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INVASIVE RODENTS ON ISLANDS

Early colonisation population structure of a Norway rat island invasion

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Abstract Colonists undergo non-equilibrium processes such as founder effects, inbreeding and changing population size which influence the mating system and demography of a population. Understanding these processes in colonising populations informs management and helps prevent further invasions. We sampled and genotyped most individuals of a Norway rat (*Rattus norvegicus*) reinvasion on Moturemu island (5 ha) in New Zealand. Population size was most likely between 30 and 33 rats. Genetic methods detected a clear bottleneck signal from the founding population. Parentage assignment revealed promiscuous mating dominated by a few individuals with increasing inbreeding, both putatively a result of small island size. Combining ecological and genetic data from a single sample allowed inferences on population structure and functioning. Invading Norway rats rapidly achieve population structure similar to established island populations despite a small number of colonists and associated inbreeding. Overcoming these initial obstacles to population establishment contributes to the global success of invasive rats.

Keywords Bottleneck · Catch-effort · Founder effect · Inbreeding · Parentage · Removal

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Introduction

Invasions of non-native species continue to increase around the world and are a leading cause of global biodiversity loss (Vitousek et al. 1997). Individuals colonise new locations, establish populations and can rapidly expand (Colautti and MacIsaac 2004). Understanding the early stages of the colonisation growth curve is important for the management and prevention of invasion, for instance, how many invaders are needed for colonisation, and what is the best way to control them prior to establishment. Unfortunately this period of invasion is the least commonly studied (Puth and Post 2005), as once most invading populations are detected, let alone of sufficient sample size for study, populations are usually well established.

Population biology and genetics can give complementary insights to invasion processes (Sakai et al. 2001), and many methods are now available to analyse population structure and functioning (Excoffier and Heckel 2006). However, invasions generate rapid changes in population size and density associated with

population foundation and expansion, which creates specific conditions where many methods that assume stable population size, structure, and functioning, may not be appropriate for investigating invasion dynamics (Estoup et al. 2001; Herborg et al. 2007). Therefore equilibrium analytical methods must be cautiously tested on invading populations with known history.

Islands have always provided valuable opportunities to study invasion dynamics, partly because the number and impact of invasions have been perceived as greater on islands (Allen et al. 2006). Islands also allow explicit definition of the spatial extent of invasion, something which can be difficult elsewhere. Islands therefore provide a valuable unit of study in biological invasions as the area of invasion is exactly defined, and by reducing the scale of investigation to small island systems sampling a large proportion of the population is possible (D'Antonio and Dudley 1995).

Invasive rats are one of the most prolific invasive species, having colonised over 80% of the world's island groups (Atkinson 1985). Their impacts on the flora and fauna of island ecosystems have been devastating, often resulting in species extirpation or extinction (Towns et al. 2006). The magnitude of these impacts has been attributed to the plasticity in rats which allows them to colonise and persist in almost any habitat (Jones et al. 2008). Invasive rats are now routinely eradicated from islands for conservation purposes (Howald et al. 2007), but are capable of reinvasion (e.g., Thorsen et al. 2000), sometimes even despite island biosecurity measures (e.g., Russell et al. 2005). Research on invasive rats has predominantly focused on high-density populations, however, populations of rats at low-density, such as during colonisation, may display profoundly different behaviours. Any such changes in individual or population functioning during colonisation require studying in order to develop effective methods to prevent rat reinvasion (e.g., Russell et al. 2008).

We investigated a small island recently reinvaded by Norway rats (*Rattus norvegicus*), focusing on four commonly investigated aspects of population biology which are relevant for a better understanding of the dynamic of the early stages of colonisation. Firstly, we investigated the spatial distribution and structure of the population using both trapping and genetic data. Secondly, we verified if genetic methods allowed us to detect a population bottleneck from the suspected small number of founders, thereby discounting continued gene flow to the island. Thirdly, we wished to estimate population size from combined multiple sources of ecological data. Finally, we looked at what could be learnt from parentage analysis about the mating structure of a population during colonisation, such as variation in breeding success among invaders, and how this might influence population establishment.

Methods

Study species

Norway rats are the dominant introduced rat on most continents, but in New Zealand they are most commonly found on offshore islands, where they have often been eradicated (Clout and Russell 2006). Compared to the more common ship rat (*R. rattus*) Norway rats are difficult to trap and are rarely found on the mainland where they are the subordinate rat species. Despite their low density on the mainland they are the most frequent island invader, possibly swimming up to 2 km offshore (Russell and Clout 2005). In high-density populations Norway rats can breed rapidly and, although not always, in all seasons, with a gestation period of 21–24 days and average litter sizes of 6–8 (Innes 2005). They have a life expectancy of 1–2 years in the wild, and almost all wild rats weighing over 200 g are sexually mature (Glass et al. 1988).

Study site

Moturemu (5.0585 ha) island lies 2.5 km offshore in the inner eastern reaches of the Kaipara Harbour, New Zealand (Fig. 1). Norway rats and mice (*Mus musculus*) were eradicated from the island in 1992 to prevent predation on a large colony of grey-faced petrels (*Pterodroma macroptera*), concentrated on the northern slopes, which could have resulted in substantial ecosystem alteration (Imber et al. 2000; Fukami et al. 2006). In order to prevent reinvasion poison bait stations were established and the island was monitored annually. The island remained rat free until February 1999, when rat sign was detected. A contingency response using traps and poison to confirm presence apparently resulted in eradication, although no bodies were recovered. No further sign was detected until April 2002, when a new population was confirmed on the island 10 years after the first

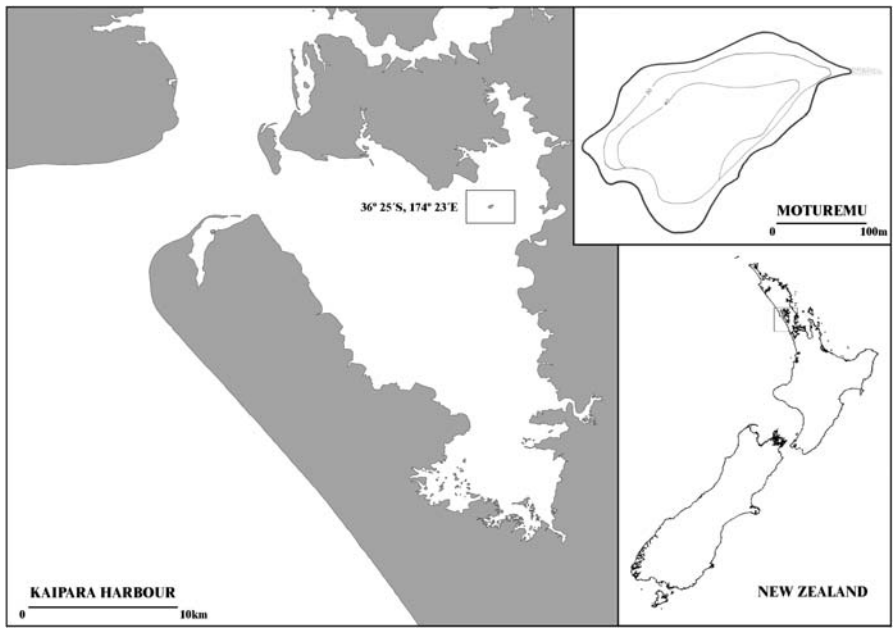

Fig. 1 Kaipara Harbour (Moturemu and New Zealand *inset*)

eradication. Therefore, it is likely that a new population became established in 2002, and 2 years later the eradication effort provided an opportunity to study invasion dynamics.

A new eradication was conducted in May 2004, providing us with a single opportunity to sample most individuals from an approximately 2 year old invasion of a small island. We removal trapped the entire island for a total of nine nights (6–8 April and 21–26 April 2004) as part of an eradication programme, with a combination of 30 Tomahawk live traps and 20 Supreme Ezeset snap traps alternately placed in a regularly spaced grid approximately every 25 m across the island. Live traps were permanently placed and remained closed in situ between trips, while snap-traps were relocated around the island based on rodent interference with waxtag detection devices (Pest Control Research, Christchurch), which register rodent presence through gnawing of wax (Thomas et al. 1999). All rats captured were sexed, weighed, assigned either adult or juvenile, and morphologically measured for head-body length (HBL) and tail length (TL) (sensu Cunningham and Moors 1996). Paws and tail tips were preserved in 70% ethanol for subsequent genetic analysis. In May 2004 the Department of Conservation undertook standard brodifacoum poisoning (Towns and Broome 2003) to kill any remaining rats. Poison was distributed in bait stations and hand-spread over cliffs. This was repeated 1 week later and bait stations were removed in the third week.

In order to obtain samples from the putative source population, trapping programmes were also conducted at three different sites on the surrounding mainland for a total of 400 trap nights. This resulted in the capture of 4 ship rats and 14 mice but no Norway rats were obtained, consistent with their rarity outside offshore islands.

DNA extraction and genotyping

Genomic DNA was extracted using the DNeasy 96 tissue kit (Qiagen). Eight microsatellite markers characterised for *R. norvegicus* genome mapping (Jacob et al. 1995) previously published on other invasive rat populations (Abdelkrim et al. 2005a, b) were used (D10Mit5, D11Mgh5, D13UW1, D19Mit2, D10Rat20, D7Rat13, D5Rat83 and D16Rat81). 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 performed in 10 µl volumes, containing 1 µg DNA, 0.1 µM of one primer labelled with 5′ fluorescent labels and 0.2 µM of the other primer, 0.2 µM of each dNTP, 1 unit Taq polymerase, and 1X reaction buffer with 1.5 mM $MgCl_2$. PCR products were pooled for a single run using an ABI prism 310 capillary

electrophoresis system (Applied Biosystems). Amplification size was scored using GeneScan Analysis v.3.1.2.

Genetic diversity and population structure

For each locus we calculated the frequency of each allele, the observed heterozygosity, the expected heterozygosity (Nei 1973), significant deviations from Hardy–Weinberg expectations with a Fisher's exact test of Hardy–Weinberg proportions (Weir 1996, p. 98) and F_{IS} values (sensu Weir 1996). All calculations were done with Bonferroni correction using Genepop 3.3 (Raymond and Rousset 1995).

Spatial structure in genetic variation across the island (e.g., family groups) 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. All calculations were done using *R* 2.0.

Detection of population bottleneck

We investigated bottleneck signal using three commonly used methods. The first method is based on the detection of heterozygosity excess, as expected in a recently bottlenecked population (Cornuet and Luikart 1996). A second method, the 'mode-shift indicator', is a qualitative descriptor of allele frequency distribution where a shifted allele frequency distribution is expected following a bottleneck, when the number of alleles classified as rare is reduced compared with the number of intermediate frequency alleles. A stable population, by contrast, is expected to exhibit an evenly distributed L-shaped allele frequency class distribution (Luikart et al. 1998). For these two methods, analyses were performed using Bottleneck v1.2 (Piry et al. 1999) with mutational specifications as used in Abdelkrim et al. (2005b) for introduced ship rats. The third method uses the ratio *M* defined as the ratio of the number of alleles to the range in allele size, with the value of *M* and its significance level computed following Garza and Williamson (2001). We assumed the conservative range of values $(N_e, \mu) = (10, 10^{-5})$ to $(60, 10^{-3})$ for effective population size and the mutation rate, respectively, therefore performing the test of the *M* ratio for two values of $\theta = 4N_e\mu$ of 0.0004 and 0.24.

Estimation of population size

Population size (N) was estimated using catch-effort removal models with the trapping data (Seber 1982, p. 297), supplemented by additional models for interference with waxtag detection devices. For each rat still alive on night *i,* we modelled the probability of capture on night *i* by $p_i = 1-\exp(-kf_i)$, where k is the Poisson catchability coefficient and f_i is the number of traps set on night *i*. The catch-effort estimates of N and k were obtained by maximum likelihood using the nightly capture data. Confidence intervals were calculated using profile likelihood (Hirst 1994). This method performs best on small populations when >50% of the population is removed (Gould and Pollock 1997).

The removal method is highly sensitive to failure of the assumption that all rats have equal probability of capture, so we also considered two further models that incorporated field observation on the number of waxtags interfered with per night. Device avoidance is expected to be less severe for waxtags than for traps (Thomas et al. 1999). For each model, rats were assumed to leave sign on waxtags according to a Poisson process. The first model gave rats free access to all waxtags, while the second model assumed a monopoly on waxtags so that each gnawed tag represented sign from a single rat. The extra parameter of the waxtag Poisson process was estimated by maximum likelihood in addition to the catch-effort parameters. All calculations were done using *R* 2.0.

Parentage and reproductive success

Kinship between individuals was investigated using genetic data. First, the samples were divided into two cohorts (candidate parents and offspring) based on morphological characteristics. Then, for each offspring, parentage of one or both parents was tested 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 programme a total of 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 the default value of 1% for typing errors, 0% for missing data from our observed rate, and conservatively that we had sampled 82% of the population following our largest population size estimate. Data on parentage were then used to estimate an index of variability for reproductive success $\left(\frac{\sigma_k^2}{\mu_k}\right)$ between male and female adults, where μ_k and σ_k^2 are the mean and variance, respectively, in the number of offspring per parent (Heiberg et al. 2006; Russell and Fewster 2009).

A single sample from a population can be used to estimate the inbreeding effective population size, N_e, via its inverse, $1/N_e$, which is the probability that two successful gametes in the offspring pool derive from the same parent, and is related to the rate of increase in the coefficient of inbreeding per generation (Russell and Fewster 2009). Reproduction in a small population leads to spurious associations between otherwise independent microsatellite loci, due to small genetic sample sizes from the mating parents. These correlations between loci are described as linkage disequilibrium, and the linkage disequilibrium estimator of $1/N_e$ from a single sampled generation is:

$$\frac{1}{N_e} = 3(r^2 - 1/n)$$

where, r^2 is the average squared correlation between pairs of alleles at different loci, averaged across all alleles and loci, and n is the harmonic mean sample size, averaged across all alleles and locus pairs. The estimate has 95% confidence intervals based on an approximate chi-square distribution for r^2. All calculations were done using *R* 2.0.

Results

Genetic diversity and population structure

A total of 27 Norway rats were captured over 335 trap nights (Table 1), all but three being captured on the second trapping occasion. Rats were not trapped uniformly across the island (Fig. 2). No significant difference was detected between the number of males and females in the population (two-tailed binomial test, $P = 0.70$). Twice as many adults as juveniles were caught. No significant interaction was detected between the number of individuals caught in each sex and age class (Table 1; $\chi^2 = 0.14$, $P = 0.71$, $df = 1$). No pregnant or lactating females were caught. There was a clear trend over the trapping period for adult males to be trapped earlier, followed by juveniles, and finally adult females (Table 2).

Table 1 Captured rats by sex and age class

	Male	Female	Subtotal
Adult (>200 g)	11	8	19
Juvenile (<200 g)	4	4	8
Subtotal	15	12	27

Between two and four alleles were present at each locus. No evidence against Hardy–Weinberg equilibrium was found, except at one locus which had significant heterozygosity excess (Table 3). F_{IS} scores were low, and frequently negative, suggesting avoidance of inbreeding. The unweighted average population F_{IS} was −0.06 with a mean number of alleles of 3.125 per locus. The global Hardy–Weinberg test showed no significant deviation from equilibrium ($\chi^2 = 19.0$, $P = 0.27$, $df = 16$) and no genetic structure (i.e., isolation by distance) was detected using the Mantel test ($P = 0.108$).

Detection of population bottleneck

All three methods indicated a recent significant reduction in population size. Heterozygote excess was detected under the two-phase mutation model ($P = 0.002$), and a shift in the distribution of allelic frequency classes was also detected, with rarer allelic classes less represented than intermediate classes. The *M* ratio was significantly inferior to the expected value for a population at demographic equilibrium ($M = 0.527$, $P < 0.001$). This value was in the range of those obtained for populations known to have experienced a bottleneck (Garza and Williamson 2001).

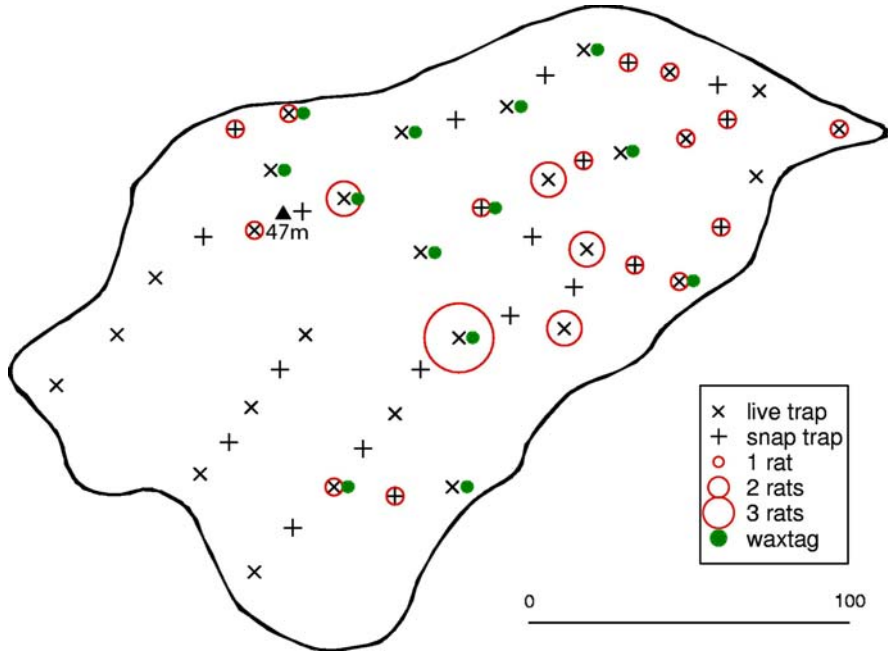

Fig. 2 Trap and capture locations, and locations of waxtags interfered with on the penultimate night (*grey-faced petrel* colony concentrated on the northern side of the island)

Table 2 Trapping results per night, number of traps in field (effort), and waxtag interference

Date (April 2004)	6	7	8	21	22	23	24	25	26
Adult ♂	1	1	1	5	1	2			
Juvenile					5	3			
Adult ♀				1		1	5		1
Total caught	1	1	1	6	6	6	5	0	1
Live traps	15	30	30	30	30	30	30	30	30
Snap traps						20	20	20	20
Total traps	15	30	30	30	30	50	50	50	50
Waxtags gnawed					25			14	
Waxtags set					30			30	

Estimation of population size

Removal data and waxtag interference are shown in Table 2. Data from the first trip from 6 to 8 April were not included in the removal model because the low capture rate was indicative of neophobia and could not be fitted. Using data from the second trip (21–26 April), the standard removal model gave a unimodal likelihood surface with maximum likelihood estimates $\hat{N} = 24.2$ rats, and Poisson catchability $\hat{k} = 0.013$ (Fig. 3). A goodness-of-fit test indicated model adequacy ($\chi^2 = 0.97$, $P = 0.91$, $df = 4$). Adding the three rats caught on the first trip (6–8 April), and rounding up, gave the estimated total population size $\hat{N} = 28$, with 95% profile likelihood confidence interval (27.0, 32.6).

We used the Poisson catchability coefficient, $\hat{k}$, to estimate the individual nightly trap capture probabilities, $\hat{p}_i = 1 - \exp(-\hat{k}f_i)$, where f_i is the number of traps (Seber 1982, p. 296). With $f_i = 30$ live-traps we estimated $\hat{p}_i = 0.33$, with 95% confidence interval (0.19, 0.45). With the addition of 20 snap-traps ($f_i = 50$), we estimated $\hat{p}_i = 0.49$ (0.29, 0.63). We trialled the model with different catchability weightings for the two trap types, but this did not alter the population estimate.

The model estimated a total population size just over the number of rats caught, suggesting a density of approximately 6 rats/ha. However, 14 of 30 waxtags were interfered with on the penultimate trapping night (Fig. 2; Table 2), and fieldworkers visually observed many rats still present after trapping. We therefore fitted extra models for the waxtag data, giving estimated total population sizes $\hat{N} = 30$ (27.8, 35.5) when waxtags were available to all rats, and $\hat{N} = 33$ (28.8, 43.7) when rats monopolized tags. The first of these models estimated that each rat would make 4.0 (2.2, 6.6) waxtag interferences per night, and reduced the estimated 50-trap capture probability to $\hat{p}_i = 0.38$ (0.24, 0.53). The second model estimated that each rat monopolized an

Table 3 Summary statistics for microsatellites

Locus	*n*	Length (bp)	Proportion	H_e	H_o	*P*	F_{IS}
D7Rat13	27	125	0.55	0.59	0.63	0.76	−0.06
		145	0.28				
		157	0.17				
D13UW1	27	171	0.26	0.46	0.33	0.10	0.29
		173	0.68				
		175	0.06				
D10Rat20	27	102	0.35	0.60	0.70	0.80	−0.15
		112	0.15				
		118	0.50				
D10Mit5	27	142	0.69	0.48	0.44	0.03	0.09
		146	0.20				
		150	0.11				
D5Rat83	27	164	0.42	0.67	0.74	0.21	−0.08
		166	0.26				
		186	0.04				
		190	0.28				
D11Mgh5	27	232	0.85	0.25	0.30	1.00	−0.16
		236	0.15				
D16Rat81	27	149	0.41	0.63	0.74	0.66	−0.15
		153	0.18				
		155	0.41				
D19Mit2	26	204	0.31	0.71	0.85	0.31	−0.18
		206	0.38				
		214	0.19				
		216	0.12				
Total				0.55	0.59	0.27	−0.06

n, Sample size (number of individuals); H_e, Expected heterozygosity (Nei 1973); H_o, Observed heterozygosity; *P*, *P*-value of Fisher's exact test for Hardy–Weinberg equilibrium; F_{IS}, Within population inbreeding coefficient, (*f*; Weir and Cockerham 1984; Weir 1996)

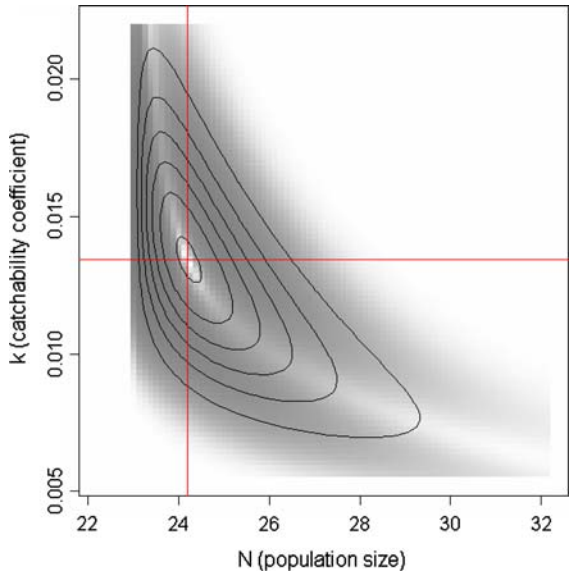

Fig. 3 Catch-effort model joint parametric likelihood surface for estimation of *N* (population size) and *k* (Poisson catchability coefficient). The maximum likelihood estimates are marked by the *cross-lines*

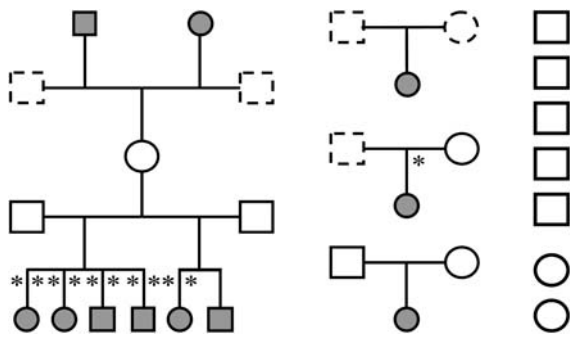

Fig. 4 Moturemu pedigree. □, Male; ○, female; *shading* indicates juvenile; *Asterisks* indicate 80% confidence in assignment, otherwise most likely parent. *Dashed lines* indicate unknown parent. Unassigned parents (5 males; 2 females) are on the right

average of 1.6 (0.8, 2.7) tags per night, and reduced $\hat{p}_i$ to 0.32 (0.17, 0.48).

Parentage and reproductive success

With 5 candidate mothers and 11 candidate fathers, using an increased weight bracket of 220 g to classify three sub-adults as candidate offspring, both most likely parents from the candidates were assigned to 7 of the 11 offspring (Fig. 4). Eleven of the parents were assigned with greater than 80% confidence. Parentage assignment was generally consistent regardless of which sex was run first in the two-stage process, although where conflicts occurred the parent was considered unknown. These unknown parents may be the same or even a parent from the candidates, but this could not be statistically determined. Parentage was dominated by one male (at least four surviving offspring) and one female (at least eight surviving offspring). The dominant female sired offspring with at least two males in the most recent breeding season. For her prolific family group (eight offspring by at least two fathers) the maximum

geographic distance between family group member captures was almost 200 m, with an average distance between captures of 66 m.

For calculating reproductive success we estimated the most likely parent for all 11 offspring (ties in parentage were assigned 0.5 to each parent). This gave estimates of $\mu_{\mathrm{m}} = 1.00$, $\sigma_m^2 = 2.40$, $\mu_{\mathrm{f}} = 2.20$, and $\sigma_f^2 = 11.08$. Indices of variability $\left(\frac{\sigma_k^2}{\mu_k}\right)$ were therefore 2.4 for males, and 5.04 for females. The probability $1/N_{\mathrm{e}}$ estimated from linkage disequilibrium in the offspring generation was estimated as 0.52, with chi-square 95% confidence interval (0.23, 1). This suggests a substantial rate of increase in the inbreeding coefficient per generation.

Discussion

The morphology of Norway rats on Moturemu is similar to those found on other northern islands of New Zealand (Innes 2005). Breeding appears to have been seasonal on Moturemu as no reproductively active females were found during our trapping in April (autumn). The threshold for adulthood can vary, but there was a clear size gap (no individuals) between 180 and 200 g, delimiting those born in the most recently completed summer breeding season (Innes 2005). The low trapping success in the first trip could be attributed to either poor weather or neophobia in the Norway rats (Brigham and Sibley 1999). Subsequent trapping results revealed adult males were more likely to be caught first, followed by juveniles, and adult females may have shown the highest levels of neophobia, as others have found (Moors 1985; Thorsen et al. 2000).

Genetic evidence suggests that the Norway rats on Moturemu clearly went through a substantial founder effect during colonisation of the island. This is demographically supported by the presumably small number of founders who initially evaded detection. It would be valuable to confirm the extent of the bottleneck by comparing genetic diversity to a mainland source population, however, this was not possible because a source population could not be identified. All three bottleneck detection methods worked well, for this situation with known history. Nevertheless, the small and recently founded population exhibited a non-negligible level of genetic polymorphism at all loci, as others have found for introduced mammals founded from a small number of colonists on islands (Thulin et al. 2006; Kaeuffer et al. 2007). The upper limit of four alleles across all eight loci is consistent with a limited number of founders, possibly even a single pregnant female. Using a similar number of markers, however, other insular Norway rat populations have been found to have some loci with more than four alleles (Robertson and Gemmell 2004; Abdelkrim et al. 2005a). With the same eight microsatellite markers, French Norway rat populations had similar allelic diversity to that on Moturemu, on larger islands such as Trielen Island (14.5 ha) and Molene Island (45.3 ha) on the Brittany coast (Abdelkrim et al. 2005a). The rats on Moturemu therefore had genetic diversity similar to other larger and longer established island populations.

Incorporating auxiliary information substantially improves removal models (Routledge 1985), and the waxtag models are likely to give more realistic answers than the removal model alone, due to trap-shy behaviour of some rats. However, field observation of waxtag interference is needed to establish the appropriate model, and we recommend in future that waxtag data are collected for every trapping night instead of just a subset. The density of Norway rats on Moturemu was at least 6 rats/ha, similar to densities of other, but longer-established, Norway rat populations on New Zealand islands (Moller and Tilley 1986; Taylor and Thomas 1993). The catch-effort model estimated the total population size at just over the exact number caught, because the catch rate declined to almost zero over the last two nights. Other rodent studies have also estimated population size at just over the total number caught (Brown et al. 1996; Liu et al. 2003). The last few animals in an eradication require disproportionately more effort to remove (Routledge 1985; Parkes 2006), which violates the assumption of equal catchability due to significant individual variation. Estimation with individual heterogeneity is much harder and requires long periods of low trapping success (Mäntyniemi et al. 2005). Although catch-effort models have been used successfully in marine systems (Gould and Pollock 1997), they have limited applicability where there is individual variability (Seber 1982, p. 305). Use of supplementary models such as our waxtag models has the potential to provide more realistic estimates, although fieldwork is needed to validate plausible models. Observations on Moturemu suggested rats

possibly monopolize waxtags by consuming all the attractive bait upon first encounter. The final individuals on Moturemu were ultimately only eradicated through a 'change of method' approach with poisoning (Parkes 2006).

The successful assignment of 17 out of 22 parents (77%) provides a corroborating estimate of the proportion of the population originally sampled (Marshall et al. 1998), assuming no trapping bias between juveniles and adults. Parentage analysis also suggested the surviving rats were most likely males that were unassigned parents. The parentage assignment success rate was high, for the most part due to dominance by one family group which was sampled. Siblings of the offspring were unlikely to be considered candidate parents due to clear adult-offspring separation by morphology, while siblings of the true parents have little effect on assignment confidence (Marshall et al. 1998). High relatedness within the population still gives the same assignment success rates but with decreased confidence (Marshall et al. 1998), although accurate estimates of mating success can be made using a relaxed confidence level (Slate et al. 2000).

Parentage assignment suggested promiscuity and dominance by a few individuals, as others have found for Norway rats (Heiberg et al. 2006). Multiple matings are common for female Norway rats (MacDonald et al. 1999) and this can lead to multiple paternity within single litters (Heiberg et al. 2006; A.-C. Heiberg et al., unpublished data), and subsequently to higher reproductive success (Stockley 2003; Solomon and Keane 2007). Reproductive success of Norway rats on Moturemu was within the range reported by Heiberg et al. (2006) for wild rats in Denmark, however, in contrast we found reproductive success was more variable for females than males. Overall, our estimates of reproductive success suggested the population was stable or declining ($\mu_k \leq 2$), possibly as a result of density dependence after reaching carrying capacity. Density dependence plays an important role regulating invasive rat populations at the breeding level (Efford et al. 2006), however, survival rates of offspring and adults are likely to be high given the absence of predators on the island and abundant food resources following the previous rat eradication.

The area over which the single family group existed suggests family members probably remain close to their parents and birth site, despite having the ability to disperse much larger distances (Russell et al. 2005). During the Norway rat invasion of Frégate Island dispersing offspring also remained near the natal site (Thorsen et al. 2000). This is not surprising given that Norway rats are social animals with strong parent-offspring associations (Dewsbury 1985). Nonetheless, spatial genetic structure was homogeneous due to the small size of this island relative to the spatial size of family groups. When individuals are not widely dispersed the male mating system should resemble non-competitive polygyny (Waterman 2007), while females will usually solicit multiple male matings (Solomon and Keane 2007). This system would result in either a dominance hierarchy or random mating, as has been observed for other Norway rat populations (Macdonald et al. 1999). The dominance of mating by a few individuals in the small population probably contributes to the increasing inbreeding rate calculated using the linkage disequilibrium method. Despite the apparently increasing inbreeding the population of invading rats had still reached a high density and probably the carrying capacity of the island. Breeding was most likely seasonal but breeding cessation may also have been linked to density dependence or increased inbreeding. However, genetic effects on population demography usually only have long-term consequences on population persistence, and inbreeding is not likely once established beyond a certain size (Jamieson et al. 2007). Unfortunately it is in the short-term, during and immediately following colonisation, that invasive rats have the most devastating effects on islands (Towns et al. 2006).

Combining ecological and genetic data from a single sample allowed insight into the early colonisation dynamics of invading Norway rats. Two years after invasion was detected, the population consisted mainly of adult animals that had demographic and genetic structure similar to other longer established island populations. Norway rats appear to be capable of establishing populations, such as on Moturemu, despite founding populations of only a small number of individuals, and increased rates of inbreeding. This apparent lack of short-term genetic consequences on immediate establishment should explain in part why Norway rats have successfully colonised so many islands.

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