



Insular pest control within a metapopulation context

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ABSTRACT

Introduced pests threaten many species and their control is generally beneficial for conservation, particularly on islands where complete eradication is possible. Unfortunately on 'nearshore' islands neighbouring source populations exist and unaided reinvasion is likely. Pest control programmes at these sites thus require a metapopulation context to adequately manage movements between source and sink populations. We investigated the ecology of introduced ship rats (*Rattus rattus*) on a nearshore island, and gene flow with adjacent mainland populations, in order to understand the metapopulation dynamics and relative levels of pest control required within the landscape. We sampled the entire population by trapping ($n = 30$), achieving eradication, and found a low rat density (3.2 ha^{-1}) indicative of a sink population. Seed and other plant material constituted the major dietary component of rats. Despite its proximity to mainland source populations, the island population was genetically distinct with reduced allelic diversity caused by a recent reinvasion founder effect. Genetic analyses also detected recent migrants between the populations. In contrast, two mainland populations separated by a similar distance displayed complete genetic mixing. The small water gap therefore provides a sufficient barrier to lower the migration rate to the island and delay reinvasion, which nonetheless eventually happens. In order to maintain nearshore islands pest-free, conservation management will require a metapopulation approach simultaneously focusing on both island and source population pest control.

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1. Introduction

Pest control is an important management tool for conservation of threatened species, particularly so on islands, where introduced species are the primary agent of decline (Veitch and Clout, 2002). Unfortunately local removal of a population is often only temporary, creating a vacuum which can be soon reinvaded by immigrants from neighbouring populations (Parkes and Murphy, 2003). Whole island eradications of many pest species are possible (Clout and Russell, 2006), and are preferable to ongoing control operations (Pascal et al., 2008), when the islands are unlikely to be reinvaded. However, as eradications become more common, the ability of pests to recolonise unaided over surprisingly large water gaps is becoming apparent (e.g. Russell et al., 2005). This poses a substantial problem for conservation on islands close to large land masses which act as source populations for reinvasion

(e.g. Møller, 1983; Cheylan et al., 1998). Because of the ongoing threat of reinvasion, these 'nearshore' islands are often overlooked for conservation, in deference to more isolated islands. Nearshore islands may not have the high endemism rates of isolated islands (Grant, 1998), yet they can account for substantial potential conservation estate. In New Zealand, 128 offshore islands accounting for over 50% of the total island area (75,000 ha) can be classified as 'nearshore', i.e. within 2 km of one of the three main islands of New Zealand. These islands are currently considered difficult for conservation since introduced pests can colonise many of them unaided by humans (Russell et al., 2004), and so pest populations often remain unmanaged on them.

When distinct populations of pests can be identified, such as those on islands and nearby reinvasion source populations, classical metapopulation dynamics will occur (Hanski, 1999). Islands will generally act as 'sink' populations, with increased rates of species turnover and extinctions (Brown and Kodric-Brown, 1977), whereas mainland populations should act as more stable 'source' populations for recolonisation of islands. Eradication for conservation purposes further and artificially increases the rate of species 'extinction' on islands. Management of islands where recolonisation is possible thus requires a metapopulation context (e.g. Abdelkrim et al., 2005a). Additionally, island populations are likely to function differently to those on adjacent mainlands due to island

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biogeographic mechanisms of area and isolation (Adler and Levins, 1994). This should particularly be the case on small islands, as it is for species richness (Lomolino and Weiser, 2001). However, on small islands immigration from neighbouring populations can supplement the population, reducing isolation, and buffering against demographic and genetic stochasticity, preventing extinction and inbreeding (Frankham, 1998).

Globally, three species of invasive rats have been introduced to over 80% of the world's archipelagos (Atkinson, 1985) and are responsible for many species extinctions (Townsend et al., 2006). Ship rats (*Rattus rattus*) have invaded at least 50% of these archipelagos. The eradication of invasive rats is now a common management tool for island restoration (Howald et al., 2007), though the greatest successes in eradication have been with Norway rats (*Rattus norvegicus*). In New Zealand ship rats have been extensively studied on the three main islands, (e.g. Innes, 2005 and references within), hereafter referred to as the 'mainland'. Ship rats have been eradicated from a number of islands (Clout and Russell, 2006) but have not been as extensively studied upon them. Considering ship rats are the dominant rat species on many larger islands of New Zealand (Russell and Clout, 2004) a greater understanding of their population biology on these islands would benefit conservation management (Sakai et al., 2001), as it has elsewhere (e.g. Cheylan et al., 1998).

We investigated the ecology and metapopulation dynamics of a small population of introduced ship rats on a nearshore island where reinvasion from the mainland had previously occurred rapidly following an earlier eradication. Given the previous rapid reinvasion, no further conservation management was anticipated on the island until such time as an adequate level of mainland pest management could be matched to prevent reinvasion. We wished to ascertain this relative level of effort required to maintain the island pest-free within a wider metapopulation context of mainland and island pest control, by comparing populations. We trapped the island population to extinction as part of an eradication program. This enabled us to describe the population structure, morphology, breeding biology and diet of the entire island population, in order to ascertain its status as a 'sink' population. We then analysed metapopulation structure and gene flow by comparing neutral polymorphism at nine microsatellite loci with adjacent mainland populations, and parentage within the exhaustively sampled island population. This allowed us to assess the relative permeability of land and water to dispersal and population mixing, and ultimately the overall metapopulation dynamics of our study site.

2. Methods

2.1. Study site

Goat Island (Motu Hawere; 9.3 ha; 36°16S, 174°48E; Fig. 1) is a Scientific Reserve situated in the Cape Rodney-Okakari Point Marine Reserve, Leigh, adjacent to the University of Auckland Leigh Marine Laboratory in northern New Zealand. Public access is discouraged although visitors to the reserve frequently use the large flat rock platform on the south-western side of the island. At low tide the channel between the island and mainland is only 50 m, well within the swimming range of introduced rats and mustlids present on the adjacent mainland. Rats have been present on the island since at least 1970 (Esler, 1975), although probably arrived much earlier. Craig (1977) recorded densities of around 12–20 ha⁻¹. In 1994 rats were eradicated from the island by Department of Conservation staff but were re-detected in 1996 (Clout and Russell, 2006). The vegetation of the island was described by Esler (1975) as a coastal fringe of pohutukawa (*Metrosideros excelsa*) forest screening shrubland further inland,

although this has now developed into regenerating coastal broad-leaf forest.

2.2. Eradication

Ship rats were eradicated from Goat Island by an exhaustive trapping regime of 50 snap-traps (Victor Professional) on a 50 m grid to recover all bodies for analysis, followed by poisoning of any survivors. Trapping took place between 26th April 2005–1st May 2005 and 20th June 2005–24th June 2005. All rats caught were weighed, sexed, assigned as adult or juvenile depending on weight and sexual characteristics, and measured for head–body length (HBL) and tail length (TL) (*sensu* Cunningham and Moors, 1996). The stomachs were removed from all rats caught and preserved in 70% ethanol for diet analysis.

On 23rd June 2005 brodifacoum (PestOff Rodent blocks, 0.02 g/kg; Animal Control Products, Whanganui) was laid across the island on a 50 m grid in 50 bait stations (baits tied under plastic covers) with five bait blocks per station. Brodifacoum pellets (PestOff 20R, 0.02 g/kg; Animal Control Products, Whanganui) were also hand-spread around inaccessible coastal cliffs at 10 kg/ha. Bait-take was monitored and the trapping grid remained active on the island to catch any surviving rats during the poisoning operation.

On 9th July 2005 10 rodent 'Protecta' bait stations (Bell Laboratories, Wisconsin) baited with six 50 g rodent blocks and a handful of sawdust and 20R pellets were placed across the island for biosecurity monitoring (*sensu* Russell et al., 2008a). On 15th September 2005 eradication was rapidly confirmed (three months) by a DOC predator control programme rodent dog (Jak and handler Fin Buchanan). Fifteen tracking tunnels and 15 waxtags were additionally placed on the island to monitor for reinvasion. From May 2006 only the 10 'Protecta' bait stations remained on the island for ongoing passive (unmonitored) biosecurity.

Rats were also simultaneously trapped to extinction with 15 snap-traps at two sites on the adjacent mainland (Fig. 1), to investigate metapopulation structure across different barriers (land and water). Traps were placed in the forested gully east of the marine reserve access road (Site A; 2.3 ha) and along the forested coastal path east of the marine laboratory (Site B; 3.9 ha), both adjacent to the coast and likely source populations for dispersal to Goat Island.

2.3. Diet

Rat stomachs were opened and their contents washed into a 500 µm mesh sieve with a 250 µm mesh sieve beneath. A jet of water was then used to rinse the stomach contents to remove any finely chewed matter. The contents of the 500 µm sieve were then examined under a dissecting microscope and the contents assigned to groups and classified according to volume (trace (<10%); medium (10–50%), large (>50%); *sensu* Moors, 1985). The 250 µm only contained small fragments of the same contents found in the larger sieve. All nematodes present were collected and counted and any easily recognisable items (e.g. insect pupae) were collected and counted.

2.4. Genetics

Genomic DNA was extracted using the DNeasy 96 tissue kit (Qiagen). Nine microsatellite markers characterised for *R. norvegicus* genome mapping (Jacob et al., 1995), but suitable for *R. rattus*, were used (D15Rat77, D18Rat96, D20Rat46, D2Rat234, D11Mgh5, D10Rat20, D5Rat83, D16Rat81, and D19Mit2). To avoid physical linkage markers were chosen on different chromosomes. Each forward locus primer was labelled with fluorescent dyes before amplification by polymerase chain reaction (PCR). PCR was per-

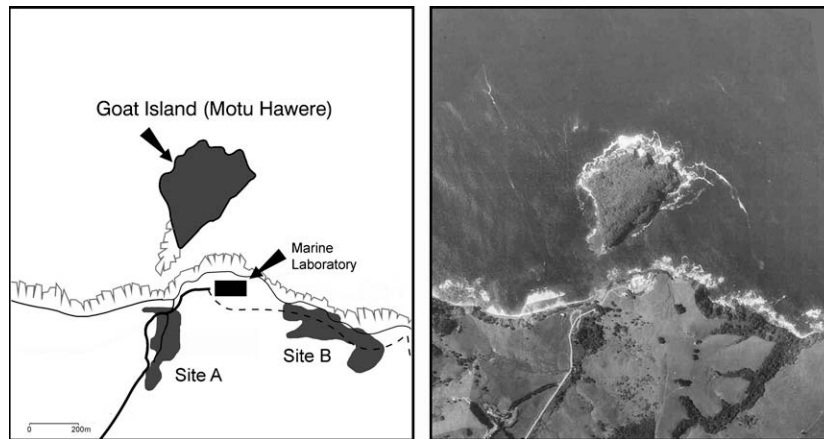


Fig. 1. Goat Island and adjacent mainland sites. Leigh Marine Laboratory buildings indicated. Shading indicates forested rat-trapping locations. Aerial photo sourced from Orthophoto R09 Warkworth. Crown Copyright Reserved.

formed in 10 μ L volumes, containing 1 μ g DNA, 0.1 μ M of one primer labelled with 5' fluorescent labels and 0.2 μ M of the other primer, 0.2 μ M of each dNTP, 1 unit *Taq* polymerase, and 1 \times reaction buffer with 1.5 mM MgCl₂. PCR products were pooled for a single run using an ABI prism 310 capillary electrophoresis system (Applied Biosystems). Amplification size was scored using GENE SCAN ANALYSIS V.3.1.2.

Standard genetic parameters were computed to estimate genetic diversity within each sampled site (one island and two mainland sites). In each case, the mean number of allele per loci, allelic frequencies, observed and expected heterozygosities (Nei, 1973) were calculated. Significant deviations from Hardy–Weinberg expectations were assessed with a Fisher's exact test of Hardy–Weinberg proportions (Weir, 1996, p. 98). We also compared the allelic diversity between the insular population and each of the mainland samples with one-tailed (expecting fewer alleles in the island population) paired *t*-tests of the number of alleles at each locus. The level of genetic differentiation between each pair of sites was estimated using F_{st} parameters (*sensu* Weir, 1996) and their significance level was tested by making 10,000 permutations of genotypes among samples using MSA (Dieringer and Schlötterer, 2002).

Spatial structure in genetic variation across Goat Island was tested for by comparing the genetic distance matrix (g_{ij}) for all rats with their spatial capture distance matrix (s_{ij}). Genetic distance was measured for every pair of rats using the similarity measure proposed by Chakraborty and Jin (1993) which estimates the proportion of shared alleles between each pair of rats. Spatial distance was taken as the true (Euclidean) distance between capture sites for each pair of rats. We then assessed spatial genetic structure using a Mantel test (Manly, 1985, p. 176) with 10,000 permutations of the spatial matrix. Genetic variation across the island was considered non-random if the observed test statistic was significant at the 5% level. We then investigated genetic similarity among individuals of all three populations, but regardless of population assignment, using the same similarity measure. A principal coordinate analysis was then performed on the resulting distance matrix (i.e. multi-dimensional scaling) and the results plotted in reduced space.

Parentage of individuals on Goat Island was investigated by classifying individuals into two cohorts (candidate parents and offspring) based on morphological characteristics. Then, for each offspring, parentage was assigned using the two-stage process implemented in the software CERVUS (Marshall et al., 1998). This method is particularly appropriate for our dataset since a clear

age structure is defined and a high proportion of the population was sampled, but we do not have any known parent–offspring bonds. We ran the program four times, giving the first assignments alternately to males and females, and for each sex using two different confidence levels of assignment (strict 95% and relaxed 80%). We assumed our observed value of 5% for typing errors. Cross-assignment of parentage between island and mainland populations was also investigated by the same method.

To test if the recent reinvasion of Goat Island still impacted genetic diversity of the population, we used three different methods to detect a bottleneck. The first method is based on the detection of 'heterozygosity excess'. In a recently bottlenecked population, the observed heterozygosity is higher than the heterozygosity expected from the observed number of alleles under the assumption of a population at mutation-drift equilibrium (Cornuet and Luikart, 1996). The results obtained separately for each locus were combined using the Wilcoxon test (Cornuet and Luikart, 1996; Piry et al., 1999). Secondly, we used a qualitative descriptor of allele frequency distribution (the mode-shift indicator). For a stable population, it is assumed that rare alleles are the most common, whereas in a recently bottlenecked population, intermediate classes are better represented (Luikart et al., 1998; Luikart and Cornuet, 1998). A shift in the mode of the distribution of allelic frequency classes is thus expected. For these two methods, analyses were performed using BOTTLENECK v1.2.02 (Piry et al., 1999). The third method (Garza and Williamson, 2001) uses the ratio M of the number of alleles to the allele size range. The observed value is compared to a distribution obtained by simulating 10,000 times a population at equilibrium. The test is significant if more than 95% of the simulated values are superior to the observed value. The value of M and its significance level were computed using the software MPVal (Garza and Williamson, 2001). For all tests, a two phase model (TPM) was assumed with 90% of single-step mutations (mutations that increase or decrease the size of the allele by one repeat) and 10% of multi-step mutations, with an exponential distribution of step numbers having an average of 3.5 steps, following the authors' suggestions (Piry et al., 1999; Garza and Williamson, 2001).

3. Results

3.1. Eradication

A total of 30 ship rats (3.2 ha⁻¹) were caught on Goat Island during the intensive trapping to extinction. On the mainland 23

ship rats were caught at Site A and 39 at Site B, corresponding to at least 10 ha⁻¹ in each forest patch. Both alexandrinus and frugivorus morphs were caught in all populations, although the distinction was not clear. A single adult (weight = 200 g) Norway rat (*R. norvegicus*) was caught around marine laboratory buildings.

Ship rats less than 120 g were classified as juveniles. On Goat Island more adults than juveniles were caught, but roughly the same number of adults and juveniles were caught on the mainland. No significant difference was detected between the number of males and females on Goat Island (two tailed binomial test, $p = 0.57$), although the small number of adult male rats on Goat Island were significantly heavier ($F_{1,51} = 10.06$, $p < 0.01$) and longer (HBL; $F_{1,51} = 5.52$, $p = 0.02$) than all other rats (Table 1). Three pregnant females (litter sizes 5, 6 and 8) were caught on Goat Island in April indicating late autumn breeding. The tail tips of eleven rats (37%) on Goat Island were white (5 mm), presumably a genetic mutation. Three rats (5%) on the mainland also displayed this abnormality.

Reinvasion of the island was detected by the passive biosecurity devices in May 2007, within 2 years of our eradication.

3.2. Diet

Fruit and seeds dominated the stomach contents of rats from the island (Table 2) but a large number of stomachs were almost completely empty. All seed material found in the stomachs had been well chewed and no whole seeds were found. No differences were found between males and females for the quantity or type of stomach contents ($F_{1,42} = 0.40$, $p = 0.53$). One rat had digested meat in its stomach and another had a single feather but no other trace of animal or bird material was found. Insect remains were found in 46% of stomachs but only one stomach had a large (>50%) volume of insect matter. Two nematode species were present in 58% of rat stomachs.

3.3. Genetics

Missing data occurred for just under 5% of loci typed. Significantly fewer alleles were detected on Goat Island (mean 3.2; range 2–4) compared to both mainland populations ($A = 6.0$, range 5–8, t_8 , $p < 0.01$; $B = 5.7$, range 3–9, t_8 , $p < 0.01$). Only two (Goat Island and Site B) or three (Site A) loci departed from Hardy–Weinberg Equilibrium ($p < 0.05$). Most alleles were shared between the two mainland populations. Moreover, almost all the alleles present in the Goat Island population were also present on the mainland. Only three private alleles at two loci were found on Goat Island, generally at low frequencies. F_{st} values were all significant but were lower between the two mainland sites (0.034, $p < 0.01$) compared to the values observed between the Goat Island population and each of the mainland site ($A = 0.213$, $p < 0.01$; $B = 0.223$, $p < 0.01$).

No correlation between genetic and geographic distances was detected in the Goat Island rat population (Mantel test, $p = 0.63$). Individuals of the Goat Island population are clearly differentiated genetically from those on the adjacent mainland (i.e. axis 1), whereas much greater mixing between the mainland populations is apparent (Fig. 2). One pregnant adult female captured on Goat

Island was genetically more similar to the mainland rats. This rat was in poor condition with evident scars, and probably a recent immigrant to Goat Island.

For eleven juveniles (six females, five males) parentage was successfully assigned (>80% confidence) for eight fathers (four with 95% confidence) and ten mothers (six with 95% confidence) (Fig. 3). Three unknown fathers (not identical) and one unknown mother were identified. These correspond to individuals no longer present on the island (i.e. death or emigration). The presence of white tail tips showed no simple inheritance pattern in the pedigree suggesting complex genetic and/or environmental expression. Six females and one male had no apparent offspring on the island. This included the apparent 'mainland' pregnant female rat. Cross-population parentage was assigned with an average success rate of 80% with relaxed confidence (80%). All juveniles except one were assigned parents from within their population. One mainland juvenile was assigned a Goat Island mother, and this female had no offspring on Goat Island.

While no significant value was observed for the M ratio method, a genetic bottleneck signature was detected on Goat Island with the two other methods used. Both a significant heterozygote excess ($p < 0.01$) and a shifted distribution of the allelic frequency classes were detected.

4. Discussion

Trapping most likely eliminated all rats from Goat Island, although it is unlikely to be successful alone on islands much larger. Because of the small size of the island eradication could be rapidly confirmed within three months of completion, much faster than the standard 2 year lay-down period (Clout and Russell, 2006). This was achieved by ongoing monitoring for survivors across the island using a combination of poison, traps, passive devices and rodent detection dogs. As we anticipated passive biosecurity devices ('rodent hotels' containing shelter, bedding, tracking cards and poison) used to prevent the anticipated reinvasion were not successful (Russell et al., 2008a), re-emphasising that biosecurity for invasive rats when reinvasion rates are high (e.g. >1 invader per annum) requires active management. Nonetheless the small water gap delayed reinvasion from neighbouring populations which is usually within six months for mainland rat control programmes (Innes et al., 1995).

Rats were morphologically typical of New Zealand ship rats (Innes, 2005). However, only a small number of large male rats were found on Goat Island, and more adults than juveniles despite sampling at the end of the breeding season. This may indicate male-biased juvenile dispersal, as occurs in other mammal populations (Hansson, 1991), or alternatively elevated juvenile mortality. Adult male rodents commonly guard multiple females, possibly excluding juvenile males from the population (Waterman, 2007). Interestingly, one Norway rat was trapped on the mainland associated with the marine laboratory buildings. Norway rats are uncommon on the New Zealand mainland but are likely reinvasers of islands (e.g. Russell et al., in press). Nonetheless ship rats have been the successful reinvasers of Goat Island, suggesting where isolation

Table 1

Body measurements (mean and range) of adult ship rats from Goat Island and adjacent mainland (pooled) following Innes (2005).

Site	Sex	<i>n</i>	Weight (g)	Head and body length (mm)	Tail length (mm)
Goat Island	M	6	183 (151–233)	189 (163–206)	220 (212–238)
	F	11	143 (120–184)	168 (148–178)	209 (186–234)
Leigh	M	19	147 (122–188)	173 (153–200)	203 (187–238)
	F	19	145 (124–182)	168 (139–184)	214 (191–235)

Table 2
Items found in rat stomachs classified by volume ($n = 26$).

Item	Trace (<10%)	Medium (10–50%)	Large (>50%)	Frequency of occurrence (%)
Seed	3	15	3	81
Fruit	2	7	6	58
Nematode	10	1	4	58
Insect	4	7	1	46
Hair	5	6	0	42
Unidentified	0	1	3	15
Vertebrate	2	0	0	8
Vegetation	0	1	0	4

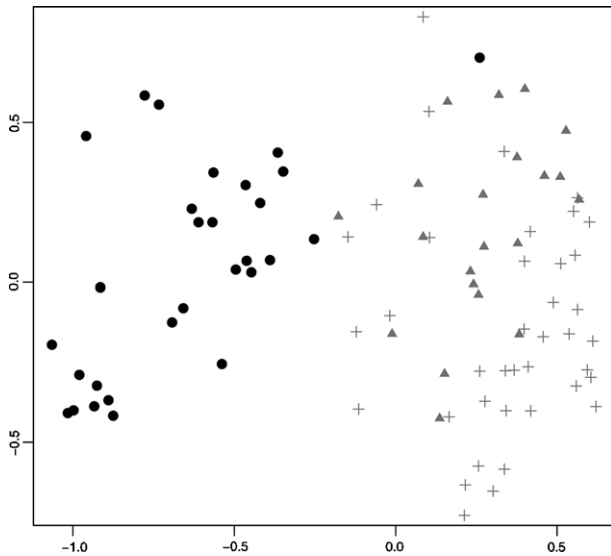


Fig. 2. Principal coordinates analysis (PCA) of the genetic similarity distance matrix for all rats (i.e. multi-dimensional scaling [MDS]). ●: Goat Island; ▲: Mainland A; +: Mainland B.

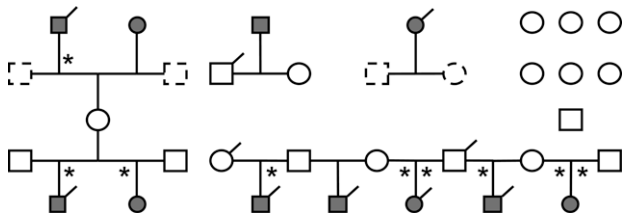


Fig. 3. Goat Island pedigree. □: Male; ○: female; shading indicates juvenile; tail indicates white tail tip. Asterisks indicate 95% confidence in assignment, otherwise 80% confidence. Dashed lines indicate unknown parent. Unassigned parents (six females; one male) are in the upper right corner.

does not affect colonisation by either species, ship rats will be the dominant reinvader (Russell and Clout, 2004).

The density of ship rats on Goat Island was unexpectedly low. Generally rodent populations on islands have elevated densities relative to equivalent habitats on the mainland (Adler and Levins, 1994). However, our density estimate on Goat Island was more similar to other mainland density estimates (Dowding and Murphy, 1994; Hooker and Innes, 1995; Brown et al., 1996; Wilson et al., 2007). Diet analysis of rats caught in March on Stewart Island, New Zealand found that the diet of female rats contained significantly more animal material than that of mature males (Gales, 1982) whereas no differences were found in this study. The general lack of invertebrate material found in stomach contents is also unusual compared to other studies, although in native forest rats

tend to eat more plant food in winter (Innes, 2005). Simultaneous research on Goat Island found low soil fertility and arthropod biodiversity (Fukami et al., 2006; Towns et al., in press), as has been found on other rat invaded islands in New Zealand (Fukami et al., 2006; Harper, 2006). Pan-trapping studies carried out on Goat Island in 1999 and 2000 found invertebrate communities dominated by amphipods with low numbers of other invertebrates (Ussher, 1999, 2000). This suggests that Goat Island is a relatively poor quality habitat for rats, more characteristic of degraded mainland forest patches. Indeed, two male Norway rats subsequently released on the rat-free island swam to the adjacent mainland within one month (Russell et al., 2008a).

Seed predation by introduced rats on islands off northern New Zealand is known to depress recruitment of vulnerable species (Campbell and Atkinson, 2002). An abundant cohort of young *Pseudopanax lessonii* and other plant species corresponding to the previous rat-free period (1994–1996) was found across the island (pers. obs.), suggesting that rats were having a significant impact on the forest structure. The two nematode species we found are likely to be those reported from rat stomachs in New Zealand; *Physoleptera getula* and *Mastophorus muris* (Charleston and Innes, 1980; Innes, 2005). The infection rate of rat stomachs on Goat Island by nematodes was usual for ship rats in New Zealand (Charleston and Innes, 1980; Clout, 1980; Miller and Miller, 1995). No sign of grey-faced petrel was found in rat stomachs despite abundant prospecting adult birds, but our study did not coincide with the chick-rearing phase where rats may consume fledglings (Imber et al., 2000).

Genetic analysis revealed significant population isolation of Goat Island from the adjacent mainland populations, with a high F_{st} and significantly reduced genetic diversity, characteristic of a founder effect with low ongoing immigration. Similar genetic results for ship rats were found on Western Mediterranean island populations at the same distance offshore (<100 m; Cheylan et al., 1998), although we found lower genetic diversity likely correlated with the lower rat density on Goat Island. The M ratio has most power for detecting historical bottlenecks, whereas the two significant methods here are more powerful for detecting recent bottlenecks, such as the recent reinvasion of Goat Island (Abdelkrim et al., 2005b). Such a founder effect could also explain the abundance of the white tail tip abnormality which is less common on the mainland. This phenotypic trait could have been, by chance, over represented in the limited number of founders and thus widely spread in the next generations. In contrast, the two mainland sites were genetically mixed with low F_{st} , despite separation by 400 m of grazed pasture and intermittent poisoning around the marine laboratory. Identifying the most likely source population of immigrants to Goat Island was not possible due to the thorough genetic mixing of the mainland populations. Nevertheless, there is no doubt that founders came from one (if not both) of these sites as the genetic diversity observed on Goat Island is clearly a sub-sample of the diversity observed on the mainland.

Parentage analysis can reveal mating systems (Jones and Ardren, 2003) and metapopulation dispersal (Telfer et al., 2003). On Goat Island rats had multiple mates, indicating a promiscuous mating system, and juvenile survival was apparently low, typical of rodents (Solomon and Keane, 2007; Waterman, 2007). Although ship rats have large litter sizes, on Goat Island no more than a single offspring from any parent-pair litter appeared to have survived. However, this excludes any half-siblings that may have occurred in single litters with multiple paternity. The parentage analysis also suggested that at least one parent-offspring pair was cross-population. One of the individuals may have migrated following birth, or alternatively the genetic signal may indicate a more diffuse F_1 generation descent from a historical migrant.

The management of 'nearshore' islands requires a metapopulation approach for conservation management (Cheylan et al., 1998). Like their mainland reserve counterparts, ongoing resources are required to maintain these 'eradicated' islands free of pests. Island biosecurity protocols (e.g. Russell et al., 2008b) are able to protect islands with arrival rates greater than one per year, but when islands are very close to source populations, island biosecurity will require complementary pest control in adjacent mainland source populations. On Goat Island, the mainland source population density was much higher than the pre-eradication island density, revealing that to maintain the island pest-free following eradication, relatively more pest control effort would be required within the source populations. Identifying these source populations, particularly for cryptic species, can be difficult (e.g. Russell et al., in press) and can benefit from genetic analyses (e.g. Cheylan et al., 1998; Abdelkrim et al., 2005a). Focusing on source population control targets individuals before they can become potential dispersers (e.g. Fig. 1 in Russell et al., 2007). Furthermore, the effects of island size, isolation and relative immigration rates on population dynamics will differ between species. For such metapopulations further research is required on the relative trade-offs between pre- (source) and post- (island) arrival biosecurity efforts given limited resources.

For nearshore islands there is little benefit in seeking absolute 'eradication'. Instead, focus should be on ensuring that ongoing control operations at both the island and source population sites maintain the target pest species below a critical threshold at the conservation site (i.e. the island) (Parkes and Murphy, 2003). Adaptive management would allow control programmes to change the relative levels of investment between island and source populations in future given site-based experience.

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