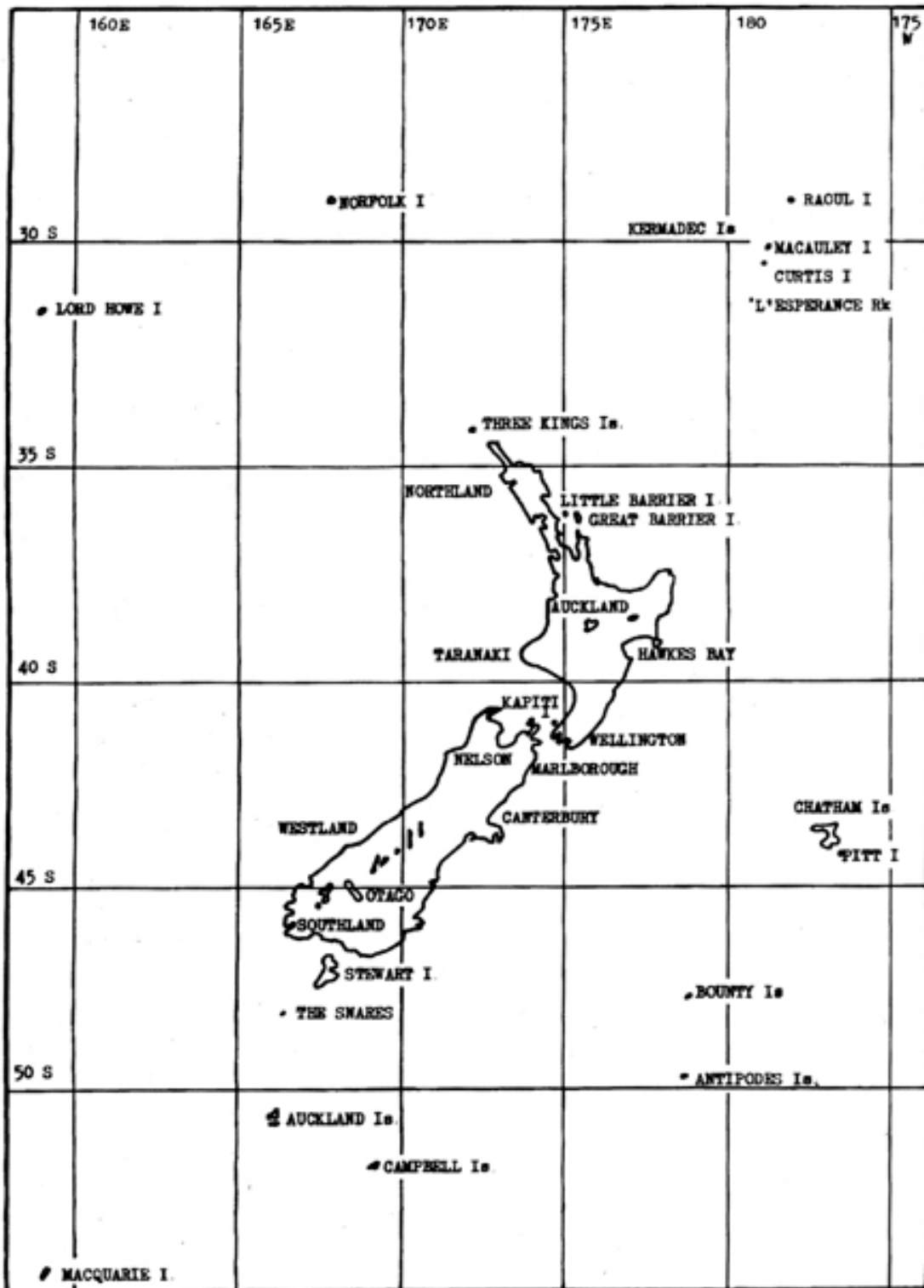


# **Modelling the Distribution and Species Richness of Introduced Vertebrates on New Zealand Offshore Islands**

A thesis submitted in partial fulfilment of the requirements for the degree of Master of  
Science in Environmental and Marine Science

by  
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New Zealand and its outlying islands

## *Abstract*

The offshore islands of New Zealand provide a unique opportunity to investigate insular biogeography with respect to relatively recently introduced vertebrate taxa (c. 200 years ago), whose colonisation and expansion across an entire archipelago is well documented.

In the past the factors that have influenced the distribution of introduced species have generally been qualitatively assumed. This thesis uses statistical modelling to quantitatively establish which factors currently correlate with the distribution of individual introduced mammal species and with the species richness of introduced mammals and exotic landbirds.

The distribution of individual introduced mammal species is generally reflected by a number of limiting factors, which vary widely, though not unexpectedly, between species. These factors are reflections of both the history of human-mediated introduction of species, and their natural dispersal across the archipelago. The use of islands as stepping stones by stoats to colonise islands outside their natural swimming distance is highlighted, as is the nature and intensity of interactions between the four rodent species found in New Zealand.

The species richness of introduced mammals is found to differ predictably between large and small mammals. The former is controlled by human activities, while island biogeographic processes control the latter. Correlates of the species richness of exotic landbirds on offshore islands are difficult to assess, primarily because of sampling effort bias in the avian data, however there are indications that habitat and biotic interactions play an important role.

Some common trends across taxa are also highlighted, including the consistent macro-scale effect of latitude on the species richness of both introduced mammals and birds, as well as the not so readily apparent negative relationship between island elevation and introduced species richness.

The thesis concludes with a discussion of the results in a wider biogeographical context, and also a number of recommendations for further work. The most paramount of these being the establishment of a centralised New Zealand Islands Database (NZID) which contains updated information on the distributions of introduced species on islands, and the types of habitat present on them.

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# *Chapter 1: Introduction*

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## *1.1 General Introduction*

### *1.1.1 'Natural Laboratories'*

Islands are valuable to ecologists. The simplification of phenomena observed on adjacent mainland areas means ecological problems are often more easily understood (Williamson 1981). Because of this islands have been described as 'natural laboratories' within the real world (Brown and Lomolino 1998). Whittaker (1998) states on the first page of his book:

*"It is that islands, being discrete, internally quantifiable, numerous, and varied entities, provide us with a suite of natural laboratories, from which the discerning natural scientist can make a selection that simplifies the complexity of the natural world, enabling theories of general importance to be developed and tested."*

Naturalists have long acknowledged such properties of islands from well before the 20<sup>th</sup> century (Darwin 1869; Wallace 1880).

Islands provide relatively independent observations (Mayr 1967 terms them 'experiments'), from which comparisons may be made over any number of characteristics, often measured as variables. This also gives them great potential for the application of mathematical and statistical ecology. Islands can be used as subjects for formulating theories that can be tested, refined and (if successful) finally applied to the mainland, where habitat can often be an 'island' within a 'sea' of grassland or buildings (Atkinson and Bell 1973). Examples of this include Robert MacArthur and Edward Wilson's work in the 1960s (Wilson 1961; MacArthur and Wilson 1963, MacArthur and Wilson 1967) applying mathematical ecology to biogeography, and later Jared

Diamond's work (Diamond 1975; Gilpin and Diamond 1981) combining statistical and community ecology.

### *1.1.2 Thesis Organisation*

This thesis is divided into seven chapters. *Chapter 1* introduces the topic of the study. *Chapter 2* outlines the data sources and methodology used, while *Chapter 3* describes the raw data and variables. *Chapter 4* investigates the distribution of introduced mammal species on New Zealand offshore islands while *Chapter 5* investigates the species richness of introduced mammals on New Zealand offshore islands. *Chapter 6* contrasts with previous chapters by considering the species richness of a different taxon - introduced birds. *Chapter 7* concludes the thesis by discussing the results within a wider scientific context, drawing conclusions from the overall study and suggesting areas for further research.

### *1.2 Aims*

The principal aim of this thesis is to investigate the variables that correlate with the distribution and species richness of introduced vertebrate species across New Zealand offshore islands. The suite of factors to be investigated includes physical, geographical, geological, biological, ecological and historical descriptors of islands, making this a truly interdisciplinary biogeographical approach.

More specifically, this thesis aims to quantify which of the variables have the strongest relationship with the distribution of introduced species and their species richness. It will then discuss the underlying processes that appear to drive and limit the establishment of such species, or mediate their total species richness on New Zealand offshore islands. From this, general conclusions can be reached regarding the behaviour of New Zealand's insular systems with respect to introduced vertebrate species and how these systems might be better managed in the future to avoid further introductions of species to pristine offshore islands. Such a study is important, as researchers and managers of New Zealand

offshore islands have often asked similar questions; such as Atkinson (1986) – “*what factors are currently influencing the spread of rodents to further islands?*”

This thesis unabashedly attempts to explain the pattern of introduced species distribution and richness across New Zealand islands before fully understanding the processes, an important distinction (McArdle 1996). Biogeography is the study of ‘pattern and process’ in species distributions (Brown and Lomolino 1998), but it has been emphasised that it is ordinarily more appropriate to investigate and understand the patterns before embarking upon studies of processes (Gotelli and Graves 1996). I believe that such an approach is favourable in studies of species distribution, which often take observed patterns and then assume what processes are driving them. Until conclusive evidence of the processes is demonstrated, the pattern is merely one hypothesis (McArdle 1996). Atkinson (1986), for example, assumes that the expansion of rodent distribution across New Zealand islands can be restricted by rigorously monitoring marine vessel access to them. More recently Holdaway (1999) assumes that “*the presence of a population of Pacific rats on an island implies a visit to that island, of whatever duration, by humans.*” Studies such as Veltman *et al.* (1996) provide a preferred example of studying the patterns before inferring the processes.

### *1.3 Hypotheses*

Hypothesis generation and testing is an integral component of modern science (Popper 1959; Underwood 1997). By creating an alternative hypothesis to a model it can be tested, and if found to be false, then discounted. This subsequently supports the corresponding null hypothesis, usually of no effect or the norm (Krohne 1998).

Only recently has there become an awareness of the importance of null hypotheses, and hypothesis testing in general, in the framework of ecological science (Hurlbert 1984; Underwood 1990, 1997; Gotelli and Graves 1996). There has been considerable debate though, on the applicability of null hypotheses and models in various studies, causing heated debate in the early 1980s (see review in Chapter 1 of Gotelli and Graves 1996).

Although hypotheses may sometimes appear difficult to formulate objectively, especially in complex branches of natural science, they nonetheless are an essential basis for scientific rigor.

Hypotheses can be presented both statistically, and in versal English. They essentially confer the same ideas, although the versal hypotheses are perhaps more easily understood, while the statistical hypotheses are more scientifically empirical. Both are presented for models in *Chapters 4, 5 and 6* as appropriate. Hypotheses by nature tend to be specific to what is being investigated, and so no overall hypothesis is presented in this introduction.

#### *1.4 Scope of the Study*

##### *1.4.1 A Definition of 'Island'*

A definition of 'island' is necessary to discriminate a threshold for islands within the scope of this study – principally to fix a definitive number.

Whittaker (pp. 7-8 1998) adopts a loose and encompassing definition of island, claiming *“even thistle heads may count as islands for some purposes.”* He does, however, indicate to the reader that for the most part the term 'island' refers to a discrete area of land surrounded by sea. Rosenzweig (pp. 210-212 1995) proposes a clearer definition of 'island'.

*“An island is a self-contained region whose species originate entirely by immigration from outside the region”*

This avoids arbitrary definitions based on water or inaccessibility. It also transforms islands from geographical entities to biological ones, and serves my study well by 'delegating' the effects of speciation to the mainland. It should be noted though, that Rosenzweig's definition does not incorporate distant islands, where speciation occurs.



Type of archipelago	Prominent theories
Large, very distant	Adaptive Radiation
Large, distant	Taxon Cycle
Medium, mid-distance	Assembly Rules
Small, near	Equilibrium Theory of Island Biogeography
Small, very near	Metapopulations

Table 1.1. Prominent island theories and the geographical configurations of islands for which they are most relevant.

Only ‘offshore’ islands (*sensu* Atkinson and Bell 1973) within 50km of the New Zealand ‘mainland’ (which includes Stewart Island – see *Section 3.1.2.5.1*) and those larger than five hectares are considered in this study. Beyond 50km species endemism becomes a significant insular process – contrasting with those islands within 50km of the mainland where the immigration of new species occurs at a much higher rate than that at which they are generated by evolution (Williamson 1981). This also retains our dataset within Rosenzweig’s definition of ‘island’. Whittaker (1998) more generally equates such near to mid-distance islands as those most pertaining to assembly rules (Diamond 1975; Weiher and Keddy 1999) and the equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967), whilst those further away are driven by the taxon cycle (Wilson 1961) and adaptive radiation. Table 1.1 summarises these island configuration themes. Outlying islands also lie off the New Zealand continental shelf (Kelly and Marshall 1996), and are termed ‘oceanic’ - presenting a more significant isolation barrier.

There are three reasons for only considering islands larger than five hectares. The first is that for most of the introduced species studied, islands less than five hectares are not sufficiently ecologically diverse (Brown and Lomolino 1998) to maintain a complete trophic web capable of supporting a permanent population (rodents being the notable exception, Taylor 1989; King 1990a). In part this is because they can not sustain a permanent supply of freshwater (Menard 1986; Hugget 1995) and are generally inhospitable stacks. The second reason is statistical. There are almost 300 islands larger than five hectares, which provides an adequate and robust dataset, while still being manageable. The final reason is logistical. Work carried out in the early 1990s by Ian

Atkinson and Rowley Taylor (Atkinson and Taylor 1991; Atkinson 1992) provides much of the data for analysis. This data is mostly for islands over five hectares – 289 in total (a few notably exceptional islands less than five hectares are also included, as they are here). Atkinson and Taylor limited their study to islands larger than five hectares for reasons of time constraints, which seems practical to repeat here. Within the context of ‘island’ only the North and South Islands of New Zealand are excluded and considered ‘mainland’ (see also *Section 3.1.2.5.1*).

A subset of ‘offshore’ islands have been termed ‘inshore’ islands. These are islands that do not lie off the coast but instead within harbours and fiords. The best examples are those within Fiordland. Although this term is generally recognised, I have chosen not to differentiate between the inshore islands and true offshore islands.

New Zealand also has approximately 30 lacustrine islands, being those islands lying within freshwater lake systems. These have been investigated with regard to island equilibrium theory (Kelly *et al.* 1989), however they are not considered here due to the different dynamic processes occurring upon them, notably that they are susceptible to invasion pressure from all directions, and often have significantly different climates. They do stand to make an interesting comparison to those offshore islands investigated here however.

#### *1.4.2 Introduced Species*

Although the term ‘introduced species’ is widely used, its meaning is ambiguous. A species that has been introduced has arrived at a location that it was not previously at by some means. By that definition, all species have been introduced to an area at some stage in their history. These species though, can be further divided into those ‘self-introduced’ and those ‘human-introduced’. The latter are more commonly termed ‘exotic’ or ‘alien’ species. Such species are recognised as those that have been purposefully transported outside their natural range by humans (Mooney and Hobbs 2000). They do not necessarily have to have established yet (Table 2.2 in Williamson 1996). Most consider

the term ‘introduced species’ to be synonymous with ‘exotic species’, as I shall do. In this study it should be noted that the introduced species selected have all established on the mainland. Once established a species will begin natural range expansion, which in time will bring it to encounter geographical barriers that may prevent it dispersing to other locations, such as islands. This natural range expansion may be confounded by further human-mediated introductions beyond the first though (Blackburn and Duncan 2001, *in press*), whether to augment the original release or to introduce the species to a new locality, which it may not have naturally been able to reach (such as islands).

Introduced species are increasingly being recognised as excellent subjects for the study of theoretical biogeography (Abbott 1974; Sax 2001; Blackburn and Duncan *in press*). Lockwood *et al.* (1999) recognised the potential of introduced avifaunas in their study of island dispersal and establishment processes. Because the introduction of such species is usually recent, and often well documented (Veltman *et al.* 1996), it allows the complete history of the species to be incorporated into a study. In this thesis it is the factors that facilitate species progressing from being absent to established on offshore islands that are of interest. It is important to note that islands where introduced species have never occurred are also considered, in contrast to studies of introduction success (Duncan 1997; Forsyth and Duncan 2001; Blackburn and Duncan 2001, *in press*; Duncan and Forsyth unpubl.) where only islands where the species have been introduced are considered. The intermediate period of introduction, where species are not yet established, is more difficult to quantify (Brown and Lomolino 1998). A general requirement of ‘establishment’ is that a population is breeding and has a viable (ecologically) long-term population on an island. Throughout this thesis the term ‘introduced species’ is used to describe those mammals and birds that were purposefully introduced by humans to the New Zealand archipelago.

The study encompasses 17 introduced mammal ‘species’. All major species are included, while those species of infrequent distribution are either discounted, or included within a larger taxonomic distinction (e.g. ‘Deer’), but still termed ‘species’ (see *Section 2.1*). The introduced avian species in the study are those which were present in the 1960s – 1970s

Ornithological Society of New Zealand's (OSNZ) national survey for the Atlas of Bird Distribution in New Zealand (Bull *et al.* 1985). These total 41 exotic terrestrial bird species.

The study is 'species neutral' (*sensu* MacArthur and Wilson 1963, 1967), in contrast to 'individually neutral' (see Hubbell 2001). This means species are considered identical and are modelled by extrinsic factors. The original 'species neutral' approach adopted by MacArthur and Wilson serves well for studies of species richness (see *Chapters 5 and 6*). It can be validly argued that individual species attributes (autoecology) also affect distribution, but *Chapter 4*, although not specifically investigating autoecological traits, renders species neutrality trivial by only modelling single species. Many of the external variables measured are also counterparts to autoecological traits (e.g. Distance to Mainland ~ Dispersal Ability; Area ~ Resource Requirements).

## *1.5 Background Review*

### *1.5.1 New Zealand Offshore Islands*

The Otiran glacial maximum 20,000 years ago was the last period when the offshore (<50km) islands were joined to the mainland (Fleming 1979). The sea level was at least 350 feet lower than at present. New Zealand was also very volcanically active at this time. The distribution of organisms was limited by glaciation to refugia scattered throughout the country, or otherwise forced to northern extremes in the 'North Island' (Anderson and McGlone 1992), as it is today recognised. As glaciers retreated, sea levels rose and species gradually expanded their distributions (Fleming 1979).

Currently the number of offshore islands around New Zealand is estimated as somewhere between several hundred (Fleet 1986) up to 600 - 800 (Daugherty *et al.* 1990; Molloy and Dingwall 1990; Veitch and Bell 1990). Such values are regularly unreferenced though, and estimates for the total number of islets have ranged as large as 10,000 (Lee 1997).

New Zealand's offshore islands can be readily classified into three groups – the northern, central and southern islands (Atkinson and Bell 1973). This division is geographically orientated, but is also reflected in the ecological differences between the three groups. Atkinson and Bell (1973), Atkinson (1989) and papers in Towns *et al.* (1990) provide excellent coverage of the biological values of New Zealand's offshore islands. Much of the work on New Zealand's islands has involved, or been inspired by, Ian Atkinson, whose studies of New Zealand's islands span almost half a century.

The arrival of humans approximately 1,000 years ago saw drastic changes to New Zealand's islands. Maori settlement was seasonal on many islands, and permanent only on some of the larger ones (Hayward 1986; Holdaway 1999). Settlement saw the hunting of much of the indigenous avifauna (McGlone 1989), including seabirds on offshore islands (Moller 1996). Islands were burned to allow fortification construction and crop planting. Also disruptive to offshore islands was the first introduction of mammals (Fleet 1986). Both kiore (*Rattus exulans*) and kuri (*Canis familiaris*) accompanied Maori settlers to New Zealand, and its offshore islands. Although the scale and nature of the destructive effects of these first two species is argued (Atkinson 1978; Holdaway 1989; McGlone 1989), it is naive to say that there was no effect. Following this the arrival of the first Europeans in 1769 saw the establishment of many more mammal species on offshore islands, both purposefully and accidentally (Fleet 1986).

### *1.5.2 Introduced New Zealand Mammals*

Before the arrival of humans, New Zealand had only three native terrestrial mammals, the New Zealand long-tailed bat (*Chalinolobus tuberculatus*), the lesser New Zealand short-tailed bat (*Mystacina tuberculata*) and the greater New Zealand short-tailed bat (*M. robusta*). All three species were volant.

The arrival of humans saw a subsequent explosion in the number of terrestrial mammals (Gibb and Flux 1973), with some 53 different species being introduced (Cochrane 1973). Although initially only two species (kiore and kuri) followed the original Maori ancestors

(Anderson 1990; Atkinson and Moller 1990), the arrival of Europeans saw the much more rapid expansion of New Zealand's mammal fauna, to over 25 successfully established terrestrial mammals (Gibb and Flux 1973; King 1990a). Table 1.2 lists those species which have established. In only 200 years many of these mammals have expanded their distributions across the length of New Zealand, although there have been some areas where recent range expansion has occurred (Gibb and Flux 1973; Taylor and Tilley 1984).

There is an abundance of descriptive natural history for introduced mammals in New Zealand (Thomson 1922; Wodzicki 1950; Gibb and Flux 1973; King 1984, 1990a). Wodzicki (1950) was the first comprehensive account of introduced mammals in New Zealand. Before then little scientific assessment of the effects of introduced mammals had been undertaken. When an update was required Gibb and Flux (1973) temporarily filled the gap, although no formal survey was undertaken. They did note that New Zealand's unique situation was "*great for studying the explosive nature of mammal populations.*"

King (1990a) is generally considered the authoritative current work on New Zealand mammals. It compiles individually contributed papers for the 46 mammals, both terrestrial and marine, currently found within New Zealand's territorial region. For the relevant introduced mammals each chapter contains the history of its introduction and establishment, its current distribution, notes on studies of its ecology within New Zealand, data on its zoology and other applicable material. The introduction provides a synopsis of the mammals within New Zealand, and reviews literature to date.

Introduced Mammals		
ORDER MARSUPIALIA	Family Macropodidae	
	<i>Macropus eugenii</i>	Dama wallaby
	<i>M. r. rufogriseus</i>	Bennett's wallaby
	<i>M. parma</i>	Parma wallaby
	<i>Petrogale p. penicillata</i>	Brushtailed rock wallaby
	<i>Wallabia bicolor</i>	Swamp wallaby
	Family Phalangeridae	
	<i>Trichosurus vulpecula</i>	Brushtail possum
ORDER INSECTIVORA	Family Erinaceidae	
	<i>Erinaceus europaeus occidentalis</i>	West European hedgehog
ORDER LAGOMORPHA	Family Leporidae	
	<i>Oryctolagus c. cuniculus</i>	European rabbit
	<i>Lepus europaeus occidentalis</i>	Brown hare
ORDER RODENTIA	Family Muridae	
	<i>Rattus exulans</i>	Kiore, Polynesian rat
	<i>R. norvegicus</i>	Norway rat
	<i>R. rattus</i>	Ship rat
	<i>Mus musculus</i>	House mouse
ORDER CARNIVORA	Family Canidae	
	<i>Canis familiaris</i>	European dog
	Family Mustelidae	
	<i>Mustela erminea</i>	Stoat
	<i>M. nivalis vulgaris</i>	Weasel
	<i>M. furo</i>	Ferret
	Family Felidae	
	<i>Felis catus</i>	House cat
ORDER PERISSODACTYLA	Family Equidae	
	<i>Equus caballus</i>	Feral & domestic horse
ORDER ARTIODACTYLA	Family Suidae	
	<i>Sus scrofa</i>	Feral and domestic pig
	Family Bovidae	
	<i>Bos taurus</i>	Feral & domestic cattle
	<i>Rupicapra r. rupicapra</i>	Chamois
	<i>Hemitragus jemlahicus</i>	Himalayan tahr
	<i>Capra hircus</i>	Feral & domestic goat
	<i>Ovis aries</i>	Feral & domestic sheep
	Family Cervidae	
	<i>Cervus elaphus scotius</i>	Red deer
	<i>C. elaphus nelsoni</i>	Wapiti
	<i>C. nippon</i>	Sika deer
	<i>C. u. unicolor</i>	Sambar deer
	<i>C. timorensis</i>	Rusa deer
	<i>Dama d. dama</i>	Fallow deer
<i>Odocoileus virginianus borealis</i>	White-tailed deer	
	<i>Alces alces andersoni</i>	Moose

Table 1.2. Introduced mammals established in New Zealand.

Most species have been studied in proportion to their perceived effects on the environment. The brush-tailed possum has received much attention (Clout and Efford 1984; Clout and Gaze 1984; Cowan 1990; Clout and Sarre 1997; Montague 2000), as have the rodents (Atkinson 1986; Efford *et al.* 1988; Innes 1990; Ji *et al.* 1999). Recently emphasis has also been placed on the mustelids (Ragg and Moller 2000; Caley and Morriss 2001) and hedgehogs (D. Jeffries unpubl.). Studies have tended to concentrate on the ecology of the species in its new environment (Miller and Miller 1995; Norbury *et al.* 1998; Ji 2000) in an effort to optimise control methods. This is because the ecology of invasive species changes when they enter new ecosystems - a phenomena recognised as niche shift (Williamson 1981). Studies have also looked at the detrimental effects these species have had and continue to have on the native biota (Atkinson 1978; Craig 1986; Brockie 1992; Pekelharing *et al.* 1998). Forsyth and Duncan (2001) investigated introduction effort and life-history traits with regard to exotic ungulate (large mammals) introductions to New Zealand. Although the data was confounded, they found that propagule size (number of individuals introduced) was a highly significant predictor of invasion success. Duncan and Forsyth (unpubl.) also studied the invasion success of six mammal species on 82 islands across New Zealand. They specifically investigated the effects of island latitude and habitat modification, finding both to significantly affect the long-term survival of mammal species on islands. Interestingly they did not find evidence that island area, biotic interactions or the species involved affected the survival times of populations. Although this result appears in conflict with other studies, it differs subtly since it looked at population survival times, not successful establishment or species distribution.

The appeal of studying introduced mammals on New Zealand islands is that many otherwise confounding biogeographical processes can be discounted. All non-volant terrestrial mammals of New Zealand are recent immigrants and their history is relatively well documented through Acclimatisation Society records. The species all belong to a single distinct taxonomic group, and no speciation has occurred since arrival, despite early predictions that it might (Thomson 1922). Evolutionary processes can thus be discounted with respect to introduced mammals. Vicariance can also be dismissed as a



means of arrival since all mammals were not introduced until after the Pleistocene, at which time the offshore islands became finally separated from the mainland. This means that all mammal dispersal to offshore islands has and still does occur over a water barrier, and is thus mediated by dispersal processes.

### *1.5.3 Introduced New Zealand Birds*

New Zealand separated from the Gondwana landmass before the evolution of land mammals (Gibb and Flux 1973). This meant New Zealand's avifauna evolved in the absence of interactions with mammals. This has been commented on by Diamond (1990) as making New Zealand "*as close as we will get to the opportunity to study life on another planet*".

Despite the diverse native avifauna present in New Zealand upon their arrival, immigrants from Europe sought to 'enrich' it further with the introduction of species more familiar to them from their homelands. The history of avian species introductions were well documented from Acclimatisation Society records by Thomson (1922). At least 137 species of birds have been introduced to New Zealand (Veltman *et al.* 1996), from a number of families. Only 20% of those species (28) established populations, much lower than observed success rates overseas (Lodge 1993), although this can in part be explained by the greater completeness of Thomson's (1922) records.

Introduced birds in New Zealand have not been studied to the same extent as introduced mammals. This can primarily be attributed to their inconspicuousness amongst the native avifauna, both in terms of identity and interactions. Introduced birds in New Zealand have thus enjoyed a less hunted existence since they are not seen as such an immediate threat to the native biota. However this may only have been because their interactions with the native biota were not as directly measurable. Few introduced birds directly predate native birds, instead subtly ousting them through resource competition (P. Keeling pers. comm.). Only recently have studies begun investigating introduced birds, and these have accordingly concentrated on interactions with the native avifauna (Tindall

1996; Wright and Clout 2001). The effects these studies investigate are harder to measure though, often being difficult to quantify because of their diffusive nature.

The relative abundance and thoroughness of New Zealand avian species data makes their study appealing. It also provides an excellent opportunity to compare the distributions of mammals and birds and the factors that might cause these differences. Gibb and Flux (1973) note similarly that *'the range of habitats occupied by the mammals makes interesting comparison with that of introduced birds.'*

#### *1.5.4 Insular Biogeography Theory*

Prior to MacArthur and Wilson's contribution to insular biogeographic theory, *'most research had been taxonomic in origin and historically orientated'* (Whittaker 1998). Island species assemblages were assumed to be the result of independent deterministic events – if a species could reach an island, it would be present on it, otherwise not (Brown and Lomolino 1998; Lomolino 1999).

This situation changed in the 1960s however, when Robert MacArthur and Edward Wilson published their ecological monograph *'The Theory of Island Biogeography'* (MacArthur and Wilson 1967), earlier published under the working title *'An equilibrium theory of insular zoogeography'* (MacArthur and Wilson 1963). The core of their theory presented the idea that the species numbers on an island could be related to both the immigration and extinction rates of species to that island. These processes are in turn dictated by the distance (now more generally acknowledged as *'isolation'*) of the island from the mainland, and the area of the island respectively. MacArthur and Wilson proposed that together these processes mediated species richness at an equilibrium level. The relationship was displayed in graphical form (Figure 1.3). Although Munroe (1948) and Preston (1948, 1962a, 1962b) independently presented several of the key elements of the final equilibrium theory of island biogeography (Brown and Lomolino 1998; Whittaker 1998), it was not widely adopted by ecologists of the time (Brown and Lomolino 2000). It took the clear writing style and mathematical framework of

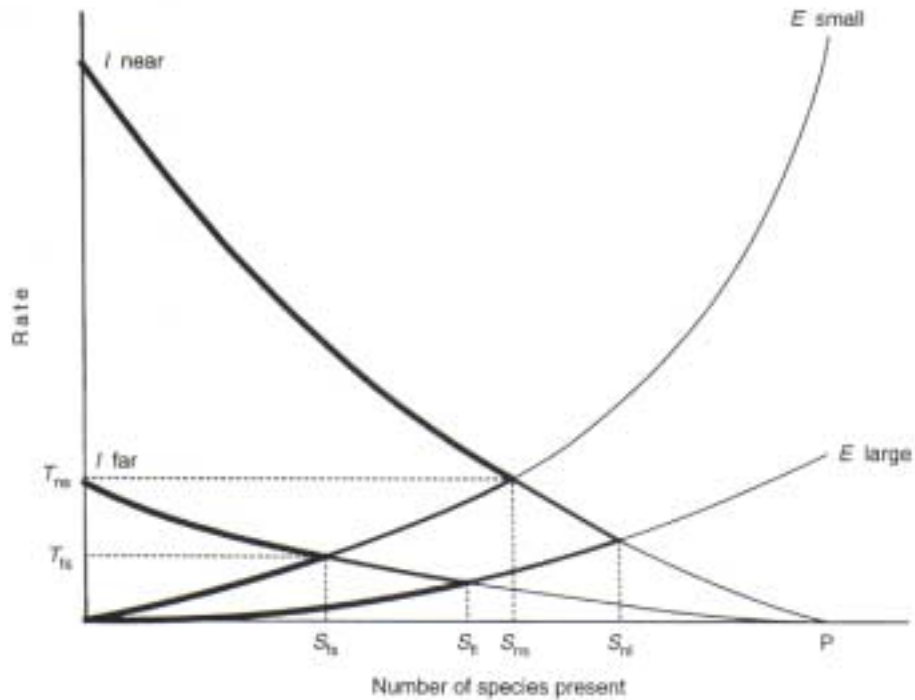


Figure 1.1. The core of MacArthur and Wilson's (1963, 1967) equilibrium theory of island biogeography. The graph demonstrates how species turnover and species richness vary as functions of island extinction ( $E \sim \text{Area}$ ) and immigration rates ( $I \sim \text{Distance}$ ).

MacArthur and Wilson's publications (1963, 1967) to present the theory in an easily understandable manner which would thrust biogeography into a new era.

In the decade following the publication of their theory, the literature became inundated with studies either supporting (Simberloff and Wilson 1969; Johnson and Simberloff 1974), or disputing (Whitehead and Jones 1969; Abbott and Grant 1976) the stance taken by MacArthur and Wilson. It has been noted though, that very few studies actually addressed the underlying premises of the theory (Williamson 1981; Gotelli and Graves 1996), instead trying to prove the theory inductively case by case. There are examples in the New Zealand literature of application of the theory of island biogeography. Williams (1986) discusses and critiques the theory within a New Zealand context, and applies it to reserve design, while Flux (1989) uses the species-area curve to predict the number of moas in different habitat types across prehistoric New Zealand.

Following from island biogeography theory, Jared Diamond coined seven 'island assembly rules' (Diamond 1975). The essential finding of Diamond's work in Papua New Guinea was that the distribution of avian species on islands was dependent on what other species were already present, through a process of diffuse competition. The results were presented graphically as 'incidence functions', plotting species presence against the total number of species, yielding different species classes depending on at what species saturation level a species would occur on an island. Although the first part of Diamond's theory seemed altogether reasonable, his conjecture that such observed assemblages were the result of competition, and his construction of island assembly rules, sparked fierce debate. Daniel Simberloff and others (Simberloff 1978; Connor and Simberloff 1979) argued that Diamond had not specified accurate null models with which to compare to his observed distributions, and that there was no evidence to invoke competition as the driver of any observed distribution patterns. Although the debate was never suitably resolved, studies have since expanded on Diamond's island assembly theory (Booth and Larson 1999; Fox 1999; Lockwood *et al.* 1999), which its intrinsic interest at least warranted (Weiher and Keddy 1999).

Charles Elton (1958) produced the first comprehensive text on invasion ecology and recognised that islands are more susceptible to invasions than adjacent continental zones. It has been noted since though, that his initial differentiation between invasion ecology and all other branches of ecology may have created more division between disciplines than was necessary, and that such division has deprived the various disciplines from exchanging knowledge (Davis *et al.* 2001). It is accepted that islands are ecologically impoverished with respect to equally sized adjacent areas of the mainland (MacArthur and Wilson 1967; Williamson 1981), and that this facilitates invasion. The reasons are not well understood though, with several hypotheses induced to explain the phenomenon (Williamson 1981; Rosenzweig 1995; Whittaker 1998). Corbet (1961) first recognised that the distribution of mammals across British islands was the result of human-mediated accidental transportation, prompting a reevaluation of past studies that had assumed natural dispersal. The British Isles though, were predisposed to human effects (Williamson 1981), and so other work instead concentrated on pristine insular systems

such as Grant's (1970) work on Canadian islands. Today biogeographers must still be reminded that their studies "*must take into account human effects*" (Spellerberg and Sawyer 1999).

Insular biogeography studies have generally investigated only one taxon at a time (Lomolino 1982; Martin 1984), although some have, to their benefit, covered multiple taxa (Abbott 1983; Ricklefs and Lovette 1999; Morand 2000). For the most part in the past, studies have considered either mammals or birds, although that is not to say other taxa have not been considered (insects – Dennis 1998; Welter-Schultes and Williams 1999; reptiles – Woinarski *et al.* 1999; marine – Haynes 1990). Although originally authors may have chosen to study a taxon based on personal predisposition towards it (Robert MacArthur, himself an ornithologist, complemented the entomological knowledge of Edward Wilson), it also served the more subtle purpose of highlighting the differences between such taxa. Mammals are characterised by poor dispersal ability. This predisposes them to studies of localised archipelagos, where isolation can be investigated with dispersal as the limiting factor (Williamson 1981). In contrast to this birds are characterised by their excellent dispersal ability, and instead find their distribution limited by area and its correlates. For distant archipelagos where birds are limited by dispersal, speciation then exceeds immigration and the system becomes dominated by evolutionary processes (Williamson 1981), which falls beyond the scope of an ecological study, and is otherwise negated by the recent nature of the introduced species studied. The work that has perhaps contributed most to studies of limiting factors in avian distribution is that by David Lack (1969, 1976). Lack staunchly believed habitat was the primary limiting factor to avian distribution across islands, notwithstanding habitat being generally correlated with area. His work was also some of the first to present an alternative theory to MacArthur and Wilson, one that suggested that the distribution of species on islands was not limited by dispersal, but in fact by habitat requirements. He provided many examples to support this. Lack's work though, was predominantly qualitative and emphasised individual avian species. He also neglects to discuss the processes by which biotic constituents of the 'habitat' might arrive (Williamson 1981). Ultimately both dispersal

ability and habitat availability most likely limit species, although the predominance of either may differ between archipelagos.

With respect to the dispersal ability of mammals in New Zealand there are few studies. Whitaker (1974) is the only study that has experimentally investigated the swimming ability of an introduced mammal. Observing nine kiore swimming at the Mokohinau Islands Whitaker found, among other statistics, a mean swimming distance of 66m (interval 10 – 130m). This was then related to the inter-island distances of the island group, and the presence of kiore. Since then all other distances that introduced mammals can swim (see Atkinson and Taylor 1991) have been deduced from island distributions or overseas studies.

The new millenium has marked a turning point for biogeographers. With little substantial change to the ruling paradigm for over 30 years (Brown and Lomolino 2000; Lomolino 2000a), it was felt necessary, if not overdue (Brown and Lomolino 2000; Whittaker 2000; Lomolino 2001) to consider fresh ideas in island biogeography. Mark Lomolino (Lomolino 2000a, 2000b, 2000c; Lomolino and Weiser 2001) has recently drawn attention to the fact that at different spatial and temporal scales, different island biogeographic processes appear dominant, a sentiment also acknowledged by Robert Whittaker (Whittaker 1998, 2000; Whittaker *et al.* 2001). The underlying tenets of MacArthur and Wilson's equilibrium theory of island biogeography have also finally begun to be addressed. The theory is now seen as only one of many possible theoretical outcomes for island turnover (Whittaker 1998, 2000; Anderson and Wait 2001) and is also divided into its integral deterministic component, and its embellishing stochastic components (Whittaker 1998, Whittaker 2000).

Finally, new theories benefiting from the increased discussion of island biogeography are being proposed. Whereas some (Lomolino and Weiser 2001) extend on the ideas presented in the original theory, others are more radical. Stephen Hubbell (Hubbell 2001) has in late 2001, as I complete my thesis, published through Princeton University Press (as MacArthur and Wilson's theory originally was) a 'Unified Neutral Theory of

Biodiversity and Biogeography'. This theory differs by modelling at the more complex level of individual neutrality rather than species neutrality, thus accounting for the differences between species, one of the major criticisms of the original MacArthur and Wilson theory (Rosenzweig 1995; Brown and Lomolino 1998). Although biogeographers have not yet had the opportunity to discuss, and perhaps debate, the fundamentals of the theory, it nonetheless appears to be an exciting step forward in biogeography and biodiversity theory. It also further unifies the disciplines of island and community (mainland) ecology, as Jared Diamond and others once attempted to do, though I foresee the customary discord between plant and animal ecologists occurring, with Hubbell's roots grounded firmly in the plant camp.

## *Chapter 2: Data Sources and Methods*

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### *2.1 Data Sources*

The following section outlines the sources used in this thesis to gather data on New Zealand offshore islands and the distribution of introduced species on them.

#### *2.1.1 Distribution of Alien Mammals on New Zealand Islands (Atkinson and Taylor 1991)*

The objective of Ian Atkinson and Rowley Taylor's 1991 project was to create a national database of New Zealand Islands (offshore and outlying) for purposes of conservation management. This project was initiated following the 1990 conference on the 'Ecological Restoration of New Zealand Islands' (Towns *et al.* 1990). The database (in its hard copy form) brings together both published and unpublished surveys of alien mammals on islands larger than five hectares, along with records of flightless birds and archaeological and historical evidence of human settlement. Recommendations are also made for further studies to enhance the value of the database. The report itself details the database and its constituent variables, with references for each island. Some key points are also reiterated here as they reflect on the conversion of the database into a dataset for this thesis.

Symbols for species occurrence were originally presented in a comprehensive manner. Table 2.1 gives abridged definitions of these symbols, and their conversion for this study.

Of the 17 species of introduced mammal identified in the database, 15 are identified to the species level. 'Deer' and 'Wallabies' are in fact the agglomeration of several species. For the sake of simplicity such nomenclature is kept in this study. Although this makes it appear that there are fewer mammals on New Zealand offshore islands, for deer the distributions of most species are exclusive, and wallabies are only present on three islands, so ultimately any bias is negligible. It is also important to distinguish the 'dogs'



Symbol	Interpretation	Conversion
+	present	+
-	not found during surveys or trapping	-
(no symbol)	inadequate surveys or trapping to confirm absence	NA
E	eradicated	+
?	presence suspected, but not confirmed	NA
d	deer not present, but island within swimming distance (c. 1km)	-
s	stoats not present, but island within swimming distance (1.2km)	-
r	rats not present, but island within swimming distance (c. 300m)	-

Table 2.1. Symbol conversion for introduced mammals from Atkinson and Taylor (1991). Interpretations are abridged.

that roam free on islands as the European breed, not the kuri – the extinct Polynesian dog that arrived with Polynesian settlers. A species is only considered present if it is feral or there are free roaming populations that sufficiently influence the ecosystem (*sensu* Atkinson and Taylor 1991).

There is also an issue that, despite adequate invested sampling effort to locate a species, its absence may not necessarily be confirmed. An error is introduced where a species may have once established (or even only invaded) and subsequently gone naturally extinct without any record (a temporal error), or may be present in such low numbers so as not to be detected (a spatial error). This error may also vary with other factors, either measured in the study (area, settlement history, species type) or not measured (directly) in the study (island visitation rate, sampling effort). Unfortunately measurement of such an error would require a thorough knowledge of the sampling effort and assumed rarity of each species at the least (see McArdle 1990; McArdle *et al.* 1990).

### 2.1.2 Major Habitats on New Zealand Islands (Atkinson 1992)

Atkinson (1992) is the consequence of the fourth recommendation in Atkinson and Taylor (1991) – that an island habitat classification system be created for New Zealand's offshore and outlying islands.

The database that was created contains information on the different geographical habitats (landforms) on offshore and outlying islands larger than five hectares, and the number of biological (vegetation association) habitats within each geographical habitat (i.e. a nested structure). Major rock types for islands are also listed, along with elevations. The data in the study are of variable quality, ranging in source from in-depth field studies to only inspection of aerial photos or topographic maps. This means that the magnitude of any variable estimates based on these descriptors may be partially correlated with sampling effort or island visitation rates. Atkinson (1992) classifies each island based on its data source, but it was not an objective of this thesis to investigate whether or not any differences in data source had a quantifiable effect on the descriptors. Even if an estimation of this effect was undertaken, other variables such as area, and the biological value of the islands themselves (assuming more interesting islands are visited more often) would most likely confound it.

The range in offshore islands around New Zealand means that there is a large amount of variation in habitat and rock types, with islands often containing unique examples of one or both. The interpretation of worded habitat and rock type descriptions for statistical analysis therefore presented some difficulty. It was decided that the best way to summarise these descriptors was to convert them into index counts – a Geographical Habitat Diversity Index (*GHDI*), Biological Habitat Diversity Index (*BHDI*) and Geological Diversity Index (*GDI*). These indices concisely summarise the magnitude of variety on an island, but are limited in that they can not convey any uniqueness or abundances of the subsumed types; they are quantitative and not qualitative measurements. By this it is meant that two islands that share identical habitat index counts may not share any common habitats whatsoever, and could be completely ecologically distinct. Although this may appear to be a significant shortcoming, in actuality all it prevents is the investigation of individual species-habitat relationships (such as rabbits to grasslands). The indices still provide a measure of habitat or rock type heterogeneity, which may itself be a significant correlate of individual species presence or overall species richness.

### *2.1.3 The Atlas of Bird Distribution in New Zealand (Bull et al. 1985)*

The Ornithological Society of New Zealand (OSNZ) Bird Atlas was a joint undertaking by the OSNZ, Ecology Division of the Department for Scientific and Industrial Research (DSIR) and the New Zealand Wildlife Service. It contains data on bird distribution collected over the decade between 1969 – 1979. Field observers compiled lists of bird species from points located in 10,000 yard grid squares across the country (3675 squares in total). In total over 19,000 species lists (cards) were compiled, although these were not evenly distributed among grid squares. The atlas itself has presence information for over 250 bird species, which can be classified following OSNZ practice into three categories:

1. Terrestrial (including freshwater)
2. Waders
3. Seabirds

Summary maps were only provided for the first category.

Island species lists were taken as the grid in which the island was found. Islands spanning multiple grids had their species lists combined. This unfortunately renders the data ‘coarse’ when comparing islands, as island groups within a single grid square have species lists that are unrealistically identical. Some islands were also in grids that contained small parts of the mainland. The atlas card summaries do not identify where they were collected in the grids, although it would seem most reasonable to assume that in these cases it would have been the mainland for logistical reasons, as the volunteer field observers would be less likely to sample from offshore islands. This means that the ‘island’ lists for grids that contained the mainland are probably more realistically ‘mainland’ lists. Equilibrium island biogeographic theory (MacArthur and Wilson 1963, 1967) and common sense suggest that some of these species would not have colonised the islands in these grids; in fact that is the goal of this study to identify the factors that do correlate with the distribution of such species on offshore islands. The application of the atlas data is thus limited by the assumption that ‘all bird species within a 10,000 yard

grid square have the capacity to colonise any site throughout it'. This assumption appears reasonably realistic for the latter two species categories identified earlier (provided that macroscale habitat availability is relatively consistent throughout each grid). However for landbirds it was decided that such an assumption would most likely be violated, since many land bird species are restricted by geographical barriers, especially water (M. Clout pers. comm., Martin 1984). The 'coarseness' of the data also means that microscale biogeographic variability is subsumed within the 10,000 yard grid squares, or rendered irrelevant for cases where the mainland is included. Meanwhile broader scale variability such as in *Latitude* is instead expected to dominate. Thus the data for avian species richness should be considered somewhat unreliable overall.

Some birds could not be classified to species level during field recording for the atlas. This was either because visual identification required close inspection of plumage, or vocal calls of related species could not be differentiated. Of the 245 species that were found on New Zealand's offshore islands 30 were general taxon groups. However the constituent species of the taxon groups were also recorded, and so in some cases it was possible to have both an unidentified taxon and one or more of its constituent species also present. This means species richness values for those islands may be overestimated, but this is rare.

There is also a bias from observer effort. This is addressed in *Section 3.1.7* where it is detrended to account for the bias. Caution must nonetheless be maintained while interpreting results from the data, although other studies (Harvey 1996) have analysed data from the atlas overlooking the bias generated by observer effort.

Codes for species were gathered from the microfiche summary sheets for each grid provided with the atlas. 26 of the 203 (13%) grid squares that contained islands had no information available. These codes were then converted into species richness counts for each class. Islands spanning multiple grid squares had their species counts combined, with duplicates removed, before summing species richness.

The Ornithological Society of New Zealand is currently collecting data for a second atlas, which they aim to publish by 2005.

#### *2.1.4 Land Information New Zealand Database (LINZ 2000)*

The LINZ database contains values for the latitude, longitude, land district code and NZMS 260 map grid reference of most New Zealand offshore islands. The first three variables were used in model construction, while the NZMS 260 map grid references were used to locate islands for further measurements. For some larger islands, multiple values for latitude and longitude were given, taken from the different locations of place names on the maps. The latitude and longitude of the place name located closest to the geographic centre of the island was taken. In any case these were found to only differ by 0.02 degrees from other values.

#### *2.1.5 New Zealand Map Series (NZMS) 260 Measurements*

Islands were located on NZMS 260 topographic maps (scale 1:50,000). Measurements of each island's distance to the mainland, and distance to its nearest intermediate neighbour that minimised across-sea distance (*Section 3.1.2.7* elaborates on this measurement) were taken to the nearest 0.5mm (250m). These were measured as a straight line from the closest point on the island to the closest adjacent point on the appropriate landmass. Elevations of islands were also updated from Atkinson (1992), as corrections had been made to the map series. Latitudes and longitudes for islands with missing values were also recorded.

## *2.2 General Methods*

### *2.2.1 Linear Modelling*

All models have been created using linear modelling, a technique widely used in the natural and life sciences to disentangle the effects of various independent (explanatory) variables on a single dependent (response) variable. The results are used to predict what response value a new observation might have, to estimate the effects of each variable and to identify the structure within a system (Glantz and Slinker 2001). All of this can be achieved from a single model, although the strength of inferences for each can vary depending on the validity of implicit assumptions in the dataset. Linear modelling methodology follows Glantz and Slinker (2001).

#### *2.2.1.1 Generalized Linear Models*

Due to the particular distributions of the response values in the study, the Generalized Linear Model (GLM) family proposed by Nelder and Wedderburn (1972) was chosen for model construction. In these models the relationship between the dependent and independent terms must be linear. This is achieved through the link function and transformations of the explanatory variables. The distribution of the response (dependent) variable is also assumed to be from the exponential family, most commonly:

1. Gaussian (normal)
2. Binomial (logistic)
3. Poisson

The second and third cases are most appropriate in ecology. The binomial distribution simulates presence – absence of species, while the Poisson (‘rare events’) distribution is right skewed with discrete positive values and is generally a good approximation for species counts (although others such as the negative binomial perform well).

Generalized linear models take the form:

$$F(y_i) = \beta_0 + \sum_j \beta_j x_{ij} + e_i \quad F \sim \text{link function}$$

Where  $y_i$  is the response value of the  $i$ th observation,  $x_{ij}$  is the  $i$ th value of the  $j$ th explanatory variable (i.e.  $x$  is a data matrix of  $i$  observations and  $j$  explanatory variables),  $\beta_0$  is the intercept,  $\beta_j$  is the coefficient of the  $j$ th variable and  $e_i$  is the residual error of the  $i$ th observation.  $F$  is a monotonic link function which depends on the response family's distribution (from the list earlier).

The coefficients are estimated using an iteratively reweighted least squares algorithm (Glantz and Slinker 2001), and are not standardised. This means that comparisons of them can not be made between variables (except for categorical/dummy terms) as they remain scale dependent. The coefficient measures the effect of  $x_{ij}$  on  $y_i$  at the scale on which it was measured (units are given in *Section 3.1*). Although it would be informative to compare effects between variables, the mathematics required to do so is complicated and more difficult to interpret. Instead these families use the natural logarithm in the link function, and their model coefficients are the proportional change in the remainder of the link function of the response for a change in one unit of the explanatory variable, keeping all other explanatory variables constant. If the explanatory variables had been standardised then the interpretation of coefficients would be for a change in one standard deviation of the explanatory variable.

Proof using regression of a single explanatory variable and natural log link (intercept and coefficient):

$$\begin{aligned} \log_e E(w_i | x_{i1}) &= \beta_0 + \beta_1 x_{i1} \\ \Rightarrow E(w_i | x_{i1}) &= e^{\beta_0 + \beta_1 x_{i1}} \\ &= e^{\beta_0} \cdot e^{\beta_1 x_{i1}} \end{aligned}$$

where  $w_i = y_i$  for the Poisson family and  $y_i / (1 - y_i)$  (odds function) for the binomial family.

For  $(x_{i1} + 1)$  (a change in one unit of the explanatory variable)

$$\begin{aligned} E(w_i | (x_{i1} + 1)) &= e^{\beta_0} \cdot e^{\beta_1(x_{i1}+1)} \\ &= e^{\beta_0} \cdot e^{\beta_1 x_{i1} + \beta_1} \\ &= e^{\beta_0} \cdot e^{\beta_1 x_{i1}} \cdot e^{\beta_1} \end{aligned}$$

Substituting  $w_i$  from earlier

$$E(w_i | (x_{i1} + 1)) = w_i \cdot e^{\beta_1}$$

Therefore  $w_i$  has increased proportionally by  $e^{\beta_1}$  (or decreased proportionally by the inverse) – where  $\beta_1$  is the explanatory variable coefficient.

P-values are quoted to three decimal places (3 d.p.) unless otherwise noted. Significance is noted if  $p$  is less than 0.100, although the more usual cut-off for statistical significance is 0.050. This lower significance level was chosen so that variables which may be having a smaller influence with respect to other more significant variables on the response could still be detected, though this is at the expense of a higher probability of detecting spurious relationships. Significance codes are given in Table 2.2.

P-value range	Sig. code
0 - 0.001	***
0.001 - 0.01	**
0.01 - 0.05	*
0.05 - 0.1	.
> 0.1	ns

Table 2.2 Significance codes.



### 2.2.1.2 Model Construction

There are numerous stages to linear modelling. The first of these requires selection of the model building technique. Two approaches are generally available. One is to construct the model and its constituent terms ('terms' includes the transformations and interactions of variables) from *a priori* hypotheses (see Woinarski *et al.* 2001). The other is 'step-wise selection' (see Burbidge *et al.* 1997; Millien-Parra and Jaeger 1999), an iterative process whereby a computer package adds or removes terms based on an arbitrary cut-off significance value, until a final 'best' model is reached. This approach though, can be prone to becoming trapped in local minima of sub-optimal models.

The second approach perhaps allows a more informative model to be created, but it is limited in that the actual significance of each term no longer holds any meaning. Philippi (1993) words this quandary well:

*“Because of the multiple analysis of a given set of data, the appropriate null hypothesis to be tested is: Given the complete series of analyses, what is the probability of obtaining a fit at least as good as the observed fit ... There is no general way to compute the appropriate hypothesis tests, and even bootstrapping the sampling distribution would require specifying the universe of all transformations and models that might have been tested in the overall analysis.”*

The sounder scientific methodology lies in the first approach, whereby significance values can be interpreted and compared. A third possible approach is to divide the dataset randomly in two and create the model on one half of the data followed by testing it on the other half of the data (D. Simberloff pers. comm.).

Because the processes that drive introduced species distribution across New Zealand islands are generally well suspected qualitatively, and the only unknowns are quantitative comparisons, the first method was considered most applicable. The *a priori* models

combine variables that are individually considered most relevant to the response based on a literature review and personal discretion. Although some variables not selected could reasonably be expected to explain variation in species richness, criteria for selection also aimed to limit the total number of variables in the original model, by selecting only those which would have the most explanatory power. Increasing the number of variables will always lead to an increase in explanatory power of the model, but this also creates added complexity in the model itself, which is not an aim of model construction where simplification of complex systems is the goal.

### *2.2.1.3 Model Diagnostics*

Initially a linear model must be tested for adequacy. Following that it is necessary to test its validity with respect to the assumptions it was created on. Namely:

1. Observations are statistically independent
2. The explanatory variables are a linear function of the response
3. The errors (residuals) are appropriately distributed

The adequacy of a generalized linear model using Poisson or binomial errors can be tested using a chi-squared test for adequacy of fit between the observed and predicted values.

$H_0$ : Model is an adequate fit for the data

The test statistic is the residual deviance, which is a measure of the unexplained variation (measured in terms of likelihood approximation) left in the model. If the p-value approaches significance then the null hypothesis should be in doubt and significant over-dispersion is present implying that the model is misspecified either in the explanatory variables or the error distribution or both.

The first of the assumptions is readily met if we consider islands as statistically independent. The occurrence of non-independent islands (*Section 3.1.2.7.1*) can be considered exceptional. To test the last two assumptions it is necessary to examine the residuals. For the binomial and Poisson distributions it is best to use deviance residuals (T. Yee pers. comm.), as they are least distorted by the inherent trends of the distributions. First it is necessary to inspect plots of the deviance residuals against the predicted values, and each explanatory variable. If these plots suggest non-random scatter of any sort, further investigation is necessary. Glantz and Slinker (Chpt. 4 2001) suggest methods to correct violation of the assumptions.

During investigation of the deviance residuals it is also possible to identify outlying and high leverage observations. Outlying observations have large residual values, and could suggest an error in sampling or an exceptional case. High leverage observations are those which take an extreme (influential) value at either end of an explanatory variable's range. They have a disproportionate effect on the fitted regression line (see pp. 145-146 in Glantz and Slinker 2001). It is generally wise to run the model having dropped high leverage observations to see if there is any significant change in coefficients. If observations are dropped this must be noted in the discussion.

The diagnostic techniques described have been used to assess the validity of the models created.

#### *2.2.1.4 Model Refinement*

Following *a priori* model construction and diagnostics, some aspects of the models which have either under-performed, not performed as might have been expected, or simply merited further interest have been refined. This exploratory refinement negates significance testing of terms, but it does allow further insight into the system's patterns that may not have otherwise been revealed under the stricter *a priori* hypothesis conditions.

Model exploration consisted of investigating other forms of some variables and inclusion of variables not originally hypothesised to have any significant predictive power.

### 2.2.2 Z-values

MacArthur and Wilson (1963, 1967) first introduced z-values in the 1960s as part of their equilibrium theory of island biogeography investigating total species richness. Since then they have been widely accepted as the most elegant way to explain the species-area relationship (Whittaker 2000).

The species-area relationship is usually taken as Arrhenius' (1921) power model:

$$S = cA^z$$

Where  $S$  is the total species richness within the sample,  $A$  is the total area sampled and  $c$  and  $z$  are mathematically determined coefficients unique to the sample.

Taking the logarithm of both sides this becomes:

$$\log S = z \log A + \log c$$

This equation allows linear regression estimation of  $z$  (slope) and  $\log c$  (intercept). It does not matter to what base the equation is logged (for proof see p. 22 in Rosenzweig 1995). It should be noted that non-linear fitting methods have also been suggested for fitting the species-area curve (e.g. Wright 1981). However the use of such methods appears not to have become popular, most likely due to the inherent simplicity of fitting the linear regression line on an Arrhenius log-log plot (Arrhenius 1921).

Z-values themselves quantify the relationship between species richness and area for a particular archipelago, and tend to vary very little between and within taxa across the world (MacArthur and Wilson 1967). However z-values are also dependent on elevation,

and archipelago distance from the mainland (Wright 1981), should they be correlated with area. The effect of area on species richness is generally more substantial for islands further from the mainland (Abbott 1980), although occasionally the opposite has applied for birds (Schoener 1976). This concept is intuitively illustrated in the original theory of island biogeography (p. 28 in MacArthur and Wilson 1967).

Because of the interactive effect between distance and area, it is necessary for comparative values of  $z$  to be from the same geographical scale. In fact the scale dependence of the theory of island biogeography has recently been highlighted as one of the primary causes for contradictory results in island biogeographic studies (Hubbell 2001; Whittaker *et al.* 2001).

Z-values also render species richness estimates independent of the non-linear effects of area. These effects manifest themselves by biasing species richness estimates across samples of different sizes. A simple estimate using

$$\text{total number of species} / \text{total area}$$

is inappropriate, biased by the non-linear effect of area on species richness (for a complete explanation see p. 31 in Rosenzweig 1995).

It is important to recall when interpreting  $c$  however, that the calculated regression value is for  $\log c$ . The original model is multiplicative and by back-transforming and comparing different values of both  $z$  and  $c$  they clearly have different interpretations. It becomes apparent that  $z$  is positively related to the asymptote of species richness, and is inversely related to the time it takes for that asymptote to be reached. The back-transformed intercept  $c$  in fact designates the differing rate of increase in species richness between different taxa or locations (Gould 1979; Lomolino 1989) – i.e.  $c$  now also determines the form of the slope.

The intercept  $c$  depends on the taxon and biogeographic region. It is also dependent on the units  $A$  is measured in, while the slope  $z$  is unit independent (for proof see p. 21 in Rosenzweig 1995). Thus  $c$  values calculated at different units of area require transformation before they can become comparable (Lomolino 1989).

However  $z$ -values have not been without their criticism. What originally appeared as an inherently simple summary statistic (May 1975; Diamond and May 1976; Schoener 1976) became fraught with both mathematical (Sugihara 1981; Wright 1981, 1988; Williams 1996) and biological (Connor and McCoy 1979; Abbott 1983; Lomolino 1989) difficulties. Gotelli and Graves (p. 224 1996) provides an extensive review of  $z$ -values and their interpretation. Now  $z$ -values are more cautiously used, and it is realised that the true mathematics of  $z$ -values lies within the assumed underlying species-abundance distribution (see p. 223 in Gotelli and Graves 1996).

## Chapter 3: Raw Data

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### 3.1 Variables

This section specifies the variables used in the study; defining them, describing any transformations performed on them and considering any missing values. All variable names as used or abbreviated in statistical analysis are given in *italics*.

Many of the processes being investigated are represented by complex configurations in reality. In some instances the processes may not be well understood. This requires that simpler measurements be taken as surrogates for these processes. The complex nature of one particular relationship, between species and area, has been well studied and has an entire section dedicated to it (*Section 3.2.3*). For the other variables in the study, a brief discussion of what process or processes they may represent is given in the following section.

Before describing each variable individually, the reasoning for consistent use of the  $\log_{10}$  transformation will be given. This transformation is appropriate in many situations, and is used in most studies (see Johnson and Raven 1970; Burbidge *et al.* 1997; Conroy *et al.* 1999; Millien-Parra and Jaeger 1999; Blackburn and Duncan *in press*). It often provides a more interpretable and appropriate axis, both with respect to the original form of the variable and in comparison to other transformations. More importantly it removes size-effects. Statistically this means that right skewed variables, common in the life sciences, have the biasing effect of their large values reduced, eliminating much of the skew. Subsequently the variables may approach normality, which can be a prerequisite for some statistical tests. Most importantly though, a  $\log_{10}$  transformation can substantially improve the linearity between the response and explanatory variables that is an implicit assumption of linear modelling. For all transformed variables in the study non-linearity with respect to the response ceases to be an issue.

There is also a mathematical justification for using the log transformation. If the probability of a species dispersing to an island takes the form of a negative exponential, then it would be most sensible to work with a logarithm of distance, and similar arguments can be put forward for other variables (p. 68 in Williamson 1981).

### *3.1.1 Island Name*

The *Island* name is presented as the common name of the island with its translated name, when also in common use, in brackets. The commonest name is presented first and may be either the English or Maori version. When the island is a member of a larger group or chain, the collective title is presented in upper case before the common name. For solitary islands a geographic marine location is usually given after the common name. *Island* name is used to order the observations alphabetically. Some islands are unnamed; they are titled as such and their geographic location is accurately recorded.

There is a total of 297 offshore islands in the dataset.

### *3.1.2 Geographical Variables*

#### *3.1.2.1 Latitude*

*Latitude* is given in Southern Hemisphere degrees (a negative value) with the minutes (1/60) converted to decimals (1/100) to remain consistent with the LINZ database format. Patterns of variation have long been associated with Latitude. Terborgh's pattern is perhaps the most well known (Rosenzweig 1995): it simply surmises that globally there is greater species diversity in the tropics because there is more land occupying that part of the globe, thus it is at the upper boundary of the species-area curve. Terborgh's pattern is coarse though, and regionally we would expect gradients such as climate and productivity to exert an effect. Sax (2001) suggested *Latitude* was a good surrogate for frost-free days, whilst Duncan and Forsyth (unpubl.) suggest it as a surrogate for primary productivity.



Pianka (1966) still offers one of the best reviews of the latitudinal gradient (Rosenzweig 1995). *Latitude* is also a correlate of human settlement intensity. As *Latitude* increases, coupled with the extremity of the environment, human settlement becomes sparser, to the extreme polar regions of the globe where no self-sustaining settlement can survive.

There are no missing values for *Latitude*.

### 3.1.2.2 *Longitude*

*Longitude* is also given in decimal degrees. All longitudes are East of 0°. *Longitude* is generally not recognised as a surrogate for any environmental patterns or processes, however together with *Latitude* the two variables give Cartesian (x,y) coordinates for all islands.

There are no missing values for *Longitude*.

### 3.1.2.3 *Area (ha)*

*Area* is measured in hectares, consistent with Atkinson and Taylor (1991). *Area* is also  $\log_{10}$  transformed, consistent with most other studies. The  $\log_{10}$  transformation removes most of the right skew in the distribution of *Area*, but Stewart Island, being the largest island by a factor of five, remains an influential observation.

*Area* is perhaps the most readily identifiable island descriptor, but perhaps also the most deceptive. It has been the most studied of island biogeographic parameters with respect to what it may act as a surrogate for, but because of confounding with other measurable variables it has a latter section dedicated to it (*Section 3.2.3*).

One variable related to *Area* that has occasionally been used (Blake and Karr 1987) is the perimeter of an island – its measured boundary. Island perimeter is not defined in this study and will therefore not be used.

There are no missing values for *Area*, but a general threshold of five hectares was chosen as the lower value for islands to be included in the study. Eight islands of less than five hectares have been included as they represent geographically or ecologically unique islands (*sensu* Atkinson and Taylor 1991; Atkinson 1992).

### 3.1.2.4 Elevation (m)

*Elevation* records the highest peak on an island in metres. Before transforming, *Elevation* has two large outliers; Resolution Island and Secretary Island, both in the glaciated valleys of southwestern Fiordland. Once  $\log_{10}$  transformed the right skew is removed, but some left skew is generated, with the smaller islands where *Elevation* is less than 20m possibly being influential. The skew present in *Elevation* both before and after  $\log_{10}$  transformation is shown in Figures 3.1 (a) and (b).

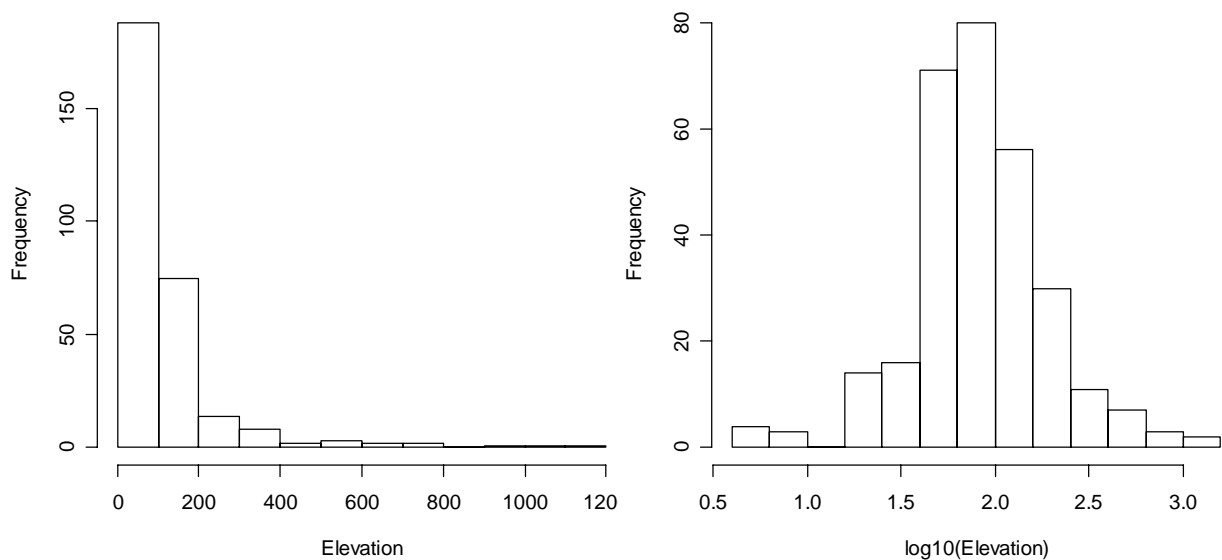


Figure 3.1. (a) Histogram of untransformed *Elevation*. Note the right-skew common in ecological data. (b) Histogram of  $\log_{10}$  *Elevation*. Note the left-skew generated by the transformation.

*Elevation*, measured as the highest peak, may be an inaccurate measure of island height as it describes only the maximum point of an island, which may be a geographic anomaly. Better surrogates for island height may be some measure of average height, or a combination of highest peaks. *Elevation* measured as the highest peak is the simplest measure though. Mueller-Dombois (1999) particularly believes elevation should be included as a third vertical component of the original island biogeographic theory, as a surrogate for water-flow or hydrology. Lomolino (1990) though found elevation was an excellent correlate of active dispersal, whereby a dispersing animal may seek a destination that is more visible on the horizon. There are thus a number of possible interpretations for the role *Elevation* may have in island biogeography.

There are no missing values for *Elevation*.

### 3.1.2.5 *Distance to the Mainland (m)*

Distance to the mainland is abbreviated to *Dist.Main* and measured to the nearest 250m. It is also  $\log_{10}$  transformed to remove the right skew present in its original distribution. In the literature distance to the mainland, as the measurement originally proposed by MacArthur and Wilson (1963, 1967), is now acknowledged as a surrogate for isolation from the mainland (Whittaker 1998). The true 'isolation' of an island is in fact the result of a number of interacting factors, including its distance from the mainland, tidal activity between the island and mainland and wind activity and storm events in the intervening distance. Burbidge *et al.* (1997) are perhaps optimistic in their view that distance from the mainland is a direct surrogate of isolation. Nonetheless distance from the mainland is easily measured and most commonly used in island biogeographic studies.

MacArthur and Wilson (1963, 1967) used distance from the mainland as an inverse approximation for immigration rates. The shape of the relationship between immigration and distance to the mainland is not known, but that did not interfere with the theoretical particulars of their work.

Atkinson (1989) gives deduced maximum swimming distances for introduced mammals, calculated from the islands to which they have been unable to naturally disperse. Studying the autoecology of species presents its own inherent difficulties however, as one must consider cues for dispersal – what are the factors that compel a terrestrial species to enter a foreign marine environment with the goal, perhaps not even realised, to reach an offshore island?

There are no missing values for *Dist.Main*.

#### 3.1.2.5.1 Rakiura (*Stewart Island*)

The variable *Dist.Main* does generate a sequence of anomalous values. Stewart Island is generally considered part of the New Zealand mainland. It is the third largest island in the New Zealand archipelago and is geographically similar to the mainland by virtue of being surrounded by smaller offshore islands. In this geographical respect distance from the mainland for these smaller offshore islands should be measured as from Stewart Island. Ecologically however, Stewart Island is not identical to the New Zealand ‘mainland’. Many introduced species found throughout the rest of New Zealand are absent from Stewart Island (King 1990a), notably stoats and mice. It also has only one settlement, the rest of the island constituting old-growth native forest. In this ecological respect Stewart Island should not be considered part of the mainland. However if this is done, then the surrounding offshore islands become located substantially further from the mainland, by up to 100km and well beyond the range of Atkinson and Bell’s (1973) ‘offshore’ islands, despite still being on the continental shelf.

The statistical artifact generated is that  $\log_{10}$  *Dist.Main* now interacts with *Latitude*, the anomalous group being the islands located around Stewart Island. There appears to be no simple solution to this problem. What is occurring is a complex stepping stone system whereby some species have colonised Stewart Island and only then been able to reach the

surrounding islands. Other species most probably can not colonise these islands unless Stewart Island is first colonised.

### 3.1.2.6 *Stepping Stone*

The categorical variable *Stepping.stone* codes for the presence or absence of an intermediate island between an island and the mainland. The variable does not differentiate between the number of islands that are intermediate. Such a measurement would be complex, requiring consideration of distances and angles relative to the mainland. *Stepping.stone* thus considers only a simple, single stepping stone system.

There are no missing values for *Stepping.stone*.

### 3.1.2.7 *Distance to Nearest Source (m)*

Distance to the nearest source, abbreviated to *Dist.Source*, is an extension of both the variables *Dist.Main* and *Stepping.stone*. Similarly it is  $\log_{10}$  transformed to remove right skew and achieve linearity with respect to response variables. Isolation as a measurement should in fact consider the distance of an island from the nearest source population, which may not necessarily exist on the coast of the mainland. Such a source population could be further inland, although this measurement would be difficult to quantify without data on species distributions throughout the mainland, ignoring the varying spatial natures of such populations over time. A source population may also already exist on a neighbouring island. It is most likely that such an island would be closer to the mainland (though not always), and the species would then not have as far to travel over water to colonise the island. These sequences of colonising steps are termed stepping stones.

*Dist.Source* only considers a single stepping stone system, as *Stepping.stone* did earlier. The measurement of this relationship however, is somewhat more difficult than was simply categorising it as done earlier. Minimising for all possible stepping stones the distance from the nearest point of an island (A) to the nearest point of an intermediate

island (B) added to the distance from the nearest point of that intermediate island (not necessarily the same two points on the intermediate island) to the nearest point of the mainland (M), if the first measurement is less than the original island's distance to the mainland, then it is taken as the distance to the source. Intermediate islands were only considered if they too were larger than five hectares. This is more clearly demonstrated graphically in Figure 3.2. The purpose of this system was to minimise the total of the two dispersal distances, though not necessarily either particular distance. It is thus the most conservative estimate for the distance that would have to be traveled from the source. There were instances where an island would have more than one intermediate island – a multiple stepping stone system, but for the sake of simplicity these had to be overlooked.

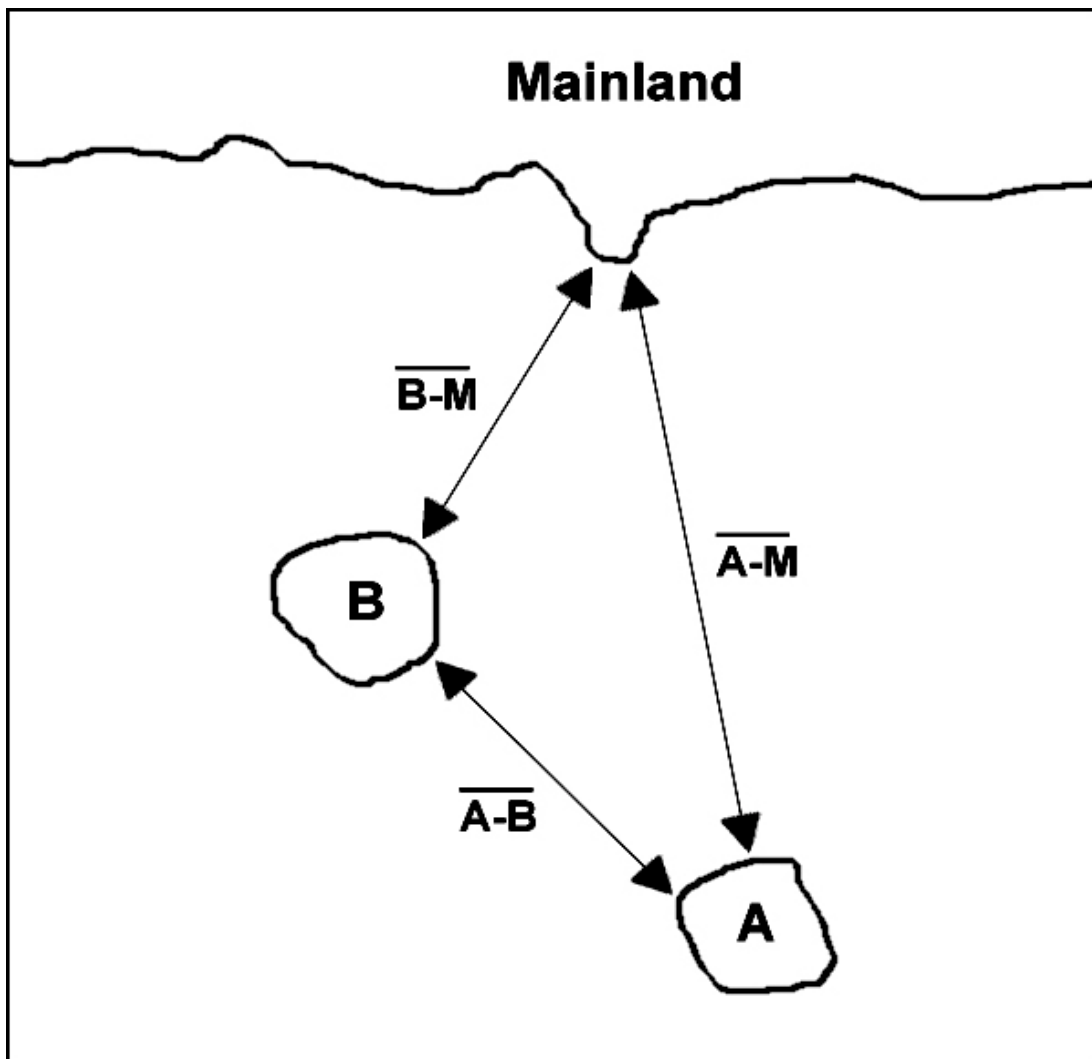


Figure 3.2. A single stepping stone system where  $A-B + B-M$  is minimised for all possible stepping stones and  $B-M < A-M$  (i.e. Island B is closer to the mainland).

Welter-Schultes and Williams (1999) use a similar measure; distance to the nearest considerably larger island (NCLI), although no precise definition is ever given. Millien-Para and Jaeger (1999) use the more defined measures of distance to the mainland or nearest larger island as well as distance to the mainland. The problem with these measures is the ecological assumption they are based on. Does a species colonise larger islands first, such as Welter-Schultes and Williams and Millien-Para and Jaeger believe, or nearer islands first, as I have assumed for my variable *Dist.Source*? MacArthur and Wilson's theory assumed that dispersal was related only to distance. While this seems reasonable for passive dispersers, Lomolino (1990) found that for the actively dispersing mammals he studied, elevation was a significant predictor, and as shall be illustrated in *Section 3.2.4* island *Elevation* is highly correlated with island *Area*. Regardless such variables are obviously gross simplifications of highly complex systems. Millien-Para and Jaeger (1999) found the distance to the mainland or nearest larger island was not significant, yet remarkably go on to conclude intra-archipelago dispersal is an important process. They conclude this because the depth of channels between islands was a significant predictor of species richness, although this might reasonably be correlated with local geological processes. Adler and Wilson (1985) partly evade the dilemma by including both distance to the nearest island and distance to the nearest larger island in their study of small mammals, although the two would be highly collinear (*Section 3.2*).

*Dist.Source* is normally distributed when  $\log_{10}$  transformed (Wilks-Shapiro test,  $p = 0.095$ ) and has no missing values.

#### *3.1.2.7.1 Motutapu-Rangitoto Island*

*Dist.Source* has one anomalous value. Motutapu Island technically has a *Dist.Source* value of zero as it is connected to Rangitoto Island. Such a value would be geographically nonsensical (they are then the same island), but they are considered separately for both historical and ecological reasons. Motutapu Island, formed following the last sea-level rise, is composed of sedimentary rock and has been intensively cleared and farmed in the

past. Rangitoto was formed within the last eight hundred years by an underwater eruption (Thompson 1977), and although it did not initially join Motutapu, it lay only ten metres from it. Subsequent coastal morphology generated a tidal bank between the two islands, which settlers later bridged. Rangitoto Island is composed of igneous rock, and is currently being revegetated via primary successional pathways in a manner similar to Krakatau Island (Whittaker 1998). The bridge is small relative to the size of both islands however, and it is considered that a colonisation event over it is as likely as an immigration event across water. The islands are still considered separately by geographers (Thompson 1977), and so to prevent confusion they remain separate in the dataset. This does mean though that they have different values for *Dist.Source*.

### 3.1.3 Geological Variables

#### 3.1.3.1 Geological Diversity Index (GDI)

The geological diversity index (*GDI*) of an island is a count of the number of different geological rock types found. Its major drawback is identified in Atkinson (1992) as the fact that accuracy of the data varies considerably. For islands visited by geologists the geology was well documented. For other islands the geology was only taken from geological maps of New Zealand. The effects of this have been discussed in *Section 2.1.2*. *GDI* is  $\log_{10}$  transformed to remove the right skew caused by the few geologically diverse islands, this also corrects for linearity.

The geological diversity of an island could very likely be correlated with its floral diversity, and thus be a good surrogate for it (P. de Lange pers. comm.). As abiotic habitat heterogeneity increases, so too should biotic heterogeneity, at least at the trophic level of vegetation. Johnson and Raven (1970) use the almost identical variable ‘number of soil types’ for estimating plant species richness, even measuring it on a similar scale of 1 – 5. Williamson (1981) notes that both soil types and geological types are good estimates of the broader term environmental heterogeneity.



There are six missing values for *GDI*. These values are correlated with small values of *Area*, and missing values in *BHDI*. They are not of an overly concerning nature however.

The presence of the three major rock types – sedimentary, igneous and metamorphic, were also summarised from the geological data. Although not used in any models, the factors are included in the event that any future studies may wish to investigate any differences between islands based on major rock types. Of the 297 offshore islands, only 17 were composed of more than one of the major types.

### *3.1.4 Ecological Variables*

#### *3.1.4.1 Biological Habitat Diversity Index (BHDI)*

The biological habitat diversity index (*BHDI*) is a count of the number of different biological habitats on an island. Biological habitats are the unique interaction between forest types and occasionally animal populations that significantly influence the ecosystem (*sensu* Atkinson 1992). Its derivation has been discussed in *Section 2.1.2*. Correlated with *BHDI* is the Geographical Habitat Diversity Index (*GHDI*) ( $r = 0.920$ ), a count of the number of different landforms on an island (*sensu* Atkinson 1992). Biological habitats are nested within geographical habitats. For every geographical habitat type on an island there are one or more biological habitat types within it, thus causing the high correlation. This clearly makes one of these variables redundant, and it is most sensible to remove the least descriptive one, *GHDI*.

The habitat diversity indices are a good measure of habitat heterogeneity on an island. Other studies have used abiotic surrogates (Johnson and Raven 1970). *Elevation* is a popular correlate (Millien-Parra and Jaeger 1999; see *Section 3.2.3*). Davidar *et al.* (2001) used a measure of forest cover. As can be seen both the meaning and measurement of habitat is open to liberal interpretation.

Both habitat indices require  $\log_{10}$  transformation for the same reasons as *GDI*. Whenuakura Island has a *BHDI* value of zero which can not be transformed (log zero is undefined). It is a small (3 ha.) outcrop with no significant biological habitat. Due to inadequate data, both habitat indices are missing 70 values for the same islands. This represents almost a quarter of the islands, and would prompt variable removal from the analysis if they were not the only ecological measures for islands. It is important to have an ecological habitat measure for islands as habitat is identified as one of the key predictors of species distribution in island biogeography. The missing values tend to be correlated with low values of *Area* and with missing values in species presence. The linking factor here is a bias towards visiting and collecting habitat and species data on larger islands. Small islands tend to have fewer habitats though, and the abundance of low *BHDI* values indicated by the right skew suggests that the smaller missing values are not as concerning as absent values for less-common larger islands might be.

The large habitat diversity values of Stewart Island make it influential in both *BHDI* and *GHDI*.

### *3.1.5 Historical Variables*

All four historical variables are unordered categorical factors, each with a number of levels. These levels are generally coded for by single letters, for brevity during statistical analysis, and the levels themselves are considered terms in the models. These levels are thus also given in *italics*.

#### *3.1.5.1 Land District Code*

Land District Code (*LDC*) is effectively a categorical cross-classification of *Latitude* and *Longitude*. As stated earlier the interaction of *Latitude* and *Longitude* creates a continuous variable where each island is represented on a Cartesian plane as an  $(x,y)$  coordinate. Instead of this it would be simpler to classify each island into a geographical region. These regions can then be assigned regional names, which the LINZ database

Land District	Code	Islands
North Auckland	AK	79
South Auckland	HN	43
Gisborne	GS	3
Hawkes Bay	HB*	1
Taranaki	NP	0
Wellington	WN	3
Nelson	NN	12
Marlborough	BM	16
Westland	HK	1
Canterbury	CH	2
Otago	DN	3
Southland	IN	110

Table 3.1. Land District Codes (*LDC*) and the number of islands in each region.

\* HB replaces NA in the LINZ database as this code is required for missing data in statistical packages

terms ‘Land District Codes’. These regions though, are not all of equal area and also have a differing numbers of islands in them. Seven of the twelve regions have three or fewer islands in them, one notably having none (Taranaki). Such low counts can not detect significant statistical departure. These regions are almost negligible in their number of islands compared to the larger regions, effectively reducing the number of regions to only five. Table 3.1 gives the land district codes and the number of islands in each region.

There are no missing values for *LDC*.

### 3.1.5.2 Maori Occupation

*Maori* indicates the presence of archaeological evidence of Maori occupation at some time in an islands history. Unfortunately archaeological surveys of islands have not been widespread, and of the 297 islands only 95 have been considered sufficiently well surveyed, the other 202 then being missing values. These missing values are not surprisingly correlated with low values of *Area*, but do not appear correlated with any other variables.

The variable, as a measure of Maori presence, has little application. Most introduced mammals and birds arrived after European colonisation. The only species where *Maori* might have significant predictive power is with kiore, a small Polynesian rodent that arrived with Maori between 1,000 to 2,000 years ago (Holdaway 1999). The presence of Maori occupation however is correlated with a number of other factors. Maori brought about widespread forest clearance across islands, as well as harvesting of native bird populations, sometimes to extinction. These were the first human-attributed environmental disturbances to occur on New Zealand islands. These initial effects may have predisposed those islands to subsequent establishment of introduced species on the arrival of Europeans, but such effects would be much better judged when more complete data are available for New Zealand islands. Holdaway (1999) supposes that if an island was close to the mainland, then it undoubtedly would have had Maori on it, but such a broad generalisation may not hold for islands in remote regions such as south-west New Zealand.

### *3.1.5.3 Landing Structure*

*Landing* codes for the presence of a permanent landing structure on an island, in all but one case a wharf<sup>†</sup>. With no replication its statistical value was nil, so it was reclassified to indicate a landing structure similar to all other islands. In the past the presence of an airstrip on an island may have also been considered relevant (C. Veitch pers. comm.), however with the advent of helicopter transport to remote regions, airstrips have virtually become redundant (M. Browne pers. comm.). They may code for a higher level of human settlement but that would be subsumed within the categorical variable for human settlement.

The presence of a landing structure should act as a simple categorical surrogate for the frequency of visits by marine vessels to an island, the causal vector by which mammals, particularly rodents, have generally been assumed to reach an island by (Atkinson 1989).

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<sup>†</sup> Kapiti Island has a slipway, a less rigorously constructed landing structure because it is used less often.

Six islands have missing values for *Landing*. These islands also tended to have missing values in other variables, indicating a lack of general scientific data for those islands altogether. This small number of missing values is not considerably concerning though.

#### 3.1.4.4 European Settlement

The categorical variable for European settlement history (*Settlement*) has five levels. These are given in Table 3.2. As can be seen the number of islands in each is not equal, with some low replication possibly preventing detection of statistical significance in two levels (<10 observations). Although there is some intrinsic ordering in the levels of settlement, it was not considered linear enough for *Settlement* to be an ordered categorical variable.

*Settlement* is a reasonably accurate surrogate for distinguishing types of European activity and disturbance on an island. Islands distinctly fall into one of the five levels. It should be noted that *Ranger Station* represents an island with a manned government station on it. These are now generally all Department of Conservation operated ranger stations for management of high conservation-value islands.

Twelve islands have missing values. These are also correlated with islands where there were missing values in other variables. They also tended to be for smaller islands, although the low number of missing values and abundance of smaller islands in the dataset means these missing values are not overly concerning.

Code	Settlement Type	Islands
-	Never Inhabited	230
R	Government Station	8
F	Unmanned Farm	4
A	Abandoned Settlement	14
I	Currently Inhabited	29

Table 3.2. The number of islands in each level of the categorical variable *Settlement*.

### 3.1.6 Introduced Mammals

#### 3.1.6.1 Species

Presence data are given for 17 species of introduced terrestrial mammals. Table 3.3 illustrates the number of missing values for each species. For most species data are absent for approximately one quarter of all islands, though not necessarily the same islands between species. For rodents the number of missing values increases due to the difficulties in determining particular species presence from just rodent sign. For stoats only 10% of the data is missing values. This is a reflection of the effort put into identifying stoat distribution for conservation purposes.

Species	Missing Values	Percentage
Cattle	78	26.3
Horses	79	26.6
Pigs	80	26.9
Deer	66	22.2
Goats	80	26.9
Sheep	79	26.6
Dogs	76	25.6
Wallabies	78	26.3
Cats	76	25.6
Possums	77	25.9
Rabbits	77	25.9
Hedgehogs	77	25.9
Stoats	30	10.1
Norway	82	27.6
Shiprats	77	25.9
Kiore	112	37.7
Mice	110	37.0

Table 3.3. Missing values in presence data for introduced mammal species in New Zealand.

### 3.1.6.2 Species Richness

Species richness is given as three values; total introduced mammal species richness  $S$ , large mammal species richness  $S_{large}$  and small mammal species richness  $S_{small}$ . These are only calculated for islands without missing values for individual species. This is so that they are not conservative estimates that assume missing values are absent species (see *Section 5.1.2*). All three measures of species richness are described fully in *Chapter 5*.

Missing values in the three variables are also dealt with in *Chapter 5*, where a reduced dataset without the observations containing missing values is used. This includes a statistical analysis of the distribution of missing values.

### 3.1.6.3 Mammal Interactions

The mammal interaction variables (*species.Inter*) were created for use with the corresponding mammal species variable. They give the number of other mammals on an island, not including the mammal species in question. This is the number of mammals that could potentially interact with a mammal species on an island.

The reason for including such a variable comes from both theory and observation. Pimm (1991) discusses the complex and large number of interactions between species in any ecosystem. These are expressed as trophic-webs. The diversity-stability debate (McCann 2000) follows from this, suggesting that a more diverse, and thus interactive, ecosystem will be more stable and less likely to be invaded by a new species. Taylor (1978, 1984) also noted that for New Zealand's four introduced rodent species, no more than three have ever been found in any one location. These reasons together suggest that the number of other mammals on an island may affect the presence of any new mammal. The largest problem with such a variable is that it can not account for different colonisation times of species in the past. Whereas species A may have arrived first on an island excluding species B, on another island species B may have arrived first and not affected the establishment of species A, depending on the nature of the interaction between the two.

This also mimics Gilpin and Diamond's (1981) incidence functions, whereby species presence depends on the number of species already on an island.

Following the same theoretical reasoning Burbidge *et al.* (1997) used two dummy variable measures of potentially interacting species depending on trophic levels and evolutionary families.

Missing values in the number of interacting mammals are for the same islands missing values in species richness counts, for the same reason that they would be conservative estimates only, however they are not correlated with any particular values in the other variables.

#### *3.1.6.4 Rodent Interactions*

Previous work (Atkinson 1978, Atkinson 1986; Taylor 1978, Taylor 1984) has investigated the interactions among rodent species, and with their predators (namely cats and stoats). It is known that the ability of one species to successfully establish will depend on the incidence of the interacting species. The rodent interaction variables (*species.Rodents.Inter*) give the number of other rodent species on an island for the corresponding mammal species.

#### *3.1.7 Avian Species*

Avian species richness estimates were recorded in four distinct classes; seabirds, waders, native terrestrial and exotic terrestrial. The latter two are a subdivision of the first OSNZ class in *Section 2.1.3*. A total of 245 species were distributed across New Zealand's offshore islands. These counts are only estimates of species richness, as a total census of the large number of avian species on New Zealand islands is more difficult to obtain than for the few mammal species.



### 3.1.7.1 Sampling Effort Bias

As described in *Section 2.1.3*, avian distribution data was collected from cards returned by field observers. The number of cards returned by observers varied between grid squares. Magurran (1988) notes “*it is of course not always possible to ensure that all sample sizes are equal and the number of species invariably increases with sample size and sampling effort*”. As can be seen in Figure 3.3 (a) this has occurred, as the number of sampling cards returned (sampling effort) has increased so too has the number of bird species recorded. Figure 3.3 (b) illustrates the linear relationship between the two variables when the number of sampling cards returned is  $\log_{10}$  transformed. If a linear regression fit were to be made to the semi-log relationship it would have intercept  $a$  and slope  $b$ . Some researchers have interpreted  $a$  and  $b$  as the number of common species and the number of rare species recorded for a sampling unit increase respectively (R. Hankin pers. comm.). Although the definition of ‘common’ will differ between species depending on body and home range size, it serves as a reasonable approximation with respect to the effect of sampling effort.

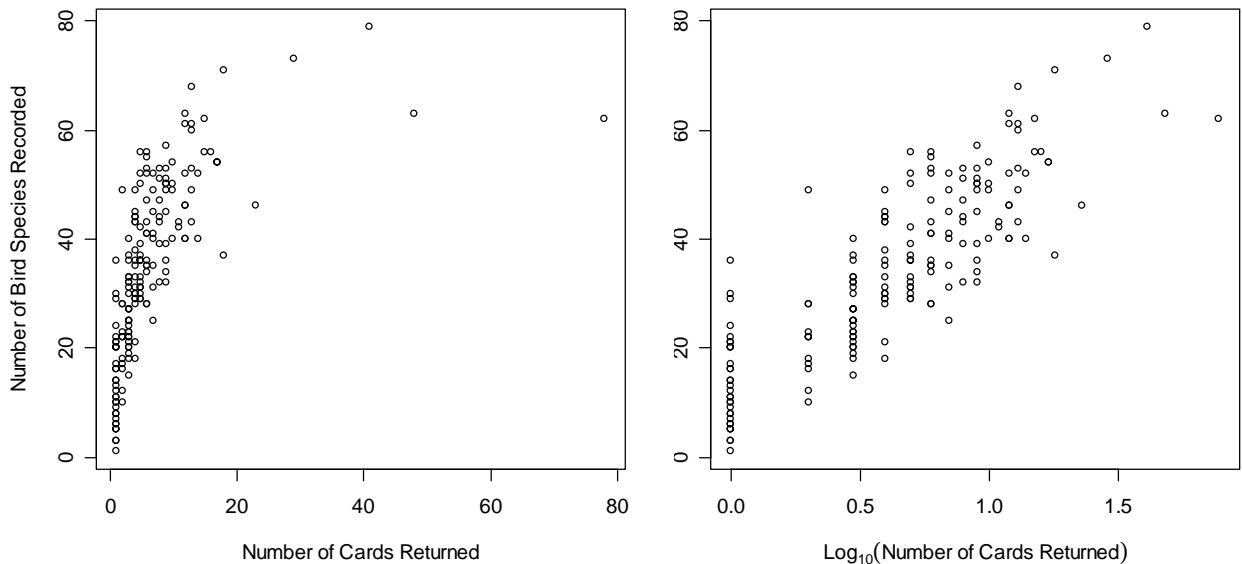


Figure 3.3. (a) The relationships between the number of *Cards* returned and the number of bird species recorded indicates a sampling effort bias. (b) When *Cards* is  $\log_{10}$  transformed the relationship becomes linear.

Unfortunately sampling effort itself may be correlated with locations of high avian species richness. Put more simply, volunteer field observers may preferentially sample areas where there is greater bird diversity. Thus the larger number of bird species in grid squares with more cards returned might be a result of both the increased sampling effort and a naturally high number of bird species which has attracted observers. Both are systematic (predictable) variations

It is highly desirable to remove the first effect of increased sampling effort, so that it does not bias the estimates of species richness. Detrending the data with respect to the sampling variable, thus removing the systematic error in it, can achieve this. Unfortunately this also removes the systematic error that may be associated with observer preference for areas of higher bird diversity, leaving only the unsystematic error – the variation in bird diversity between grid squares not *a priori* recognised by observers.

### *3.1.7.2 Statistical Detrending*

One of the most popular methods of standardising data biased with respect to sampling effort is rarefaction (originally Sanders 1968 but see discussion in Magurran 1988; Gotelli and Graves 1996). Unfortunately this, along with most other methods, requires both the species counts and the abundances within them. To do this properly from the OSNZ Atlas would have required sorting through all 19,000 microfiche summary cards – a daunting task.

A much simpler method (following from Figure 3.3 (b)) would be to regress the number of species recorded against the logarithm of the number of cards returned. This estimates the variation in species recorded explained by the number of cards returned. The residuals of this regression would then be independent of the number of cards returned. This can easily be done for species counts of the four categories. However there are additional complications that arise from the form of the original data in the OSNZ Atlas. Since the data was from 10,000 yard grid squares, an island which spanned multiple grid squares

required its species count to be the sum of the individual grid squares, discarding repetition of the same species. The number of cards returned in each grid square cannot be combined in the same manner as this would be too liberal an estimate of the number of cards required to record the number of species that resulted from the combination of grid squares. As referred to earlier, for each grid square the first card returned records all common species (the intercept), although in reality it will be some number of the first cards. The subsequent cards returned each increase the number of rare species recorded (the slope). When species lists are combined for multiple grid squares the species common to both are only counted once in the summed list. These can be considered the 'common' species of the grids. Therefore when combining the number of cards returned, the 'common' cards between grid squares would theoretically require counting only once. However there is no adequate way to estimate what proportion of the cards returned record only the common species. In contrast to this, the grid square with the highest number of cards returned could be taken as the minimum number of cards required to obtain the summed species count of an island. This would instead be a conservative estimate of the imaginary value for the number of cards returned for an island of combined grid squares, as it only counts the extra cards required to find rare species from one grid square, when rare species found in other grid squares will have also been counted. If either value for the number of cards returned for islands spanning multiple grid squares were to be used, it would bias the detrending regression equation either negatively for summed cards (as the residuals for these values would be negative) or positively if using the single grid with the highest number of cards (as the residuals for these values would be positive). This is illustrated in Figure 3.4.

The detrending regression equation is generated from the grid square species counts, instead of from island species counts. This prevents weighting towards grid squares that contained more islands. However the final estimates of relative avian species richness are calculated from the logarithm of the number of cards returned for each island, which means the issue of islands spanning multiple grid square described earlier must be considered during interpretation. Possible complex mathematical solutions to this problem were considered, but it was decided to continue with combined (liberal) card

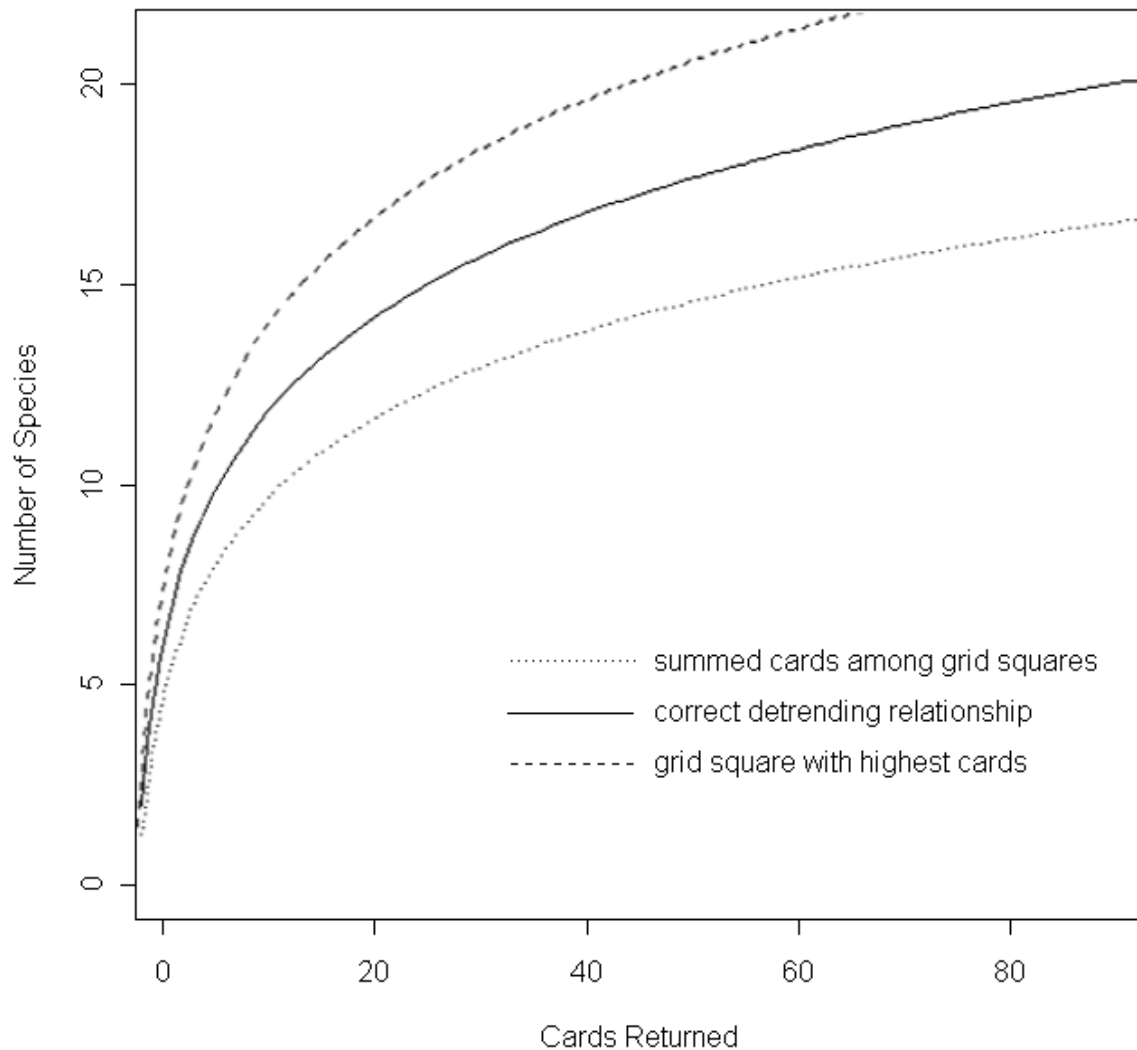


Figure 3.4. Bias generated in the detrending equation when combining 'cards returned' counts for islands spanning multiple grid squares. The solid line is the hypothetical true detrending relationship. The dotted line is the positive bias in the detrending equation generated by summing the total cards returned across all grid squares (over estimating the number of cards required). The resulting detrended values would be under estimates (too many species removed). The dashed line is the negative bias in the detrending equation generated by taking the single grid square with the highest number of cards returned (under estimating the number of cards required). The resulting detrended values would be over estimates (not enough species removed). The problem is most manifest for large numbers of cards returned (from across multiple grid squares or highest single grid square).

counts which would give conservative estimates of relative avian species richness for those islands. All categories except waders were best detrended assuming the regular Gaussian distribution. The distribution of wader species was better fitted by a Poisson

distribution, due to their relative rarity in nature. This was supported by the negative intercept for wader species recorded (thus no common species).

It is initially appealing to not add the intercept of the detrended equation to each observation. Detrended estimates would then have large positive residuals, which could be likened to a genuine species estimate (or for identical values the intercept could be added to each residual of the full detrended model). This would be misleading for three reasons though. Firstly, it constrains the detrending model to a zero intercept. Although it is true that if no cards are returned no species are recorded, the first card returned theoretically records all 'common' species (i.e. the intercept in the detrending model), but the number of common species varies between categories. For waders, there are almost no common species and it is not until a large number of cards are returned that waders begin appearing. The opposite is true for exotic species, most appearing in the first few cards. Secondly, depauperate areas with particularly low counts could take nonsensical values below zero. Thirdly, the new estimates will have been constrained to different distributions from the original species richness counts. Although the detrending does remove the bias in the distribution, the distributions of the new values are constrained by the regression method chosen. If a variable has been successfully transformed it is not beneficial to further transform it to resemble the original measurement. It is transformed to remove bias, acknowledging that this may complicate interpretation with respect to the original system.

Table 3.4 gives the correlation between the logarithm of the number of cards returned and the species counts in each category both before and after detrending with respect to the logarithm of the number of cards returned. The changes in sign from positive to negative (except for the most correlated native landbird category) illustrate the over detrending (under estimation of species) that has occurred as a result of using summed cards over all multiple grid squares (Figure 3.4 earlier).

Category	$\log_{10}$ Cards correlation	
	Original	Detrended
Seabirds	0.522	-0.102
Waders	* 0.563	-0.172
Native Land	0.712	0.128
Exotic Land	0.651	-0.120

Table 3.4. Correlation of sampling effort (logarithm of cards returned) with species counts before and after detrending with respect to sampling effort.

\* The untransformed wader species counts were used here, but detrending used the poisson log link

### 3.1.7.3 Relative Avian Species Richness

The final detrended values for avian species richness in each category (*Rel.category*) behave differently to the original measurements. They are no longer discrete positive values, but now continuous variables. The residuals of the regression should average to zero. However, due to weighting by islands, and the bias generated by multiple grid square islands where counts are conservative, they average to values less than zero. They can be interpreted as approximately the number of species above or below the detrended average for that class. They require no further transformation. Counts between categories are only comparable for relative density, not absolute density.

Detrended seabird and wader species counts are right skewed. The distributions of both the native and exotic land bird species counts tend to be closer to normally distributed, although exotic land birds are bi-modal. The linear relationship between the number of species and the logarithm of cards returned is strongest for the exotic land birds ( $r = 0.723$ ).

Estimates of avian species diversity should be a good surrogate for ecosystem intactness or health. Unfortunately avian species themselves are causally affected by a number of interacting biogeographic variables. In most cases, as an ecosystem is modified or destroyed, native biodiversity (including seabirds, waders and native landbirds) decreases

(Craig *et al.* 2000). Landbirds generally require adequate vegetated habitat (though not necessarily native), seabirds are particularly sensitive to the introduction of predatory mammals, while waders are particularly sensitive to habitat, requiring specific feeding grounds. However exotic biodiversity (exotic landbirds) should increase with the human modification of ecosystems and habitats (Norton 1992). Many exotic land birds (such as the finches) prefer open grassland habitat that is only present as a result of human modification (Falla *et al.* 1996). It should be noted that the degree of modification of habitats, which the relative avian species richness may be a surrogate for, does not necessarily have to be related to habitat heterogeneity (*BHDI*) – native habitats may be modified into exotic ones on a *pro rata* basis (i.e. habitat heterogeneity may not change, although the constituent types have). However such an effect would need to have *Area* partialled out first, as larger islands will nearly always have more species due to the species-area relationship. Such estimates are also still complicated by the bias in sampling effort, even when statistically detrended, as the detrending itself may have also removed some natural variability. Because of the complex cause and effect relationship that the relative avian species richness estimates have with mammals, the variables are only applied cautiously (do less birds mean a mammal species can more easily establish, or are there less birds because a mammal species has established?).

Interestingly, the total detrended avian species count is not correlated with *Latitude* ( $r = 0.237$ ), but when split into the four categories each is related to a varying extent (although not necessarily linearly) with *Latitude*. This suggests some type of equilibrium where the total number of species is constant across *Latitude*, but where the composition does vary. This may not be a direct relationship, but it could be indirectly linked by one or more intermediate factors such as the number of mammal species or human settlement patterns. This once again illustrates the complex nature of the avian species data and the caution required when including any part of it as an explanatory term in a model due to its high correlation with other explanatory variables.

Avian species counts are absent for 24 islands, where no data were available. The missing data appeared to have been ‘lost’ between summary sheets, which were geographically

ordered by *Latitude* and *Longitude*. This meant that for some clusters of islands data were missing throughout. The most concerning of these is for a large number of islands in the Hauraki Gulf. Otherwise the missing values are not correlated with any other variables.

## 3.2 Collinearity

### 3.2.1 Definition

Collinearity (also known as multicollinearity) is generated when there is redundant information among explanatory variables resulting in them varying together. When this is most severe, a substantial part of the information in one or more variables is completely redundant, making it difficult to separate the effects of the different explanatory variables on the response variable (Glantz and Slinker 2001). The result is a loss of precision in the estimates of the regression coefficients. The standard errors are increased, and the coefficients themselves may be distorted.

There are various ways of detecting and dealing with sample-based collinearity; where explanatory variables can not be independently manipulated. Visual inspection of scatter-plots between explanatory variables can reveal non-independence. A quantitative test of this is the *Variance Inflation Factor* (VIF). This measures the change in variance of the regression parameter for each set of  $k - 1$  variables. If a variable contains significant redundant information, then dropping it from the set of explanatory variables will significantly lower the variance estimate of the regression parameter. VIF values exceeding ten are generally considered signs of serious collinearity.

The most obvious solution when severe collinearity is present is to delete the redundant variable(s). Unfortunately this requires a somewhat arbitrary decision of which variable contains the ‘better’ information. When modelling systems where processes are *a priori* hypothesised as important it is often not possible to objectively delete a variable, as the quality of conclusions can be reduced. Perhaps the most appealing solution is principal components regression. By performing a *Principal Components Analysis* (PCA) on the



explanatory variables a set of PCA axes (linear combinations of the explanatory variables) are created which are statistically independent<sup>†</sup>. After dropping the components associated with the collinear relationships the remaining axes can be used in a regression with no collinearity, and the coefficients obtained then back-transformed on the linear weightings within the original axes. It is also sometimes possible to interpret the PCA axes as complex variables; combinations of related variables which act as surrogates for a single unmeasurable process (see Adler and Wilson 1985). The problem with PCA regression is that by dropping the less explanatory PCA axes (those associated with the collinear relationships), some information from all variables is removed, and the regression is thus constrained because of this (Glantz and Slinker 2001). Some statisticians see this as a valid reason for not using PCA regression.

### *3.2.2 Species-Area Relationship*

The species-area relationship is perhaps the foremost ecological example of collinearity. One relationship can be explained by a number of different processes. Each process can be measured, however due to the unifying relationship of each with area, they are subsequently collinear. It has been recognised since the 19<sup>th</sup> century (Watson 1859; Williams 1943) and has been called as close to a law as an ecological pattern can become (Schoener 1976). Lomolino (2001) reviews the history of the species-area relationship.

MacArthur and Wilson (1963, 1967) originally believed that area was a surrogate for the probability of a species going extinct. Unfortunately they neglected the interactive effect it might have with distance (Brown and Kodric-Brown 1977; Gotelli and Graves 1996), whereby new species may immigrate from the source pool to supplement a population, thus reducing the probability of extinction. This was termed the ‘rescue-effect’ (Brown and Kodric-Brown 1977).

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<sup>†</sup> For a complete description of Principal Components Regression see pp. 230 – 237 of Glantz and Slinker (2001) ‘Primer of Applied Regression and Analysis of Variance’ (2<sup>nd</sup> edition)

Since then a number of alternative hypotheses have been postulated for the observed relationship between area and the number of species on an island (pp. 118-125 in Williamson 1981; pp. 190-192 in Rosenzweig 1995; Chapter 8 in Gotelli and Graves 1996; pp. 123-124 in Whittaker 1998). These hypotheses are essentially:

1. Random Placement – if individuals are distributed at random, a larger sample will contain more species
2. Habitat Diversity – Larger islands have more habitats supporting more species
3. Equilibrium – Total species number is a dynamic equilibrium between immigration and extinction
4. Disturbance Hypothesis – Smaller islands are disturbed more often, preventing the establishment of many species

The most popular means by which to distinguish between these competing hypotheses has been multiple regression, which allows us to tease out the different effects from extra data (Rosenzweig 1995).

Several investigations have investigated the relationship between area and habitat diversity (Harner and Harper 1976; Ricklefs and Lovette 1999; Welter-Schultes and Williams 1999). It is the most popular hypothesis, but also the most difficult to assess (Gotelli and Graves 1996). Studies have also investigated population densities (Wright 1981), but Connor *et al.* (2000) found no correlation, at least for mammals. Elevation has also been investigated to a lesser extent (Lomolino 1984; Burbidge *et al.* 1997), although only recently has it received attention as a further correlate of area, habitat and the number of individuals. The addition of elevation renders island biogeographic models three dimensional (Millien-Parra and Jaeger 1999), and thus more complex still. The disturbance hypothesis (McGuinness 1984) has generally been limited to marine systems.

Measurements of the number of individuals, habitats, extinction rate and disturbance rate are all correlated with area, and thus all explain very similar variability within species richness models. It is yet unclear which, if any, is the true manifestation of the underlying

process controlling the species-area relationship (Whittaker 1998). The one conclusion that has been firmly reached is that the processes generating the species-area relationship are much more difficult to establish than the pattern is. It is always imperative to consider alternative explanations for an observed relationship, beyond what might perhaps be immediately apparent. Connor and Simberloff (1978) stated upon their reexamination of data collected from the Galapagos Islands that

*“the number of botanical collecting trips to each of the Galapagos Islands is a better predictor of species number than are area, elevation, or isolation.”*

However the explanation of a possible correlation between the number of botanical collecting trips and the island descriptors, by reason of researcher preference, eluded them (Williamson 1981).

### *3.2.3 Area-Elevation-Habitat*

Within this thesis are three variables that are highly correlated and subsequently collinear. They are  $\log_{10}$  *Area*,  $\log_{10}$  *Elevation* and  $\log_{10}$  *BHDI*. The theoretical cause of their correlation has been discussed in the previous section. Larger New Zealand islands tend to have higher elevations, which appears to be a relic of geological processes. The large islands in Fiordland are the result of glacial processes, while other larger islands are peaks that have been separated from the mainland during the Pleistocene.  $\log_{10}$  *Area* is thus correlated with  $\log_{10}$  *Elevation* ( $r = 0.688$ ), except for very small islands where it appears independent. Larger islands can also support more habitats, due to a greater variety of abiotic and biotic conditions. Thus  $\log_{10}$  *Area* is correlated with  $\log_{10}$  *BHDI* ( $r = 0.840$ ). For an increase in island elevation, there is also a corresponding increase in habitat heterogeneity (Abbott 1978). This is because higher islands can support more novel habitats due to the variant climatic conditions (Whittaker 1998). Despite its small size (3083 ha.), Little Barrier Island supports ‘montane-cloud forest’ surrounding its 722m summit (pers. obs.). Thus  $\log_{10}$  *Elevation* is correlated with  $\log_{10}$  *BHDI* ( $r = 0.696$ ).

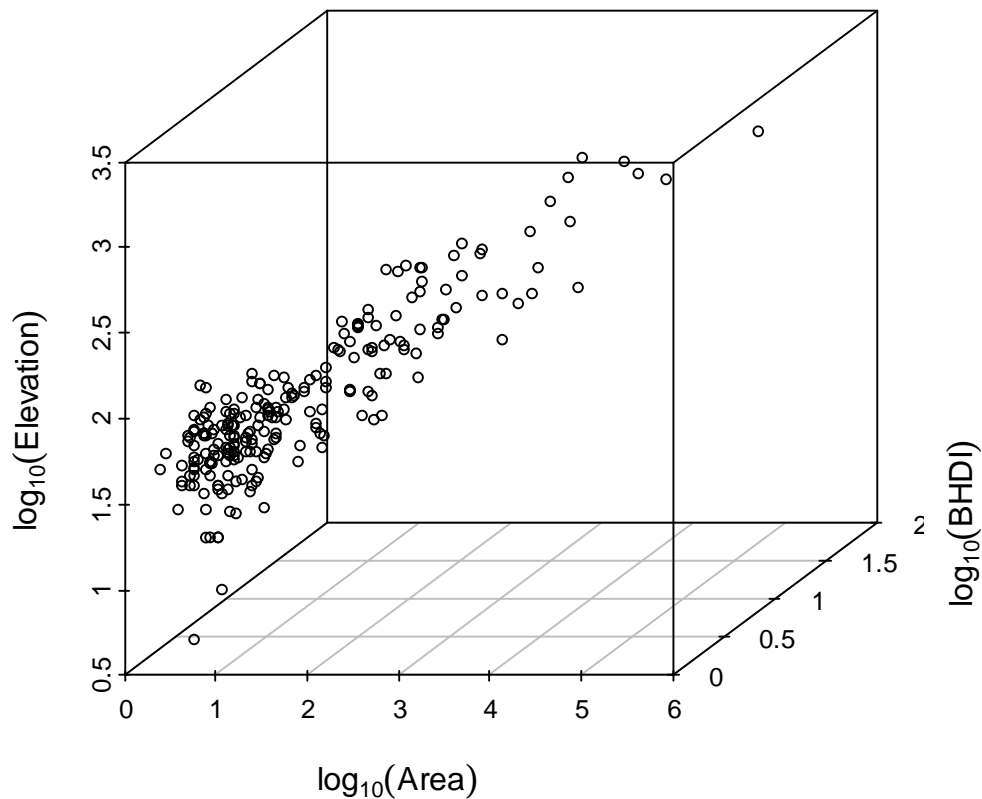


Figure 3.5. Three dimensional scatterplot of  $\log_{10}$  *Area*,  $\log_{10}$  *Elevation* and  $\log_{10}$  *BHDI*. The one-dimensional linearity illustrates high collinearity between all three variables. Only complete observations were used to generate the plot.

The relationship between all three variables is shown in Figure 3.5. Only small islands appear relatively independent for values of each variable. This may be a manifestation of the ‘small-island effect’ (Lomolino 2000c; Lomolino and Weiser 2001).

Inspection of VIFs reveals both  $\log_{10}$  *Area* and  $\log_{10}$  *BHDI* are above the threshold value of ten. This suggests that both should not be included together in a model, due to high collinearity with other explanatory variables. Unfortunately it would be a subjective decision regarding which should be dropped, and the model would lose some ecological explanatory power with respect to the myriad of variables operating in the system. By leaving both in they can partial each other out to reveal the unique effect each variable has on the response value. The estimate of the coefficients should still be reasonably accurate, as other variables in the regression model will stabilise the fitting surface. The

precision may be compromised however, with inflated standard error values and an increased chance of non-significant p-values for collinear variable terms. This is not as concerning in *a priori* models as it would be in step-wise regression, where variables are included depending on arbitrary p-value thresholds.

Although the relationship between area and habitat heterogeneity has long been realised (Williams 1943; Lack 1969, 1976; Williamson 1981; Rosenzweig 1995; Gotelli and Graves 1996; Whittaker 1998), the correlation of both of these with elevation appears to be less well realised (although see Abbott 1978). As it stands all three variables together essentially represent the same underlying characteristic of an island. The variable *BHDI* poses difficulties though, as it is itself a measure of some biotic characteristics of an island, which are dictated by the species-area relationship. Atkinson (1992) also discusses the limitations of the habitat data as it may be a better reflection of research effort on an island than actual habitat diversity itself, a problem acknowledged by Connor and Simberloff (1978). However if we consider the original, although less informative, *GHDI* – a purely abiotic descriptor of island landform diversity, along with both *Area* and *Elevation*, then all three together compose a physical descriptor of an island. Using PCA it would be possible to find the first axis, a linear combination of all three variables, that maximises the variation explained. This can be visualised as a line-of-best-fit through Figure 3.5. This idea has great intuitive appeal, but the methodology was considered complicated for the timeframe of this thesis, and by including the variables individually it is much easier to interpret their relative meaning.

# *Chapter 4: Modelling Introduced Mammalian Species Distribution*

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## *4.1 Introduction*

### *4.1.1 Investigating the Distribution of Species*

The investigation of the distribution of species is essentially what constitutes biogeography, although such investigations have occurred since long before the discipline itself was recognised (Brown and Lomolino 1998). Early practitioners include Charles Darwin, Alfred Wallace and Joseph Hooker, who all noted the distribution of species during their journeys around the globe.

The distribution of a species is limited by environmental factors (Krohne 1998). Hutchinson (1957) developed the concept of the ‘ecological niche’ – a multidimensional abstract representation of a species’ environment in which it is limited at particular upper and lower boundaries for every environmental factor, both biotic and abiotic (Brown and Lomolino 1998). By assessing correlates of a species distribution, it is not only possible to describe where a species may or may not be found, but also to detect which factors are limiting to its distribution and which are not (Krohne 1998). Theoretically every factor will be limiting at some level, and because of this it allows us to say that variables which do not appear to correlate with the distribution of a species are simply not limiting at the scale upon which we measured them (Whittaker 2000).

What an investigation of species distributions does require is that the populations are relatively statically established over ecological time-spans. Of course as the time frame is increased all populations are doomed to extinction and so none are truly permanently established (Williamson 1981), but so long as the population is resident permanently over

ecological time-spans (decades to centuries, although a better measure is generation time) then it can be considered established.

#### *4.1.2 Processes Controlling Introduced Mammalian Distribution*

In the past, the processes that have mediated introduced mammals dispersing to and establishing on offshore islands have been qualitatively assumed. Holdaway (1999) for example assumes '*the presence of a population of Pacific rats on an island implies a visit to that island, of whatever duration, by humans.*' Similarly Atkinson (1986) suggests that rodent distribution on New Zealand islands is '*largely a reflection of intensity of European settlement, competition between the four species, and in the case of rats, the distances between the islands and source populations*' and later notes that sea-going vessels are also an important vector. As is evident, these processes have tended to be based on historical assumption. Thus, the examination of historical introductions and how they have influenced current species distributions goes some way in suggesting factors that might predict the distribution of introduced mammals on New Zealand islands. The dominant factors appear to be the physical characteristics of islands and the history of their anthropological modification, although the influence of ecological factors is known to be harder to delineate (Burbidge *et al.* 1997; Woinarski *et al.* 2001). More specifically, Atkinson (1986) identifies the settlement history, distance from the source and the intensity of mammal interactions as correlates of rodent distribution. This was calculated from chi-square counts however, not multiple regression, and so other confounding effects identified by Craig (1986) may not have been considered.

Although *Latitude* may affect rodent morphology and population demography (Yom-Tov *et al.* 1999) it is not considered limiting to their actual distribution, as rodents have been recorded throughout most regions of the world except the polar extremes. Interactions between the four rodent species present in New Zealand have also been hypothesised and supported by circumstantial evidence (Taylor 1978, 1984); Yom-Tov *et al.* 1999).

### 4.1.3 Hypotheses

#### 4.1.3.1 Versal Hypotheses

It is hypothesised that the distribution (presence) of individual mammal species across New Zealand offshore islands can be adequately predicted by a combination of their *Latitude*,  $\log_{10}$  transformations of *Area*, *Elevation*, distance to the mainland (*Dist.Main*), distance to the nearest source (*Dist.Source*), geological diversity (*GDI*) and biological habitat diversity (*BHDI*) and the presence of an intermediate stepping stone island (*Stepping.stone*), the relative species richness of seabirds (*Rel.Seabird*) and exotic land birds (*Rel.Ex.Land*), the number of interacting mammals (*species.Inter*), the presence of landing structures (*Landing*), archaeological evidence of Maori occupation (*Maori*) and their European settlement history (*Settlement*). No interaction between variables is hypothesised. The corresponding null hypothesis for each species is that none of this combination of variables will affect its distribution. Table 4.1 shows which variables were *a priori* hypothesised to be correlates with the distribution of each introduced mammal species across New Zealand offshore islands.

#### 4.1.3.2 Statistical Hypotheses

H<sub>0</sub>: All coefficients and the intercept in each linear model are equal to zero.

$$a, b_1, b_2, b_3, \dots, b_n = 0$$

H<sub>1</sub>: One or more of the terms in each linear model has a coefficient not equal to zero.

$$a \text{ or } b_1 \text{ or } b_2 \text{ or } b_3, \dots, b_n \neq 0$$



	Latitude	Area	Elevation	Distance Main	Stepping Stone	Distance Source	GDI	BHDI	Relative Seabird	Relative Exotic	Mammal Inter	Maori	Landing	Settlement	Total
Cattle	X	X	-	-	-	-	X	X	-	X	-	-	X	X	7
Horses	X	X	-	-	-	-	X	X	-	X	-	-	X	X	7
Pigs	X	X	-	-	-	-	X	X	-	X	-	X	X	X	8
Deer	X	X	X	X	-	-	X	X	-	X	-	-	X	X	9
Sheep	X	X	-	-	-	-	X	X	-	X	-	-	X	X	7
Goats	X	X	X	-	-	-	X	X	-	X	-	-	X	X	8
Dogs	X	X	-	-	-	-	X	X	X	X	-	-	X	X	8
Wallabies	-	X	-	-	-	-	X	X	-	X	-	-	X	X	6
Cats	X	X	X	-	-	-	X	X	X	X	X	-	X	X	10
Possums	X	X	-	-	-	-	X	X	-	X	-	-	X	X	7
Rabbits	X	X	-	-	-	-	X	X	-	X	X	-	X	X	8
Hedgehogs	X	X	X	-	-	-	X	X	X	X	X	-	X	X	10
Stoats	X	X	X	X	-	-	X	X	X	X	X	-	-	-	9
Norway	-	X	X	-	X	X	X	X	X	X	X	-	X	X	11
Shiprats	-	X	X	-	X	X	X	X	X	X	X	-	X	X	11
Kiore	-	X	X	-	X	X	X	X	X	X	X	X	-	X	11
Mice	-	X	X	-	X	X	X	X	X	X	X	-	X	X	11

Table 4.1. Variables *a priori* hypothesised to influence the distribution of introduced mammals across New Zealand offshore islands. X signifies inclusion of the variable in the species model

## 4.2 Methods

### 4.2.1 Linear Modelling

Linear modelling methodology follows that outlined in *Section 2.2.1*. For modelling species distributions as presence or absence, it was assumed that the response was binomially distributed. This is mathematically depicted as  $y = 0 \dots 1$ , which is analytically identical to the probability of a species being present. The generalized linear model with binomial family error utilises the logarithm of the odds function (logit) as the link in the equation equality:

$$\text{odds function} = (p / (1 - p))$$

$$\text{logit} = \log_e (p / (1 - p))$$

where  $p$  = the probability of the species being present

As can be seen, the odds function is a measure of the probability of a species being present divided by the probability of it being absent (the likelihood of its presence). The logit link is required to constrain the values of the response to between zero and one, otherwise nonsensical values outside this range may be obtained.

The final model presented is thus:

$$E(y_i / (1 - y_i)) = e^{\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_n x_{in}} \quad y_i \sim \text{Binomial}(E(y_i), n)$$

### 4.3 Results

#### 4.3.1 Model Adequacy

Chi-squared tests for adequacy of fit had insignificant values for all models. These are given in Table 4.2. This means the null hypotheses that each model is adequate are accepted.

#### 4.3.2 Effects

Table 4.3 gives significant variables and their significance codes for all individual mammal models. The horse, dog, wallaby and hedgehog models all had less than 10 islands where the species occurred in the wild. This meant that the iteratively reweighted least squares algorithm did not converge because the model fitted the (absence) observations exactly. This is termed over-fitting (see p. 82 in Collett 1991). Between one to six variables were significant at the 10% level for each other model.

#### 4.3.3 Collinear Variables

The variables  $\log_{10} Area$  and  $\log_{10} BMDI$  are both identified in *Section 3.2.3* as collinear and were terms in all 17 original models. The variable  $\log_{10} Elevation$  was included in a further nine of these. However only two in models were any combination of these correlates significant. In both the cat and ship rat models the effect of  $\log_{10} Elevation$  is negative, while the effect of  $\log_{10} BMDI$  and  $\log_{10} Area$  respectively is positive.

#### 4.3.4 Residuals

Plots of indexed deviance residuals for all models generally showed no abnormal variation in random scatter about zero. There was some trend towards increased random scatter above the zero line (species more often observed where not expected), but this

Species	Adequacy	d.f.
Cattle	1	154
Horses	1	154
Pigs	0.953	56
Deer	1	158
Goats	1	152
Sheep	1	155
Dogs	1	157
Wallabies	1	156
Cats	1	113
Possoms	1	155
Rabbits	0.949	115
Hedgehogs	1	113
Stoats	1	120
Norway	0.876	112
Shiprats	0.995	112
Kiore	0.334	42
Mice	1	112

Table 4.2. P-values for chi-square adequacy of fit tests for individual mammal models. Non-significant values ( $p > 0.050$ ) indicate model adequacy.

was only concerning for the possum model, where random variation in deviance residual values above the zero line ranged as high as three (Figure 4.1).

Deviance residuals can only be calculated for observations with complete data for all variables. This meant that in some cases, where an *a priori* variable included a large number of missing values, it was not possible to calculate a broad range of deviance residuals. *Section 3.1* discussed the biases in missing values of variables. Overall it can be considered that the missing values were not biased against other explanatory variables. Table 4.4 gives the number and percentage of complete observations in the deviance residuals. For most models the number of complete observations is between 40 – 60%, but for pigs and kiore it drops to an alarming 20%.

	Cattle	Horses <sup>1</sup>	Pigs	Deer	Goats	Sheep	Dogs <sup>1</sup>	Wallabies <sup>1</sup>	Cats	Possums	Rabbits	Hedgehogs <sup>1</sup>	Stoats	Norway	Shiprats	Kiore	Mice
(Intercept)	ns	ns	ns	- **	- .	ns	ns	ns	ns	- *	ns	ns	+ .	ns	ns	- *	ns
<i>Latitude</i>	+ .	ns	ns	- **	ns	ns	ns		ns	ns	ns	ns	ns				
$\log_{10}$ <i>Area</i>	ns	ns	+ *	ns	ns	ns	ns	ns	ns	ns	ns	ns	+ *	ns	+ **	ns	ns
$\log_{10}$ <i>Elevation</i>				ns	ns				- *			ns	ns	ns	- *	ns	ns
$\log_{10}$ <i>Dist.Main</i>				ns									- ***				
<i>Stepping.stone</i>														ns	ns	ns	- .
$\log_{10}$ <i>Dist.Source</i>														ns	- *	+ *	ns
$\log_{10}$ <i>GDI</i>	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	- .	ns
$\log_{10}$ <i>BHDI</i>	ns	ns	ns	ns	ns	+ *	ns	ns	+ *	ns	ns	ns	ns	ns	ns	ns	ns
<i>Rel.Seabird</i>							ns		ns			ns	ns	- *	ns	ns	ns
<i>Rel.Ex.Land</i>	ns	ns	ns	ns	+ **	+ **	ns	ns	ns	+ .	ns	ns	ns	+ *	ns	ns	ns
<i>M.Inter</i>									ns		+ .	ns	ns	ns	ns	ns	ns
<i>Maori</i>			ns														+ .
<i>Wharf</i>	ns	ns	ns	ns	+ .	ns	ns	ns	ns	+ .	ns	ns		ns	+ .		ns
<i>Abandoned</i>	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns		ns	ns	ns	ns
<i>Farmed</i>	+ .	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns		ns	ns	ns	ns
<i>Inhabited</i>	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns		ns	+ *	ns	ns
<i>Ranger</i>	+ *	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns		ns	ns	ns	ns

Significance codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 'ns' not significant. Prefixes: '+' positive effect, '-' negative effect  
Table 4.3. Significant variables in the individual mammal distribution models. Shaded symbols are for significant variables ( $p < 0.100$ ).  
<sup>1</sup> iteratively reweighted least squares algorithm did not converge

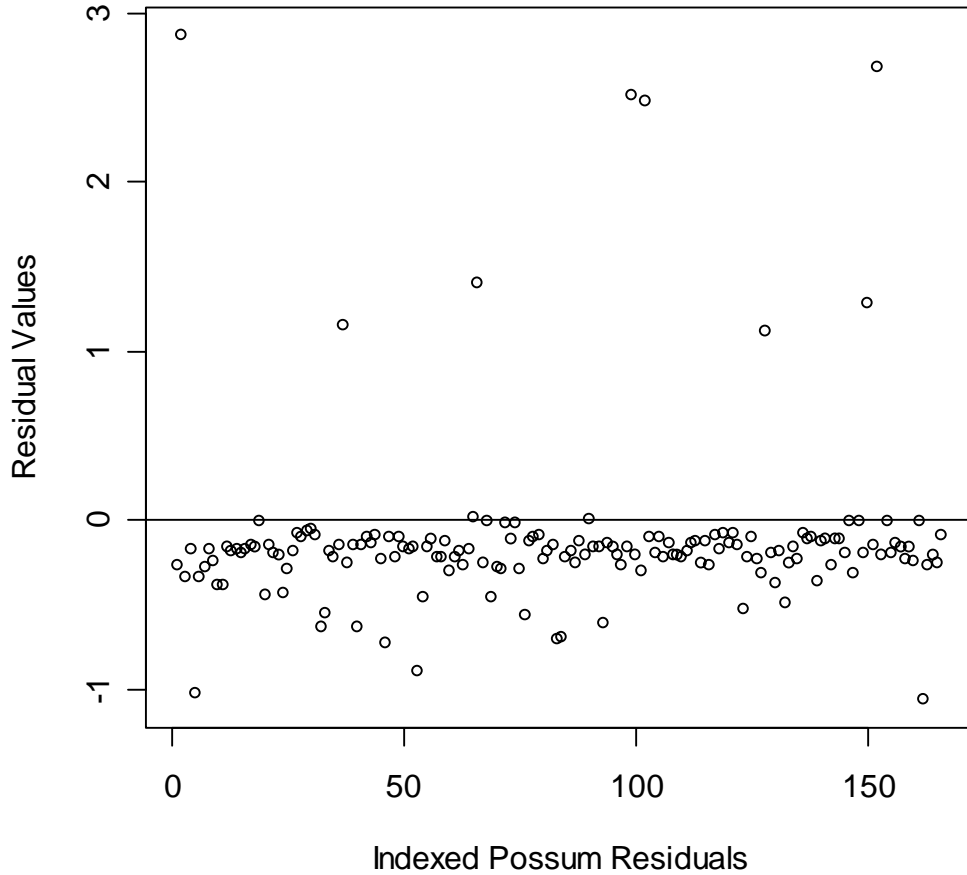


Figure 4.1. Residual values for the possum distribution model. Note the greater variability in positive residuals.

#### 4.3.5 Outliers

Outliers were identified from plots of indexed deviance residuals as values outside the range  $[-2,2]$ . Table 4.5 lists the islands in each model that were outlying values. 44 positive outliers (observed  $>$  expected) were identified. Only five negative outliers (observed  $<$  expected) were identified. Except for the four models with no convergence, each model had between two to six outliers.

Species	Complete observations	
	Number	Percentage
Cattle	165	55.7
Horses	165	55.7
Pigs	68	23.0
Deer	171	57.8
Goats	164	55.4
Sheep	166	56.1
Dogs	169	57.1
Wallabies	166	56.1
Cats	127	42.9
Possums	166	56.1
Rabbits	127	42.9
Hedgehogs	127	42.9
Stoats	130	43.9
Norway	127	42.9
Shiprats	127	42.9
Kiore	57	19.3
Mice	127	42.9

Table 4.4. Number and percentage of complete observations for calculation of deviance residuals in individual mammal species models.

#### *4.3.6 Model Refinement*

##### *4.3.6.1 Predator-Prey Relationships*

To more adequately explore known predator-prey relationships between some mammals (cats, stoats, rabbits and rodents) extra terms were added to their models. These terms and their significance are given in Table 4.6. The presence of stoats on an island significantly affected the presence of rabbits, but no other significant interactions were detected.

	Observed > Expected	Observed < Expected
Cattle	CHICKEN IS Marotiri (Lady Alice) GREAT BARRIER, Rangiahua (Flat)	GREAT BARRIER, Aotea (Gt Barrier)
Horses	*	
Pigs	CAVALLI IS Panaki CAVALLI IS Hamaruru	
Deer	PASSAGE IS, Dusky Sd, Passage KAWAU I. CHETWODE IS Nukuwaiata NATIVE I., Paterson Inlet GREAT BARRIER, Kaikoura (Selwyn)	
Goats	CAVALLI IS Nukutaunga MOTUORUHI (GOAT) I., W. Coromandel HAULASHORE I., Nelson ALLPORTS I., Queen Charlotte Sd STEEP-TO I., Preservation Inlet HEREKOPARE (TE MARAMA) I.	
Sheep	MOTUKIEKIE I., Bay of Islands OKAHU (RED HEAD) I., Bay of Islands RANGITOTO IS, Whakaterepapanui PICKERSGILL I., Queen Charlotte Sd BLUMINE (ORUAWAIRUA) I., Queen Charlotte Sd	D'URVILLE (RANGITOTO KI TE TONGA) I.
Dogs	*	
Wallabies	*	
Cats	GREAT BARRIER, Rangiahua (Flat) HEREKOPARE (TE MARAMA) I.	
Possums	NATIVE I., Paterson Inlet MOTUTAPERE I., W. Coromandel TARAKAIPA I., Tennyson Inlet ALLPORTS I., Queen Charlotte Sd	
Rabbits	RANGITOTO IS, Puangiangi MERCURY IS, Korapuki MOTUNAU I., Pegasus Bay	
Hedgehogs	*	
Stoats	ENTRY I., Breaksea Sd WAEWAETOREA I., Bay of Islands PICKERSGILL I., Queen Charlotte Sd	
Norway	HAWEA I., Breaksea Sd BENCH (COLL) I., E. Stewart I.	
Shiprats	GREAT BARRIER, Okokewa (Green) TAWHITINUI I., Tennyson Inlet MOTUKAHAUA (HAPPY JACK) I., W. Coromandel GREAT BARRIER, Junction RAKITU (ARID) I.	D'URVILLE (RANGITOTO KI TE TONGA) I.
Kiore	RURIMA I., Bay of Plenty	POOR KNIGHTS IS., Aorangi MERCURY IS, Ahuahua (Great Mercury)
Mice	BLUMINE (ORUAWAIRUA) I., Queen Charlotte Sd ADELE I., Tasman Bay PICKERSGILL I., Queen Charlotte Sd TARAKAIPA I., Tennyson Inlet	

Table 4.5. Islands which had outlying values in the individual mammal species models.



Model	Term	P-value	Signif.	Effect
Cats	Number of rodents	ns		
Rabbits	Stoat presence/absence	0.047	*	–
Stoats	Number of rodents	ns		

Table 4.6. Predator-prey relationship terms in three individual species models. Only the presence of predators (stoats) appears to affect the distribution of prey (rabbits). Not vice-versa (prey mediating predators).

#### 4.3.6.2 Rodent Interactions

To test if the number of other rodent species on an island affects the presence of a rodent species, rodent interaction terms were included in the four rodent models. Results are presented in Table 4.7. Only the three rat species (Norway, ship rat and kiore) were significantly affected by the presence of other rodent species on an island. The effect was most significant for the Norway rats, but strongest for the kiore.

To specifically test for interactions between kiore and all other rodent species, the distribution of each species was also included individually in the kiore model. Results are presented in Table 4.8. Kiore were most significantly negatively affected by the presence of ship rats, although the presence of Norway rats also significantly influenced the presence of kiore negatively to a lesser extent. The presence of mice did not significantly affect the presence of kiore.

Model	Coefficient	P-value	Signif.
Norway Rats	-1.540	0.028	*
Ship Rats	-1.469	0.055	.
Kiore	-2.768	0.063	.
Mice	-0.517	ns	

Table 4.7. Rodent interaction terms for all four rodent species models. Only the three rodent species were negatively affected by the presence of other rodents.

Model	Coefficient	P-value	Signif.
Norway Rats	-4.0712	0.09	.
Ship Rats	-11.053	0.024	**
Mice	0.1984	ns	

Table 4.8. Interactions between kiore with the three other rodent species. The distribution of kiore is most severely affected by the presence of ship rats. The presence of mice has no effect on the distribution of kiore.

#### 4.4 Discussion

##### 4.4.1 Linear Models

The original models were all adequate at predicting the distribution of introduced mammal species on New Zealand offshore islands. The chi-square adequacy tests support the plausibility of the model specifications, as well as providing no evidence that over dispersion is occurring. The only model with a low p-value suggesting an inadequate fit might be occurring was the kiore model ( $\chi^2$ ,  $p_{large} = 0.334$ ,  $df = 42$ ), which was related to its low degrees of freedom.

##### 4.4.1.1 Individual Models

##### 4.4.1.1.1 Cattle

Only three terms were significant in the cattle model. *Latitude* ( $p = 0.053$ ) and the levels for *Unmanned Farm* ( $p = 0.069$ ) and *Ranger Station* ( $p = 0.038$ ) in *Settlement*. It is important to remember that the large domestic mammals were only considered present on an island if they were relatively free-roaming and unmanaged populations, which significantly affected the ecosystem (*sensu* Atkinson and Taylor 1991). Truly feral populations of livestock only exist on a few islands now (Rudge 1990a, 1990b). In fact for cattle there are no longer any truly feral populations on offshore islands due to the

advance of land development, permanent settlement and more intensive farming (Taylor 1990). It is thus not surprising that islands which contain *Unmanned Farms* or *Ranger Stations* would be significantly more likely to have a cattle population, as populations on these islands would not be securely managed. On a permanently inhabited island populations of cattle (and other livestock) would be fenced off and securely managed, so they would not have been considered 'present' by Atkinson and Taylor (1991). Because of this relationship between cattle and human settlement distribution across New Zealand islands, it is not surprising that *Latitude* is also significant, acting as a surrogate for human settlement patterns and farming modification (Duncan and Forsyth unpubl.). It is unlikely that any latitudinal effect would be related to climate or productivity. Aside from human settlement, cattle populations have been established across the complete latitudinal range of New Zealand islands, including those outlying, from the subtropical Kermadecs to the subantarctic Auckland Islands, although the survival of such populations is affected by *Latitude* (Duncan and Forsyth unpubl.).

#### 4.4.1.1.2 Horses

Due to the small number of wild horse populations established on offshore islands (<10), and the subsequent over-fitting, no variables were significant correlates of wild horse distribution across New Zealand offshore islands.

#### 4.4.1.1.3 Pigs

Only  $\log_{10}$  *Area* was significantly related ( $p = 0.028$ ) to pig distribution across New Zealand offshore islands. There are a number of possible explanations. It may be that area is a limiting factor to the establishment of pig populations. If so it would more likely be because of home-range requirements, than of habitat requirements. The variable  $\log_{10}$  *BHDI* was not significant in the pig model, suggesting habitat heterogeneity does not play a role in pig distribution. Instead it seems more likely that the relationship between the number of individuals and area is the explanation. McIlroy (1990) notes that the key factors for feral pigs are reliable supplies of appropriate food and water and adequate

cover; resources that would be mediated by island area and would control population sizes. However pig distribution may be a relic of past historical introductions by early human explorers such as Captain James Cook (McIlroy 1990; Park 1995), who would have only landed on the larger islands, at a time before settlement of islands was occurring or wharves were present, thus negating those variables. It may be that both explanations contribute to the distribution of pigs across New Zealand offshore islands, but unfortunately it is not possible to tell from observational data. More in-depth investigation of the introduction of pigs to New Zealand, combined with experiments of minimum area requirements would be needed to establish the true explanation.

#### 4.4.1.1.4 Deer

Both the intercept ( $p = 0.001$ ) and *Latitude* ( $p = 0.007$ ) were highly significant in the deer model. The strong negative relationship with *Latitude* means deer are much more likely to be found on southern islands, and the significant negative intercept means the change from predominantly present to absent occurs early in the relationship with *Latitude*. Deer have been known to swim to islands, although this appears to be mainly among ‘inshore’ islands, as found in the Fiordland system. The *Latitude* effect may also be a relic of the historical introduction of deer to New Zealand. Deer have a restricted distribution on the mainland of New Zealand, occurring in pockets scattered throughout the country, except in the Northland where legislation bans the farming of red deer (*Cervus elaphus scoticus*). King (1990a) maps the distribution of all deer species, where they predominantly occur on the western side of the South Island (where the only islands are around southern-most Fiordland). They have tended not to expand their range across the entire country as other introduced mammal species have. Their main restriction has been human occupation, and to a lesser extent competition with other ungulates (Challies 1990). Thus to a large extent the only islands that could be colonised by deer would be those located near the release sites of mainland populations. For the more common red deer these release sites were near large tracts of forest in order to facilitate their rapid spread and multiplying (Challies 1990). Fiordland is New Zealand’s largest national park, containing large tracts of continuous forest, and it would only be here that deer would have been able to disperse

unrestricted to islands. The low human population and absence of modified habitat barriers would thus facilitate deer dispersing to islands.

#### 4.4.1.1.5 Goats

The intercept in the goat distribution model is also negative and significant ( $p = 0.084$ ), although not to the same level as for deer. Once again the change is early in the relationship, although in this case the change is from absent to present with respect to the relative species richness of exotic land birds on islands ( $p = 0.008$ ). The presence of a landing structure may also increase the probability of goats being on an island ( $p = 0.081$ ). The positive relationship with exotic land birds suggests that goats are more likely to be found on islands with modified habitat, since exotic land bird species richness tends to be a good surrogate for this (see *Section 3.1.7.3*). This is not surprising as goats are themselves known to drive habitat modification (Townes *et al.* 1997), although their presence may be indirectly related because humans modified the habitat initially, and then introduced goats. Goats were in fact bought onto islands as a convenient stock animal to control woody weeds (Rudge 1990a), which could only invade modified sites and would also be a good indication of modification. Although the relationship with the presence of a landing structure is only weak, it still suggests that the presence of goats reflects their original distribution following their introduction. Truly feral goat populations are now present on only four islands (Rudge 1990a).

#### 4.4.1.1.6 Sheep

The presence of sheep has a significant relationship with the relative species richness of exotic land birds ( $p = 0.007$ ), as did goats. Once again this also suggests sheep may occur on islands which have been modified by humans, and that the sheep themselves may be modifying the habitat, which was originally a prerequisite of Atkinson and Taylor's (1991) inclusion of their presence. However the two models differ in that sheep presence is also positively related to biological habitat diversity ( $p = 0.043$ ) as well as the degree of habitat modification. This relationship may be because sheep are only on islands where

humans have generated multiple land uses, although one might then expect some relationship to human settlement or the presence of a landing structure as has been found for other large mammals. Sheep do require multiple habitats to survive, they feed in open pasture, but require forest for shelter (Rudge 1990b). This may explain their occurrence on islands with higher habitat diversity, independent of *Area* which was not significant. It may be that sheep are in fact both modifying the habitat, and increasing its heterogeneity. Because goats are such aggressive browsers, invading even native forest and climbing trees, they tend to homogenise habitat. Sheep on the other hand may only be able to modify smaller habitat patches, subsequently creating increased habitat heterogeneity. Sheep are only truly feral on Arapawa Island (Rudge 1990b). All other populations are human escapees, although the distinction was once quite unclear (Wodzicki 1950). Their original distribution would have reflected this.

#### *4.4.1.1.7 Dogs*

Due to the small number of wild dog populations established on offshore islands (<10), and the subsequent over-fitting, no variables were significant correlates of wild dog distribution across New Zealand offshore islands.

#### *4.4.1.1.8 Wallabies*

Due to the small number of wallaby populations established on offshore islands (<10), and the subsequent over-fitting, no variables were significant correlates of wallaby distribution across New Zealand offshore islands.

#### *4.4.1.1.9 Cats*

The presence of cats was negatively correlated with island *Elevation* ( $p = 0.050$ ) and positively correlated with island habitat heterogeneity ( $p = 0.044$ ). Within the New Zealand landscape, the islands with the highest elevation also happen to be the most well

preserved, retaining a high degree of ecological intactness. It is possibly because of this intactness that these islands are less likely to be invaded. Mandon-Dalger *et al.* (1999) found a similar negative correlation with elevation for the colonisation of Reunion Island by the Red whiskered Bulbul (*Pycnonotus jocosus*), an endemic bird species. This they associated with the different micro-climates of elevations on the island. New Zealand islands with higher elevation tend to have damper climates (pers. obs.), and it is known that cats are extremely sensitive to micro-climate and habitat, especially increased moisture exposure from which they require shelter. This is also supported by the relationship between cat presence and biological habitat diversity. Cats use multiple habitats (Fitzgerald 1990) and their presence may be controlled by the availability of suitable habitat, as predicted by Lack's (1969, 1976) habitat hypothesis. Habitat could thus be considered one of the limiting factors to the distribution of cats.

The distribution of cats was not related to the abundance of prey such as bird species or rodents, as others have suggested (Towns *et al.* 1997). This is not entirely strange though, because in the absence of one prey type generalist predators can always switch to another, thus not relying on any one species (Curtis and Barnes 1989). Originally sealers and whalers introduced cats, but since then many populations have naturally gone extinct (Fitzgerald 1990). Reasons for these extinctions have not been discussed in the literature, however it is likely that some aspect of island existence has restricted the long-term establishment of cats on offshore islands. Taylor (1984) suggested cats compete with stoats for food during shortages and so require rabbits or close human habitation to survive. Taylor cited the mutual exclusion of both species on islands less than 750 hectares in support of this. However this mutual exclusion does not consider other factors that might differ between islands with separate cat and stoat populations. There are also examples such as Little Barrier Island where feral cat populations have thrived with neither rabbits nor close human habitation (Veitch 1985). Instead it would seem that the limits to cat distribution on islands are abiotic conditions (elevation/habitat) rather than biotic conditions (prey/competition) as suggested by others (Taylor 1984; Fitzgerald 1990).

#### 4.4.1.1.10 Possums

The factors that predict the distribution of possums are barely significant at the 10% level. It is known that possums do not voluntarily swim, and so dispersal across significant water barriers would have to be by human vector (M. Clout pers. comm.). Cowan (1990) states possums were purposefully introduced onto 17 (including outlying) islands. The positive relationship with relative exotic bird species richness ( $p = 0.073$ ) once again suggests that the species is only present on islands modified by humans. The presence of a landing structure ( $p = 0.074$ ) quite possibly explains the vector by which possums would have arrived at an island. Possums were introduced to New Zealand in the late nineteenth century to establish a fur trade (Cowan 1990). They would have been transported by ship to areas where they were not established. The lack of a relationship with *Settlement* suggests that the choice of island sites for possum introduction was independent of European settlement types. It is also possible that since the introduction of possums to islands, some populations have gone naturally extinct. This would obscure what factors were operative at the time of introduction.

#### 4.4.1.1.11 Rabbits

Only one variable was barely significant at the 10% level in the rabbit distribution model. The presence of rabbits appears to be positively related to the number of interacting mammals ( $p = 0.083$ ). Originally rabbits were introduced to shore stations on islands as a common food item of trade (Gibb and Williams 1990), however since then their distribution has changed. Now it appears that rabbits are only on islands where other mammal species occur. Prior knowledge of the interactions of rabbits with other mammals, including the misguided introduction of stoats as a biological control (King 1990b) suggests that the presence of stoats on an island would coincide with the absence of rabbits. When the distribution of stoats is included in the rabbit distribution model, the two are indeed negatively related. Although such a relationship can not be proven to be causal from this analysis, it would seem most likely to be, since an indirect correlation



due to similar area or distance effects would produce the opposite result (a positive correlation).

#### 4.4.1.1.12 Hedgehogs

Due to the small number of hedgehog populations established on offshore islands (<10), and the subsequent over-fitting, no variables were significant correlates of hedgehog distribution across New Zealand offshore islands.

#### 4.4.1.1.13 Stoats

The stoat distribution model illustrates island biogeographic parameters operating on a dispersing population well. This was to be expected as stoats have never been purposefully introduced to an island (Taylor and Tilley 1984). Both  $\log_{10} Area$  ( $p = 0.027$ ) and  $\log_{10} Dist.Main$  ( $p < 0.001$ ) were significant predictors of the distribution of stoats. The intercept was also just significant ( $p = 0.056$ ) at the 10% level. As predicted by island biogeography theory, *Area* has a positive effect on the presence of stoats. Populations are less likely to go extinct on larger islands. The underlying nature of this species-area relationship is probably due to individual abundances, since  $\log_{10} BHDI$  was not significant. Distance from the mainland (*Dist.Main*) has a negative effect. Stoats are less likely to be established on islands further from the mainland because of a lower immigration rate. All of these results suggest that island populations of stoats are conforming to island biogeographic theory (*sensu* MacArthur and Wilson 1963, 1967).

The alarming possibility of stoats colonising offshore island nature reserves and decimating threatened bird populations requires that managers be aware of islands within the swimming distance of stoats. Taylor and Tilley (1984) investigated 26 islands known to be colonised or visited by stoats at that time and concluded that 1.2 kilometres was the safe distance for islands. Atkinson and Taylor (1991) list a further 9 islands which are known to have stoat populations established on them. Table 4.9 lists the 33 islands greater than five hectares (Taylor and Tilley included two islands less than five hectares)

Island	Latitude	Longitude	Area (ha)	Elevation (m)	Distance from Mainland (m)	Number of >5ha Stepping stones	Last >5ha Stepping stone	Distance (m)	Stoats on Last Island
* CAVALLI IS Motukawanui	-35.00	173.91	380	177	2650	1	Motukawaiti	1250	No
WAEWAETOREA I., Bay of Islands	-35.20	174.21	52	79	3250	1	Urupukapuka	175	Yes
URAPUKAPUKA I., Bay of Islands	-35.20	174.23	220	106	750				
MOTUROA I., Bay of Islands	-35.21	174.07	157	82	375				
* MOTURUA I., Bay of Islands	-35.22	174.16	162	99	1500	1	Motuarohia	975	Yes
MOTUAROHIA (ROBERTON) I., Bay of Islands	-35.23	174.14	66	78	1650	1	Moturua	1000	Yes
* RIMARIKI I.	-35.42	174.44	22	60	400				
* KAWAU I.	-36.42	174.88	2050	182	1475				
* NOISES IS, Hauraki Gulf, Otata	-36.69	174.97	15	67	17550	2/3	Rakino	2275	NA
MOTUORUHI (GOAT) I., W. Coromandel	-36.73	175.38	57	169	2575				
WAIHEKE I., Hauraki Gulf	-36.81	175.07	9333	231	5100	2	Ponui	1175	Yes
* RANGITOTO/MOTUTAPU I., Hauraki Gulf	-36.81	174.85	2321/1560	260/121	3000	1	Brown	1800	No
PONU I (CHAMBERLINS) I., Hauraki Gulf	-36.86	175.20	1795	173	3200	1	Pakihi	1150	No
D'URVILLE (RANGITOTO KI TE TONGA) I.	-40.85	173.84	16782	729	500				
FORSYTH (TE PARUPARU) I., Pelorus Sd	-40.95	174.09	775	356	275				
ADELE I., Tasman Bay	-40.98	173.06	88	169	775				
MAUD (TE HOIERE) I.	-41.02	173.90	309	368	850				
TAWHITINUI I., Tennyson Inlet	-41.05	173.80	22	103	475				
PICKERSGILL I., Queen Charlotte Sd	-41.16	174.28	103	186	4250	1	Arapawa	250	Yes
BLUMINE (ORUAWAIRUA) I., Queen Charlotte Sd	-41.16	174.24	377	298	1700	1	Arapawa	350	Yes
ARAPAWA I.	-41.18	174.33	7785	559	600				
* HAULASHORE I., Nelson	-41.26	173.24	6	5	225				
SECRETARY I.	-45.23	166.92	8140	1196	925	2	Bauza	200	Yes
* BAUZA I., Doubtful Sd	-45.29	166.91	480	383	650	1	Utah	225	No
ELIZABETH I., Doubtful Sd	-45.41	167.11	75	117	150				
* ENTRY I., Breaksea Sd	-45.59	166.69	38	147	1075	1	Resolution	1000	Yes
RESOLUTION I.	-45.68	166.65	20860	1069	500				
COOPER I., Dusky Sd	-45.73	166.82	1780	523	175				
ANCHOR I., Dusky Sd	-45.76	166.51	1525	417	2500	1	Resolution	1250	Yes
SMALL CRAFT HARBOUR IS, Chalky In.	-45.96	166.63	48	65	550				
CHALKY I., Chalky Inlet	-46.04	166.51	475	151	2750	3	Passage	825	No
WEKA (LONG) I., Preservation Inlet	-46.09	166.68	108	88	725				
COAL I., Preservation Inlet	-46.11	166.63	1163	251	425				

Table 4.9. New Zealand offshore islands (> 5 ha) known to be colonised by stoats.

\* not included in Taylor and Tilley (1984)

where stoats have been recorded. Rangitoto and Motutapu Islands are combined into one island (see *Section 3.1.2.7.1*). Distance measurements differ by up to 150m between Table 4.9 and Taylor and Tilley (1984). Where the difference is larger, it is because of intermediate islands less than five hectares which are not included in Table 4.9. *Elevation* is included as Lomolino (1990) found it acted as a cue for the active dispersal of small mammals. The status of stoats on a further 30 islands is not identified in Atkinson and Taylor (1991).

Generally 1200 metres is still a good estimate for the distances stoats are known to have crossed to colonise islands, but there are three islands where stoats appear to have swum further. These are Motuoruhi, Kawau and Otata (Table 4.9). For Motuoruhi island there is an island intermediate to the mainland, slightly under five hectares, which could act as a stepping stone and is not included in this dataset. Kawau Island is only just over the 1.2 kilometre limit. However Otata Island in the Noises appears to be an exceptional case of stoat colonisation, clearly over two kilometres from the nearest island, Rakino. Otata is the last island in a chain of stepping stones where the first island (Rangitoto/Motutapu) is colonised by stoats, but the status of stoats on the second island (Rakino) is unknown (although it would be quite likely that they were at some point present). Table 4.9 illustrates how stoats are in fact using islands as stepping stones to reach more distant islands, another prediction of island biogeographic theory. It is also noteworthy that these exceptional cases are all in the far north where the water temperature is warmer, and the islands are in relatively sheltered locations. These other factors are also considered important when considering islands that may be within the swimming distance of stoats (Taylor and Tilley 1984).

The stoat model illustrates the interactive effect between *Area* and *Dist.Main*. Taylor and Tilley (1984) suggest that stoats can colonise accessible islands over 90 hectares in size. What is actually happening is that the further an island is from a source population of stoats, the larger it needs to be to minimise extinction and compensate for the lower immigration rate. Considering a model with only *Dist.Main* removes the interactive effect with *Area*. In fact the *Area* term only governs population extinction (MacArthur and

Wilson 1963, 1967). A stoat does not have to establish nor even survive long to wreak havoc on threatened fauna. Therefore in considering islands which stoats only have to reach (c.f. survive on) the effect of *Area* is inconsequential. By considering a logistic model that relates stoat presence only to island distance from a source population it is possible to calculate the probability of stoat presence (from the current distribution) for islands at different distances using the sigmoidal curve. Such a value could be considered the 'probability of invasion' for an island by stoats, and would have application in population viability analyses where knowledge of the probability of catastrophes occurring is integral. However to do this one would need a dataset which considers complex stepping stone systems. The dataset here only considers single stepping stone systems, and would be fine for 32 of the islands, but for Otata, which is part of a multiple stepping stone system, the *Dist.Source* measurement is over 10 kilometres. If this value was corrected to compensate, so too would every other value have to be for islands where stoats are absent (so as not to make them also seem further from the source). What is required is a measurement of island distance from the nearest stoat population, or even just distance to the nearest stepping stone island (c.f. single minimising stepping stone island as done here). Such an overhaul of the dataset is not possible within the timeframe of this thesis, and not worthwhile for such a small (though significant) component of it.

A final point is that these figures and conclusions are based on the current distribution of stoats, which has only considered permanently established populations. There may be cases where stoats have reached more distant islands but failed to be recorded because they did not establish due to low immigration rates failing to supplement the population. By using only established populations, estimates of the distance of water that stoats can cross may be conservative.

It should be a priority to remove stoats from island groups such as in the Bay of Islands where stepping stone systems may rapidly facilitate the dispersal of stoats to more distant islands. By preventing stoat establishment on the first island in a stepping stone chain, all other islands are subsequently protected. To this end the status of stoats on islands included in Table 4.9, where they are not known, should be established to further

elucidate the distance stoats may be able to cross (such as on Rakino Island). Some islands should also have the status of stoats on them reconfirmed, considering the current distribution and cases where an intermediate island will most likely have them, despite being recorded as absent (such as on Brown, Pakahi, Motukawaiti, Utah and Passage Islands)

#### *4.4.1.1.14 Norway Rats*

The Norway rat model makes predictions consistent with early introduction linked to European settlement. Norway rats are present on islands with low relative seabird species richness. This would arise from direct predation upon the seabirds (Bettesworth 1972; Atkinson 1985). The positive relationship with relative exotic bird species richness, as found in other models, once again suggests human modification of the island ecosystems where Norway rats are found. A more complex explanation is also possible in this case however, one that reflected the behavioural ecology of exotic birds which might be adapted from their native ecosystems to the presence of rats. They would be better adapted than native species to survive on islands where Norway rats are present, where the decimation of native bird populations may have been followed by establishment of exotic bird species. It is surprising that neither island biogeographic nor human activity variables are significant – yielding no further insight as to how Norway rats may have colonised offshore islands.

Norway rats were introduced early relative to the other rodents (Atkinson 1973), and subsequently reached many islands early too. Around the early 1900s their numbers were observed to drastically decline to their much reduced distribution today (Moors 1990). It is quite likely that interactions with other species caused this decline. Although the mammal interaction variable is too broad to reflect this, the rodent interaction variable does have a significant negative relationship ( $p = 0.028$ ) with the presence of Norway rats. This indicates that the greater the number of other rodent species on the island, the less likely Norway rats are to be present. It would be dangerous to attribute this causally to competitive interactions based solely on these results, but most of the available

evidence in the literature supports the notion of negative interactions between the four rodent species on offshore islands (Taylor 1978, 1984; Atkinson 1986; Yom-Tov *et al.* 1999). The relationship with relative seabird richness may reflect the need for an abundant food supply to prevent resource competition with the other rodent species.

#### 4.4.1.1.15 Ship Rats

The distribution model for ship rats had more significant variables than any other species. This in itself suggests that the distribution of ship rats is relatively predictable from a number of limiting factors. Since ship rats have dispersed widely throughout the New Zealand archipelago (Atkinson 1973; Innes 1990) it could be that their distribution reflects a larger number of their limiting factors compared to less widely dispersed species whose distribution remains a relic of their human-mediated introduction. The distribution of ship rats on offshore islands is predicted by the variable  $\log_{10} Area$  ( $p = 0.005$ ). Without habitat heterogeneity ( $\log_{10} BHDI$ ) being significant this suggests the number of individuals and the associated probability of extinction is the limiting factor, although there are other explanations which should be considered. The significant negative relationship with  $\log_{10} Elevation$  ( $p = 0.040$ ) can, as for cats, be explained by the lower invasibility of offshore islands with high peaks, or an unknown component of these islands that this might be a good surrogate for. As would be expected, the further an island is from a potential source population ( $\log_{10} Dist.Source$ ) the less likely ship rats are to be present ( $p = 0.023$ ). This might suggest that stepping stone islands play a role in island dispersal, as has been suggested within island groups (Atkinson 1986). However if  $\log_{10} Dist.Main$  is included in the model it is more significant ( $p = 0.0167$ ) than  $\log_{10} Dist.Source$  as a predictor of ship rat distribution. Ship rat presence is barely negatively related ( $p = 0.08686$ ) to  $\log_{10} GDI$ , which is a good surrogate for floral complexity.

Originally (from the 1880s) ship rats reached islands from ships moored to wharves (Atkinson 1985; Innes 1990). Since then they have established successfully throughout the mainland though, and naturally dispersed to islands as evidenced earlier. Nevertheless the presence of a *Wharf* is still a (barely) significant predictor ( $p = 0.089$ ) of ship rat

presence. This illustrates how significant the presence of a landing structure must have once been in the past for allowing ship rats onto islands for it still to be significant now. The presence of ship rats is even more significantly related to whether an island is *Inhabited* or not ( $p = 0.035$ ). This is not surprising given that ship rats have for a long time known to be particularly commensal with humans (Thomson 1921; Atkinson 1985), and is probably related to the presence of a landing structure. A permanent island settlement with a landing structure would have had ships moored to it often, allowing ample opportunities for ship rats to invade an island. Ship rats are not more likely to be on islands with any of the other settlement types though. For the less intensive settlement types of *Unmanned Farm* and *Ranger Stations* this is probably reflected by the relative infrequency of ship visits; lighthouse stations were generally restocked only once every four months by the national lighthouse tender (N. Ritchie pers. comm.). *Abandoned* settlements (those which were once *Inhabited*) might also reasonably be expected to have a higher likelihood of ship rat presence, however this is not so. It may be that the settlements did not remain long enough for invasion to occur, or there may be some indirect relationship with whatever reason the settlement was abandoned for.

As in the Norway rat model, there appears to be a negative interaction between the rodent species that affects the distribution of ship rats. However in this case the relationship is not as significant as it was for Norway rats. This may be because ship rats are the superior competitor (Atkinson 1986; Yom-Tov *et al.* 1999).

#### 4.4.1.1.16 Kiore

There have been two general points of view in the past regarding how kiore may have colonised offshore islands. Holdaway (1989, 1999) believes Maori purposefully transported kiore to offshore islands. Atkinson (1986) admits that this may in some part explain their distribution, but he believes kiore have also dispersed naturally to offshore islands. Each cites examples supporting their hypothesis. In the kiore model both  $\log_{10}$  *Dist.Source* ( $p = 0.011$ ) and evidence of previous *Maori* occupation ( $p = 0.082$ ) are significant predictors of the presence of kiore. The significance of the intercept ( $p =$

0.013) indicates that the shift from presence to absence is marked, as Atkinson (1973) noted for islands situated at 1.5km from the mainland. *Maori* was significant despite missing over two thirds of its observations, which illustrates the intensity of the relationship between Maori on islands and the presence of kiore. Although this relationship may not be causal, it is suggestive of this, and supports Holdaway's views. What is strange is that  $\log_{10} \text{Dist.Source}$  has such a strong positive relationship with the presence of kiore. What this means, is that the further an island is from a source island, the more likely it is to have kiore. A similar relationship is also evident for  $\log_{10} \text{Dist.Main}$ . This initially appears to contradict Atkinson's hypothesis of natural dispersal, but it is possible that there are more complex processes operating than can be seen in what is essentially a simplified linear model. For both other species of rats, a negative relationship with other rodent species has been found which affects their presence. This relationship is also present and is strongest (though not as significant) for kiore, who tend to be absent when there are more rodent species present. Yom-Tov *et al.* (1999) discussed these interactions and found circumstantial evidence that kiore compete with both mice and ship rats. In this study the relationship was found to be strongest for ship rats, followed by Norway rats. There was no evidence of any interaction between kiore and mice. It was earlier found that the presence of ship rats was negatively related to the distance of an island from a potential source population. Together, this suggests that what we are seeing is a reduced distribution of kiore, which were once more widely spread (Atkinson and Moller 1990). This is probably the outcome of competitive interactions with ship rats colonising near-shore islands and driving kiore populations on them to extinction. This would have left kiore only on distant islands where they could only have arrived with Maori travelers, as kiore can themselves only swim up to a few hundred metres (Whitaker 1974). Similar exclusion on the mainland has been found when the spread of ship rats coincided with the final disappearance (though not the earlier decline) of kiore from most of the New Zealand mainland (Atkinson 1973).



#### 4.4.1.1.17 Mice

The mouse model is the most inexplicably uninformative of the mammal distribution models. The absence of an intermediate island which might act as a stepping stone was the only significant ( $p = 0.094$ ) predictor of the presence of mice, but this by itself is only a weak relationship with little interpretability. It has been found through examination of distributions that Norway rats and mice do not often occur together on offshore islands. This result prompted Taylor (1984) to suggest that Norway rats limited the distribution of mice. However, from this study there is no evidence that either the presence of Norway rats or interactions with other rat species in general limits mice on an island. It is generally assumed that humans accidentally transported mice to New Zealand offshore islands (Taylor 1984), but in many cases the populations did not expand or establish (Murphy and Pickard 1990). This suggests that there is some limiting factor to the distribution of mice, however it does not appear to be related to any of the variables *a priori* hypothesised in the model. It may be that the limiting factor is not deterministic, but stochastic in nature. For example, the distribution of mice may be a relic of stochastic introduction events, such as shipwrecks. The first population of mice in New Zealand was apparently established on Ruapuke Island in Foveaux Strait following the wreck of the *Elizabeth Henrietta* in 1823 (Thompson 1977; Murphy and Pickard 1990). This of course could not explain the entire distribution of mice, which will have also closely followed human journeys to offshore islands, usually in food stocks.

#### 4.4.1.2 Collinear Variables

Although all three collinear variables have been demonstrated to be highly positively correlated, it is interesting that for both the cat and ship rat models one effect is positive, while the other is negative. This suggests that the regression has partitioned out the unique variability in each collinear variable to reveal the true underlying effect. It is not surprising that  $\log_{10} BUDI$  and  $\log_{10} Area$  are positively related to the presence of cats and ship rats respectively – this can be explained by the species-area relationship and its associated explanations. The unique effect of  $\log_{10} Elevation$ , when not confounded by

either other variable appears to be negative however. This has been explained earlier by the relative invasibility of islands with higher elevations. Without including all three collinear variables it would not have been possible to discern such an obfuscated effect.

#### *4.4.1.3 Residuals*

The slightly greater variation in the positive residuals suggests that species are more often observed where the model would predict them not to occur, than the opposite (absence where expected to be present). This suggests that species occur through a means not accounted for sufficiently in any of the explanatory variables. This was most clearly demonstrated in possums, suggesting that there are cases where they would definitely not be expected by the model, but are in fact present due to some other unknown factor. Possums were specifically introduced in the latter part of the nineteenth century to establish a fur trade, and so it would seem likely that, on the few islands where they are present, this is because of factors governed by the necessities of the fur trade.

#### *4.4.1.4 Outliers*

For positive outliers, the species is observed on an island when it was most likely expected not to be. For negative residuals, the species was absent from an island where it was most likely expected to be present. As can be seen in Figure 4.5 most outlying values were positive values. This means that in most cases a species was observed where it was not expected to be, suggesting that for each island there are factors not considered in the *a priori* model which influence the presence of the associated mammalian species on that island. The distribution of mammals across New Zealand offshore islands thus appears to be related to many variables, some of which are not considered here.

The fewer cases of negative outliers are perhaps more intriguing. For both cattle on Great Barrier (Aotea) Island and sheep on D'Urville Island their 'absence' is merely a relic of Atkinson and Taylor's (1991) classification. Both species are in fact present on these islands, only they are not considered to sufficiently be influencing ecosystem dynamics.

For ship rats on D'Urville Island it would appear to be because of chance alone that they have not established, despite the island having the correct characteristics in significant variables to predispose it to colonisation. Buckingham and Elliott (1979) note that soon after their liberation possums were eradicated by residents of D'Urville Island, suggestive of an unusually early pro-conservation attitude. Atkinson (1986) has previously identified Aorangi Island in the Poor Knights as an anomalous case for kiore absence, when all other islands in the group were colonised. He attributes its lack of colonisation to the unavailability of Maori landing sites and its distance from the other islands in the archipelago. The absence of kiore on Great Mercury Island is most likely due to the presence of ship rats, which are not present on any other island in the Mercury group. The competitive interactions between rodent species are known to be harshest on kiore, which are usually driven to extinction shortly after colonisation by ship rats (Atkinson 1975; Yom-Tov *et al.* 1999).

#### *4.4.1.5 Rodent Interactions*

The interactions between rodent species have already been briefly considered in the discussion of each individual model. This section draws together those discussions into concluding remarks on the overall patterns of rodent interaction, and how these results can be placed within the context of other investigations of rodent interactions.

As discussed earlier, all four species of rodents in New Zealand are considered to interact to some extent (Innes 1990), this being evidenced by their exclusive distribution across New Zealand, with no location where the four species occur sympatrically (Taylor 1978). However the exact nature of these interactions have never been fully addressed. The disappearance of kiore from the mainland has been linked both with the spread of ship rats (Atkinson 1973) and that of mice (Taylor 1975). The link with mice was based on the similar response that both mice and kiore (but not the other two rodent species) exhibited to beech mast seeding (Murphy and Pickard 1990). However it has recently been found that ship rats also respond to mast seeding of beech (King and Moller 1997), and so this explanation no longer differentiates any competitive effect of either ship rats or mice

upon kiore. The theory itself was questionable, given that mast seeding provides an abundant resource, and the species tracking it should not therefore need to compete over a resource which would not be limiting to them. After mast seeding overly abundant populations may compete, but as population levels return to normal so too would the dynamic interactions, and then resource dependency might switch to the usual and perhaps non-overlapping resources. All that was evidenced by mast seeding relationships was the dependence of each species on it, but nothing concerning competition. Yom-Tov *et al.* (1999) suggest that the similar body sizes of kiore and mice may predispose them to competition, but that argument seems relatively unsubstantiated given that competition equally occurs between species of quite differing body sizes. It has also been suggested that the spread of Norway rats partly influenced the decline of kiore (Wodzicki 1950). This seems likely, given that negative rodent interactions were only found for the three rat species, and the inclusion of Norway rats individually was just significant in the kiore model. However Norway rats also appear to have suffered considerably from rodent interactions, as their negative interaction was most significant of the three individual rodent models. Atkinson and Moller (1990) suggest three alternative hypotheses for the decline of kiore, but do not appear to take a firm stance on any of them. Of the three hypotheses, the results found here support the first; that the absence of kiore is most strongly linked with the presence of ship rats. Both species negatively interact with each other, but it is not possible to determine whether it is cause or effect in either of them. The available literature suggests ship rats are the cause and kiore suffer the effects. The distribution of kiore was most significantly negatively related to the distribution of ship rats. Kiore distribution on islands was not in any way affected by the distribution of mice. Yom-Tov *et al.* (1999) admit that their evidence of interaction is only circumstantial, and likewise here no causation has been established. However, in light of the evidence of interactions presented, it would appear that the absence of kiore on offshore islands is currently most strongly influenced by the presence of ship rats.

#### 4.4.2 Conclusions

It is consequential to note that much of the early work on New Zealand islands and the distribution of mammals (Taylor 1984; Atkinson 1986) used data that would later be compiled in Atkinson and Taylor (1991). Thus to a large extent the results presented here have not reached different conclusions by looking at new data. Instead they should be seen as a complementary reappraisal of the same data. This is inevitable since there is only one set of New Zealand offshore islands, and any work on them will be using the same data, although perhaps updated since last investigated.

Duncan and Forsyth (unpubl.) investigated factors affecting the probability of successful introduction (i.e. the establishment) of selected exotic mammals to New Zealand. They found similar effects of *Latitude*, and farming modification on species population survival, but they found no evidence of effects of *Area* or biotic interactions between species. It is important to note though, that because of the questions addressed in their study, their dataset was subtly but significantly different (Figure 4.2). This difference is consistent for other studies that also address questions of introduction success in a similar manner (Blackburn and Duncan *in press*). The results of this study and how they relate to the distribution of species must therefore be considered within this context. What has been modelled here are the predictors of the current distributions of mammals on New Zealand offshore islands (disregarding human eradication of populations). These distributions will have changed from what they originally were when the species was first introduced.

Duncan and Forsyth (unpubl.)	Present	Extinct	Never Introduced
Russell (2002)	Present	Absent	

Figure 4.2. A comparison of population statuses and how they are reflected in the datasets of Duncan and Forsyth (unpubl.) and this thesis. Investigating introduction success, Duncan and Forsyth only used islands where species were either ‘Present’ or ‘Extinct’, omitting islands where the species was ‘Never Introduced’. Investigating species distributions, Russell (2002) treats islands where those species either naturally went ‘Extinct’ or were ‘Never Introduced’ collectively as ‘Absent’. Duncan and Forsyth (unpubl.) only considered species which had not naturally dispersed. The datasets reflect the different questions addressed by each study.

Over time, both biotic and abiotic factors will have limited the dispersal of introduced species to new islands and governed their extinctions on them. However in some cases the distribution of the species may not have changed significantly from its original distribution (i.e. its distribution is relatively static). This appears quite common for the larger mammals that cannot naturally disperse over water, or have not rapidly expanded their ranges on the mainland. The distribution of feral pigs, for example, may still reflect introduction patterns by early explorers of New Zealand, given the low dispersal rate of pigs in New Zealand. Thus for the larger mammals the significant variables may be a good indication of the characteristics of islands chosen to historically introduce species to. Patterson (1999) did in fact conclude that

*“history is shown to represent an important parameter for island biogeography; over ecological time spans, trenchant differences arise in patterns of species richness and species composition as a reflection of island history”.*

Lack (1969, 1976) found that suitable habitat availability was almost exclusively the driver of the distribution of avian species. However in this study habitat was only found to be a significant predictor of species presence for those species which were particularly sensitive to it. Ricklefs and Lovette (1999) also found that although habitat did drive avian distribution in their study as Lack suggested, it rarely influenced the distribution of mammals.

Determinism and stochasticity can both play a role in insular biogeography depending on the timeframe or window of investigation (Whittaker 1992). Ward and Thornton (2000) suggest that the natural colonisation of islands may originally be highly deterministic. The distributions of species that are naturally dispersing will ultimately be limited by factors that constrain their survival. Many of the models for smaller mammals illustrate such factors, which appear to limit their distribution on offshore islands. Where no factors are significant, it may be because the species has not yet encountered limiting factors. It might also be, for poorly dispersing species, that their distribution is limited to

the pattern of their original introduction, which might have been haphazard, or based on stochastic introduction events (such as in the model for mice distribution). Even stochastic events can be modelled over long time frames though, as they tend towards a Poisson distribution. Ward and Thornton (2000) relate the highly deterministic phase to predominantly competitive processes, which are essentially biotic limitations. This is what could be apparent in the individual rodent models that revealed significant interactions between the rodent species. It is wise, however, to consider processes beyond competition which may also produce the same result, so as not to fall into the trap of single process-orientated theories as others have in the past (see competition in Diamond 1975). Sax and Brown (2000) note that exotic species generally require multiple introductions for successful establishment, which was no less true for the New Zealand mammal introductions (Thomson 1921). It would logically follow that the distributions of species during and following that original introduction phase would be determined by anthropogenic activities, which can be deterministically modelled with relative ease. Following successful establishment, species would then begin to colonise islands independently of human processes, within a more island biogeographical framework. The proximity of source pools of species will have also changed over time as introduced species expanded their ranges on the mainland. Unfortunately there was no temporal component available in the models presented here to investigate such possibilities. Other studies (Cassey 2001; Forsyth and Duncan 2001; Duncan and Forsyth unpubl.) may provide insight into such possible colonisation stages.

Overall, the distributions of the larger mammals, which are used as livestock, tended to be related to their original distributions when introduced, as mediated by human factors. They can be considered relic populations. For smaller mammals, their distributions tended to be limited by a combination of island biogeographic parameters and biotic interactions, although some aspects of their distribution were still reflected by the patterns of their original introduction. For some species either unknown or stochastic factors may govern their current distribution.

# ***Chapter 5: Modelling Introduced Mammalian Species Richness***

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## *5.1 Introduction*

### *5.1.1 The Concept of ‘Species Diversity’*

The number of species and the relative abundances of individuals within them are together identified as the two major components of species diversity (Magurran 1988; Hubbell 2001). Unfortunately the sampling effort required to count all of the individuals in each species, within a defined sample area, means that often it is only feasible to assess species richness alone as a surrogate for species diversity. Rosenzweig (footnote p. 201 1995) argues that the concept of ‘species diversity’ should be reclaimed as a count of species, following Hurlbert’s (1971) damning of its mis-use (the ‘non-concept’ of species diversity). Still, I would agree with Gaston (1998), who suggests the two terms are often incorrectly synonymously used, as this would be misleading in depicting the full extent of information attributed to a species diversity count composed only of species richness. Regardless, the debate over the definition of species diversity seems far from over (McAllister 1991; Gaston 1996, 1998) and the concept can be bewildering to the unacquainted (see definition in Whittaker *et al.* 2001).

### *5.1.2 Measuring Introduced Mammalian Species Richness*

The limited number of introduced mammalian species on New Zealand islands (King 1990a) means that a complete census of them is a realistic goal. Such a census of species richness can also be considered more robust with respect to time-scale, as species richness varies much less than individual abundances do over time.



Use of an unmodified species richness count however, requires that it be constructed from a census of the entire species pool (Magurran 1988). If the absence of any species cannot reasonably be assumed to be accurate (see *Section 2.1.1*; McArdle 1990), then a total count of present species can only ever be a conservative (minimum) estimate. Although an analysis could be performed on such conservative data, caution would be necessary in the interpretation of subsequent results, especially when comparing between accurate and inaccurate (conservative) counts. The evident solution to this would be to analyse only islands where the complete mammal species richness has been accurately determined. This would depend on two conditions; the first being that such a sub-sample was still large enough to be statistically robust, and the second being that such a sub-sample was a fair representation of the original sample (i.e. an unbiased sub-selection with regard to individual variables). As shall be demonstrated in *Section 5.3.1* these conditions can be assessed with relative ease.

In this chapter henceforth, the term ‘mammalian species richness’ refers to the census of introduced mammals on New Zealand islands. *Chapter 6* employs a different concept for avian species richness.

### *5.1.3 Processes Controlling Introduced Mammalian Species Richness*

Studies of species richness are popular as a means of investigating whether or not the number of species on an island is in equilibrium, as proposed by MacArthur and Wilson (1963, 1967). Modelling species richness however can appear deceptively simple. Species richness is the summation of the number of individual species present, each interacting, and each limited on account of their own factors (*Chapter 4*). It has been shown that such explanatory factors can themselves interact in a multidimensional manner on species richness (Burns 1995).

Studies on introduced mammals in New Zealand have generally been characterised by the single species approach of previous decades (e.g. Taylor and Tilley 1984; Efford *et al.* 1988). Little investigation of introduced mammalian species richness has taken place in

New Zealand until recently. Results from single species studies can be used to hypothesise variables that might influence species richness. Those factors that are consistently significant in single species studies could reasonably be assumed to have an effect on any species richness count composed of those species. Recent work (e.g. Forsyth and Duncan 2001; Duncan and Forsyth unpubl.) has investigated the introduction of exotic mammals and birds to the New Zealand mainland using multiple regression and multivariate methods. Although the models concentrate on autoecological traits of species with respect to introduction success, they can still indicate processes that may drive introduced mammalian species richness on the New Zealand mainland. Investigating introduced mammals on New Zealand offshore islands can be seen as a logical progression from such work. The autoecology of species is also always going to play a role in their distribution across islands, but for species richness the differences between constituent species must be considered irrelevant, and only factors extrinsic to species can be investigated. This makes the model species neutral as the original theory of island biogeography was (for an explanation of ‘neutrality’ see Chpt. 1 in Hubbell 2001).

Overseas studies of mammalian species richness have used a number of variables as surrogates for the underlying processes potentially driving the island system in question. Area and distance are the two core elements identified by MacArthur and Wilson (1967) in their equilibrium theory of island biogeography. Thus they form the foundation for most species richness investigations (Lomolino 1982; Ceballos and Brown 1995; Burbidge *et al.* 1997; Millien-Parra and Jaeger 1999). Adler and Wilson (1985) use area, distance to the mainland, distance to the nearest island and habitat heterogeneity among other variables to investigate the biogeography of small mammals on Massachusetts islands. For terrestrial mammals, it is assumed that stepping stone islands do not play a significant role in island colonisation processes, and a direct measure of island distance to the mainland, neglecting intermediate islands, can be used as a fair surrogate for isolation. This is possible as mammals are poor dispersers, in comparison to birds whose mobility means they can colonise many islands more rapidly using such stepping stones.

Emphasis has also been placed on the predictive value of latitude (Ceballos and Brown 1995), although the exact nature of such an effect is still unclear (Sax 2001).

*Section 3.2.3* discussed the confounding effects of area, habitat diversity and to a lesser extent elevation. All of these variables have been shown to explain similar variability within species richness models, and it is unclear which may be the causal mechanism.

Other studies have highlighted the importance of including anthropogenic historical factors in any study of species richness (Abbott 1983; Patterson 1999; Welter-Schultes and Williams 1999).

#### *5.1.3.1 Splitting Species Richness*

The weight distribution of introduced New Zealand mammals shows a marked shift between small mammals and large mammals at around ten kilograms (King 1990a). Figure 5.1 illustrates the division between these two groups. Siemann and Brown (1999) found that gaps in the body size distribution of terrestrial mammals was in fact an exception, rather than a rule in itself (Holling 1992), however, the observed bias in exotic mammal introductions to New Zealand (King 1990a; Forsyth and Duncan 2001) would suggest that a human-caused exception was generated in the New Zealand landscape (Gibb and Flux 1973). It was hypothesised that the underlying processes driving total introduced mammalian species richness on islands would differ between these two distinct groups, as other mammalian and conceptual studies have found within taxa distinctions (Adler and Wilson 1985; Burbidge *et al.* 1997; Lomolino 1999). Table 5.1 lists the mammals in each group.

It was hypothesised that island biogeographic processes would drive the species richness of the small mammals and that human-mediated historical processes would predominantly drive the species richness of the large mammals (Gibb and Flux 1973).

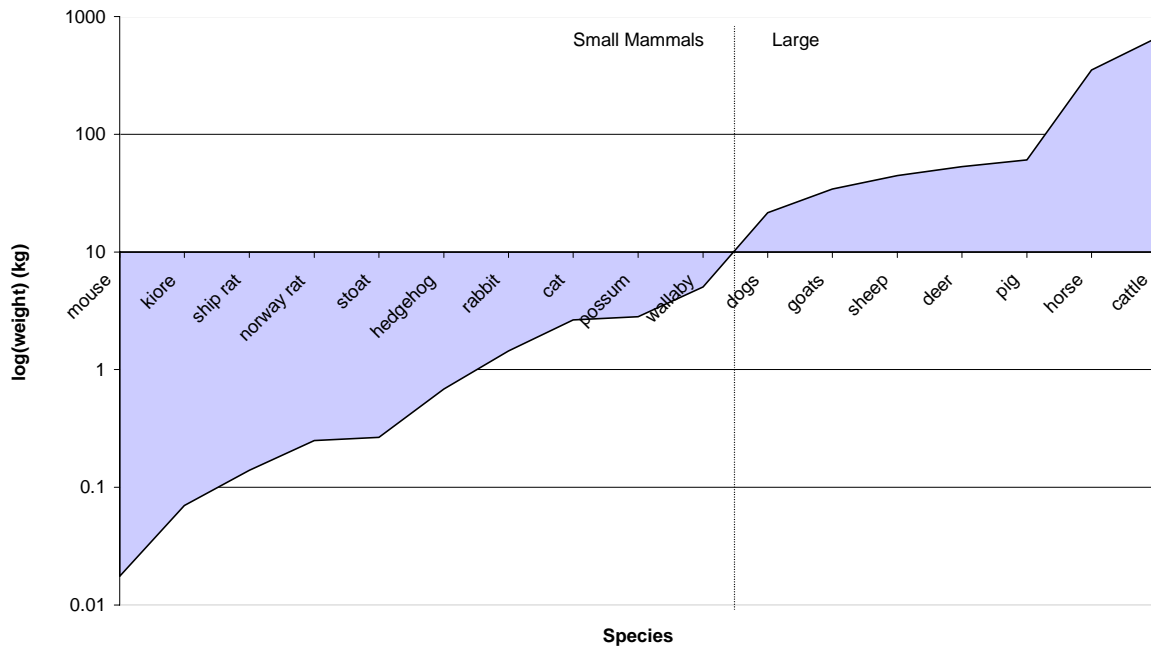


Figure 1.1. The weight distribution of introduced mammals in New Zealand. Note the division at 10kg.

## 5.1.4 Hypotheses

### 5.1.4.1 Versal Hypotheses

It is hypothesised that the introduced mammalian species richness of New Zealand offshore islands can be adequately predicted by their *Latitude*,  $\log_{10}$  transformations of *Area*, *Elevation*, distance to the mainland (*Dist.Main*), geological diversity (*GDI*) and biological habitat diversity (*BHDI*) and the presence of landing structures (*Landing*) and their European settlement history (*Settlement*). It is also hypothesised that the interaction between landing structure presence and European settlement history will have an effect on the introduced mammalian species richness. The corresponding null hypothesis is that species richness has no relationship to any of the aforementioned variables.

It is also hypothesised that the significance of the above variables will differ between small mammals (<10 kg) and large mammals (>10 kg).

< 10kg	> 10kg
<i>Mus musculus</i>	<i>Canis familiaris</i>
<i>Rattus exulans</i>	<i>Capra hircus</i>
<i>R. rattus</i>	<i>Ovis aries</i>
<i>R. norvegicus</i>	<i>Cervus sp.</i>
<i>Mustela erminea</i>	<i>Sus scrofa</i>
<i>Erinaceus europaeus occidentalis</i>	<i>Equus caballus</i>
<i>Oryctolagus c. cuniculus</i>	<i>Bos taurus</i>
<i>Felis catus</i>	
<i>Trichosurus vulpecula</i>	
<i>Macropus sp.</i>	

Table 5.1. Large and small mammal groups.

#### 5.1.4.2 Statistical Hypotheses

H<sub>0</sub>: All coefficients and the intercept in the linear model are equal to zero.

$$a, b_1, b_2, b_3, \dots, b_n = 0$$

H<sub>1</sub>: One or more of the terms in the linear model has a coefficient not equal to zero.

$$a \text{ or } b_1 \text{ or } b_2 \text{ or } b_3, \dots, b_n \neq 0$$

## 5.2 Methods

### 5.2.1 Reduced Dataset

As outlined in 5.1.2, for data where observations contain incomplete censuses, only conservative estimates of introduced mammalian species richness can be constructed. To avoid biasing the dataset with such conservative estimates only islands where complete

censuses of all introduced mammalian species (from the total pool of 17 species) were used. This allowed a relatively unbiased calculation of  $S$  (total introduced mammalian species richness). The original data source (Atkinson and Taylor 1991) used a larger number of classifications for mammal occupation on islands. These have been discussed in *Section 2.1.1*. The point to reiterate here is that observations where presence was suspected but not confirmed (presumably from a lack of adequate sampling effort) were reclassified to *NA*. This prevents the use of islands containing such reclassifications in calculating an unbiased estimate of  $S$ .

The reduced dataset consisted of 165 of the total 297 islands. Immediate observation suggests that the first of the conditions discussed in *Section 5.1.2* is readily met;  $n = 165$  islands remains a substantial sample size for robust statistical analysis (Chase and Bown 1997). The second of the conditions, that the subsample must be a fair representation of the original sample, requires considerably more testing. A comparison of quantile distributions between identical variables from the subsample and the original sample is used to highlight any differences in distribution (over-represented and under-represented values).

### *5.2.2 Z-values*

The relationship between  $\log_{10} A$  and  $\log_{10} S$  can be modelled using least squares linear regression, and the fitted line will have a slope of  $z$  and an intercept of  $\log_{10} c$  (*Section 2.2.2*).

The line was fitted for non-zero values of  $S$  (i.e.  $S > 0$ ). This is because the log of 0 is undefined, and a transformation (such as  $\log(S + 1)$ ) inappropriately biases interpretation of  $z$  and  $c$  during comparison between studies (Williamson 1981). Although removing observations is not favoured, it is the least obtrusive of a number of fixes (Williams 1996).

### 5.2.3 Linear Modelling

Linear modelling methodology follows that outlined in *Section 2.2.1*. For modelling species richness the response was assumed to be Poisson distributed. i.e. The response variable  $y$  takes a discrete value greater than zero. This is mathematically depicted as  $y = 0, 1, 2, \dots, n$ , which is analytically identical to a measure of species richness. The generalized linear model with Poisson family error utilises the natural log link in the equation equality.

The final model presented is thus:

$$E(y_i) = e^{\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \dots + \beta_n x_{in}} \quad y_i \sim \text{Poisson}(E(y_i))$$

Coefficients of model terms are presented as the proportional change in the response variable for a change in one unit of the explanatory variable (for proof see *Section 2.2.1.1*).

## 5.3 Results

### 5.3.1 Subsample Representativeness

Most variables had a similar distribution in the subsample as in the original dataset, but a few were under and over-sampled for particular values. Only two islands considered high-leverage were present in the subsample; Haulashore Island:  $\log_{10}$  *Elevation* and Stewart Island:  $\log_{10}$  *Area* and  $\log_{10}$  *BHDI*.

$\log_{10}$  *Elevation* was under-sampled for values below 1.5. Back-transformed, this means that islands with elevations less than 30m are those under-represented in the subsample of 165 islands.

$\text{Log}_{10} \text{Dist.Main}$  showed a similar trend, with islands having values less than 2.5 being severely under-represented. However this trend does not level off until values of greater than 4. Back-transformed, this means that islands closer than 300m to the shore are those severely under-represented, and this trend persists until islands are over 10km offshore.  $\text{Log}_{10} \text{GDI}$  is under represented for values below 0.3, which when back-transformed corresponds to islands with Geological Diversity Indices less than or equal to 2.

The largest departure from distribution equality is in *Latitude*, which is under-sampled for values lying between  $-45.00$  and  $-41.00$ , and correspondingly over-sampled for values lying between  $-41.00$  and  $-38.00$ . Those under represented are geographically located around the central South Island, between the south of the Marlborough Sounds and the north of the Fiordland Islands. Those over represented lie around the central North Island generally south of the East Cape and north of the Marlborough Sounds. This reflects the geographical clustering of islands in New Zealand. Figure 5.2 graphically depicts the irregularities in the subsample.

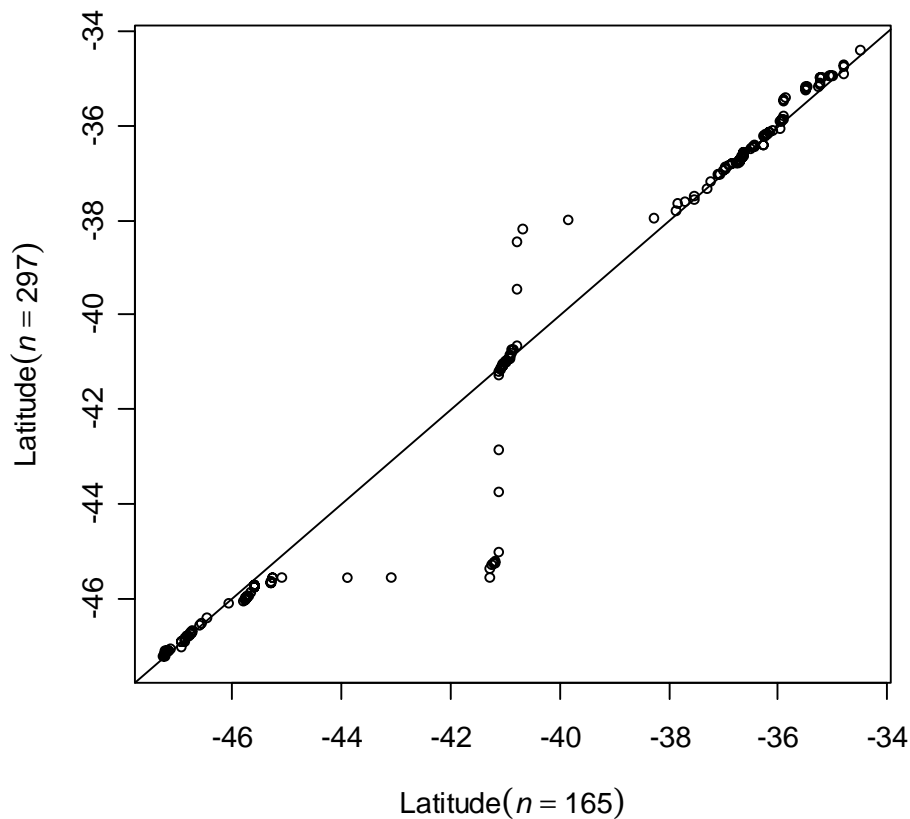


Figure 5.2. Quantile-quantile plot for *Latitude* subsample. Points below the line indicate under-sampling while points above the line indicate over-sampling.



	<i>Landing</i>						
	Total	-	W	NA			
Proportion	165/297	148/256	16/35	1/6			
95% Interval	0.56	(0.52,0.64)	(0.29,0.63)	(-0.21,0.55)			
	<i>Settlement</i>						
	Total	-	A	F	I	R	NA
Proportion	165/297	130/230	11/14	2/4	13/29	7/8	2/12
95% Interval	0.56	(0.50,0.63)	(0.56,1.02)	(-0.19,1.19)	(0.26,0.64)	(0.62,1.14)	(-0.07,0.41)

Table 5.2. Sub-sampling proportions and 95% confidence intervals for levels of the categorical variables *Landing* and *Settlement*. All intervals except NA contain the average and are thus unbiased subsamples.

Table 5.2 gives intervals of the sampling proportions for levels of both categorical variables compared to the average (total islands in subset/total islands). Intervals for most levels included the average, suggesting that the subsample of levels is not particularly biased. In *Settlement*, both *Abandoned* and *Ranger Station* islands appear to be over represented, with their respective lower-tails marginally around the average value.

### 5.3.2 Z-values

Taking only islands with positive values of  $S$  meant that the sample size was reduced for these islands from 165 to 108. Figure 5.3 shows the regression of  $\log_{10} A$  on  $\log_{10} S$ . Estimates and 95% confidence intervals ( $n = 108$ ) for  $\log c$  and  $z$  are:

$$\begin{aligned} \log c &= -0.06 && (-0.18,0.06) \\ z &= 0.21 && (0.16,0.26) \end{aligned}$$

The intercept was not significant ( $p = 0.325$ ), but the z-value was significant at the 5% level ( $p < 0.001$ ). Residuals were normally distributed (Wilks-Shapiro test,  $p = 0.140$ ).

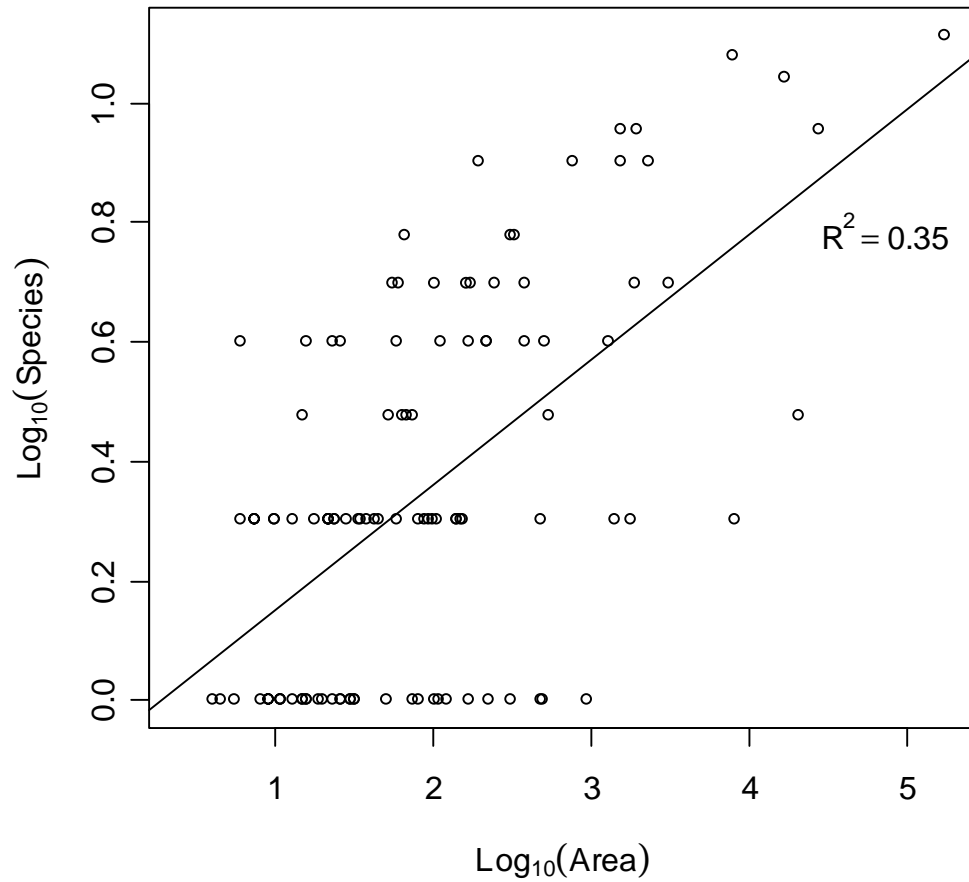


Figure 5.3. Linear regression of  $\log_{10} S$  on  $\log_{10} A$  for introduced mammals.

An insignificant  $\log c$  implies that it is not significantly different from zero.

Thus  $\log c = 0$

By back-transforming  $c = 1$

### 5.3.3 Model Summary

Introduced mammalian species richness model:

$$\begin{aligned} \text{Species Richness} = & \text{Latitude} + \log_{10} \text{Area} + \log_{10} \text{Elevation} + \log_{10} \text{Dist.Main} + \log_{10} \text{GDI} \\ & + \log_{10} \text{BHDI} + \text{Landing} + \text{Settlement} + \text{Landing:Settlement} \end{aligned}$$

### 5.3.3.1 Model Adequacy

Chi-squared tests for adequacy of fit had insignificant values ( $\chi^2$ ,  $p_{large} = 0.851$ ,  $p_{small} = 0.832$ ,  $df = 132$ ). This means the null hypotheses that both the large and small mammal models are adequate are accepted.

### 5.3.3.2 Effects

Tables 5.3 and 5.4 give the coefficients, standard errors, p-values, significance codes and proportional changes in species richness at the 10% level for the large and small mammal species richness models respectively. For the  $\log_{10}$  terms the proportional change is with respect to an order of magnitude ( $\log_{10}$  scale) change in the variable, not a linear change.

Term	Coefficient	S.E.	P-value	Signif.	Proportional change in $S_{large}$
Wharf	1.70	0.49	0.001	***	5.48
<i>Wharf:Inhabited</i>	-2.18	0.68	0.001	**	0.11
<i>Inhabited</i>	1.20	0.43	0.006	**	3.31
<i>Wharf:Abandoned</i>	-1.71	0.74	0.020	*	0.18
<i>Abandoned</i>	0.78	0.40	0.052	.	2.18
$\log_{10} Area$	0.51	0.30	0.094	.	1.66

Table 5.3. Significant model terms and their proportional changes in species richness for the large mammal model.

Term	Coefficient	S.E.	P-value	Signif.	Proportional change in $S_{small}$
$\log_{10} Area$	0.93	0.24	<0.001	***	2.53
Latitude	0.07	0.02	0.001	***	1.07
(Intercept)	3.87	1.17	0.001	***	N/A
$\log_{10} Elevation$	-0.84	0.41	0.042	*	0.43
$\log_{10} Dist.Main$	-0.21	0.12	0.080	.	0.81
$\log_{10} GDI$	-0.84	0.49	0.087	.	0.43

Table 5.4. Significant model terms and their proportional changes in species richness for the small mammal model.

Six terms were significant in the large mammal model and five were significant in the small mammal model.

### 5.3.3.3 Interactions

The only hypothesised interaction was that between the categorical variables for presence of a landing structure and the European settlement history of islands. In the small mammal model no interaction terms were significant. In the large mammal model the interaction terms for the presence of a *Wharf* with both *Abandoned* and *Inhabited* European settlements were significant ( $p = 0.020$ ,  $p = 0.001$ ), both having negative effects (Table 5.3). An interaction plot for the terms in the large mammal species richness model is given in Figure 5.4.

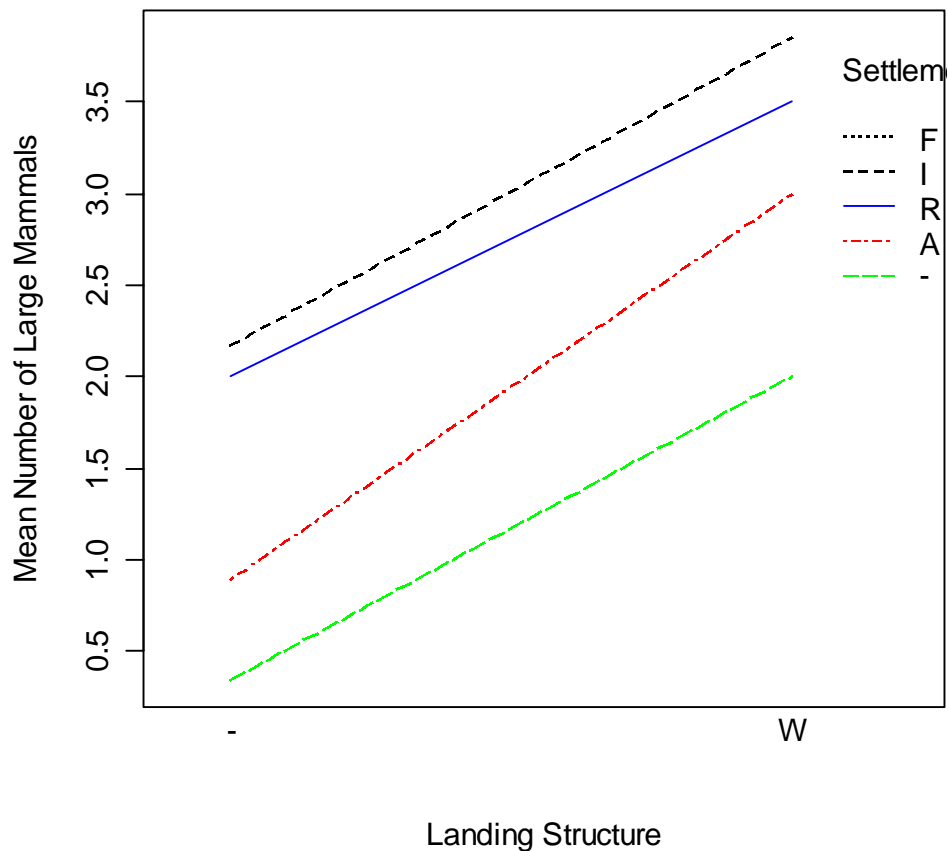


Figure 5.4. Interaction plot for the categorical variables *Landing* and *Settlement*. Parallel lines indicate no interaction. Note the two parallel groups; *Inhabited* & *Abandoned* and *Ranger Station* & *Never Settled*. There is no line for *Unmanned Farm* as those islands had no landing structures.

The proportional changes for differing levels of the categorical variables are directly comparable – they are unitless. When multiplying proportions together for interaction terms, the overall proportional effect of having an island with a *Wharf*, which is currently *Inhabited* is:

$$\begin{aligned} \text{Proportional change in } S_{large} &= \textit{Wharf} \times \textit{Inhabited} \times \textit{Wharf:Inhabited} \\ &= 5.48 \times 3.31 \times 0.11 \\ &= 2.00 \end{aligned}$$

and for an island with a *Wharf* which was settled but subsequently *Abandoned*:

$$\begin{aligned} \text{Proportional change in } S_{large} &= \textit{Wharf} \times \textit{Abandoned} \times \textit{Wharf:Abandoned} \\ &= 5.48 \times 2.18 \times 0.18 \\ &= 2.15 \end{aligned}$$

Tests for two-way interactions of continuous variables included in the original model were also undertaken. The only interacting variable was distance to the mainland (see *Section 3.1.2.5.1*), however the interactions were not significant when added to the model.

#### 5.3.3.4 Collinear Variables

The variables  $\log_{10}$  *Area*,  $\log_{10}$  *Elevation* and  $\log_{10}$  *BHDI* were all identified in *Section 3.2.3* as collinear and were terms of the original model. Tables 5.5 and 5.6 show the contribution of each collinear variable to the residual deviance of their respective models. This can be interpreted as the unique variation in the response explained by each variable.

Variable	Residual Deviance
$\log_{10} Area$	1.633
$\log_{10} Elevation$	0.023
$\log_{10} BHDI$	1.529

Table 5.5. Contribution to the residual deviance of the large mammal model by the collinear variables  $\log_{10} Area$ ,  $\log_{10} Elevation$  and  $\log_{10} BHDI$ .

Variable	Residual Deviance
$\log_{10} Area$	15.038
$\log_{10} Elevation$	4.298
$\log_{10} BHDI$	0.002

Table 5.6. Contribution to the residual deviance of the small mammal model by the collinear variables  $\log_{10} Area$ ,  $\log_{10} Elevation$  and  $\log_{10} BHDI$ .

### 5.3.3.5 Residuals

Plots of indexed deviance residuals for both the large and small mammal groups showed larger variation in random scatter above zero.

Plots of deviance residuals versus explanatory variables revealed no abnormal, non-linear trends.

### 5.3.3.6 Outliers

Outliers were identified from plots of indexed deviance residuals as values outside the range [-2,2]. Figure 5.5 displays the islands with outlying species richness values.

#### 5.3.3.6.1 Large Mammals

Four outliers were identified:

RAKITU (ARID) I.	2.48
NATIVE I., Paterson Inlet	2.37
CHETWODE IS, Nukuwaiata	2.08

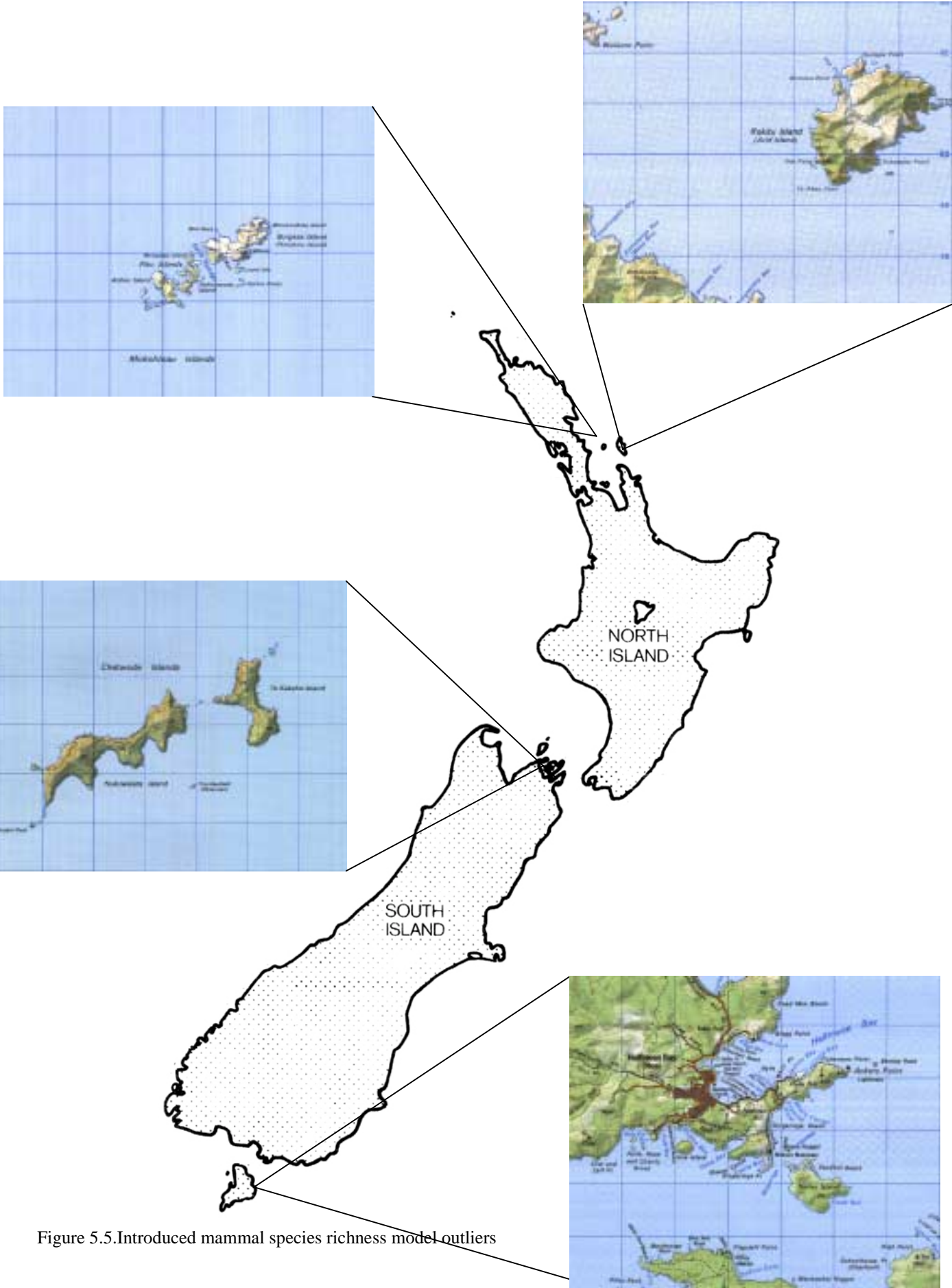


Figure 5.5. Introduced mammal species richness model outliers

MOKOHINAU IS, Burgess (Pokohinu) 2.08

#### 5.3.3.6.2 *Small Mammals*

One outlier was identified:

NATIVE I., Paterson Inlet 2.24

#### 5.3.3.7 *Model Refinement*

The following aspects of the original models were refined and yielded the following results.

##### 5.3.3.7.1 *Latitude Dummy Variable*

Figure 5.6 illustrates the tri-modal relationship between total mammalian species richness  $S$  and *Latitude*, a spatial artifact of offshore island distribution across New Zealand. To remove this non-linear effect, a three level dummy variable (*Latitude.dummy*) was created for each of the three modes of *Latitude* (shown as dotted lines on Figure 5.6). The northern latitudes equate to those islands above a line that falls above Taranaki, below Lake Taupo and above Mahia Peninsula. The southern latitudes equate to those islands below a line that falls above Mt. Cook and Banks Peninsula (Figure 5.6).

When *Latitude* from the original models was replaced with *Latitude.dummy*, the significance of other variables also changed (Tables 5.7 and 5.8). Changes in significance were measured by increments of the significance codings {0, 0.001, 0.01, 0.05, 0.1}.

For the large mammal model, taking northern latitude islands as the baseline, both other levels of *Latitude.dummy* were significantly different at varying levels. Species richness for large mammals just significantly increases ( $p = 0.074$ ) by a proportion of 1.63 for



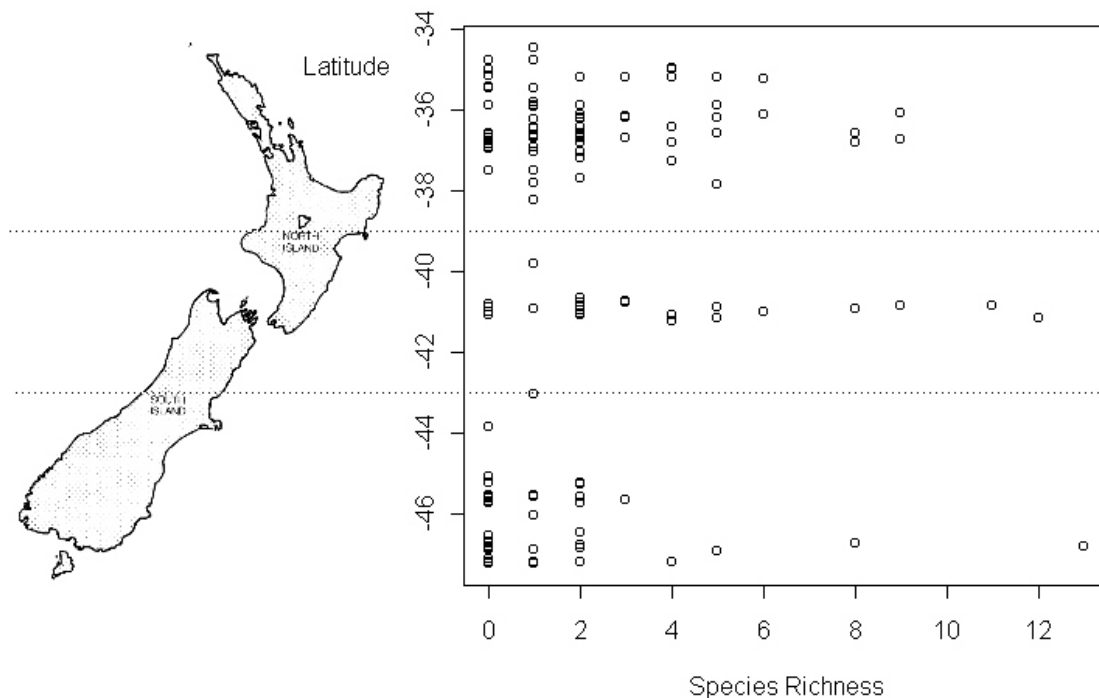


Figure 5.6. Introduced mammal species richness on New Zealand offshore islands across *Latitude*. Note the tri-modality and three distinct island groups.

central latitude islands, and significantly decreases ( $p = 0.042$ ) by a proportion of 0.50 for southern latitude islands.

For the small mammal model, only the third level of *Latitude.dummy* was significant. Again, taking the northern latitude islands as the baseline, species richness for small mammals significantly decreases ( $p < 0.001$ ) by a proportion of 0.35 species for southern latitude islands.

When *Latitude.dummy* was included in both original models with *Latitude*, the residual deviances did not significantly decrease.

#### 5.3.3.7.2. Land District Code

*Latitude* from the original model was replaced by Land District Code (*LDC*).

Term	Change	Term	Change	key
Wharf	>	log <sub>10</sub> Area	.	. no change
Wharf:Inhabited	<	Latitude	N/A	< less significant
Inhabited	<	(Intercept)	<<	> more significant
Wharf:Abandoned	>	log <sub>10</sub> Elevation	>	<< no longer significant
Abandoned	.	log <sub>10</sub> Dist.Main	<<	
log <sub>10</sub> Area	>	log <sub>10</sub> GDI	<<	

Table 5.7. Changes in significance values of large mammal model terms when *Latitude* is replaced by a three-level dummy.

Table 5.8. Changes in significance values of small mammal model terms when *Latitude* is replaced by a three-level dummy.

For the large mammal model, the *Marlborough* district had a significantly higher ( $p = 0.020$ ) proportion of species by 2.24 and *Southland* district had a significantly lower ( $p = 0.049$ ) proportion of species by 0.50 when compared to the *North Auckland* district baseline.

For the small mammal model only *Southland* district had a significantly lower ( $p < 0.001$ ) proportion of species by 0.37 when compared to the *North Auckland* district baseline.

## 5.4 Discussion

### 5.4.1 Subset Representativeness

The bias in the subsampling of islands with respect to *Latitude* appears to be an artifact of the latitudinal distribution of islands across New Zealand. As illustrated in *Section 1.5.1*. New Zealand islands are found in three main groups, with two ‘gaps’ of relatively low island occurrence, consequently islands are not linearly distributed across *Latitude*. It is within these gaps that the under-sampling and over-sampling respectively lie. Thus although the disparities in the quantile-quantile plot of *Latitude* appear large, they in fact

only represent an under-sampling of those few islands lying off the central South Island, and an over-sampling of those few islands lying off the central North Island, relative to the overall sampling proportion (165/297). As a whole the actual bias in total islands in the subsample with respect to *Latitude* is minimal, and for the three main clusters the subsample is representative.

For *Elevation* only six islands in the original dataset were under 30m, hence an under-sampling here is negligible as a proportion of the total subsample.

This is also true for the remaining variables, where the total bias within the subsample is not overly concerning.

For both the presence of a landing structure and European settlement history missing values are underrepresented in the subsample. This is not surprising as missing values in the larger dataset correlate with each other. Islands with missing values in the census of mammal species were also islands with missing values in the categorical variables. Selecting a subsample on the condition of no missing values in the mammal species census, would consequently mean under representation of missing values in all variables of the subsample. Although this does indicate a bias in the subsample that will effect the inference of results with respect to the original dataset, it is also beneficial as it minimises the unknown components in the new subsample. This adds more robustness to the predictive value of the model itself, due to the reduction in missing values.

Overall it can be concluded that the biases within the subsample are negligible and unlikely to affect the interpretation of results within the wider context of all New Zealand islands larger than five hectares. The subsample can be considered an unbiased selection from the original complete dataset.

#### 5.4.2 Z-values

Because introduced mammals are not present on all offshore islands, some had values of zero for  $S$ . Species richness and z-value studies have generally been undertaken on much larger, well established native taxa (Lomolino 1982, 1984; Abbott 1983). Williams (1996) discusses the inherent biases in regression estimates from discarding observations where  $S = 0$ . Unfortunately he is unable to suggest other methods which aren't themselves problematic. Calculating z-values for such an extreme end of the island species richness spectrum, and discarding a large portion of the sample, will accordingly require caution during interpretation.

MacArthur and Wilson (1967) originally stated that the range of insular z-values lies between 0.20 – 0.35, although this has subsequently become a more conservative 0.25 – 0.33 (Rosenzweig 1995). The z-value of 0.21 obtained here lies outside the generally accepted literature values for islands, although it is noted that for large vertebrates the z-values do tend to be low (at around 0.25). Such a low value suggests a depauperate introduced mammal diversity on New Zealand islands. However the confidence interval upper bound does include the lower-tail of literature values, including Preston's (1962a, 1962b) canonical value of 0.26. Lomolino (1984) found that for non-volant mammals z-values tended to be lower than for other island taxa, and Abbott (1983) simulated island z-values using small source pools of generic hypothetical species and also found similar low z-values. Other studies (cited in Lomolino 1982) have quoted higher z-values for mammals, however Lomolino dismisses these as being caused by distant archipelagos, where area plays a more substantial interactive role. Lomolino (2001) suggests low z-values, which cause a less linear species-area curve, mean saturation of the archipelago by the taxon. Saturation does not equate to equilibrium however, as the two are different concepts.

Some convex curvature upwards can be seen in Figure 5.3. Fitting a regression line in Gleason's semi-log space (Gleason 1922) provides a better fit ( $R^2 = 0.44$ ). Following Connor and McCoy (1979) however, the  $R^2$  difference of less than 5% would not be

significant, though it has been noted that this significance level is entirely arbitrary (Gotelli and Graves 1996). There are also no generally accepted ‘canonical’ values for parameters of the Gleasonian model (Lomolino 2000c). Lomolino (2000c) advocates a hypothetical sigmoidal shaped species-area curve based on a unimodal species distribution as originally proposed by Schoener (1976) and Gilpin and Diamond (1976). However if ‘small’ islands are not sampled, as may be the case in this study, the ‘small-island’ effect (Lomolino and Weiser 2001) depicted by the lower left-hand tail of the sigmoidal curve is neglected. The remaining segment of the curve would then appear as it does in Figure 5.3. This is depicted in Figure 5.7 and warrants further investigation. Lomolino and Weiser (2001) interpret both log-log and semi-log species-area relationships in their paper depending on applicability within datasets.

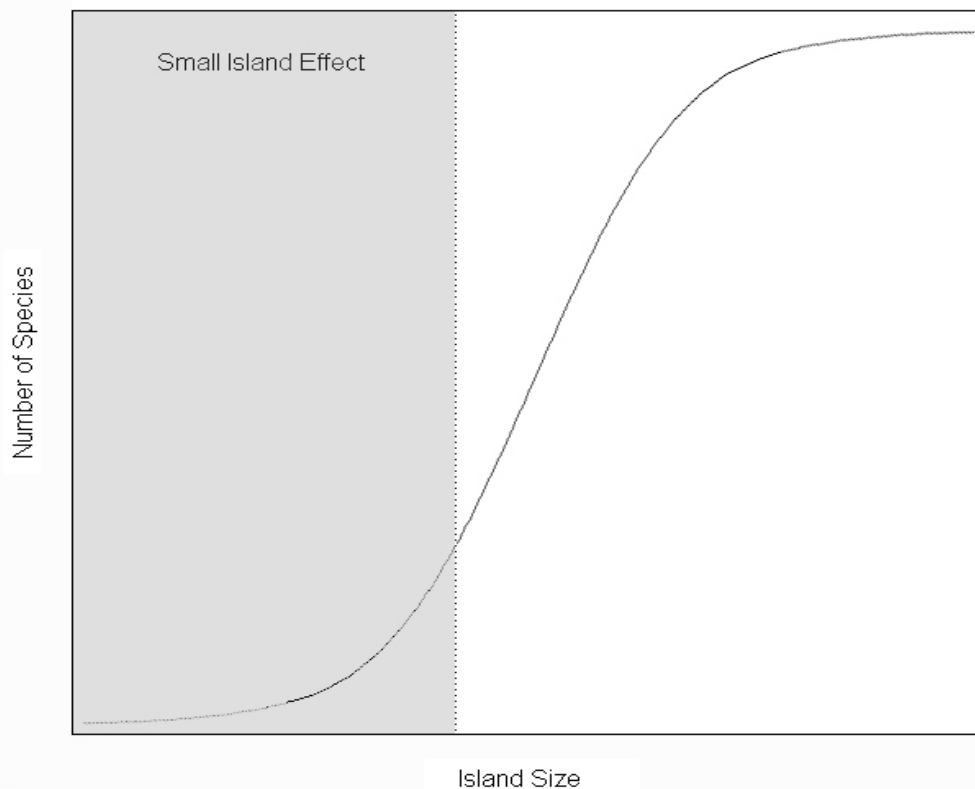


Figure 5.7. A sigmoidal species-area (most probably semi-logarithmic) relationship advocated by Lomolino (2000c) showing the hypothetical ‘small-island effect’. Islands < 5ha were disregarded in this study. The unshaded area represents the remaining part of the curve that might be observed (see Figure 5.3).

In the regression fit  $\log c$  is insignificant and so equal to zero. By back transforming the log-model to its original multiplicative state,  $c$  then has no effect on the species-area relationship, which is now entirely defined by  $A^z$ . The final form of the introduced mammal species-area curve across the range of island areas in the New Zealand archipelago is shown in Figure 5.8. Leveling off towards a saturated asymptote begins at around 8 species. The rapid rise towards an asymptote suggests New Zealand's offshore islands are saturated with respect to introduced mammals. For the largest New Zealand islands, asymptotic saturation by introduced mammal species is almost achieved, this occurs around 12 of the total possible 17 species. For all but the smallest islands at least six introduced mammal species are expected to be found. The fact that the small islands have much fewer introduced mammal species than the larger ones is most likely because their small areas limit many species establishing, as the species-area relationship would suggest. However the general intactness and ecologically novel nature of most small New Zealand islands may also prevent introduced mammals from colonising as rapidly as has occurred on the larger more disturbed islands.

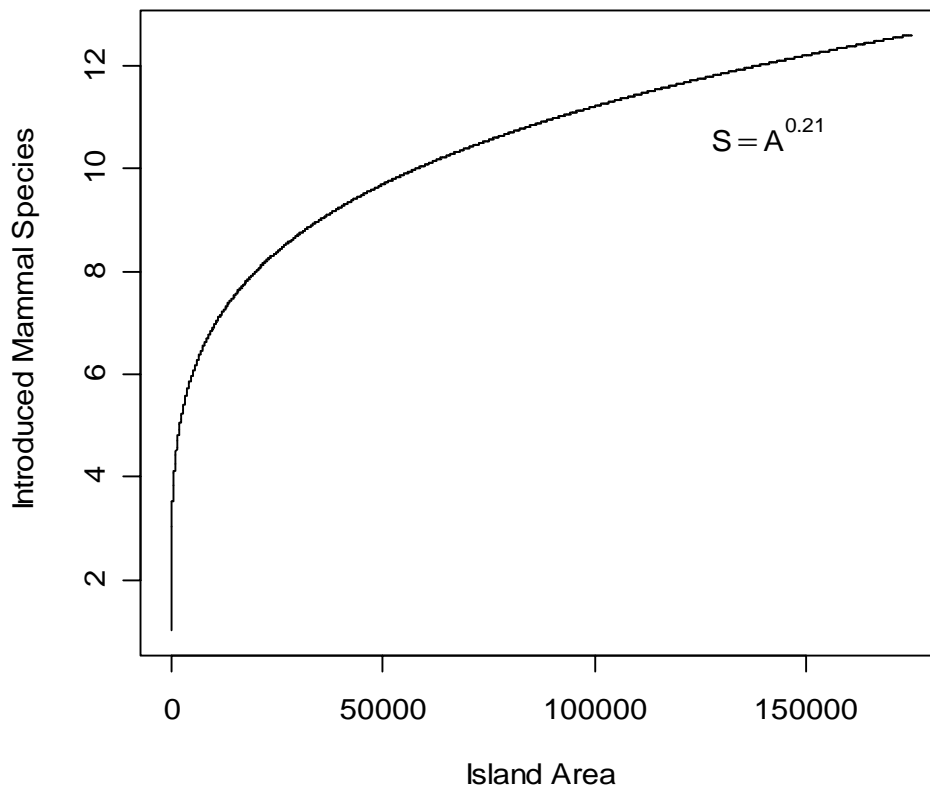


Figure 5.8. Species-area curve for introduced mammals on New Zealand islands. Generated from the power function and with coefficients calculated from regression of  $\log_{10} S$  on  $\log_{10} A$  (Figure 5.3).

The human-mediated introduction of mammals to New Zealand also means, as supported by the results of the individual species models of *Chapter 4* and large mammal model here, that the distribution of introduced mammals in New Zealand is explained in some part by human-facilitated dispersal. This effectively overcomes what may otherwise be barriers to natural dispersal. Mammalian species richness on New Zealand offshore islands appears to have a similar relationship to area as found on overseas landbridge islands (similar  $z$ -values are presented in Lomolino 1984; Millien-Parra and Jaeger 1999), suggesting that over-water dispersal is not as much a barrier in New Zealand as it is elsewhere. All mammal species, except the rodents, were introduced because of their utility to humans (Thomson 1921). To islands where one was introduced, it follows that most others were introduced as well, subsequently saturating the island.

Lomolino (1999) emphasises the importance of variable scale in uncovering the driving processes of species richness. If high  $z$ -values (Lomolino 1982) and intercepts (Williamson 1981) are the result of distant archipelagos then correspondingly low values, such as those found in this study, suggest an adjacent archipelago. That is clearly not geographically the case when the distances of islands were quite appropriately (Lomolino 1999) measured across three magnitudes (0.1 – 100s kms), whereas the swimming distance of New Zealand introduced mammals is only of the order of 0.1 – 1 kms (Atkinson and Taylor 1991). Abbott (1983) cautions against the interpretation of low  $z$ -values. A low  $z$ -value suggests the effect of area on dispersal is minimal, but it says nothing of the effect of distance. Species could be either poor colonisers, not reaching any islands irrespective of area, or good colonisers, able to live on any islands irrespective of area. In light of the widespread distribution of mammals throughout the New Zealand archipelago, and the saturation suggested by Figure 5.8, the most likely explanation is the latter. This suggests that the human-facilitated dispersal of mammals throughout the New Zealand landscape has effectively rendered the archipelago smaller within an ecological context, with area playing less of an interactive effect since distance to the mainland is now ecologically trivial (at least for the larger mammal component of species richness). Most New Zealand offshore islands are close to saturation by

introduced mammals, except for the smallest New Zealand islands, which are relatively undisturbed or can not support large numbers of mammal species.

### *5.4.3 Linear Models*

The original models were very good at predicting changes in the species richness of large and small mammals on New Zealand offshore islands. The chi-square adequacy tests support the plausibility of the model specifications, as well as providing no evidence that over dispersion is occurring. Additional variables explained very little of the remaining variation, although they were still significant and their importance should not be overlooked.

#### *5.4.3.1 Significant Variables*

##### *5.4.3.1.1 Large Mammal Model*

For the large mammal model six terms were significant predictors of species richness. Five of these terms were from only three variables: presence of a landing structure, European settlement history and their interaction as the third variable. Overall only four variables were actual predictors of species richness. The three categorical variables are all surrogates for different aspects of human activities on islands, although there is some correlation with other geographical and ecological variables, which may confound interpretation of the underlying processes. Generally the categorical variables can be considered direct surrogates for human activities – supporting the notion that species richness of large mammals on New Zealand offshore islands is driven by anthropogenic activities.

The effect of  $\log_{10}$  *Area* (barely significant in the model) is difficult to disentangle. It would seem most likely that the role of *Area* is also related to a human mediated process, suggesting a relationship between *Area* and available farming land, or put more simply



that area is related to human settlement habits ( $r = 0.55$ ). The average *Area* of islands that are considered permanently *Inhabited* is over 1,000 hectares; significantly larger than the average areas for other types of European settlement history.

We should expect the distribution of large mammals, being particularly commensal with humans, to be highly correlated with human activity across New Zealand offshore islands. Palmer *et al.* (1999) found that historical disturbances (citing introduced species) were indeed a significant predictor of species richness for endemic fauna on the Balearic Islands. It has always been assumed that the distribution of introduced mammals across the New Zealand landscape, including its offshore islands, is related to human factors (King 1990a; C. Veitch pers. comm.). The results presented here provide quantitative evidence supporting such a relationship, at least for the large introduced mammals of New Zealand.

#### 5.4.3.1.2 *Small Mammal Model*

In the small mammal model, five variables and the intercept were all significant predictors of species richness. The intercept is the value for species richness should all other variables be zero. However statistically relevant, it has little biological relevance, for all the log-transformed variables would be zero (their back-transformed variables one unit), and *Latitude* would be zero, which is equatorial and well outside the latitudinal range of any New Zealand islands. It is used for predictive purposes.

It is essential to recall that since four of the variables were log transformed to improve linearity, the proportional changes, given in Table 5.4 for a change in one unit of the variable, are in fact for a change of one magnitude (1 to 100 to 1000, etc). As can be seen, a change in one magnitude of *Area* results in a 2.53 fold increase in species richness. This is not surprising, regardless of what the underlying process may be. The evidence supporting this effect is also very strong. The effect of *Latitude* is similarly as significant, although for a change of one degree in *Latitude* (New Zealand spans just under 13 degrees latitudinally) only a small increase of 1.07 fold is experienced. Since

*Latitude* was measured in negative (Southern Hemisphere) values, the gradient of increase is northwards. The total proportional variation in *Latitude*, holding all other variables constant, is 2.38 ( $1.07^{12.8}$ ) from the southern most (Big South Cape) to the northern most (Motuopao) islands of New Zealand. Such a trend in *Latitude* for exotic species has also been found in other studies (Sax 2001).

$\log_{10}$  *Dist.Main* and  $\log_{10}$  *GDI* were only marginally significant. Both took negative values, implying that as an island is located further from the mainland, or its geological (and possibly floral) diversity increases, it becomes much less likely to have a large number of small mammal species. The negative relationship between distance and species richness is well-documented (MacArthur and Wilson 1963, 1967; Lomolino 1982, 1984, 1990, 1999; Adler and Wilson 1985; Rosenzweig 1995; Whittaker 1998), and is related to the immigration rate of species. The relationship between abiotic-biotic complexity and species richness is less well understood. Although the geological diversity may appear to be related to biological habitat diversity, they have a low correlation ( $r = 0.43$ ), which is only present for islands with geological diversities greater than four. Habitat diversity is positively correlated with species richness – greater habitat heterogeneity means a greater diversity of species can establish (Lack 1969, 1976; Adler and Wilson 1985; Ricklefs and Lovette 1999; Davidar *et al.* 2001). Geological diversity (as a surrogate for floral complexity) was included as a means of establishing whether ecological complexity affects introduced species richness. The impetus was taken from the hypothesised diversity-stability relationship, where diverse ecosystems are considered to be less invasible by exotic species (Pimm 1991; Rosenzweig 1995). The two variables, although similar in nature, therefore designate different relationships with species richness. Abbott (1980) discusses the differences between plant diversity and habitat diversity as predictors. The negative correlation between geological diversity and small mammal species richness supports the presumption that more complex systems are less invasible, although geological diversity is only just significant, and the relationship between geological diversity and floral complexity is only assumed, not tested.

The last significant variable is  $\log_{10}$  *Elevation*, which had a negative effect on small mammal species richness. As illustrated in *Section 3.2.3*  $\log_{10}$  *Area* and  $\log_{10}$  *Elevation* are positively correlated. The  $\log_{10}$  *Area* term in the model has a positive effect on species richness, which would lead one to believe that  $\log_{10}$  *Elevation* might do so as well. However when the effect of  $\log_{10}$  *Area* alone on species richness is partialled out,  $\log_{10}$  *Elevation* has a negative effect on species richness. This significant negative influence of  $\log_{10}$  *Elevation* is despite the high collinearity between it and  $\log_{10}$  *Area*, which in fact makes it less likely to be significant because of standard error inflation (*Section 3.2.1*). As it did in *Chapter 4* the negative relationship between  $\log_{10}$  *Elevation* and the response variable suggests that islands with higher elevation have been less invaded by small mammals. However  $\log_{10}$  *Elevation* may be acting as a surrogate for another unknown variable, perhaps in a manner similar to geological diversity with the ecological complexity of islands, providing more support for the notion of ecologically complex islands being less invasible. Mueller-Dombois (1999) promotes incorporating a vertical component, measured as elevation, into the theory of island biogeography. His reasoning is that elevation is a good approximation of waterflow from upland to lowland areas, providing greater habitat heterogeneity. The general relationship between area and elevation quite likely confounds the interpretation of any elevation effect in many studies. Few studies appear to have investigated the effect of elevation on mammals, which have a much lower dependency on suitable habitat availability, although Lomolino (1990) suggests elevation is a good predictor as a cue for active dispersers (which can see their destination) to islands. Such a result would promote a positive effect for elevation though, which is not the case here. More work is clearly necessary to identify the true effect of elevation on the species richness of different taxa in different regions.

Overall, it can be concluded that the best correlates of small mammal species richness on New Zealand offshore islands are those which are judged by island equilibrium theory (MacArthur and Wilson 1963, 1967) and studies based upon it (Lomolino 1982, 1990; Ceballos and Brown 1995; Burbidge *et al.* 1997; Millien-Parra and Jaeger 1999) to be indicators of self-dispersal and colonisation processes. The five variables that were the best predictors appear to be surrogates for underlying natural processes that relate to the

dispersal of species to offshore islands, and the potential for an island to be invaded based on its ecological complexity. These results are not unusual when compared with the international studies cited earlier, but do dispute the general assumption that introduced mammal distribution across New Zealand islands is for the most part determined by anthropogenic factors.

#### 5.4.3.2 Interactions

Few mammalian species richness studies appear to have addressed possible interactions between explanatory variables. This could possibly be because of a belief that any effects beyond the main terms in statistical analyses should be considered ecologically irrelevant. This may have been true for other studies where variables could generally be considered independent and non-interactive. However as hypothesised *a priori* in this case, an interaction between anthropogenic historical factors could be reasonably expected.

In the small mammal model neither the interaction term nor its constituent additive terms were significant. As already discussed, historical factors appear to have very little predictive power in explaining small mammal species richness across New Zealand offshore islands.

For large mammals the interaction plot (Figure 5.4) shows two groups each with parallel slopes. The slopes may be interpreted as the rate of increase in species richness on islands as a *Wharf* is added. As can be seen, the group with the gentler slope (where addition of a *Wharf* does not have so great an effect) is for islands which have never been inhabited, or only had a *Ranger Station* on them. The other group, comprising *Abandoned* and *Inhabited* islands, has a slope that increases much more rapidly upon addition of a *Wharf*. This reflects the consequences of adding a *Wharf* to an island that has at some stage served as a settlement – where large mammals are purposefully introduced.

Of the two significant interaction terms in the large mammal model, the interaction between *Wharf* and *Inhabited* was the most significant, however the overall proportional

effect of the interaction between *Wharf* and *Abandoned* was the largest. Interestingly the nature of both interaction terms was negative. What this means is that the combined interactive effect of the categorical variable levels on an island is less than would be expected if the levels were independently additive. This is readily interpreted as should one of the categorical variable levels be present, then species richness increases markedly by an amount. However the addition of the other categorical variable level has less effect thereafter, as most of the few species available from the source pool of seven large mammals will already be present, and fewer are available to be subsequently added to the island's pool of species.

#### 5.4.3.3 Collinear Variables

*Section 3.2.3* has already discussed the collinearity between  $\log_{10}$  *Area*,  $\log_{10}$  *Elevation* and  $\log_{10}$  *BHDI*. What follows here is a discussion of the unique explanatory power of each collinear variable when all were included in the original two species richness models.

For large mammals the collinear variability in species richness was roughly equally explained between  $\log_{10}$  *Area* and  $\log_{10}$  *BHDI*, although for large mammals only  $\log_{10}$  *Area* was a significant predictor, and only just at the 10% level. The  $\log_{10}$  *Elevation* term contributed almost nothing towards explaining the variability in large mammal species richness. Lomolino (1990) found elevation was an excellent surrogate for the cues for active dispersal in non-volant mammals. Active dispersers will seek an island that they can see, which is most readily characterised by a high elevation. It is thus not surprising that the large mammals so dominated by anthropogenic events would not be actively dispersing. The relative equality between  $\log_{10}$  *Area* and  $\log_{10}$  *BHDI* may be more correlation than causal – large feral mammals would only ever be present on large islands where they were first introduced. Regardless an explanation seems needless since none of the three collinear variables were particularly significant in the first instance.

For small mammals the collinear variability in species richness is predominantly explained by  $\log_{10}$  *Area*, although  $\log_{10}$  *Elevation* also explained a significant component of it. Both variables were significant in the original model. The variable  $\log_{10}$  *BHDI* explained almost none of the variability in small mammal species richness, once the variability explained by all other variables had been partialled out. Although habitat is considered to be the primary driver of the species-area relationship (Whittaker 1998), its insignificance is not a surprise. As Ricklefs and Lovette (1999) found, although habitat is almost exclusively the driver for avian species (Lack 1969, 1976), it rarely influences mammals (bats in their study). This result is also reflected in other studies (Burbidge *et al.* 1997). The variable  $\log_{10}$  *Elevation* plays a minor negative role, possibly representing ecological complexity (preventing invasion), although Mueller-Dombois (1999) suggests that elevation represents a measure of waterflow, by virtue of upland-lowland flow. This seems ambiguous though as waterflow is not an absolute necessity for survival, only water presence – which require only a larger area irrespective of an elevation component (Hugget 1995). The overall predictive power of  $\log_{10}$  *Area* excluding  $\log_{10}$  *Elevation* and  $\log_{10}$  *BHDI* suggests that population density (unmeasured in these models) drives the species-area relationship (Connor *et al.* 2000). This would also mean that small mammal populations may require a minimum area to establish a viable population.

#### 5.4.3.4 Residuals

The increased scatter and distribution of deviance residuals above the zero line suggests that there are islands with high species richnesses which are unexplained by variables in the model. Overall however very few of the species richness counts were considered actual outliers.

#### 5.4.3.5 Outliers

Between both models four islands were identified as outliers, although their species richness values were only one or two species over that predicted. When working with such small species richness counts, the stochastic variation which may allow an increase

of only one more species may be common enough to permit four islands (in the case of the large mammal model) to be outliers. However all the large mammal model outliers were for more species than predicted (i.e. the model under predicted). This suggests that these islands are over-saturated by large mammals, most likely because humans transported them to islands they could not normally reach.

Native Island was an outlier in both models. Native Island lies in Paterson Inlet, immediately beside the only settlement of Halfmoon Bay on Stewart Island. Being in close proximity to human settlement significantly increases invasion pressure on an island (Williamson 1996), but Stewart Island is not considered part of the mainland (*Section 3.1.2.5.1*). Native Island therefore appears inordinately far from a source pool, predicting a low species richness. Native Island illustrates a stepping stone system, whereby species colonise one island (or at least its human settlement) and only then invade neighbouring islands. The variable  $\log_{10} Dist.Main$  provides no estimate of this. It can be concluded that Native Island's outlying observed values of species richness are not exceptional, but instead expected, and are a result of stepping stone processes which are more difficult to model.

It was not considered necessary to test the model without the outliers as they represented only a small fraction of the total sample, were not considered high leverage (as identified in *Section 3.1*) and were not mistakes in the dataset.

#### *5.4.3.6 Model Refinement*

##### *5.4.4.6.1 Latitude Dummy Variable*

The original *Latitude* variable was biased by a geographical spatial artifact of the distribution of offshore islands across New Zealand. Similar bias in *Latitude* has been found in other studies (Blackburn and Duncan *in press*). Although spatial processes are identified as significant contributors to variation within ecological communities (Ricklefs and Schluter 1993; Whittaker 1998), Selmi (2001) found autocorrelation across islands in

the South Pacific was significant for most species except those with low dispersal ability – specifically mammals. Nonetheless the tri-modal pattern in *Latitude* could bias the fitted regression line and conceal the true underlying nature of any *Latitude* effect. Partitioning *Latitude* into a categorical dummy variable creates one dimensional geographical ‘regions’. These regions were approximately assigned following the intrinsically apparent boundaries of Atkinson and Bell (1973).

In the large mammal model, all three *Latitude.dummy* regions were significantly different. The central region of New Zealand is the most intensively farmed (Fleet 1986). The relative intensity of this farming may be related to the fact that the central region is also the largest area of the three *Latitude.dummy* regions. This historical explanation would seem to be a good one for the relative increase in large mammal species richness across these islands. Settlement across New Zealand generally follows a trend from most intense in the north to more sporadic settlement throughout the south (Atkinson and Bell 1973; Craig *et al.* 2000), which is not unrelated to the climatic trend across the same gradient (being cooler in the south). This historical explanation supports the observation of significantly lower large mammal species richness on southern islands. Less settlement presents less opportunity for human-facilitated introduction (as predicted by the large mammal model) on these southern islands. The replacement of the continuous variable *Latitude* by *Latitude.dummy* now appears to reflect the anthropogenic factors driving large mammal species richness.

The southern latitude islands are among the more pristine environments of New Zealand, reflected by general ecological intactness, even on the mainland, at New Zealand’s southern limits (Molloy and Dingwall 1990). The results of the small mammal model predicted biogeographic factors driving small mammal species richness. It thus follows that less opportunity has been presented to small mammal in the southern latitudes to colonise offshore islands. This would generally be due to the lack of adequate source populations, since the southern wilderness areas of the New Zealand mainland are relatively less invaded (Fleet 1986). Thus it follows that southern latitude islands should have significantly fewer introduced small mammal species.



A significant correlation also exists between human activities (measured by *Landing* and *Settlement*) and *Latitude.dummy*. This meant that when *Latitude.dummy* was introduced to the large mammal model, the significance of both *Wharf* and the different levels of European settlement history were reduced due to collinear effects. However changing *Latitude* into a dummy variable meant that  $\log_{10} Area$  also picked up some of the spatial information that was lost in the simplification.

For the large mammal model, *Latitude* was insignificant when measured as a continuous variable in the manner of a linear environmental gradient, but when split into arbitrary regions it became significant. The opposite of this was true for small mammals. This gives some indication of the way in which *Latitude* is acting as a driver of introduced mammalian species richness. Foremost, the relationship is not linear for large mammals, in fact appearing quadratic when *Latitude* is split into discrete values. For large mammals, it may act as a correlate for human activity, supported by the strong relationship between *Latitude.dummy* and the categorical variables for *Landing* and *Settlement*. For small mammals, the relationship appears more indicative of a continuous linear environmental gradient, usually related to climate or productivity (Rosenzweig 1995; Sax 2001). Although the four (latitude-climate-productivity-human activity) are all closely correlated, the predominant influence can only be teased out by inspection of the different forms in which *Latitude* (as a surrogate for these processes) is presented.

Overall *Latitude.dummy* did not explain significantly more variability beyond that explained by *Latitude*, and so as useful as the insights gained from its inclusion are, the absolute value of including it instead of the original continuous variable is negligible. What it does demonstrate is the very different interpretations that may arise depending on the form that a surrogate variable takes in a regression model (Philippi 1993).

#### 5.4.4.6.2 Land District Code

The results from the replacement of *Latitude* with *LDC* reflect the history of each region. European settlers intensively farmed the *Marlborough* district, the area itself being a network of submerged river valleys (Fleet 1986). This would explain the significant increase in large mammal species richness in this district.

*Southland* district is one of the largest districts – encompassing Fiordland and Stewart Island. Not only is this one of the most pristine areas of New Zealand (Fleet 1986), but it also contains the largest number of islands. This statistical robustness makes detection of a significant departure easier. Since the *Southland* district contains the largely ecologically intact islands of Fiordland, and the offshore refuge of Stewart Island, it is reasonable to expect that both large and small mammal species richness counts would be significantly reduced. The *Southland* district is also the southern-most in New Zealand, and a less amenable climate (Duncan and Forsyth unpubl.), another possible reason for the much reduced species richness.

As *LDC* is a two dimensional categorical extension of the one dimensional categorical *Latitude.dummy* variable, much of the discussion earlier applies when *LDC* is included in the species richness models. Specifically the differing explanations for the significance of districts with respect to large (human dominated) or small (biogeographically dominated) mammal species richness on New Zealand offshore islands, and discussion of the latitudinal gradient.

#### 5.4.4 Conclusions

The success of the models applied here suggests that predicting species richness of both large and small mammals on New Zealand offshore islands is a relatively deterministic process, governed by only a few key variables which act as surrogates for the underlying processes. Refinement of the original models, although yielding interesting results within

a regional and geographical context, did not produce significant increases in the predictive power of the linear models.

The results must be considered within a spatial context. A greater increase has been achieved recently (see Whittaker 1998) in our understanding of scale with respect to insular systems. Lomolino (1999, 2000b) presents a graphical model which illustrates how, at different spatial scales, different variables can appear to take precedent. The important message (Lomolino 1999; Lomolino and Weiser 2001) is that an array of islands must be sampled from throughout an archipelago, at all scales of all variables, before inferences can be applied to the whole archipelago. For smaller studies of fewer islands (such as Conroy *et al.* 1999; Palmer *et al.* 1999) this is cited as a possible reason for conflicting results interpreted in the light of the equilibrium theory of island biogeography. Since the sample for this study was all islands larger than five hectares in New Zealand, it is hoped that the relative importance of each explanatory variable has been established within the context of the entire New Zealand archipelago.

The results may be difficult to place within the context of the theory of island biogeography because the theory only occupies one corner of Whittaker's (1998, 2000) conceptual representation of island species turnovers. Because introduced mammals are only now completing range expansion since their arrival, we can not be sure whether they have, or (more likely) still are attaining an equilibrium or non-equilibrium condition (Gibb and Flux 1973). Patterson (1999) suggests that historical influences drive islands towards non-equilibrium. We also do not know whether the final state will be dynamic or static, but Brown and Lomolino (1998) note that new equilibrium states can be achieved following non-equilibrium conditions. It has also been suggested by Holland (2000) that the New Zealand biota was impoverished before introductions began – at a sub-equilibrium biodiversity state, and subsequent introductions have so far only served to approach an equilibrium level. However this seems absurd when considering the geological time-scales over which New Zealand's biota has evolved, and the intense predatory interactions that have been generated by the recently invading fauna (King 1984). Such predation might also hypothetically suggest equilibrium was, and still is,

present, and for a new species to establish another must go extinct. But whereas this may be the case on the New Zealand mainland, the bias in the ratio of extinctions to invaders on islands would oppose such a notion. Overall the results suggest that the introduction of mammals to New Zealand islands has instead driven our insular ecosystems into a state of non-equilibrium, in a manner similar to non-equilibrium results found for Japanese terrestrial mammal assemblages on offshore islands (Millien-Parra and Jaeger 1999). Only time can tell if New Zealand's introduced mammals will conform to island biogeographic theory principles (dynamic equilibrium) or to some alternative theory. This places the results in a 'zone of uncertainty' – but for temporal reasons, not spatial ones as suggested in Whittaker's diagram.

# ***Chapter 6: Modelling Introduced Avian Species Richness***

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## *6.1 Introduction*

### *6.1.1 Measuring Introduced Avian Species Richness*

Measuring the species richness of introduced avian species on New Zealand islands is considerably more difficult than measuring that of introduced mammals. Avian species amalgamated themselves more rapidly into the New Zealand landscape, and are generally less conspicuous alongside the native avifauna (introduced mammals having no such counterparts). Because of this, repeated counts of introduced avian species are usually required to obtain an accurate estimate of species diversity (and abundance). One benefit of this methodology is that if every island is sampled at least once, then each has an estimate, although the accuracy of such estimates will vary with the number of independent samples taken.

In this chapter henceforth, the term ‘avian species richness’ refers to the estimate of the number of introduced birds on New Zealand islands. This definition differs from that of *Chapter 5*. Note that this is not the relative detrended estimate that is used as an explanatory variable.

### *6.1.2 Processes Controlling Introduced Avian Species Richness*

Lack (1969, 1976) has been credited for much of the early work on processes controlling the distribution of birds on islands. His work investigated single species, and he found that habitat availability, not immigration rates as MacArthur and Wilson (1963, 1967) suggested, was the primary determinant of species presence.

There have been a number of studies recently in New Zealand which have investigated factors correlating with the successful introduction of exotic birds to the New Zealand archipelago. Veltman *et al.* (1996) investigated correlates of introduction success for exotic New Zealand birds. Their data was also collected from historical records (Thomson 1922), however the methods of their study differed subtly. Whereas I am investigating the patterns of species establishment across all New Zealand islands, Veltman *et al.* studied the establishment of species only where they were introduced, thus predisposing their results to the effects of human management. Duncan (1997) investigated the role of competition and introduction effort in the success of passeriform birds introduced to New Zealand. His results chiefly supported the role of the latter, but he also found the results were confounded by inadequacies in the data; including a lack of comprehensive records on introduction effort, and the observational constraints of the analysis. Both these studies differ from mine by examining the autoecological traits of bird species, rather than the extrinsic characteristics of the environment they were being introduced into. Forsyth and Duncan (2001) also briefly consider the number of propagules required for the successful introduction of a bird species, finding it to be considerably larger than the number required for successful ungulate introduction.

Overseas studies of avian species richness have predominantly investigated the roles of habitat (Ricklefs and Lovette 1999; Davidar *et al.* 2001), *Area* (Wiggins and Moller 1997; Woinarski *et al.* 2001) and (where applicable) competition (Gilpin and Diamond 1981; Lockwood *et al.* 1999). Mandon-Dalger *et al.* (1999) found elevation, through its relationship with habitat heterogeneity, was a significant influence on colonisation patterns. Isolation is also considered (Wiggins and Moller 1997; Davidar *et al.* 2001) in studies of turnover and equilibrium. Other less frequently considered factors have also been shown to influence avian species. Palmer *et al.* (1999) found historical factors significantly influenced species composition. Habitat alteration attributable to humans has also been found to significantly affect avian species (Steadman and Freifeld 1998; Walter 1998). Li and Li (1998) investigated the effects of area, elevation, minimum distance to source area, island shape and human activities on species diversity for Raniformes on the Zhoushan archipelago. Area and elevation were found to be most

significant, but it was concluded that the islands were under “non-equilibrium” status. Abbott (1980) reviews the early literature dealing with the ecology of landbirds on islands. Because exotic birds are such good dispersers, exotic landbirds are extensively distributed across the New Zealand archipelago. However whether this extensive distribution is because of rapid expansion utilising stepping stone islands or long-distance dispersal is not fully understood. Thus both stepping stones and island distances from other islands are considered in the model for exotic landbird species richness.

It should be noted that because detrending the avian species richness estimates may have removed some natural variability, the values used for exotic landbird species richness are the raw estimates. To partial out the bias of sampling effort the number of cards returned, and the number of grid squares an island covers, are included as explanatory variables. The number of cards returned was used in *Chapter 3* to detrend individual grid square avian species richness estimates independent of islands. By its inclusion here the detrending is weighted towards grid squares which contained more islands. Thus the number of grid squares an island covers is included here as for islands that covered multiple grid squares the number of cards returned was combined, which was a subsequent over-estimate of the number of cards required for them. Since this represents a further complication of the sampling effort and estimation of species richness for each island, it is also included as an explanatory variable.

### *6.1.3 Hypotheses*

#### *6.1.3.1 Versal Hypotheses*

It is hypothesised that the introduced avian species richness of New Zealand islands can be adequately predicted by the  $\log_{10}$  transformation of the number of cards returned by observers and the number of OSNZ Atlas sampling grid squares the island covers (collectively sampling effort), *Latitude*,  $\log_{10}$  transformations of *Area*, *Elevation*, distance to the nearest source island (*Dist.Source*), geological diversity (*GDI*) and biological habitat diversity (*BHDI*) and the presence of an intermediate stepping stone island

(*Stepping.stone*), relative avian species richness of native landbirds (*Rel.Nat.Land*) and European settlement history (*Settlement*) of the island. No interactions between variables were *a priori* hypothesised. The corresponding null hypothesis is that species richness has no relationship to any of the aforementioned variables (although see *Section 6.4.2*).

### 6.1.3.2 Statistical Hypotheses

H<sub>0</sub>: All coefficients and the intercept in the linear model are equal to zero.

$$a, b_1, b_2, b_3, \dots, b_n = 0$$

H<sub>1</sub>: One or more of the terms in the linear model has a coefficient not equal to zero.

$$a \text{ or } b_1 \text{ or } b_2 \text{ or } b_3, \dots, b_n \neq 0$$

## 6.2 Methods

### 6.2.1 Linear Modelling

Linear modelling methodology follows that outlined in *Chapter 2.2.1*. Species richness modelling methodology follows *Chapter 5.2.3*.

The quasi-likelihood correction factor<sup>†</sup> is used to correct for over dispersion. Over dispersion occurs when the model is misspecified either in the explanatory variables or the error distribution (in this model the Poisson distribution) or both. This generates overly significant p-values.

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<sup>†</sup> For a complete description of quasi-likelihood correction see Wedderburn (1974) 'Quasi-likelihood functions, generalized linear models, and the Gauss-Newton method' *Biometrika* 61:439-447



However if the ratio of the residual deviance to its degrees of freedom is less than 10, then the quasi-likelihood correction factor can be applied to the standard errors and correct p-values subsequently calculated.

The species-area relationship, and its corresponding z-value, were not investigated for exotic landbird species due to the inadequacies in the data (*Section 2.1.3*).

### 6.3 Results

#### 6.3.1 Model Summary

Exotic landbird species richness model:

$$\begin{aligned} \textit{Species Richness} = & \log_{10} \textit{Cards} + \textit{Grids} + \textit{Latitude} + \log_{10} \textit{Area} + \log_{10} \textit{Elevation} + \\ & \log_{10} \textit{Dist.Source} + \textit{Stepping.stone} + \log_{10} \textit{GDI} + \log_{10} \textit{BHDI} + \textit{Rel.Nat.Land} + \\ & \textit{Settlement} \end{aligned}$$

#### 6.3.2 Model Adequacy

The model failed a chi-squared test for adequacy of fit ( $\chi^2$ ,  $p < 0.001$ ,  $df = 178$ ). This indicated that there was over dispersion in the data which needed to be corrected for using the quasi-likelihood correction factor.

#### 6.3.3 Effects

Tables 6.1 gives the coefficients, standard errors, p-values, significance codes and proportional changes in introduced avian species richness at the 10% level. Note that for  $\log_{10}$  terms the proportional change is with respect to an order of magnitude ( $\log_{10}$  scale) change in the variable, not a linear change.

Term	Coefficient	Corrected S.E.	P-value	Signif.	Proportional change in Ex.Land
(Intercept)	4.70	8.62	<0.001	***	NA
$\log_{10}$ <i>Cards</i>	0.87	1.60	<0.001	***	2.39
<i>Latitude</i>	0.06	0.11	0.000	***	1.06
$\log_{10}$ <i>Elevation</i>	-0.40	-0.73	0.068	.	0.67
<i>Rel.Nat.Land</i>	0.03	0.05	0.027	*	1.03

Table 6.1. Significant model terms and their proportional changes in species richness for the exotic landbird model.

Five terms were significant in the exotic landbird species richness model. These were the intercept,  $\log_{10}$  *Cards*, *Latitude*,  $\log_{10}$  *Elevation* and the relative native landbird species richness.

#### 6.3.4 Collinear Variables

The variables  $\log_{10}$  *Area*,  $\log_{10}$  *Elevation* and  $\log_{10}$  *BHDI* were all identified in *Chapter 3.2.3* as collinear and were terms of the original model. Of these only  $\log_{10}$  *Elevation* was significant ( $p = 0.068$ ).

#### 6.3.5 Residuals

A plot of indexed deviance residuals showed erratic, but apparently random, scatter about the zero line.

Plots of deviance residuals versus individual explanatory variables revealed the following abnormalities:

<i>Grids</i>	One high leverage value (Stewart Island). Figure 6.1.
<i>Latitude</i>	Requires creation of a dummy variable. Figure 6.2.
<i>Rel.Nat.Land</i>	Abnormal scatter. Figure 6.3.

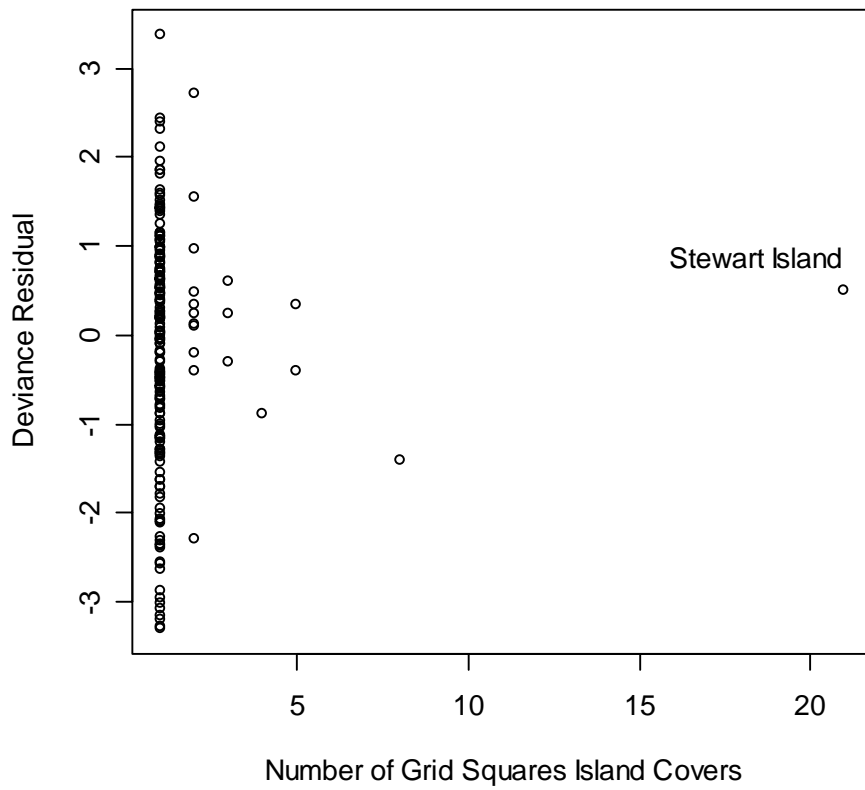


Figure 6.1. Plot of deviance residuals against the explanatory variable: number of sampling grid squares an island covers. The high leverage value 'Stewart Island' is identified.

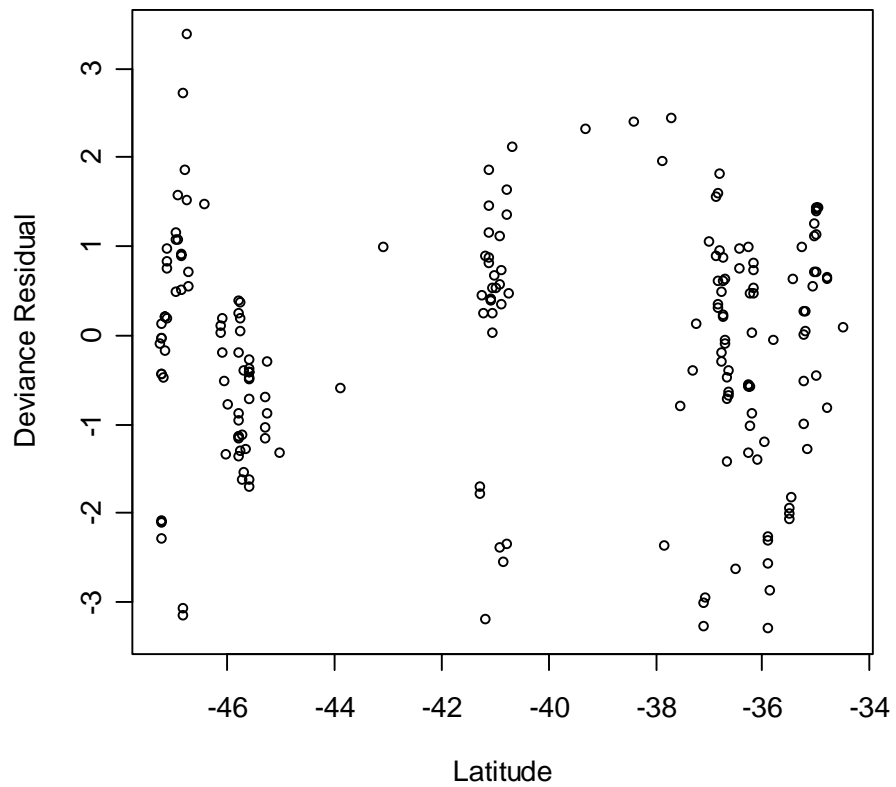


Figure 6.2. Plot of deviance residuals against the explanatory variable: *Latitude*. The clustering indicates a dummy variable (*Latitude.dummy*) should be used instead of *Latitude*.

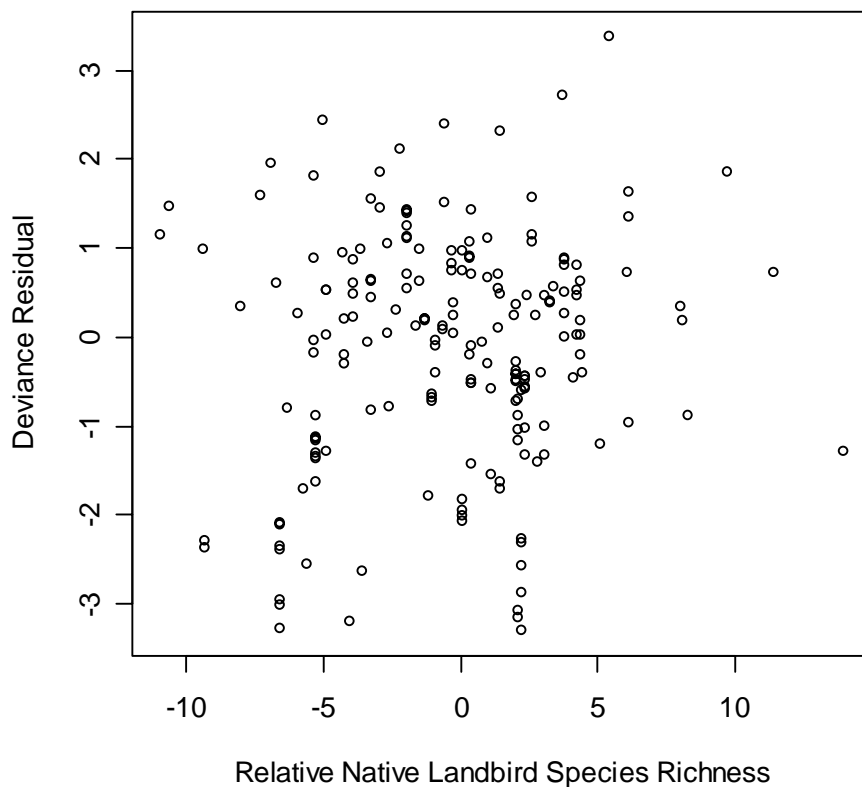


Figure 6.3. Plot of deviance residuals against the explanatory variable: relative native landbird species richness.

For reasons given in *Chapter 4*, because of the large number of missing values in some variables, residual deviances could only be calculated and inspected for 65% (193) of the islands. As in *Chapter 4* this was not assumed to be a problem during interpretation, as these are an unbiased subset.

### 6.3.6 Outliers

Outliers were identified from plots of indexed deviance residuals as values outside the range  $[-3,3]$ . This range is larger than that used in earlier chapters because the diversity of exotic landbird species is larger than that of introduced mammal species. Figure 6.4 displays the islands with outlying species richness values.

Six negative outliers were identified (observed < expected):

CHICKEN IS Muriwhenua

-3.31

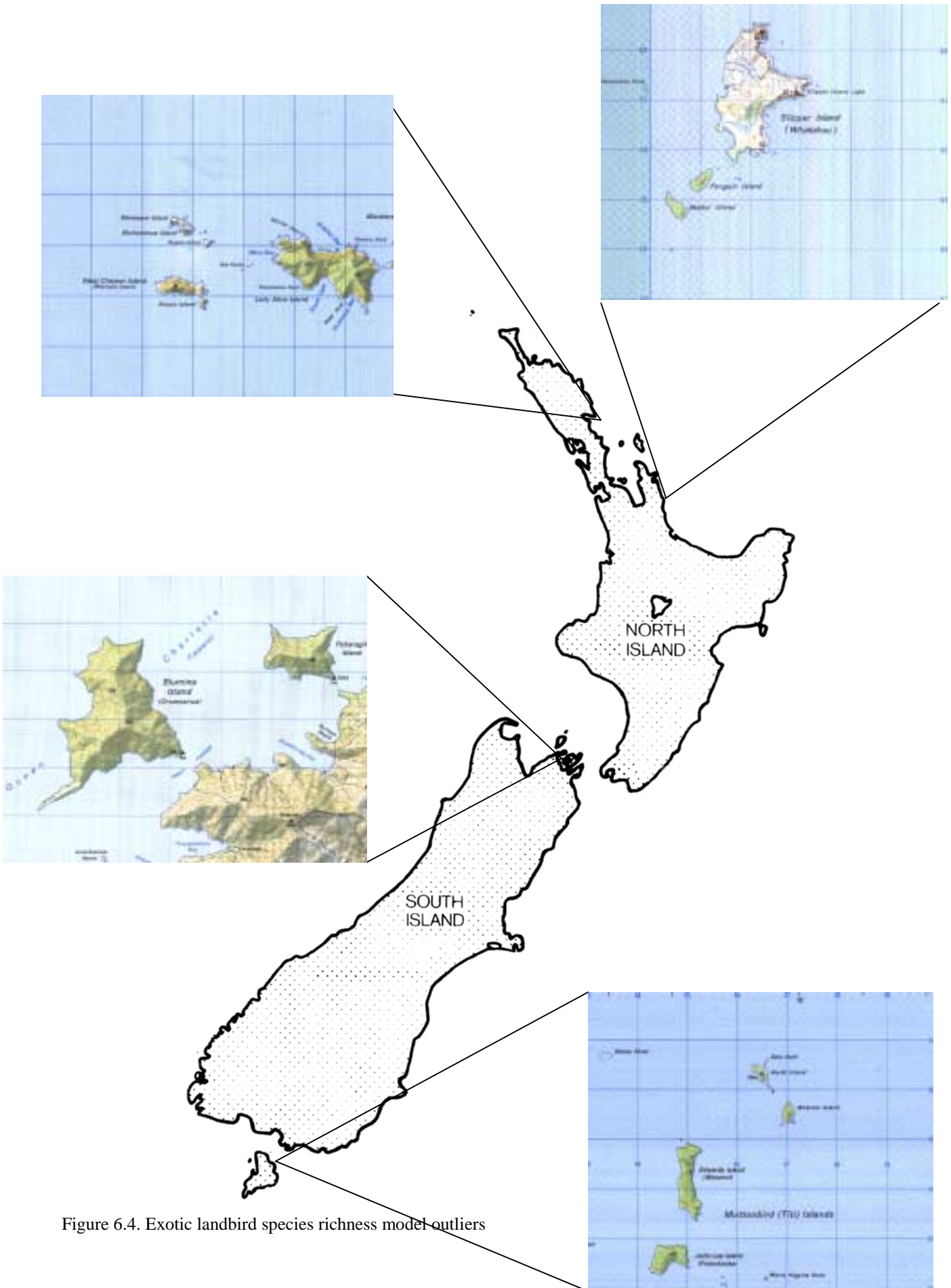


Figure 6.4. Exotic landbird species richness model outliers

SLIPPER I. GP: Rabbit	-3.27
BLUMINE (ORUAWAIRUA) I.,	-3.21
WOMENS I., E. Stewart I.	-3.16
NORTH I., NE Stewart I.	-3.08
SLIPPER I. GP: Slipper (Whakahau)	-3.02

One positive outlier was identified (observed > expected):

GREEN I., Foveaux St	3.38
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### 6.3.7 Model Refinement

Similarly to *Chapter 5*, both the three level *Latitude* dummy variable and Land District Code (*LDC*) were added to the exotic landbird species richness model.

#### 6.3.7.1 Latitude Dummy Variable

*Latitude* from the original model was replaced by the three level dummy variable (*Latitude.dummy*) created in *Chapter 5*.

The exotic landbird species richness of southern latitude islands decreased significantly ( $p < 0.001$ ) by a factor of 0.53 from the northern (baseline) latitude islands. Exotic landbird species richness on central latitude islands was not significantly different from the baseline.

The only other term to change significance was  $\log_{10}$  *Elevation*, which became no longer significant.

### 6.3.7.2. Land District Code

*Latitude* from the original model was replaced by Land District Code (*LDC*).

The *Southland* district had a significantly ( $p < 0.001$ ) lower proportion of exotic landbird species by 0.53. The only other district which differed significantly from the *North Auckland* district baseline was *Gisborne* district, which had a significantly ( $p = 0.049$ ) higher proportion of species by 2.15.

No other variables changed significance.

### 6.3.7.3 Other Relative Avian Species Richness Categories

Native landbird species richness was the only relative avian species richness category *a priori* hypothesised to have a relationship with exotic landbird species richness. This was because the two species categories were assumed to directly interact through their use of similar terrestrial habitat. It was not possible to include the total avian species richness of islands as an explanatory variable since this count included exotic landbird species. However after construction of the original model both remaining categories; relative wader and seabird species richness, were included to see if they did have a relationship with exotic landbird species richness.

Exotic landbird species richness was positively related to relative wader species richness ( $p = 0.002$ ). There was no significant relationship between exotic landbird species richness and relative seabird species richness. The relationship with relative native landbird species richness decreased to become barely significant ( $p = 0.100$ ). No other variables changed significance.

## 6.4 Discussion

### 6.4.1 Linear Model

Despite the inadequacies of the avian data, and over dispersion, the original model did highlight some significant factors influencing the species richness of exotic landbirds on New Zealand offshore islands. Inclusion of more specific geographical variables revealed more precisely which areas of New Zealand differed significantly in their exotic landbird species richness.

#### 6.4.1.1 Significant Variables

Five terms were significant predictors of exotic landbird species richness on New Zealand islands. As with the mammal species richness models, interpretation of the intercept is nonsensical, and so it is largely overlooked. It is required for predictive purposes.

As a measure of sampling effort  $\log_{10}$  *Cards* was highly significant, as anticipated. The number of *Grid* squares an island spans was not significant. This result in itself is valuable as it advocates the use of  $\log_{10}$  *Cards* alone in *Chapter 3* to detrend the avian species richness estimates.

For a change of one degree in *Latitude* only a small increase of 1.06 fold is experienced in exotic landbird species richness. Since *Latitude* was measured in negative (Southern Hemisphere) values, the gradient of increase is northwards. The total proportional variation in *Latitude*, holding all other variables constant, is 2.11 ( $1.06^{12.8}$ ) from the southern most (Big South Cape) to the northern most (Motuopao) islands of New Zealand. The *Latitude* effect per degree differs by only 0.01 from that found in *Chapter 5.4.3.1.2* for introduced small mammals that are naturally dispersing to New Zealand islands. This is interesting considering that the species pools considered for small



mammals and for exotic landbirds differ in size. This result may only be coincidental, however it might suggest that the processes mediated by *Latitude* controlling the macro-scale distribution of introduced species is similar between the two vertebrate taxa, and compels investigation into whether such an effect is similar across other introduced taxa. Sax (2001) certainly did find similar gradients across taxa, however his broad study merely appraised the qualitative similarities rather than the quantitative changes. Sax also found that islands were more susceptible to invasion than the mainland was when species were outside their latitudinal range. Rosenzweig (1995) believes the latitudinal gradient is primarily caused by the topics covering more land area. However even if this is correct on a global scale, the reasoning does not follow through adequately to regional scales. Rosenzweig then surmises that the latitudinal gradient is in fact a combination of area and environmental effects. Perhaps as scale is decreased so too does the weighting of each effect.

The variable  $\log_{10}$  *Elevation* was barely significant, and when *Latitude* was replaced by the more appropriate dummy variable it ceased to be significant. The effect is once again negative as has been consistently observed for both the distribution and species richness of mammals throughout the study. Other avian studies have found elevation to play a significant, though polar, role; sometimes being negative (Mandon-Dalger *et al.* 1999), and other times being positive (Adler 1992). Being barely significant,  $\log_{10}$  *Elevation* does not warrant a great deal of interpretation. However if any effect exists, it would most likely be for similar reasons as for the introduced mammals, namely the reduced invasibility of islands with higher peaks.

The inclusion of relative native landbird species richness is questionable as this variable could itself be influenced by a number of the other explanatory variables. In this a case path regression may have been more appropriate (see p.70 in Williamson 1981). However regardless of any cause or effect dilemma, by its inclusion a large amount of the ecological value of each New Zealand island is summarised, since these islands have in the past tended to be classified and managed based on their native avian biodiversity (J. Craig pers. comm.). Exotic landbird species richness on New Zealand offshore islands is

significantly positively related to relative native landbird species richness. Initially such a relationship would be expected; if an island can support more native landbirds it should also be able to support more exotic landbirds. However this effect is independent of any *Area* or habitat effect associated with the species-area relationship which those variables are surrogates for. In that case the literature on introduction and invasion would suggest a negative relationship is more sensible, as this would support the notion that for islands where exotic landbird establishment is occurring it is because habitat modification or some other process is causing a corresponding reduction in native landbird species richness (McLay 1974; Diamond and Veitch 1981; Case 1996). Even if the New Zealand islands were not in a MacArthur and Wilson (1963, 1967) equilibrium, but a sub-equilibrium as others have suggested (Abbott and Grant 1976; Holland 2000), the relationship should still not be positive. In this case it would more sensibly not exist at all, since exotic landbirds could establish without compromising any equilibrium scenario (Abbott and Grant 1976). The positive relationship is obviously not direct. The presence of an exotic landbird species would not be directly attributable to the presence of a native landbird species, no such associations exist. What requires uncovering is the characteristics of an island which promote the presence of larger numbers of both native landbirds and exotic landbirds. Lack (1969, 1976) and other authors (Steadman and Freifeld 1998; Davidar *et al.* 2001; Woinarski *et al.* 2001) have consistently found suitable habitat to be the appropriate link, but for this model habitat heterogeneity ( $\log_{10} BHDI$ ) was not a significant factor. However as Gotelli and Graves (1996) have shown, studies of habitat heterogeneity are fallible, since they cannot isolate the habitat dependencies of species or taxa (a shortcoming of *BHDI* identified in *Section 2.1.2*). What is probably occurring is that for islands with suitable habitat, both native and exotic landbird species can establish in greater numbers. Where this habitat does not occur, species of neither type can establish. What would be required to confirm such a relationship is some measure of appropriate habitat type being present, such as in Duncan's (1997) study of exotic ungulate introductions to New Zealand.

Also of note are the variables that were not significant. Neither transformation of *Area* nor distance (*Dist.Main*), as championed by MacArthur and Wilson (1963, 1967) played

any role in predicting exotic landbird species richness. This result further supports Lack's (1969, 1976) alternative view that habitat is the primary driver of avian species distribution (the sum of which is avian species richness).

The presence of a stepping stone island was not a significant correlate of exotic landbird species richness. This suggests that exotic landbirds are not utilising them to reach more distant islands, instead dispersing over considerable distances directly. This also explains the presence of exotic landbirds on more distant outlying islands (>50km) from the mainland where there are no stepping stones, although here oceanic ridge archipelagos such as the subantarctic islands of New Zealand have had to have been used as stepping stones to cover even greater distances in orders of hundreds of kilometres (pers. obs.).

Although initially the various types of human settlements may have differentially facilitated invasion by exotic landbirds, their subsequent rapid expansion across the New Zealand archipelago will have meant that settlement would no longer correlate with overall species richness, although it may still influence the distribution of individual species with particular habitat requirements.

Davidar *et al.*'s (2001) work on Indian islands found latitude, area and habitat were all important predictors of avian species richness in forests on offshore islands. The effect of habitat was found to be most important at a micro-scale level, once other factors had been partialled out. However Steadman and Freifeld (1998) found no effect of area, elevation or isolation; attributing most variation in species richness of the indigenous avifauna of Tongan Islands to human mediated habitat destruction. In further contrast Li and Li (1998) found for their subset of Chinese islands that area generally explained the most variation, although elevation, isolation and human effects also contributed to the variation in species richness of *Raniformes*. Overall, it is postulated that avian species richness depends on factors which are often quite archipelago specific and are reflections of both the physical locality and history of the archipelagos in question, although such meta-analysis is difficult given the different conditions under which data will have been collected and analysed.

#### 6.4.1.2 Collinear Variables

*Elevation* was the only collinear variable identified in *Chapter 3.2.3* that was significant in the final model. Its effect has been discussed earlier, and once again it appears that the confounding effects of  $\log_{10}$  *Area* and  $\log_{10}$  *BHDI* were partialled out. It is possible that standard error inflation has occurred causing the  $\log_{10}$  *Elevation* term to be less significant than it actually is, however of the three collinear terms it was the only one that did not have a VIF over the threshold value of ten, which suggests standard error inflation will not have occurred.

#### 6.4.1.3 Residuals

Three of the residuals versus explanatory variable plots were concerning (Figures 6.1-3).

For *Grids* the value for Stewart Island was extremely high leverage. However the number of *Grid* squares an island covers was not a significant variable, and Stewart Island was not an outlier in the model, so this abnormality had no problematic consequences.

*Latitude* illustrated the tri-modal clustering of New Zealand offshore islands which is corrected for during model refinement by including the *Latitude.dummy* variable term.

The plot for relative native landbird species richness was the most concerning. Although the residuals are evenly balanced, there are areas of the plot with very few residuals. The most obvious of these is for negative residuals (observed < expected) for islands with very high relative native landbird species richness. This suggests that for islands with high native landbird diversity, it is unlikely to find less exotic landbirds than expected. In other words, these islands tend to be well invaded by exotic landbirds. However it is known that the relative native landbird species richness is conservatively estimated for some values because of the detrending, and since this was the only plot to show concerning scatter in the residuals, and the overall residual plot showed no problems, it was considered that the distribution of residuals was not significantly affected.

#### *6.4.1.4 Outliers*

Six islands were identified as negative outliers, their species richness being approximately three species under that predicted. There was only one island where species richness was three species over that predicted. These outliers are located across the archipelago.

Both Womens and North Island are located off north eastern Stewart Island, while both Rabbit and Slipper Island lie in the Slipper group (Penguin Island, the third in the group, just fell short of being an outlier). This suggests that local processes affecting either the islands or source population are the cause of the low observed number of exotic landbirds on these islands. These processes are probably on too small a scale or are too specific to have been accounted for in this study.

Green Island is the only island where more species were observed than would be expected. It is located remotely from the mainland, in the middle of Foveaux Strait. However in relation to numerous other larger islands it is located much more closely. It is intermediate to Stewart Island from the mainland, and located immediately adjacent to Ruapuke Island. Both larger islands have 13 exotic landbird species, 12 of which are shared with Green Island. This sharing of common species suggests Green Island could be acting as a stepping stone, while using the mainland, Ruapuke and Stewart Island as population sources. This would then account for its positively outlying exotic landbird species richness estimate.

It was not considered necessary to test the model without the outliers because they represented only a small fraction of the total sample, were not considered high leverage and were not mistakes in the dataset.

#### 6.4.1.5 Model Refinement

##### 6.4.1.5.1 Latitude Dummy Variable

The significant decrease in exotic landbird species richness found for southern islands is similar to the result found for small mammal species richness. As for small mammals, it could follow that this is because the southern latitude islands are among the more pristine environments of New Zealand. This has in turn meant that these islands, buffered by continuous tracts of forest around them on the mainland and coastline, are relatively less invasible by exotic landbirds. Indeed only a few well-established exotic landbirds, such as the blackbird (*Turdus merula*), seem able to penetrate into such complex native forest ecosystems (pers. obs.). However this general trend could also be linked to the general absence of adequate source populations. Exotic landbirds are most strongly established in the northern areas of New Zealand, gradually declining in abundance further southwards, in some cases because of known climatic limitation (Tindall 1996). It may be that some species have not expanded into the southern areas yet. There are a number of possible explanations for the observed decline in exotic landbird species richness southwards, and it is highly likely that they all play some role in the trend, and are themselves caused by processes controlled by *Latitude*.

The non-significance of  $\log_{10}$  *Elevation* when *Latitude.dummy* is included is most likely because the highest, uninvasible islands are located in the southern latitudes, and by changing *Latitude* from a continuous to a categorical variable these tall islands are all subsumed within one category.

##### 6.4.1.5.2 Land District Code

The results of replacing *Latitude* with *LDC* support the assertion (made in the previous section) that the islands around Fiordland are those which are the least invasible, which is reflected by the significantly decreased exotic landbird species richness of the *Southland*

district. This result was similarly found for both small and large mammal species richness.

*Gisborne* district had a significantly higher proportion of exotic landbird species. The *Gisborne* district is characterised by intensive agricultural use. Forest cover was drastically reduced to such a level that legislation was passed requiring landowners to prevent erosion by planting pine trees (*Pinus radiata*). This opening of habitat into pasture and grasslands would be beneficial to the establishment of introduced exotic landbirds.

No gradual decline in exotic landbird species richness was observed which was analogous to the *Latitude* effect observed earlier. The *LDC* effect appears to be operating on a more regional scale than the *Latitude* effect. The most apparent explanation is that the *LDC* districts are surrogates for habitat modification within an area. *Southland* district is relatively unmodified, while *Gisborne* district is in contrast most heavily modified. Although the *LDC* districts are only arbitrary divisions of the mainland, they have existed since European settlement and as a result of this their land use differs due to differences in the legislation and policies of controlling authorities. Davidar *et al.* (2001) found habitat operated on a similar micro-scale for forest birds on the Andaman Islands.

#### 6.4.1.5.3 Other Relative Avian Species Richness Categories

Because waders are particularly sensitive to habitat availability and disturbance, their positive correlation with exotic landbird species richness supports the general assumption that the relative native avian species richness categories are good surrogates for suitable habitat type, although not necessarily the same habitat types being shared between categories. The corresponding decrease in the significance of the relative native landbird species richness term suggests there is some overlap in the data between waders and native landbirds, again probably also in the manner in which they act as surrogates for suitable habitat availability.

Seabirds are not as sensitive to suitable habitat availability as the other categories are. They are generally more susceptible to introduced mammalian predators which have decimated their populations on offshore islands (Bettesworth 1972; Atkinson 1985). As has been discussed earlier, exotic landbirds are evolutionarily adapted to such predators, and so it is not surprising that no link between the two categories was found.

#### 6.4.2 Conclusions

Firstly, it is imperative to note that the null hypothesis, although correctly specified statistically, was immediately biologically annulled because sampling effort had *a priori* been shown to have an effect on exotic landbird species richness. This misspecification does not have any immediate consequences upon the conclusions drawn from the model, but it is possible that other patterns which emerged from it were also generated from the measures of sampling effort, because of overlap in the information contained in the significant variables. The subsequent disregarding of the significance of sampling effort would then also imply that the significance of other variables would become questionable.

It is difficult from the results presented here to test if exotic landbirds on New Zealand offshore islands are in equilibrium or not. Some patterns certainly do exist, and these mostly appear to be types of ecological relationships that include associations with other bird species and habitat suitability. Blackburn and Duncan (2001, *in press*) found the opposite; that globally, introduced birds tend to be limited by abiotic factors, and not biotic factors. This however, may be a reflection of the different spatial scales of the studies (Whittaker 2000), and the indistinct discrimination between habitat measures as biotic or abiotic that can occur in studies. Abbott and Grant (1976) certainly found that the avifauna of New Zealand's outlying islands (>50km) were in non-equilibrium, however it is not known whether this is also true for the offshore islands in this study. On a larger scale *Latitude* certainly plays a role, although there are many possible causes for the observed trend. Overall, the conclusions that can be drawn are limited because of the difficulties that were encountered with the avian data.



## Chapter 7: Conclusions

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### 7.1 General Discussion

Gotelli and Graves (1996) decry the *ceteris parabus* ('all other things being equal') clause of island biogeography studies. Beyond the core elements of island biogeography (area and distance) are a host of other factors which differ between islands and species (Brown and Lomolino 2000). Fox and Fox (2000) specifically recommend inclusion of measures of habitat diversity, disturbance and inter-specific competition in models. The variables included in this study were selected to represent a broad range of descriptors for the physical nature of islands, ecological processes, characteristics and complexities of islands, and the effects humans have had on the islands. The results of each chapter have revealed common patterns in the observed distribution and species richness of introduced vertebrates on New Zealand offshore islands, while the discussions have highlighted the differing roles the individual variables play in each model. However when considering these findings the importance of scale must also be considered (Whittaker *et al.* 2001). Whittaker (2000) asserts that the effects of area, isolation, altitude and habitat diversity are all proportional to the scale at which they are measured. This study was undertaken at a macro-scale level (*sensu* Whittaker *et al.* 2001), encompassing the entire New Zealand archipelago and its offshore islands within 50 kilometres of the mainland, and so the significant effects found are operating at a similar such scale. There were cases where the results suggested that more localised processes were occurring. In *Chapters 5* and *6* the differences between Land District Codes (*LDC*) suggested regional processes were having an influence on species richness, while the islands which were outliers in the exotic landbird species richness model suggested that processes specific to particular island groups may also be occurring. There were also cases where the results suggested processes related to global patterns, such as the consistent effect of *Latitude* across *Chapters 4, 5* and *6*. This demonstrates the applicability of the models to understanding introduced species both at a regional scale, where local authorities may wish to control introduced species in a specific area, to a global scale where predictions can be made of

changes in introduced species distribution and richness, with respect to changes in climate. Such tools are invaluable for managers of introduced species.

It is important to remember that, with so many variables being analysed some of the significant effects may be due to chance alone (Type I error *sensu* Underwood 1990). A more liberal than usual significance level of 10% was chosen for this study, which also meant a higher probability of detecting spurious relationships. The significance of the collinear variables could also have been questionable due to standard error inflation. However by inclusion of all three collinear variables, obscure effects (which might have otherwise been subsumed in the other variables) were uncovered. Here I am specifically referring to the consistent negative effect of  $\log_{10}$  *Elevation* in *Chapters 4, 5 and 6*.

Overall this thesis has taken a complex system (the offshore islands of New Zealand and their introduced vertebrate species), stripped it into its constituent components (individual variables) and then attempted to reconstruct the system (using models) in the light of those constituent components which played the most important roles.

Modelling the biotic components of islands using abiotic factors, the variables are essentially restricted to *Latitude* and its variants (*Latitude.dummy* and *LDC*), *Area* and its collinears (species-area relationship) and the different measures of distance. Historical factors (non-interacting categorical variables) shift the relationship between the biotic and abiotic components of islands, however they do not alter its final form. All these relationships were predicted by MacArthur and Wilson (1963, 1967) in their original equilibrium theory of island biogeography, although *Latitude* was controlled for when climate was required to be held constant in their original theory. Adding biotic factors (such as other species, often lower in the trophic chain) as explanatory variables complicates the models as the distribution of these species too is determined in some part by the same abiotic factors. However it can not be overlooked that the final distribution and diversity of species on islands will also be a result of interactions between them as well as with the abiotic characteristics of the islands.

Because of the large volume of literature on biogeography studies, it has only been possible to place the results found here within the context of a selection of studies. However the selection has been broad, both temporally (incorporating studies since MacArthur and Wilson's contribution) and spatially (incorporating studies from across the globe, including both the Northern and Southern Hemisphere). Specific emphasis has been placed on discussing the results within the context of more recent studies. The discussions in each chapter have also largely been an interpretation of the available results. To this end the thesis has been useful for generating new hypotheses, however, it is still highly desirable to gather further evidence supporting the conclusions reached regarding the patterns observed in this study.

## *7.2 Applications*

### *7.2.1 Offshore Island Management*

Conservation of New Zealand's islands is paramount, because they "*function as biological reservoirs for native plants, animals, communities and habitats*" (Atkinson 1989). These conservation values are not limited to some islands. The threatened plant kakabeak (*Clianthus puniceus*) is only found in two wild populations, one of which is on the unnamed island in Kaipara Harbour, which might otherwise be considered insignificant. Lee (1997) acknowledges that conservation of islands should be undertaken for even the smallest of islets. Of the large amount of resources dedicated to the restoration of offshore islands (see papers in Towns *et al.* 1990), a significant proportion must be dedicated to considering and redressing the effects of introduced species (Towns *et al.* 1997). Offshore island nature reserves are continually threatened by the invasion of introduced mammals and birds that can prey upon or compete with native species (Pryde 1997). This thesis has shown that the likelihood of any of these species reaching an offshore island depends on a combination of physical, biological and historical factors. The recent discovery (17<sup>th</sup> January 2002) of two rats on Ulva Island native bird sanctuary, 800 metres offshore, has once again highlighted the threat of invasion. Taylor (1984)

asserts that the swimming distance of rat species is approximately 300 metres, so how is it possible that these rats could have reached Ulva Island?

The individual mammal species distribution models presented in *Chapter 4* allow island managers to see which factors are most significant in influencing the distribution of each introduced mammal species across New Zealand's offshore islands. The models in *Chapters 5* and *6* show which factors correlate with increases in species richness, which relates to the overall degradation of the native biodiversity values of offshore islands, and to their use as native flora and fauna sanctuaries. For example, the potential values of restoring Limestone Island (Brackenbury 2001) can be measured with respect to the likelihood of invasion by introduced mammals and birds.

It is also important to revise previous investigations. As time passes, the circumstances surrounding investigations can change. Taylor and Tilley (1984) found that stoat dispersal to offshore islands was a dynamic process, and so considering recent range expansion and the use of stepping stone islands, it is possible to reappraise their views pertaining to the dispersal ability of stoats (*Section 4.4.1.1.13*).

### *7.2.2 Wider Research Implications*

The results of this thesis are important when considered within the context of other island archipelagos and taxa, both native and introduced. Studies such as this one have been undertaken for islands throughout the world (e.g. Adler and Wilson 1985; Burbidge *et al.* 1997; Dennis *et al.* 1998; Conroy *et al.* 1999). To the best of my knowledge, however, this is the first time such a study has been performed using New Zealand islands. The results contribute to the wider scientific understanding of archipelagos, and the processes operating within them driving species distribution and richness at different scales. It is important within this context to recall that humans originally mediated the introduction of the species investigated here, so some effects, such as the 'small-island effect' (Lomolino 2000c; Lomolino and Weiser 2001) may differ or even not exist because of the human mediated confounding of natural colonisation processes. However this does allow the

opportunity for interesting comparisons with biogeographical studies of native fauna distribution and species richness on islands, both here (Abbott and Grant 1976) and elsewhere (Adler and Wilson 1985; Palmer *et al.* 1999). As our access to more comprehensive data increases, so to will our ability to more precisely determine the processes controlling the distribution of species on both larger and smaller scales

There are also tangible benefits from theoretically orientated investigations such as this in the application of such theory. Flux (1989) applied biogeographic theory to estimating species densities in different habitats of the extinct moa (*Dinornis spp.*). The New Zealand Department of Conservation has also recently identified practical knowledge that would best be sought through modelling the distribution of species and the factors that make particular native communities vulnerable to invasion (Department of Conservation 2001).

### *7.3 Further Work*

At the conclusion of any project, hindsight and reflection is always beneficial. This can be turned into a profitable affair by considering future opportunities; both what needs to be done in order to make similar projects more successful in the future, and also the types of research that can follow from the findings of a project.

The first and most apparent of these is to supplement the dataset. Due to the large number of islands and species that were considered in this study, it was inevitable that there would be missing values. Although these were shown not to generally affect the models and their interpretation (the avian data being a notable exception), it would nonetheless be advantageous to have more thorough data on species distributions and the characteristics of New Zealand offshore islands. For the 132 islands missing data on the presence of introduced mammal species, many only required the confirmation of a few species to become complete observations (and thus useful in investigations of species richness such as *Chapter 5*). It is also especially pertinent that attention be drawn to the biasing effect of sampling effort in ‘The Atlas of Bird Distribution in New Zealand’ (Bull

*et al.* 1985), as the Ornithological Society of New Zealand is currently in the process of collecting data using an identical methodology for an updated publication. The atlas would have even more application if it contained records of bird distribution (both native and exotic) specifically on islands, rather than solely in ‘grid squares’.

With regard to the methodology, the benefits of using *a priori* hypotheses were that biologically relevant variables could be included in models, and their relative effects within models compared using appropriate tests of significance. However there was not as much flexibility for comparison of effects between models which contained different *a priori* hypothesised sets of variables. The inclusion of many biologically relevant variables also meant there were issues of collinearity between similar variables. A different approach which may warrant investigation, if only for comparative purposes, would be to use *Principal Components* (PCA) regression (*sensu* Adler and Wilson 1985; Philippi 1993; Burns 1995). This would remove the effects of collinearity, and amalgamate the variables into compound variables that could act as broad surrogates for such insular descriptor categories as ‘physical’, ‘ecological’ and ‘human effects’. If these descriptors were consistently used in similar models of the response variables used here, then the results between models would be directly compared. However biological interpretation of the compound variables would be somewhat more difficult (variables would initially require standardising and the compound variables back-transformed to estimate the original, albeit constrained, biological effects).

The study has illustrated the large numbers of patterns that exist in the distribution and species richness of introduced vertebrates across New Zealand offshore islands. In *Chapter 1* it was stated that once patterns have been established, it is then much more practical to attempt to establish the processes behind them. The challenge that now lies ahead for researchers following this study, is to establish what processes, some of which are speculated in *Chapters 4, 5 and 6*, are causing the observed patterns. This needs to be done in a rigorous manner such that competing alternative hypotheses can be systematically discounted (see Table 8.1 in Gotelli and Graves 1996).

I foresee particular merit in establishing the underlying process that drives the species-area relationship for both native and introduced species on New Zealand offshore islands, considering that the two may differ. Kelly *et al.* (1989) attempted such an investigation for New Zealand plants, however it has been noted that the results are limited to micro-scale processes due to the spatial scale of the study (Whittaker 1998). A number of novel approaches are available for uncovering what may be the true underlying effect of the species-area relationship (Williamson 1981; p. 235 in Gotelli and Graves 1996), and it is suggested that these be considered as means by which to do so.

Other theoretical issues should also be addressed. Lomolino (2000c) advocates a ‘small-island effect’, originally considered by Whitehead and Jones (1969), in the species-area curve. There were indications in the results of this thesis that for New Zealand offshore islands, certain effects are restricted to the extremities of island parameters. The dataset was also purposefully limited to islands less than five hectares in area because such a small-island effect was in fact anticipated. What makes such a study even more engaging is that the dataset for such an analysis is already available. Taylor (1989) lists all islands, with no restriction on size, merely the condition that they are not connected to the mainland, which are within the northern latitudes of New Zealand (as specified by *Latitude.dummy*). This dataset is also available in an electronic form on permission of its author (G. Taylor pers. comm.).

For mathematically inclined researchers, the dataset provides an abundance of figures which could be quite comprehensively analysed. As has been noted (*Section 3.1.2.2*) the *Latitude* and *Longitude* of every offshore island are analogous to Cartesian coordinates. From this it would be possible to compute distance matrices for every offshore island, which could be subsequently used to investigate species compositions both across island ‘groups’ and along potential stepping stone systems. I see an exciting avenue of research here that could incorporate simulation studies and the application of null models within a New Zealand context.

Although there has recently been a shift in emphasis away from single species research and management, there is still much to be gained from investigating the components of ecosystems and how they interact with one another. This study has speculated on limiting factors for the distribution of introduced mammal species on a macro-scale. What is required now is a process-orientated investigation of these limiting factors. Such an approach would be best served by exploring the biology of individual species (autoecology) and how they interact with the physical geography of their environments. Offshore islands stand as excellent 'natural laboratories' for the successful experimental manipulation of factors, including controls, to investigate such limiting factors (Simberloff and Wilson 1969). There is the potential to use some of New Zealand's smaller, less ecologically valuable, islets as sites for the introduction and monitoring of small mammal species to achieve such an end, as has been done overseas (Crowell 1973).

As is evident, the opportunities for biogeographical work within New Zealand are vast, and there would be no better time than the present, with the recent resurgence in popularity of biogeographic theories (Lomolino 2000a, 2000b, 2001; Hubbell 2001; Whittaker *et al.* 2001) and studies (Burbidge *et al.* 1997; Chown *et al.* 1998; Millien-Parra and Jaeger 1999; Palmer *et al.* 1999; Ricklefs and Lovette 1999; Welter-Schultes and Williams 1999; Woinarski *et al.* 2001), to undertake such work in New Zealand and contribute to the global understanding of insular systems. However as MacDonald (2000) states in his paper 'preparing biogeographers for the third millenium', which succinctly sums the current necessity and potential of biogeography, achieving such a task will require participation from a range of disciplines, with broadly trained individuals from inter-disciplinary backgrounds.

#### *7.4 Recommendations*

To summarise these conclusions, a number of recommendations are made here. Following these would yield some immediate scientific and conservation benefits.



Many of the recommendations from Atkinson and Taylor (1991) and Atkinson (1992) still require acting upon, and some are re-listed below in a slightly altered form in the context of this study.

- The Department of Conservation (as the primary estate holder of most New Zealand islands > 5ha.) should establish a centralised database for New Zealand offshore islands, based on the data from Atkinson and Taylor (1991) and incorporating the updated data available here. Such a database should be similar to the species eradication database (I. McFadden pers. comm.) located in the Wellington DoC Head Office, and would benefit from being electronically linked to it.
- The status of introduced mammals on islands where this is not yet known should be established. Department of Conservation field staff could achieve this during routine island visits. This information should be made available either as an update to Atkinson and Taylor (1991) or within a centralised database as suggested earlier.
- More thorough work should be undertaken describing habitat types and variety on New Zealand offshore islands. The framework for such a project should be based on Atkinson (1992) so that those islands that have not yet been adequately described can be covered first.
- As an offshoot of the current update of the Ornithological Society of New Zealand Bird Atlas, species lists for offshore islands should be created. These could readily be generated using sampling cards which were recorded on offshore islands, and should be noted in the appendix of the atlas.
- The processes that drive the species-area relationship for both native and introduced taxa in New Zealand should be investigated with a process-orientated approach.

- Studies should be initiated to investigate the limiting factors for particular introduced species on New Zealand offshore islands. Such studies should be process-orientated and include investigation of the temporal and spatial effects of colonisation and dispersal.
- A multivariate analysis of the composition of introduced mammal populations on New Zealand's offshore islands should be undertaken. It is foreseen that this would include *Principal Components Analysis* (PCA) regression on a similar dataset so that results would be comparable to those found here.

### 7.5 Appendix

The appendix is included electronically on CD-R in the back cover of the thesis. Included are:

- 1) The complete dataset in Microsoft Excel™ 97 format (with map references)
- 2) The complete dataset in tab delimited text format
- 3) A summary of computer packages used
- 4) The entire thesis in *Portable Document Format* (PDF) format
- 5) 'R' for Windows (Version 1.3.0)

Permission is given to retain and distribute copies of the first four sections of the appendix, provided that it is for private or institutional use only, and due acknowledgement is given. 'R' is distributed under a separate GNU licence included in the installation package.

If the dataset is analysed in a form not substantially different from that included in the appendices, then reference should be given as:

Dataset from Russell, J. C. (2002). *Modelling the Distribution and Species Richness of Introduced Vertebrates on New Zealand Offshore Islands*. Unpubl. M.Sc. thesis, University of Auckland.

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## *Errata*

- p. 12 l. 14 should read "Although the data were confounded"
- p. 100 l. 4 sampe should read sample
- p. 104 Fig 1.1 should read Fig 5.1
- p. 128 l. 21 compromising should read comprising
- p. 131 l. 14 ore should read are
- p. 135 l. 16 precedent should read precedence
- p. 167 l. 6-7 *Advanced* should read *Advances in* (Vol. 11)
- p. 169 l. 2 constrained
- p. 170 l. 3 determining
- p. 171 l. 6 archipelago
- p. 173 l. 24 biodiversity
- p. 179 l. 30 university
- p. 182 l. 17 kiore
- p. 183 l. 3 distributions