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PAPER



# Modelling the distribution and interaction of introduced rodents on New Zealand offshore islands

James C. Russell\* and Mick N. Clout

*Animal Behaviour, Ecology and Conservation Research Group, School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand.*

## ABSTRACT

**Aim** To establish the factors that correlate with the distribution of the four most commonly introduced rodent species on New Zealand offshore islands — ship rat (*Rattus rattus*), Norway rat (*R. norvegicus*), Pacific rat or kiore (*R. exulans*) and house mouse (*Mus musculus*) — and examine if these distributions are interactive at the archipelago scale.

**Location** The 297 offshore islands of the New Zealand archipelago (latitude: 34° S to 47° S; longitude: 166° E to 179° E).

**Methods** Data on the distribution of all four introduced rodent species and the characteristics of New Zealand offshore islands were collated from published surveys and maps. The distribution of individual rodent species was regressed on island characteristics using a logistic generalized linear model. Interactions were examined by including the distributions of other rodent species as predictors in models.

**Results** All four rodent species appear to be limited by a variety of factors, which differ between species in both number and type. The distribution of ship rats is limited by the most factors, reflecting the extent of its distribution across the archipelago. The distribution of mice is the least explicative. Only the three rat species interacted in their distribution. The distribution of kiore on offshore islands is significantly negatively related to that of ship rats and to a lesser extent Norway rats. The distribution of mice did not appear affected in any way by the number of other rodent species on an island.

**Main conclusions** Differences in competitive ability and dispersal allow all four species to inhabit the New Zealand archipelago. Kiore distribution appears to be most limited by ship rat (and to a lesser extent Norway rat) distribution. The distribution of kiore was not found to interact with the distribution of mice on offshore islands, as has been suggested by others. The distribution of mice on offshore islands was difficult to model, which highlights the difficulties in managing this species. Overall the results offer valuable insights for management methods to assist preventing the invasion of offshore islands.

## Keywords

Distribution, interaction, islands, kiore, logistic modelling, mice, New Zealand, Norway rat, ship rat.

\*Correspondence: James C. Russell, Animal Behaviour, Ecology and Conservation Research Group, School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand. E-mail: j.russell@auckland.ac.nz

## INTRODUCTION

Worldwide, the ship rat (*Rattus rattus*), Norway rat (*R. norvegicus*), Pacific rat or kiore (*R. exulans*) and house mouse (*Mus musculus*) are identified as one of the most widespread and invasive cohorts of species (Moors *et al.*, 1992; Amori & Clout, 2002; Courchamp *et al.*, 2003). Together these four rodents constitute a grave threat

to native biota, in particular on islands (Atkinson, 1977, 1985). The entire New Zealand archipelago is characterized by this phenomenon, having been separated from the continental landmass of Gondwana before mammals had evolved. The factors that mediate rodent invasion of islands are not well understood. The pathways have generally been identified (Mooney & Hobbs, 2000), but their relative importance with respect to one another

has not been quantified (Atkinson, 1985). With quantitative information it would be possible to develop island 'risk profiles', which managers could then use justifiably to prioritize islands for conservation management (Atkinson & Taylor, 1991).

The distribution of any species is limited by environmental factors. 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. By identifying correlates of these boundaries, it is possible to understand better what limits species expansion and invasion of locations (Taylor, 1978). Theoretically every factor will be limiting at some scale, and this 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 *et al.*, 2001). Multiple species can also persist on similar resources when differing levels of competitive success and dispersal are present (Tilman, 1994). Such studies do require that the populations be permanently established over ecological time spans. Populations of *R. rattus*, *R. norvegicus* and *M. musculus* have only been established in New Zealand for less than 200 years (Wodzicki, 1950), however, the kiore (*R. exulans*) has been established for over 1000 years (Holdaway, 1996, 1999). All four species have at one stage been widespread throughout the New Zealand archipelago.

This paper sets out to quantify what island characteristics are correlated with the distribution of these four introduced rodent species at the archipelago scale, and to establish the nature of any interactions between their distributions. This is done using the extensive data available for New Zealand's 297 offshore islands larger than five hectares (Fig. 1). In the past, the processes that have mediated introduced rodents dispersing to and establishing on New Zealand offshore islands have been qualitatively assumed (Taylor, 1978). 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'. These processes have tended to be based on historical assumption, and so 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 rodents 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). More specifically, Atkinson (1986) identifies the settlement history, distance from a possible source population and the intensity of mammal interactions all as correlates of rodent distribution. However these correlations did not use methods to adjust for confounding variables. Other factors identified by Craig (1986) affecting the presence of rodents may not have been adequately considered, such as trampling by grazing stock, the presence of cats, habitat modification and the abundance of exotic birds.

Possible interactions between New Zealand's four rodent species have also long been a source of conjecture by scientists (Atkinson & Towns, 2001; Innes, 2001). Various hypotheses have been supported by circumstantial evidence (Taylor, 1978, 1984; Yom-Tov *et al.*, 1999). On the New Zealand mainland, populations of all four species of rodent have never been recorded in any one location or habitat (Roberts, 1991a; Atkinson & Towns, 2001). However, this complex matrix of mainland rodent distributions makes it almost impossible actually to quantify what pair-wise interactions may be occurring. New Zealand's offshore islands provide an array of different combinations of species presence, which can be analysed collectively to reveal what specific interactions may be occurring (Murphy & Pickard, 1990).

## MATERIALS AND METHODS

### Datasets

Data on the distribution of rodents on New Zealand's 297 offshore islands ( $\geq 5$  hectares, excluding the North and South Islands) were derived from Atkinson & Taylor (1991), with additional data on habitats taken from Atkinson (1992). Classification of species was simplified to presence (at some stage of the island's history), absence (not found on the island despite adequate investigation) or unknown (not enough information). Data on avian species categories were then taken from the *Atlas of bird distribution in New Zealand* (Bull *et al.*, 1985), and adjusted with respect to sampling effort bias (Russell, 2002).

Species absence is difficult to confirm. A species may have once established and subsequently gone naturally extinct without any record (a temporal error), or may be present in such low numbers that it is undetected (a spatial error). This error may vary with other factors measured (area, settlement history, species type) or unmeasured (island visitation rate, sampling effort) in the study. Measurement of such error would be difficult (McArdle *et al.*, 1990). The co-occurrence of species presence (at some stage of island history) and explanatory variable states (e.g. settlement history) may not coincide perfectly, but in general it is assumed that over ecological time spans the variables are characteristic of the insular systems. The order and timing of invasions (where known) could also not be incorporated into the models.

Data on 17 variables were collected for each island in the study (Table 1). Although latitude may affect rodent morphology and population demography (Yom-Tov *et al.*, 1999) it was assumed not to be limiting to their actual distribution, as rodents have been recorded throughout the world except polar extremes. The presence of potential stepping stone islands is reduced to a more tractable presence or absence, given the complex spatial matrix of islands in the archipelago.

### Statistical analysis

Some variables were  $\log_{10}$  transformed to remove right skew in their distributions. This resulted in more linear model fits and increased normality in the distributions. Generalized linear models (McCullagh & Nelder, 1994) were constructed relating

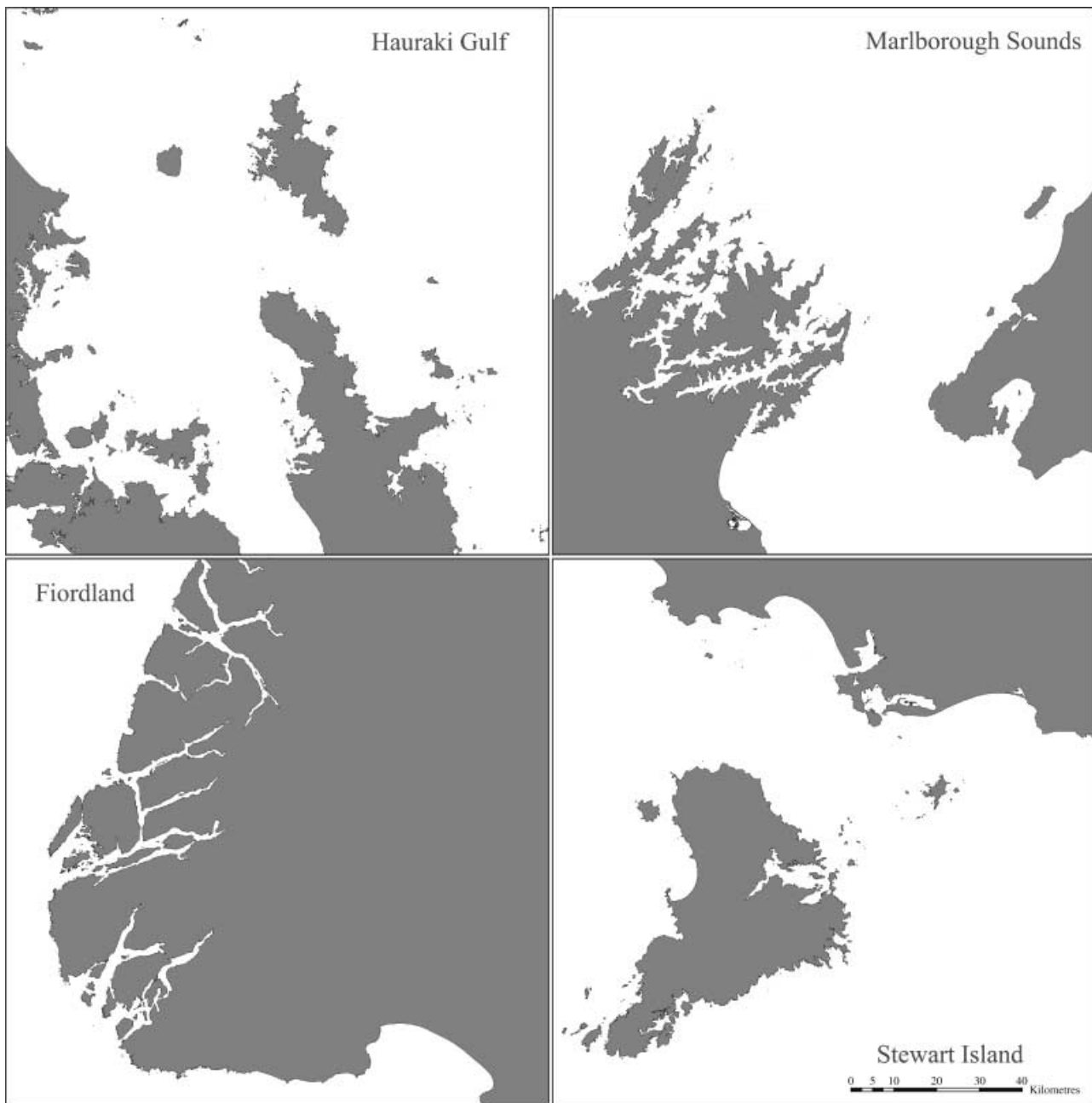


Figure 1 The four main New Zealand island groups.

the presence of each species to explanatory variables hypothesized *a priori* (Table 1), except rodent interaction in the first instance. *Maori* occupation was only used in the kiore model, and presence of a *Landing* structure was only used in the remaining three models. This reflected species arrival, where kiore initially expanded during Polynesian colonization (up to 200 years before present), before subsequently declining in their distribution following European colonization (Taylor, 1975). During this latter phase it is assumed that kiore did not disperse to new islands via wharves, because only ship and Norway rats were recorded on moored vessels (Atkinson, 1985). Following *a priori* model investigation, a rodent interaction term was included in each

model to investigate if the number of other rodent species on an island affects the presence of each species.

Models were constructed with the goal of identifying and interpreting the explanatory variables that govern rodent distribution on New Zealand offshore islands, not to maximize predictive power. As such model simplification is not required. Partial correlation coefficients are not standardized, which means that comparisons between them cannot generally be made as they remain scale dependent. Significance is noted if *P* is less than a liberal 0.10. This lower significance level was chosen so that variables which may have a smaller influence with respect to other more significant variables on the response could still be detected,

**Table 1** Variables (both response and explanatory) and their description within the context of this study

Variable	Description	Range
<i>Continuous</i>		
Area*	Land area of the island (ha)	2.5–174,600
Elevation*	Maximum elevation of the island (m)	4–1,196
Distance Source*†	Distance from the nearest stepping stone island or mainland (whichever is closer) (m)	25–39,600
Relative Seabird	Relative (adjusted) seabird species counts	–7.65–16.10
Relative Exotic	Relative (adjusted) exotic land bird species counts	–9.07–9.55
<i>Discrete</i>		
GDI*	Geological Diversity Index (number of rock types present <i>sensu</i> Atkinson, 1992)	1–6
BHDI*	Biological Habitat Diversity Index (number of biological habitat types present <i>sensu</i> Atkinson, 1992)	0–34
Mammal Interaction	Number of other introduced mammals on the island	0–13
Rodent Interaction	Number of other introduced rodents on the island	0–3
Stepping stone	Presence/absence of an intermediate stepping stone island ( $\geq 5$ ha) between an island and the mainland	0/1
<i>Binary (0/1)</i>		
Norway rats	Presence/absence of Norway rats	0/1
Ship rats	Presence/absence of ship rats	0/1
Kiore	Presence/absence of kiore	0/1
Mice	Presence/absence of mice	0/1
<i>Categorical</i>		
Maori	M: Presence of evidence of pre-European Maori occupation (earthworks or historical accounts <i>sensu</i> Atkinson & Taylor, 1991)	
Landing	W: Presence of a landing structure (wharf)	
Settlement	–: Never inhabited A: Abandoned R: Government (Ranger) station F: Unmanned farm I: Inhabited	

\* $\log_{10}$  transformed.

†distance from the source island which minimizes total dispersal distance from the mainland.

though this is at the expense of a higher probability of detecting spurious relationships. Logistic models are described in Hosmer & Lemeshow (2000). When constructing linear models it is important to consider the effects of collinearity between explanatory variables, if high collinearity is present the signs and magnitudes for coefficients of collinear variables can change considerably depending on their inclusion or exclusion. Collinearity was investigated using standard variance inflation factors for each explanatory variable. Chi-squared adequacy of fit tests were used to test the plausibility of the model specifications.

## RESULTS

Chi-squared tests for adequacy of fit found no evidence of model inadequacy. The only model with a low  $P$ -value, suggesting a possible inadequate fit might be occurring, was the kiore model ( $\chi^2$ ,  $P = 0.334$ , d.f. = 42). Data on kiore distribution contained more missing observations than the other rodents, and this was attributed as the cause for the possible inadequate fit (reflected in the low degrees of freedom). Analysis of missing observations found no severe departure from observations 'missing at random'. Collinearity was detected between the physical explanatory

variables *Area*, *Elevation* and *Biological Habitat Diversity* (all  $R > 0.65$ ). This is not surprising given the complex environmental system being investigated, and was attributed to aspects of landscape ecology and geography (see discussions in Gotelli & Graves, 1996; Whittaker, 1998). Despite this collinearity, all three terms were kept in the models, as other explanatory variables were found to stabilize the regression surface. Explanatory value would have been lost by arbitrarily dropping one of the variables, and the larger  $P$ -value threshold allows for collinearity affecting  $P$ -value precision.

The four models showed much variation in the number and nature of significant terms. Significant terms and the direction of their effects are given in Table 2. The ship rat model had the most significant terms (6), while the mouse model had only one. Three variables were not significant in any of the four models. These were *Biological Habitat Diversity*, *Mammal Interaction*, and all levels of *Settlement* except *Inhabited*.

### Norway rats

Norway rat presence was negatively correlated with relative seabird species richness, and positively correlated with relative exotic

**Table 2** Significant explanatory variables in the individual rodent distribution models. Shaded symbols are for significant variables ( $P < 0.100$ ). The categorical levels of *Settlement* are relative to the baseline *Never Inhabited*

Variable	Norway rats	Ship rats	Kiore	Mice
(Intercept)	ns	ns	-*	ns
$\log_{10}$ Area	ns	+**	ns	ns
$\log_{10}$ Elevation	ns	-*	ns	ns
Stepping stone	ns	ns	ns	-(*)
$\log_{10}$ Distance Source	ns	-*	+*	ns
$\log_{10}$ GDI	ns	-(*)	ns	ns
$\log_{10}$ BHDI	ns	ns	ns	ns
Relative Seabird	-*	ns	ns	ns
Relative Exotic	+*	ns	ns	ns
Mammal Interaction	ns	ns	ns	ns
Maori			+(*)	
Wharf	ns	+(*)		ns
Abandoned	ns	ns	ns	ns
Government station	ns	ns	ns	ns
Unmanned farm	ns	ns	ns	ns
Inhabited	ns	+*	ns	ns

Prefixes: '+' positive effect, '-' negative effect.

Significance levels: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '(\*)' 0.1 'ns' not significant.

land bird species richness. No other significant relationships were found. *Latitude* was included retrospectively in the model to test the assumption of no significant relationship, but no correlation between Norway rat presence and *Latitude* was found.

### Ship rats

The model for ship rats had six significant variables, the most of all four models. This suggests that the distribution of ship rats is relatively predictable based on limiting factors. Ship rat presence was positively related to  $\log_{10}$  Area and negatively related to  $\log_{10}$  Distance from Source, as classical island biogeographical theory would suggest. Negative correlations with the physical variables  $\log_{10}$  Elevation and  $\log_{10}$  Geological Diversity were also found. The presence of ship rats significantly increased with the presence of a Wharf or if an island was Inhabited. No biological relationships were found. When *Latitude* was included retrospectively to test the assumption of no significant relationship it was barely significant at the 10% level with a positive relationship (rarer at low latitudes).

### Kiore

Distance from Source and evidence of previous Maori occupation are significant predictors of the presence of kiore. The significance of the negative intercept indicates that the shift from absence to presence is marked, as Atkinson (1973) noted for islands situated at 1.5 km from the mainland. Maori occupation was significant despite missing over two thirds of its observations (and thus having much fewer degrees of freedom), which illustrates the intensity of the relationship between Maori occupation

**Table 3** Rodent interaction terms for all four models. Only the three rat species were negatively affected by the presence of other rodents

Model	Coefficient	P-value	Significance
Norway rats	-1.540	0.028	*
Ship rats	-1.469	0.055	(*)
Kiore	-2.768	0.063	(*)
Mice	-0.517	ns	

**Table 4** Interactions between kiore with the three other rodent species. The distribution of kiore is most severely affected by the presence of ship rats, and Norway rats to a lesser extent. The presence of mice has no effect on the distribution of kiore

Model	Coefficient	P-value	Significance
Norway rats	-4.071	0.090	(*)
Ship rats	-11.053	0.024	**
Mice	0.198	ns	

of islands and the presence of kiore. It is initially surprising that Distance from Source has such a strong positive correlation with the presence of kiore. This is contradictory to classical island biogeographical theory. It means that the further an island is from a source population (usually the mainland), the more likely it is to have kiore. When *Latitude* was included retrospectively to test the assumption of no significant relationship it was barely significant at the 10% level.

### Mice

The mouse model is the most uninformative of the models. The absence of an intermediate island, which might act as a stepping stone, was the only significant predictor of the presence of mice, but this alone was only a weak relationship with little interpretability. When *Latitude* was included retrospectively to test the assumption of no significant relationship it was not found to be significant.

### Interactions

Only the three rat species (Norway rat, ship rat and kiore) were significantly affected by the presence of other rodent species on an island (Table 3). Kiore were most strongly affected on average, while the effect on Norway rats was most consistent.

To test specifically for interactions between kiore and all other rodent species, the distribution of each species was also included individually in the kiore model (Table 4). Kiore were most significantly negatively affected by the presence of ship rats, although the presence of Norway rats also significantly negatively influenced the presence of kiore (albeit to a lesser extent). The presence of mice did not significantly affect the presence of kiore.

## DISCUSSION

### Norway rats

The Norway rat model makes predictions consistent with early introduction linked to European settlement of New Zealand. The presence of Norway rats on islands with low relative seabird species richness would arise from direct predation upon the seabirds (Atkinson, 1985). The positive relationship with relative exotic land bird species richness suggests that human modification of island ecosystems might facilitate Norway rat invasion. Many exotic species prefer habitat that is a result of disturbance modification (Courchamp *et al.*, 2003). The behaviour of exotic birds would also be genetically adapted from their native origins to the presence of rats, which endemic birds are not (Atkinson, 1985). Exotic bird establishment may also have been facilitated by the decline in unadapted native bird populations. It is surprising that neither island biogeographical nor anthropological variables are significant, as others have suggested (Bell, 1978; Atkinson, 1986). This offers no further insight as to how Norway rats may have colonized offshore islands, although the biological interactions with seabirds and exotic birds suggest some regulation at that level.

Norway rats were introduced to New Zealand earlier than ship rats and mice (Atkinson, 1973), and subsequently reached many islands (Moors, 1990). Around the early 1900s their numbers were observed to decline drastically 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 found a negative interaction between the four rodent species ( $P = 0.028$ ). This negative interaction between the four rodent species on offshore islands is frequently reported (Taylor, 1978, 1984; Atkinson, 1986; Yom-Tov *et al.*, 1999). Similarly in the Seychelles Islands, Norway rats and ship rats are not found on the same islands (Hill *et al.*, 2003). The relationship with relative seabird richness may reflect the need for an abundant food supply to prevent resource competition with the other rodent species, or competition and predation upon burrowing seabirds (Atkinson, 1985).

### Ship rats

Because ship rats have dispersed widely and successfully throughout the New Zealand archipelago (Atkinson, 1973; Innes, 1990) their distribution may reflect a larger number of limiting factors, compared to less widely dispersed species whose distribution may remain a relic of human-mediated introduction or interspecific interactions between rodent species. The fact that area is significant without biological habitat diversity suggests that the number of individuals and associated probability of extinction is the limiting factor (Gotelli & Graves, 1996). The significant negative relationship with elevation could be explained by the lower invasibility of offshore islands with high peaks, or an unknown component of these islands for which this might be a good surrogate. Within the New Zealand landscape, the islands with the highest elevation also happen to be the best preserved, retaining

a high degree of ecological intactness. It is possibly because of this intactness that these islands are less likely to be invaded. The significance of distance from source suggests that 'stepping stone' islands play a role in island dispersal (whether natural or human-mediated), as has been suggested within island groups (Atkinson, 1986). Certainly distance from a source population is a governing factor in the likelihood of ship rat presence on an island. Geological diversity has been proposed as a surrogate for floral complexity (Wardle, 1984), but was barely significant in the model.

Originally ship rats reached New Zealand islands from ships moored to wharves (Atkinson, 1985; Innes, 1990), so it is not surprising that the presence of a wharf is a significant predictor of ship rat presence, as others have suggested (Bell, 1978). Since then they have established successfully throughout the mainland, and naturally dispersed to islands. The presence of ship rats is further significantly related to whether an island is inhabited. This supports the common observation that ship rats are commensal with humans (Atkinson, 1985). A permanent island settlement with a landing structure would have had ships moored to it often, allowing ample opportunities for ship rats to come ashore. Ship rats are less likely to be on islands with other settlement types. For the less intensive settlement types of unmanned farm and ranger stations this is probably reflected by the relative infrequency of ship visits. Abandoned settlements (those which were once inhabited) might also reasonably be expected to have a higher likelihood of ship rat presence, but this is not so. It may be that the settlements did not persist long enough for invasion to occur.

As for Norway rats, there appears to be a negative interaction between 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 in New Zealand (Atkinson, 1986; Yom-Tov *et al.*, 1999; Innes, 2001). The prevalence and dominance of ship rats in the New Zealand environment provides a stark contrast to the case in Europe, where ship rats have recently undergone considerable range reduction (Pucek, 1989). In the United Kingdom ship rats were recently recorded only on two offshore islands, though reasons for this range reduction are unclear given the species' status globally (Innes, 2001). Atkinson (1985) found from records of rodents on ocean-going vessels that ship rats dominated until 1700, when Norway rats became the prevalent rodent on vessels. This coincides with the invasion of the United Kingdom by Norway rats in the early 1700s. The prevalence of Norway rats on vessels continued until 1850, when a greater number of records revealed both species. As a result, Norway rats were the primary invader of most Pacific islands during colonization in the 1700s. Certainly, the interaction between ship rats and Norway rats is historically complex.

### Kiore

There have been two contrasting views regarding kiore colonization of offshore islands. Holdaway (1999) suggested human mediation, while Atkinson (1986) admits that this implied causation may in some part explain their distribution, but believes kiore have also dispersed naturally to offshore islands. Each cites

examples supporting their hypothesis. There is some evidence in the kiore model that the distribution of kiore was positively correlated with Maori occupation. Although this relationship may not be causal, it is suggestive of this, and supports Holdaway's view. The positive relationship between kiore presence and island distance initially appears to contradict Atkinson's hypothesis of natural dispersal, but it is possible that a more complex process is operating than can be seen in what is essentially a simplified linear model. Indeed 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, which 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. Bramley (1999) found that kiore avoided various signs of 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 marked contraction in the once-widespread distribution of kiore in New Zealand (Atkinson & Moller, 1990), probably caused by competitive interactions with ship rats (and to a lesser extent Norway rats) colonizing near-shore islands and driving the kiore populations on them to extinction. There are only a few documented cases in New Zealand of 'kiore only' islands, which have resisted invasion by the other rat species (Roberts, 1991b). This invasion of inshore islands would have left kiore only on distant islands where they originally arrived with Maori travellers, as kiore can only swim up to a few hundred metres (Whitaker, 1974). Similar exclusion has occurred on most of the mainland, where the spread of ship rats coincided with the final disappearance of kiore (Atkinson, 1973). The range contraction of kiore in New Zealand contrasts with their native range in South-east Asia where range expansion is still occurring, including to offshore islands (Motokawa *et al.*, 2001), probably reflecting the incumbent advantage as the native rat species.

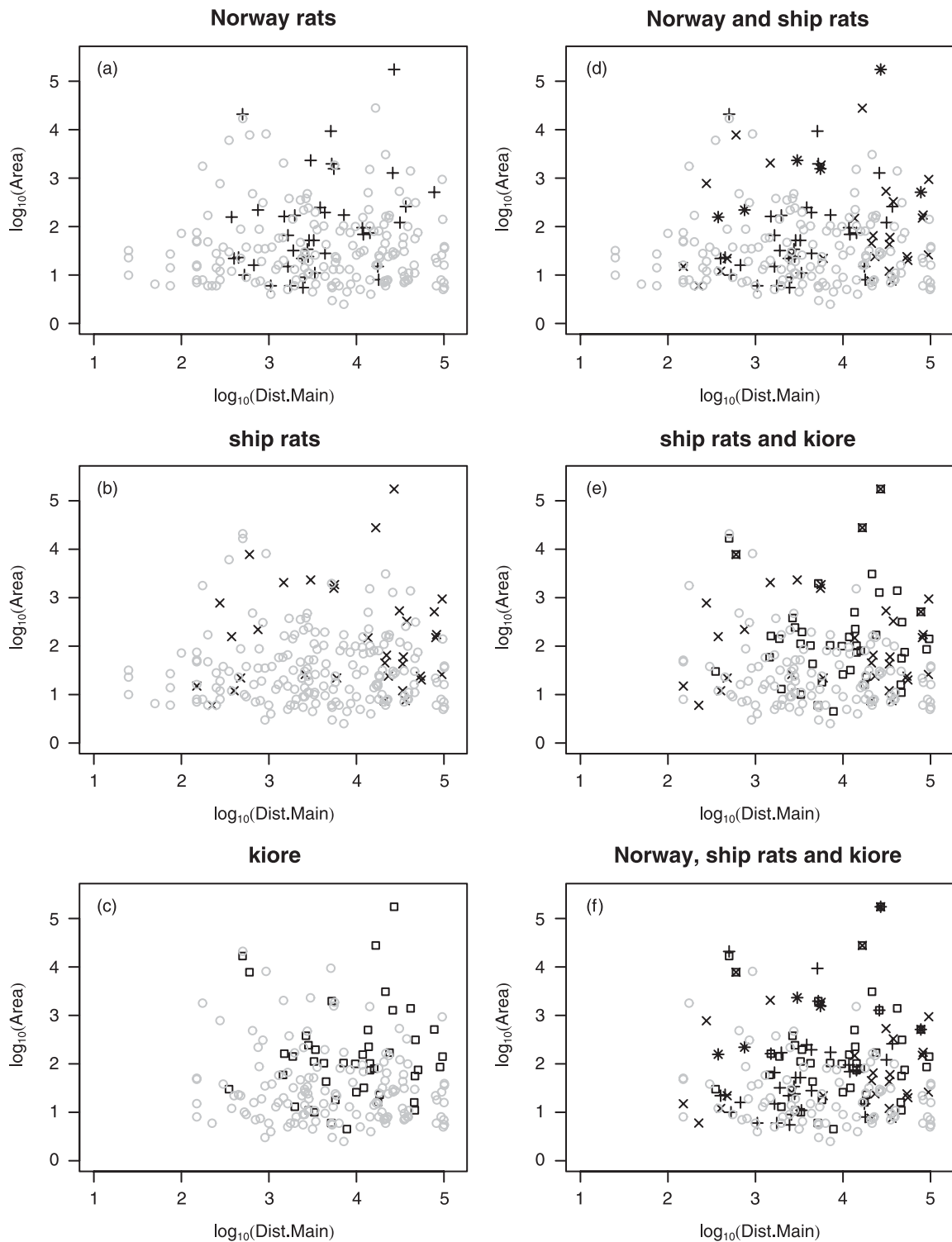
### Mice

Other studies have found the distribution of mice equally perplexing (Taylor, 1978). Through examination of distributions it has been found that Norway rats and mice do not often occur together on offshore islands. This result prompted Taylor (1978, 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 the distribution of mice on islands. This appears not to be the case on the mainland where there is a reciprocal relationship between the distributions of ship rats and mice (Innes, 2001). It is generally assumed that humans accidentally transported mice to New Zealand offshore islands (Taylor, 1975, 1984), but in many cases the populations did not expand or establish (Murphy & 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 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 (Fig. 2) in Foveaux Strait following the wreck of the *Elizabeth Henrietta* in 1823 (Murphy & 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 (Murphy & Pickard, 1990). In the United Kingdom the house mouse competes poorly with other rodents, and is largely a commensal species, along with the Norway rat (Langton *et al.*, 2001). On the New Zealand mainland-Taylor (1975) noted a negative interaction with Norway rats, but we did not detect this. Co-existence with Norway rats was found in New Caledonian nature reserves (Rouys & Theuerkarf, 2003). This result highlights the difficulties of managing mouse invasion of islands.

### Interactions

As discussed earlier, all four species of rodents are considered to interact to some extent (Innes, 1990). This is evident from their distribution across New Zealand, with no location where all four species occur sympatrically (Taylor, 1978; Atkinson & Towns, 2001). This has been observed on other islands (Hill *et al.*, 2003) because the realized distributions are the outcome of interspecific interactions between very similar species (Fox & Fox, 2000). The coexistence of these multiple species with similar niche requirements on islands is possible though, because as well as interspecific interactions, differing dispersal abilities also facilitate coexistence (Lomolino, 2000), as do possible lag times in extinction as a response to invasion (Tilman *et al.*, 2002), although the severity of biological invasions suggests this would only be in the order of years. Incumbent advantage (priority effect) may also prevent ecologically dominant invaders from establishing on new islands (Granjon & Cheylan, 1989; Lockwood *et al.*, 1999), in a manner which suggests that ecological assembly rules (Diamond, 1975) could play a role in determining the distribution of all four rodent species across New Zealand. This would explain the persistence of competitively inferior guild members on islands that the superior species is unable to colonize, as others have found (Lomolino, 2000). Given the above mechanisms, insular distribution functions (Lomolino, 2000) for all three rat species can be constructed (Fig. 2). This is possible because all three species were at one stage thoroughly dispersed throughout the New Zealand archipelago, with equal opportunity to colonize all offshore islands. In this case the functions do not illustrate resource limitations but the current outcome of dispersal opportunities and subsequent interspecific interactions. These outcomes may be dictated by first arrival (chance) or conferred by some competitive advantage (Whittaker, 1998). All three rat species have different insular distribution functions (Fig. 2a,b,c). Interactively Norway rats appear to persist on mid-distance islands, which they are better able to swim to when compared with ship rats, although some coexistence appears possible on larger islands (Fig. 2d). Ship



**Figure 2** Insular distribution functions of (a) Norway rats (b) ship rats (c) kiore (d) joint Norway and ship rats (e) joint ship rats and kiore and (f) all three rodent species (Norway, ship rats and kiore). + Norway rats, x ship rats, □ kiore, ○ absence. Area = Island area in hectares, Dist.Main = Island distance from the mainland in metres.

rats and kiore have the most noticeably exclusive distributions (Fig. 2e), although once again some coexistence occurs on larger islands. Overall, all three species appear able to coexist only on larger islands, with distribution amongst smaller islands appear-

ing generally random (Fig. 2f). Ship rats and kiore exist on islands well outside their natural swimming range — most likely a result of human transportation, while Norway and ship rats appear to be the only species swimming to closer offshore islands, at which



the Norway rat is considerably more adept. This matches current ecological thinking for these species in New Zealand. These insular distribution functions may appear to have limited value when ship rats were the only species where area and isolation were found to be limiting factors, attributed to them having obtained these limits, however, as the subdominant species Norway rats and kiore may have suboptimal ranges where area and isolation do not control distribution, which is instead more heavily mediated by the distribution of the more dominant ship rat. It is noteworthy that all four species of rodents studied here do coexist in the less severe environment of tropical Pacific Islands (Roberts, 1991a). Interactions between rodent species can also manifest themselves at the more subtle level of changes in density, particularly so for mice (Innes, 2001). Although the models presented here have shown cases of complete exclusion (particularly for kiore), it is likely that other rodent interactions at the level of density are occurring that we cannot detect.

The exact nature of these interactions has never been fully addressed though. The disappearance of kiore from the New Zealand 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 niche exclusion (Taylor, 1975) and the similar response that both mice and kiore (but not the other two rodent species) exhibited to beech (*Nothofagus* spp.) mast seeding (Murphy & Pickard, 1990). However it has recently been found that ship rats also respond to mast seeding of beech (King & Moller, 1997), 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 that 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 weak given that competition also occurs between species of quite different body sizes, and these two species are in fact not entirely overlapping in size. It has also been suggested that the spread of Norway rats partly influenced the decline of kiore (Wodzicki, 1950). This partial influence seems likely, given that negative rodent interactions were only found for the three rat species, and the inclusion of Norway rats individually was barely significant in the kiore model. However, Norway rats also appear to be substantially affected by rodent interactions, as the negative rodent interaction term in their model was most significant of the three rodent models. This is unusual considering its dominance over ship rats in Europe (Atkinson, 1985; Pucek, 1989).

Atkinson & Moller (1990) review three alternative hypotheses for the decline of kiore: competition with the other two *Rattus* species; introduction of trypanosomes (*Trypanosoma lewisi*) by rats from Europe; and competition with mice. They do not take a firm stance on any of these, but indicate a possible combination

of the first and third. The results found here support the first hypothesis, that the absence of kiore is most strongly linked with the presence of ship rats, and also (less so) with the presence of Norway rats. All three species negatively interact with each other, but it is not possible to determine precisely cause or effect. The available literature suggests the arrival of ship rats was a causal factor in kiore decline (Atkinson, 1973) and in this study the distribution of kiore was most negatively related to the distribution of ship rats. This is not the case on the large island of New Caledonia, where ship rats and kiore were found to coexist, in the absence of commensal Norway rats and mice (Rouys & Theuerkarf, 2003). According to the second hypothesis, kiore became hosts in New Zealand to parasites of the other rodent species, and these may have also contributed to their decline. However the persistence of kiore on islands infected with such parasites suggests this is not the case (Roberts, 1991b). We found that kiore distribution on New Zealand islands is not in any way affected by the distribution of mice, discounting the third hypothesis. Yom-Tov *et al.* (1999) warn that their evidence of interactions is only circumstantial, and likewise here no causation can be established from the results. However, in light of the circumstantial evidence of interactions accumulating, it would appear that the absence of kiore on offshore islands is currently most strongly influenced by the presence of ship rats.

The variables which were not significant in any of the four models also warrant discussion. The non-significance of biological habitat diversity suggests that the distribution of rodents across New Zealand islands is not limited by habitat availability. This does not necessarily mean they are in every habitat, but that at the current magnitude of expansion they have not encountered any habitats in significant numbers to appear limiting in these models. The non-significance of higher level mammal interactions suggests that within the complex modified ecosystem relationships occurring on islands with introduced mammals, the relationship between rodents and all other mammals is not particularly significant compared with other introduced mammal interactions that have been reported (Veitch & Bell, 1990; Imber *et al.*, 2000). The significance of inhabited islands alone, and no other levels of settlement, probably reflects pathways more than land use. Inhabited islands, by virtue of high visitation, provided a means for invasion that other islands did not. This has been well established already (Atkinson, 1986; Atkinson & Taylor, 1991; Russell *et al.*, 2004).

It is important to consider spatial scale in studies such as these, where scale dependence will be a controlling factor (Lomolino, 1999, 2000). A representative range of islands must be included in such studies (Lomolino & Weiser, 2001) so that all scales of variables are covered. Because the sample for this study was the population of islands larger than five hectares in New Zealand, it is expected that the relative importance of each explanatory variable has been established within the context of the entire New Zealand archipelago.

The results of this study highlight the significance of various factors (natural and anthropological) in governing the distribution of introduced rodents on offshore islands, and those factors which facilitate invasion. Interaction between the presence of introduced rodent species was also shown to be significant for some

species. The knowledge that this provides can aid management of offshore islands reserves for conservation by identifying those characteristics of islands that should be more heavily weighted when considering procedures to prevent rodent invasion or re-invasion following eradication.

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## BIOSKETCHES

**James Russell** completed his MSc in Geography & Environmental Science in 2002 before working for the Invasive Species Specialist Group (ISSG) of the IUCN based at the University of Auckland, New Zealand. Currently James is researching for his PhD jointly in Biology and Statistics at the University of Auckland. His research into the 'Invasion ecology of rats on New Zealand Islands' will incorporate statistical risk profiling of islands and field-based releases of rats onto islands followed by statistical modelling of the invasion.

**Mick Clout** is Professor of ecology in the School of Biological Sciences, and heads the Invasive Species Specialist Group of the IUCN based at the University of Auckland. His research investigates the effects of invasive species on conservation biology.