands in the area that are largely unmodified (such as the Trios), or lack a human presence and could be more fully restored (e.g. Nuku-waiata, Titi). Representatives of pre-human Marlborough Sounds islands will still be able to be found.

Appendix 1: Video camera count of fairy prion, sooty shearwater and tuatara on Takapourewa¹

INTRODUCTION

Because of the length and curvature of their burrows, nesting petrels are rarely able to be observed directly (Warham 1966), and it is difficult to take accurate censuses or determine breeding status and burrow occupancy. Some studies have been based on simple burrow counts (e.g. Skira et al. 1986, Hill and Barnes 1989), but little is known about the relationship between burrow entrance counts and the number of birds below ground. Monitoring only accessible burrows biases sampling, whereas destructive techniques involving excavating burrows are impractical, especially on hilly terrain, and ethically unacceptable. Indicators such as flattened vegetation or broken gates outside burrows (Warham et al. 1982) record only the first bird and do not allow estimation of numbers. Flexible tapes (Harper 1983) could be difficult to manipulate and would not be able to detect an unattended egg. Playing recorded petrel calls and listening for a response can determine if a burrow is occupied, but not all individuals respond to playback techniques (Norman Ratcliffe, RSPB *pers. comm.* 1997). Other techniques are equally imprecise (summarised in Dyer and Hill 1991). A method that avoids many of these problems is miniature video recording (Dyer and Hill 1991).

Takapourewa (Stephens Island) is situated off the north-eastern tip of D'Urville Island, in Cook Strait, New Zealand (41°40" E, 174°00" S) (Fig. A1.1). It is an internationally important wildlife sanctuary (Molloy and Dingwall 1990). It is rodent free and is one of the largest islands inhabited by tuatara (*Sphenodon punctatus*) (Newman 1987). An estimated one million fairy prions (*Pachyptila turtur*) (Harper 1985) and up to approximately 1000 sooty shearwater (*Puffinus griseus*) (*pers. obs.*) are seasonal breeders on the island. These birds bring nutrients, perturb soil and deplete undergrowth (Ward 1961, Campbell 1967, Walls 1978, Newman 1987). Because of the conservation significance of the island, it is important to understand ecological relationships, and

¹ Published as Markwell (1997)

FIG. A1.1. Location and map of Takapourewa.

numbers of animals involved so that risks to population viability can be assessed and impacts monitored.

As part of a larger study of the importance of seabirds, I used a modified video camera to estimate the densities of seabirds and tuatara in different habitats on Takapourewa. In this paper, I describe the design and use of this camera and compare it to a camera used by Dyer and Hill (1991) to study wedge-tailed shearwater (*Puffinus pacificus*) in the Capricorn Islands, Great Barrier Reef, Australia.

METHODS

Camera specifications

I used a Cohu 6700 series remote-head solid-state CCIR monochrome CCD camera, fitted with a Computar 3.6 mm 1:1.6 television lens. The camera and lens were enclosed inside a turned rigid nylon casing, with holes drilled in the front to hold lights. A glass disk was fitted inside the casing to protect the camera lens. The final remote head measured 49 mm in diameter and 114 mm in length (Fig. A1.2), approximately the same dimensions as the camera head used by Dyer and Hill (1991). I initially tried a wide-angle

lens, which I thought would give greater visibility in the burrows, but the protective case was too large to fit into the burrows, and so I subsequently used a smaller 3.6 mm lens.

Infra-red light emitting diodes (LEDs) were wired in parallel inside the camera casing to illuminate the burrows. I used infra-red diodes to minimise power consumption and because I expected their light to disturb the animals less than white light.

The remote camera head was connected to the camera control unit by 4.5 m of control cable, enclosed in a casing of garden hose. This length of cable enabled long burrows to be sampled, and shorter, adjacent burrows could be investigated without moving the control unit over terrain made fragile by the maze of burrows below the surface. Garden hose gave compressional strength that allowed the unit to be pushed into tight places, but was still flexible enough to get around bends in the tunnel. Electricians' insulation tape sealed the join between the camera head and the hose. The tape provided a waterproof seal that could be removed and replaced in the field in the course of running repairs on the camera. Dyer and Hill (1991) used a rubber sock to seal the join between their camera head and hose. The sock was found to be unsatisfactory because it bunched and shifted in tight burrows, allowing penetration of water and sand into the equipment. The final model designed by Dyer and Hill (1991) had a larger sock sealed with electrical

FIG. A1.2. Dimensions (in millimetres) of the remote camera head enclosed inside a protective casing and used to observe burrows on Takapourewa.

tape. The lights and camera of my system were powered by a rechargeable 12 V battery and were controlled from a box containing power switches and a rheostat for the lights. For protection when travelling to and from islands, the complete system fitted into a durable Underwater Kinetics waterproof suitcase. The camera control unit was connected via 5 m of extension cord to a JVC portable colour video monitor. The extension cord allowed positioning of the monitor in a convenient location to be observed by a single camera operator, and allowed it to be placed on firm ground.

As found by Dyer and Hill (1991), direct sunlight made the monochrome picture on the monitor almost invisible. However, I alleviated this problem by putting the monitor inside a black plastic bag and watching the picture shaded from the light. Observation was thus restricted to one person at a time.

Field methods

To see inside a burrow, I pushed the camera into its entrance. In initial field trials I stiffened the hose with number 8 fencing wire. However, the increased compressional strength did not compensate for the concomitant decrease in flexibility. The easiest way to move the camera within a burrow was to push the camera into the entrance and roll it around any corners encountered. Tensionable steering cables, as attempted (unsuccessfully) by Dyer and Hill (1991) were proposed for my camera but since reducing the width of the camera was a prime concern, they were not built. However, if they could be effectively designed without adding to the width of the camera, they could prove useful. By using the hose to roll the camera and its casing from side to side, I could negotiate most corners while pushing the camera into burrows. I could get the camera into nesting chambers up to c.2 m from their entrance. Because of the rolling of the camera head, orientation on the TV monitor was often confusing. However, with practice one soon adapted to viewing at odd angles.

A significant problem encountered when using burrow cameras is that the camera head can dig into soft material on the floor of a burrow and obscure lights or camera. I found that wiggling of the camera head alleviated this problem. The head of the camera used by Dyer and Hill (1991) was angled upwards by 25° to avoid the digging-in problem.

Our camera could not be angled, for two reasons. First, it would have increased the maximum area taken up by the camera, reducing the number of burrows able to be studied. Second, because of the rolling required to manoeuvre the camera in many burrows it was impossible to keep the same portion of the camera at the top. For much of the time, any angle imparted to the camera head could be counter-productive, causing the lens to dig into the burrow wall.

The focus on the camera was initially set at c.5 cm. This was subsequently changed to c.30 cm. With the close focus, animals could not be seen until the camera was immediately adjacent to them, and could be missed if the camera was facing slightly in the wrong direction. Because of the tight twists and turns experienced in many burrows on Takapourewa, it was not possible to get the camera into the nesting chambers of some burrows. However, with the focus set at 30 cm, it was consistently possible to determine what was in a burrow. If branches and turns in tunnels could be seen before they were reached, it was possible to manipulate the camera into them, rather than only seeing a corner about to be negotiated. Finally, a longer focal distance gave a wider field of view in focus, helping with observation of animals and negotiation of tunnels with the camera. Dyer and Hill (1991) came to the opposite conclusion, deciding that 30 cm was too long a focus because shearwater came right up to the camera to investigate, and camera manipulation was easier.

I made four trips to Takapourewa, in June, September, November and December 1994. Four different areas were studied: grazed pasture, tussock grassland, scrubland and forest (Fig. A1.1). Because of the fragile nature of the terrain, movement was restricted to boardwalks arranged haphazardly across quadrats. Burrows easily reached from these boards were sampled with the video camera.

I was not able to investigate every selected burrow within each study area because the camera could not negotiate turns of greater than c.90°, and some tunnels became too narrow for the camera. However, I was able to observe c. 85% of burrows attempted. I marked each successfully investigated burrow with an individually numbered garden tag so that it could be identified and reinvestigated on future trips. Some tags were removed, presumably by wind or animals, buried, or grown over in the interval between visits. I measured the distance from the surface to the nesting chamber of a sample of 53 burrows using a graduated scale on the camera hose.

In each of the four habitats, five 10×10 m quadrats were positioned using random distances from a baseline (the main track for the grassland, shrub and bush sites and the railway line for the pasture). In each of these quadrats the number of burrow entrances visible on the surface was counted. These burrow counts were used in estimation of density in each habitat.

RESULTS

The narrowest point of most burrows was the entrance, which was sometimes blocked with leaves and debris. Beyond the entrance, the tunnels became slightly wider and then opened into the birds' nesting chamber. Tunnels usually had some kind of twist or bend, so that the nesting chamber was blocked from light during the day. The shortest burrows (20 - 30 cm) often had a very sharp initial bend to achieve this. The length of prion burrows from the surface to the nesting chamber ranged from c.20 cm to at least 200 cm deep. The average length from the surface to the nesting chamber of the burrows investigated was 76 ± 7 cm (mean $\pm$ 1 SE).

To determine the relationship between below-ground burrow architecture and entrance counts, it was necessary to find out how many burrow entrances opened onto multiple nesting chambers, and how many nesting chambers had more than one entrance. In four trips to Takapourewa, I scanned a total of 180 different burrow entrances with the camera. Fourteen of these were found to have an additional entrance, usually at least one metre away from the first; hence I determined what was inside 194 burrow entrances. Twenty-two burrows had two nesting chambers opening off a single entrance and one entrance in the pasture study area had three nesting chambers, all with a prion sitting on an egg. No burrow with multiple chambers and multiple entrances was found. Therefore, the 194 entrances on the surface corresponded to 204 different nesting chambers, an increase of c.5%. I found no significant difference between the proportion of burrows in different habitats with multiple chambers ($G_{[3]} = 4.6$, $P > 0.05$) or multiple entrances ($G_{[3]} = 1.8$, $P > 0.05$).

Fairy prions were found breeding on the island during November and January. Therefore, only data from burrows investigated on these trips are included in analysis of

burrow occupancy. I calculated the proportion of burrows occupied by tuatara, prions and sooty shearwater in different habitats (Table A1.1). Using Friedman's test, with tuatara, prions and sooty shearwater as blocks, I found no significant difference between burrow occupancy in different habitats ($S_{[3]} = 1.5$, $P > 0.05$). All three species were found in all habitats, apart from sooty shearwater which were not found in the pasture.

I multiplied the mean burrow counts from each of the different habitats by the burrow occupancy figures determined with the video camera. These values were then

TABLE A1.1. Number (and percentage) of burrows inhabited by tuatara, fairy prion, and sooty shearwater, or empty, in different habitats on Takapourewa.

	<i>n</i>	Tuatara	Fairy prion	Sooty shearwater	Empty
Pasture	44	4 (9.1)	30 (68.2)	0 (0)	10 (22.7)
Grassland	35	1 (2.9)	25 (71.4)	1 (2.9)	8 (22.9)
Shrubs	19	1 (5.3)	15 (79.0)	2 (10.5)	1 (5.3)
Forest	36	6 (16.2)	24 (67.6)	1 (2.7)	5 (13.5)

TABLE A1.2. Number of burrows and density of tuatara, fairy prion and sooty shearwater in different habitats on Takapourewa. All values are mean/m² ± SE.

	Number of burrows	Tuatara	Fairy prion	Sooty shearwater
Pasture	1.1 ± 0.4	0.11 ± 0.04	0.8 ± 0.3	0.00 ± 0.00
Grassland	1.4 ± 0.2	0.04 ± 0.01	1.1 ± 0.2	0.04 ± 0.01
Shrubs	0.5 ± 0.3	0.03 ± 0.01	0.4 ± 0.1	0.06 ± 0.02
Forest	0.9 ± 0.3	0.15 ± 0.04	0.6 ± 0.2	0.02 ± 0.01

increased by 5% to account for multiple chambers and burrows with multiple entrances to give density figures for each habitat (Table A1.2). Although there are differences between densities in each habitat, they are not significant ($S_{[3]} = 5$, $P > 0.05$).

DISCUSSION

Usefulness of miniature video cameras

If statistically meaningful conclusions are to be drawn from ecological studies, sample sizes must be reasonable large. However, excessive disturbance of burrow-nesting

animals may lead to changes in behaviour which, for nesting seabirds, can include desertion or hatching failure (Harris 1966, Warham et al. 1982). Miniature video technology allows adequate numbers of burrows to be sampled without destroying or damaging them and without shining white light into the nesting chamber. White light disturbs both tuatara (Newman 1987) and petrels (Warham 1966). When it is considered that some of these birds share burrows with tuatara, a significant predator, especially of chicks (Walls 1978), and still manage to breed successfully, the relatively brief disturbance caused by the intrusion of the camera is presumably slight. Fibre-optic endoscopes allow burrow sampling in a manner similar to a video camera (P. Ellis, N. Ratcliffe, and D. Suddaby, RSPB *Unpubl. data*), but the cost of the equipment is considerably greater.

Efficiency of my video camera

It took me c.4 h to census 20 fairy prion burrows. This is considerably less than the time it takes to dig observation holes in the top of 20 burrows. Dyer and Hill (1991) sampled 20 wedge-tailed shearwater burrows in 45 minutes. Wedge-tailed shearwater are twice the size of fairy prion (Falla et al. 1993) and sampling speed probably increases when a bird with a larger burrow is being studied. The difference in the size of the birds appears to be the factor causing many of the differences between my camera and that used by Dyer and Hill (1991). In designing a camera with which to study fairy prion burrows, the most important consideration was small size. To this end, potentially valuable modifications such as steering mechanisms and angled camera heads had to be forgone. Because burrows were often angular and narrow, focus length had to be pre-set to allow observation from a distance in case nesting chambers could not be reached. A rigid connector between the remote head and the camera control unit would have been easier to push into burrows and lift over obstacles on burrow floors. However, the narrow convoluted nature of the burrows meant that a flexible hose was most useful.

Tuatara and seabird densities on Takapourewa

The absence of sooty shearwater from the pasture site can be explained by its location. The grassland, shrub and forest sites were all adjacent to the cliff on the western,

seaward side of the island (Fig. A1.1). Because sooty shearwater require a high point from which to get airborne (Richdale 1963), none are found nesting away from the cliffs (e.g. at the pasture site).

Comparison with other studies of burrow occupancy on Takapourewa can serve as a check on the accuracy of figures calculated with the burrow camera. Crook (1975) estimating fairy prion density on Takapourewa, found occupancy rates up to 78%. This is within the range calculated in my study (Table A1.1), yet his counts of burrow entrances were up to 3.7 per m², above my estimates (Table A1.2). Crook worked in the Ruston Bush area of Takapourewa, which according to Newman (1987) has higher numbers of burrows and more multiple entranced burrows than other sites on the island. The burrow densities reported by Crook (1975) are likely to be overestimates of burrow numbers (Newman 1987). In a five year study involving 60 study burrows in the Keepers Bush area of Takapourewa, Newman (1987) calculated tuatara burrow occupancy to be 14% and density to be 0.14×0.04 tuatara per m². My forest study area was also within Keepers Bush and both my occupancy and density calculations encompassed those of Newman (1987) (Tables A1.1, A1.2). These results show how relatively quick, efficient video camera observation can yield results similar to those calculated in more detailed and labour-intensive studies.

Conservation value of video camera monitoring

To determine whether conservation programmes are successful, or to discover if human activity is having a deleterious impact on a population, it is necessary to collect baseline data and repeatedly monitor those populations, noting changes in factors such as breeding success and overall density. A miniature video camera can be a valuable tool for this type of monitoring. For example, on Takapourewa revegetation projects are at present being carried out. Because tuatara require open areas for incubation of eggs (Thompson 1990), revegetation of pasture areas could have an impact on tuatara breeding success. Future study with a video camera will be able to show if densities of tuatara have changed in conjunction with an increase in vegetation cover.

Simberloff (1990) identified the potential value of keystone species in restoring damaged ecosystems. Burrow-dwelling animals carry out many roles in the ecosystems in

which they live. Their burrowing activities homogenise soil horizons, and aerate the soil. Nutrients from their excretion affect plant growth (Furness 1991) and may also promote a prolific invertebrate fauna (Crook 1975, Walls 1981) with concomitant effects up the food chain. For these reasons, burrow-dwelling animals - and seabirds in particular - may fulfil keystone roles at the sites at which they occur. Restoration projects could well be based around seabirds and hence a knowledge of their abundance and behaviour could be especially valuable in conservation projects. However, many breeding colonies of seabirds occur on offshore islands and other isolated locations (Mizutani and Wada 1988). Video cameras allow relatively efficient monitoring and censuses in possibly inhospitable terrain, and can facilitate the collection of valuable baseline data for restoration and conservation of unique seabird-dominated ecosystems.

CONCLUSION

Dyer and Hill (1991) noted that different environmental conditions and burrow geometries require modifications of the basic burrow camera design. This paper presents one such modification. A camera can be designed and built for the often narrow and convoluted burrows dug by small prions, and can be used to collect data useful for study of the inhabitants of these burrows.

ERRATUM

Although the data in Tables A1.1 and A1.2 are correct, their derivation is not clear from the text. The number (and percentage) of burrows inhabited by tuatara, fairy prion and sooty shearwater were calculated using data collected from video camera study of two quadrats in each habitat type. In Table A1.1, n represents the total number of burrows investigated in each habitat type. The other columns in Table A1.1 represent the total animals of each taxa observed in the burrows in each habitat.

In Table A1.2, the number of burrows is the mean burrow count ($\pm 1SE$) in five quadrats in each habitat type. To calculate the densities of tuatara and seabirds, the percentage of burrows occupied by each taxa in each habitat (from Table A1.1) is

multiplied by the number of burrows in that habitat. These values were then increased by 5% to account for multiple chambers and burrows with multiple entrances to give the density figures for each habitat (Table A1.2).

n.b. The SE for the shrubs habitat in Table A1.2 is incorrect, and should read 0.2. Other values are unchanged.

Appendix 2: Relationship between tuatara and fairy prion densities in different habitats on Takapourewa¹

Tuatara *Sphenodon punctatus* and fairy prion *Pachyptila turtur* both nest in burrows on 150-ha Takapourewa. The birds form a major component of tuatara diet (Moller 1985, Fraser 1995) and provide a source of food and moisture in the summer months when invertebrates are scarce (Walls 1981). As part of a broader systems study, the aim of this work was to investigate possible levels of tuatara predation on fairy prions and determine if this feeding relationship was reflected in the distribution of the two species.

I used a Cohu 6700 series remote-head CCD miniature video camera to examine burrows in four different habitats on Takapourewa (Markwell 1997).¹ Two 100 m² quadrats were investigated in each of pasture, long grassland and forest habitats, and one in a scrub habitat. Burrows were selected opportunistically within each quadrat, and their contents determined with the camera. I calculated the proportion of burrows surveyed that was occupied by tuatara in each quadrat. To estimate tuatara density I multiplied the occupancy rates by surface counts of burrows in each quadrat. The density figure thus calculated was then corrected to account for the proportion of multiple chambered or entranced burrows discovered with the video camera (Markwell 1997).

Prions are only present on the island in any number over the breeding season (October-January, Falla et al. 1993). Data on fairy prion density were collected in November 1994 and January 1995. Prion densities were calculated in the same manner as tuatara densities.

Adult fairy prions appear able to defend themselves against tuatara (Newman 1987, Gaston and Scofield 1995), but the reptiles consume chicks (Walls 1978, Fraser 1995). Therefore, a measure of the effect on chicks was necessary to show the effect of tuatara predation on fairy prion populations. I measured the survival rate of fairy prion chicks in different areas on Takapourewa and compared this rate with tuatara density in these areas to ascertain if chick survival decreased as tuatara density increased. To determine survival

¹In press as Markwell (1998)

of chicks, I investigated the same burrows on two separate trips. Burrows empty in both November and January were not included in the analysis. In total, I studied 80 burrows during both incubation and pre-fledging times. I deemed the nest to be successful if a live chick was recorded in a burrow in January. Failures were scored when an empty nest or an unattended egg (i.e. without a parent) was found in January. Fairy prions incubate eggs for *c.* 55 days and have a *c.* seven-week fledging period (Falla et al. 1993). It was possible that some unattended eggs in burrows in January were still viable and would hatch. However, these would need to have been laid at the extreme end of the breeding season and were unlikely to be in any great number or affect the results significantly. On Takapourewa, fairy prion chicks begin to fledge in late January (Walls 1978), and so the possibility that empty nests in early January had previously contained fledged chicks seems unlikely. Because tuatara drag chicks away from their burrows before eating them (pers. obs.), I used empty burrows where previously an egg had been observed as an indication of the predation rate. Movement of prey is thought to be the prime stimulus triggering feeding by tuatara (Falla 1935, Dawbin 1962) so chicks that died of causes other than predation are not likely to have been removed from the nest by tuatara. A dead chick or unhatched egg was counted as a failure due to another cause (e.g., cold, malnutrition, abandonment).

Calculated tuatara density ranged from 0 in one grassland quadrat up to 0.40 tuatara/m² in one forest quadrat (Table A2.1). In the same quadrats, fairy prion densities were up to approximately 10 times greater than were tuatara densities (Table A2.1). Because of the significant imbalance in the numbers of fairy prions and tuatara, large changes in fairy prion density are likely to lead to small changes in tuatara density. To

TABLE A2.1. Burrow counts, occupancy rates and densities of tuatara and fairy prion in different habitats on Takapourewa in 1994/1995.

Habitat type	% burrows containing tuatara	% burrows containing prions	Burrow entrances/ quadrat	Correction factor	Chambers/ m ²	Tuatara/ m ²	Prions/ m ²
Pasture	9	67	192	1.05	2.02	0.18	1.34
Pasture	11	70	138	1.05	1.45	0.17	1.01
Grassland	0	88	193	0.88	1.7	0	1.5
Grassland	7	65	89	0.88	0.78	0.05	0.51
Scrub	13	79	124	1	1.24	0.17	0.98
Forest	25	69	164	0.98	1.61	0.4	1.1
Forest	20	63	56	0.98	0.55	0.11	0.35

compensate for this, I carried out a logarithmic transformation on the tuatara density data (Sokal and Rohlf 1981). Prion density was significantly positively correlated with $\ln$ tuatara density ($r = 0.80$, $t_{[5]} = 3.04$, $P < 0.05$).

Adult prions were found sitting in most of the burrows observed during November. I attempted to nudge birds from the nests with the camera to see the egg, but this was not possible in 20 (27%) of cases. In the November samples, unattended eggs were found in five (6%) of the 80 burrows. In January, the only live prions found in the burrows were down-covered chicks. A burrow containing an egg or an unmoved sitting prion in November was occupied by a chick in January in 58 cases (73%). In two (2%) cases, empty burrows in November contained chicks in January. Eleven (14%) failures were shown by empty nests. One dead chick was found in a burrow and eight (10%) burrows contained unattended eggs.

In the different habitats, failure rate due to predation ranged from 7% to 33% (Table A2.2). I arcsine-transformed the chick predation data to maintain normality and homoscedasticity in percentage data (Sokal and Rohlf 1981). No significant relationship was found between arcsine predation rate and $\ln$ tuatara density ($r = 0.43$, $t_{[5]} = 1.07$, $P > 0.05$).

Tuatara densities are positively correlated with seabird densities. This relationship indicates either that tuatara are responding to the presence of prions or that both are responding to some other factor. Fairy prions are an important food source for tuatara (Moller 1985, Fraser 1995). The birds also deplete understorey vegetation in forested areas (Campbell 1967) and possibly increase the invertebrate biomass by nutrient addition

(Dawbin 1962) thus potentially improving hunting conditions for tuatara. For these reasons, it seems likely that the distribution and abundance of tuatara is in some way influenced by fairy prions. If prion abundance was significantly affected by

TABLE A2.2. Percentage of fairy prion chicks successful and preyed upon in burrows in different habitats on Takapourewa, 1994/1995

Habitat type	n	% nests successful	% nests predated
Pasture	8	88	13
Pasture	13	62	15
Grassland	14	79	14
Grassland	9	78	11
Scrub	14	86	7
Forest	12	58	33
Forest	10	80	10

predation from tuatara, fairy prion densities should be low at sites with high tuatara densities and the correlation should be inverse, in contrast to my finding.

Because of the relatively small number of fairy prion thought to be taken by tuatara, the lack of significant correlation between predation rate and tuatara density provides only an indication that tuatara do not have a great effect on fairy prion density. However, comparison of this study with other studies on petrel breeding success provides support for the conclusion that fairy prion numbers are not significantly influenced by predation. A total of 10 different studies were selected, based on a (non-exhaustive) literature search. The studies chosen reflected a range of species and geographic locations (Table A2.3). The studies on Marion Island (Schramm 1983, Fugler et al. 1987, Newton and Fugler 1989, Cooper et al. 1995) and Lavezzi Island (Thibault 1995) report data taken before and after the removal of predators from habitats on the islands (feral domestic cats *Felis catus* on Marion and black rats *Rattus rattus* on Lavezzi). The remaining data were gathered from areas with or without predators throughout the course of the study. In predator-free areas the breeding success rate is significantly higher than in predator areas ($t'_{[12.6]} = -5.46$, $P = 0.0001$). Although breeding success of some species (i.e. whitechinned petrel *Procellaria aequinoctialis*) is not significantly improved by the removal of predators (Cooper et al. 1995), a clear pattern of success at over 60% in predator-free areas and 35% or lower in areas with predators can be seen. The value of 49% for fairy prion from Richdale (1944a) was calculated one year on Whero Island in Foveaux Strait, New Zealand. Richdale (1944a) notes that the climate was severe at this site, and chicks succumbed to excessively wet burrows. The survivorship pattern observed in my study matches the pattern seen for sites where predators are absent or in low numbers rather than situations where predators are having a significant impact on petrel breeding.

Although tuatara numbers may be controlled by factors in addition to food supply, such as space for burrows and open areas for breeding (Thompson 1990), fairy prions may be important in allowing high tuatara densities to be maintained, and higher tuatara densities are found in areas with more prions. In contrast, fairy prion numbers do not appear to be significantly influenced by tuatara. The proportion of chicks lost in a season does not seem any greater than that in areas without predators. The most likely factor controlling prion numbers is mortality while the birds are at sea.

TABLE A2.3. Burrowing petrel breeding success in localities with and without mammalian predators

Species	Success (%)	Locality	Reference
Without mammalian predators			
Cory's Shearwater <i>Calonectris diomedea</i>	78	Lavezzi Island (Corsica)	Thibault 1995
Fairy Prion <i>Pachyptila turtur</i>	76	Takapourewa	Walls 1978
Fairy Prion	76	Takapourewa	This study
Fairy Prion	74	Poor Knights Island (New Zealand)	Harper 1976
Fairy Prion	49-71	Whero Island (New Zealand)	Richdale 1944a
Manx Shearwater <i>Puffinus puffinus</i>	75	Skokholm Island (Wales)	Harris 1966
Greatwinged Petrel <i>Pterodroma macroptera</i>	64	Marion Island (Subantarctic)	Cooper et al. 1995
Blue Petrel <i>Halobaena caerulea</i>	64	Marion Island	Cooper et al. 1995
Whitechinned Petrel <i>Procellaria aequinoctialis</i>	22	Marion Island	Cooper et al. 1995
With mammalian predators			
Black Petrel <i>Procellaria parkinsoni</i>	26	Little Barrier Island (New Zealand)	Imber 1987
Cory's Shearwater	34	Lavezzi Island	Thibault 1995
Greatwinged Petrel	5	Marion Island	Schramm 1983 Newton & Fugler 1989
Blue petrel	24	Marion Island	Fugler et al. 1987
Whitechinned Petrel	36	Marion Island	Cooper et al. 1995
Westland Black Petrel <i>Procellaria westlandica</i>	4	Punakaiki (New Zealand)	Baker & Coleman 1977

APPENDIX 3: Predominant vegetation in the different sites

Site	Predominant vegetation
Takapourewa pasture	<i>Avena sterilis</i> , <i>Lolium perenne</i>
Takapourewa grassland	<i>A. sterilis</i> , <i>L. perenne</i> with patches of <i>Poa cita</i>
Takapourewa scrub	<i>A. sterilis</i> , <i>L. perenne</i> and <i>P. cita</i> interspersed with <i>Coprosma repens</i> , <i>Muehlenbeckia complexa</i> and <i>Hebe urvilleana</i>
Takapourewa forest	<i>C. repens</i> , <i>Melicytus ramiflorus</i> , <i>Dysoxylum spectabile</i> , <i>Hedycarya arborea</i> . Sparse undergrowth of <i>Macropiper excelsum</i> , <i>Urtica ferox</i> and <i>Solanum nigrum</i>
Maud Island	<i>D. spectabile</i> , <i>Melicytus ramiflorus</i> , <i>H. arborea</i> and <i>Laurelia novae-zelandiae</i> with <i>C. repens</i> on forest margins. Understorey of <i>Macropiper excelsum</i> and ground ferns such as <i>Asplenium bulbiferum</i> and <i>Blechnum filiforme</i>
Nuku-waiata	<i>D. spectabile</i> , <i>Melicytus ramiflorus</i> , <i>Rhopalostylis sapida</i> . Understorey of <i>Macropiper excelsum</i> , <i>A. lucidum</i> and other small ferns
Whakatere-papanui	<i>A. sterilis</i> , <i>L. perenne</i> , <i>P. cita</i> with patches of <i>Phormium tenax</i> , <i>Pseudopanax arboreus</i> and <i>Cassinia leptophylla</i>
Titi Island	<i>C. repens</i> , <i>Myoporum laetum</i> , <i>Melicope ternata</i> , <i>D. spectabile</i> , <i>H. arborea</i> , <i>Pseudopanax arboreus</i> , <i>Myrsine australis</i> , <i>Melicytus ramiflorus</i> , <i>Olearia paniculata</i> . Understorey of <i>Macropiper excelsum</i> , <i>Urtica ferox</i> and <i>Asplenium bulbiferum</i>
North Brother	At low levels, bare rock with patches of <i>Sarcocornia quinqueflora</i> , <i>Disphyma australe</i> , <i>Senecio sterquilinus</i> <i>Lepidium oleraceum</i> . At higher elevations, <i>Poa cita</i> , and low shrubby <i>Coprosma repens</i> and <i>Hebe elliptica</i>

Nomenclature follows Connor and Edgar (1987) and Webb et al. (1988). Data from Grant et al. 1992 (Takapourewa), Cannington 1982 (Maud), Walls 1984 (Nuku-waiata), Mazey 1982 (Titi), Gillham 1960 (North Brother) and Markwell *unpublished data* (Whakatere-papanui).

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