.

Rat invasion of Tetiaroa Atoll, French Polynesia

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Abstract All three species of invasive rats are found throughout the Pacific Ocean: *Rattus rattus, R. norvegicus* and *R. exulans*. Polynesians historically introduced *R. exulans*, after which competitively dominant *R. rattus* and *R. norvegicus* were introduced by Europeans. However, the competitive processes in island invasion among rats have never been well documented. Tetiaroa atoll, in the Society Islands, consists of 12 small coral islets ("motu") with remnant coconut plantations from the early 20th century. *Rattus exulans* was the only species present on the atoll until *R. rattus* was first documented in the 1970s. We review the history of Tetiaroa, and document the current extant distributions of *R. rattus*, *R. exulans* and the seabird community. Genetic studies confirm the species and locality of introduced rats with COI barcoding. Microsatellite analyses suggest recent isolation of the *R. exulans* populations on separate motu, whereas *R. rattus* on the north-west motu appear to be one meta-population. Colonies of small seabird species are generally associated with sandy areas on small motu with only *R. exulans* present. Only larger seabird species such as frigates and boobies successfully breed on motu with *R. rattus* present. With hotel development and pest control now under way, the challenge is to manage rat eradication and biosecurity measures both within and from outside of the atoll in coordination with preserving the seabird community. Studies such as this provide novel opportunities to understand competitive interactions between species.

Keywords: Biosecurity, competition, genetics, island, microsatellite, *Rattus*, seabirds

INTRODUCTION

The sequence of introductions (or assembly history) of introduced species can play an important role in their establishment and the final community composition where multiple invasive species interact (Drake 1990; Chase 2003; Courchamp *et al*. 2003). For example, where one invasive species is already established, the introduction of a second species can either exclude competitively inferior species or lead to changes in their abundance, behaviour, or trophic position (Grosholz 2005). Three species of the genus *Rattus* are widely distributed invasive pests (Amori and Clout 2003). Across 123 of the world's archipelagos, Pacific or Polynesian rats (*R. exulans*) are found on 24% ($n = 30$), brown or Norway rats (*R. norvegicus*) are found on 36% ($n = 44$) and black or ship rats (*R. rattus*) are found on 50% ($n = 61$) (data from Atkinson 1985). *Rattus exulans* is invasive throughout the Pacific Ocean, where it was introduced by Polynesian immigrants dispersing from south-east Asia over the last 3,500 years (Matisoo-Smith *et al*. 1998; Matisoo-Smith *et al*. 2009). The cosmopolitan invasive rats (*R. norvegicus* and *R. rattus*) did not reach islands in the Pacific until the arrival of European explorers 300 years ago, with a colonisation peak following World War II (Atkinson 1985). Upon arriving at islands already colonized by *R. exulans*, *R. norvegicus* and *R. rattus* competitively dominated (e.g. Baker 1946; Storer 1962; Williams 1972; Twibell 1973; Spennemann 1997; Russell and Clout 2004; Harper and Veitch 2006), although *R. exulans* may have resisted invasion on some islands due to an incumbent advantage (e.g. Roberts 1991; Russell and Clout 2004).

Identification of some species of *Rattus* can be difficult if based on morphological traits alone (Robins *et al*. 2007). *Rattus rattus* is a particularly problematic cryptic species 'complex', possibly comprising multiple species, sub-species and lineages (Aplin *et al*. 2003; Robins *et al*. 2007, 2008). Two different chromosomal forms are generally recognised, one Oceanian ($2n = 38$) and the other Asian ($2n = 42$) (Yosida *et al*. 1974; Baverstock *et al*. 1983). The Oceanian form (also known as European), named *R. rattus* by Musser and Carleton (1993), is generally the most invasive. However, the Asian form, named *R. tanezumi* by Musser and Carleton (1993), recently invaded McKean Island in the Phoenix Islands (Pierce *et al*. 2006). DNA barcoding based on mtDNA regions such as COI may provide more reliable species identification within the *R. rattus* complex (Robins *et al*. 2007).

Tetiaroa atoll (3366 ha; 17°07'15"S 149°29'30"W), lies 50 km north of Moorea and Tahiti in the Society Islands of French Polynesia (Fig. 1). Tetiaroa is one of 115 sites of important conservation value in French Polynesia (Meyer *et al*. 2005). The atoll comprises 12 low-lying vegetated coral islets, locally called "motu", and an emerging sandbank
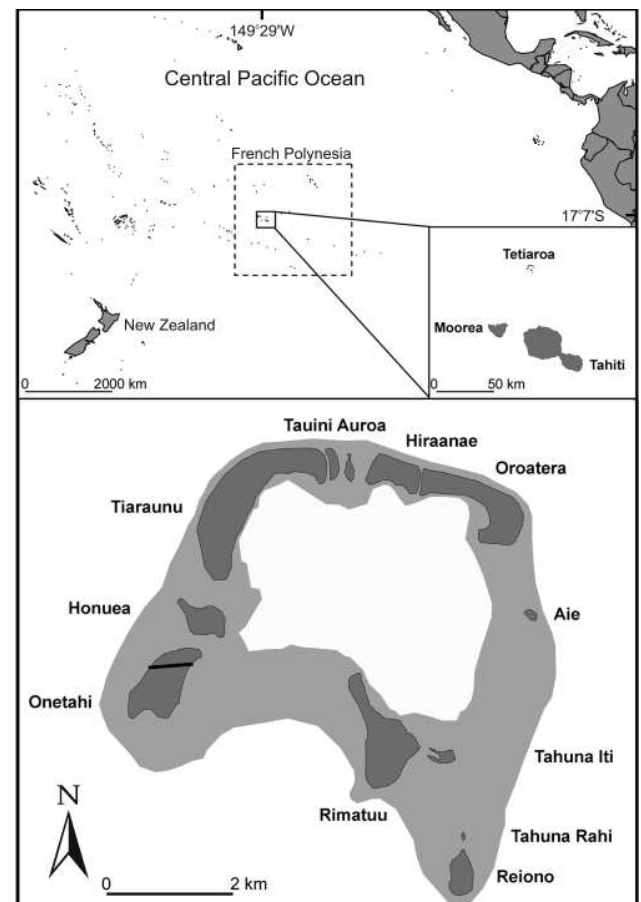
Fig. 1 Dark grey indicates land and light grey submerged coral reefs. Landing strip indicated on Onetahi. Tahuna Iti is colloquially named 'the bird island' (« Ile aux Oiseaux »). Tahuna Iti and Tahuna Rahi have changed substantially over the past 50 years.

(Motu One) east of Tahuna Rahi, all roughly circling a large lagoon. Names of motu vary among reports due to typographic errors, and the changing geography of the landscape. Tahuna Rahi and Tahuna Iti have dramatically changed size and moved over the last 50 years (comparison to a 1955 aerial photo). Tahuna Rahi has decreased from 2.0 to 0.5 ha, while Tahuna Iti has increased from 5.2 to 5.9 ha, and more notably shifted from 350 m to less than 10 m offshore of Rimatuu. Tahuna Iti was presumably also the smaller island of the two historically, based on its name ('iti' translates as small). Most motu are dominated by abandoned coconut plantations formely exploited for copra (coconut oil), although Reiono retains substantial native vegetation dominated by a 20 m canopy of the tree *Pisonia grandis*. Archaeological sites from Polynesian settlement on Tetiaroa have been dated to 1500-1600 A.D., including pig remains (*Sus scrofa*) on Onetahi (Sinoto and McCoy 1974), although these early radiocarbon dates may be inaccurate (Spriggs and Anderson 1993). There has been short- and long-term human habitation since that time. Recent habitation, and hotel development on Onetahi, has led to further species introductions and vegetation alteration.

The first Europeans on the atoll were three deserters from the H.M.S. Bounty in 1789. In 1904 King Pomare V gifted the island to dentist Johnston Walter Williams, who developed intensive coconut plantations across the atoll managed from a small village of workers on Rimatuu. When he died in 1937 his daughter, Madame Duran, inherited the atoll and continued to live on Rimatuu. In 1961 the actor Marlon Brando investigated buying the atoll, and after obtaining government approval in 1965, paid 17,492,000 French Pacific francs for most of Tetiaroa on October 17 1966 and bought the remainder the following January. Only the terrestrial component rests in private ownership; the lagoon and reef remaining in the public domain. Brando transferred operations from Rimatuu to Onetahi, and in 1971 hired an architect to build a small 'eco-hotel' of 13 modest thatched fares, meeting with scientists at the Smithsonian Institution in late 1972 to discuss his proposed development. Hotel Tetiaroa Village opened on Onetahi in March 1973. Brando lived on the island occasionally until 1990, and died on July 1, 2004 passing ownership to the Brando Trust. In 2005 a building permit was issued to Tahiti Beachcomber SA to develop 40 'eco-friendly' hotel units, and construction began in 2006.

The archaeology was assessed in the early 1960s (exact date unrecorded) by Pierre Vérin, Raoul Teissier and Henri Picard (Teissier 1962, Vérin 1962) and in December 1972 by Yosihiko Sinoto and Patrick McCoy (Sinoto and McCoy 1974). The avifauna (predominantly seabirds) was assessed from 1972-1975 by Jean-Claude Thibault (Thibault 1976), and in 1992-1993 by Philippe Raust and Albert Varney (Raust and Varney 1992, Raust 1993). The ecology of the atoll, focusing on vegetation, was studied by Marie-Hélène Sachet and Francis Raymond Fosberg in 1973-1975 and 1982-1983, resulting in an exhaustive plant list for each motu (Sachet and Fosberg 1983). Further botanical visits and a revised plant list were made by Jean-François Butaud in 2003 and 2006 (Butaud 2006).

In the early 1960s, *R. exulans* were the only rats described on the atoll (Teissier 1962), but by the early 1970s there was a 'recent population explosion of a tree-dwelling rat' (Sachet and Fosberg 1983), and 'large sized rats' were seen under red-footed booby (*Sula sula*) colonies on the northern islands around 1972-1975 (Thibault 1976). Both observations are presumed to be of *R. rattus* and coincide with new ownership and development on Tetiaroa. Cats were reportedly introduced to Tetiaroa to control abundant rats after 1904, but by the 1970s only remained on Onetahi (Thibault 1976). Fourteen semi-wild cats were removed from Onetahi in early 2009 by trapping (N. Leclerc pers.

comm.). Rat eradication was also attempted commencing in June 2009 with a 50 m grid of bait stations and hand-spread Talon wax baits at a rate of approximately 10 kg/ha^{-1} over two sessions. After surviving rats were detected, a third follow-up application was made. Domestic pigs and dogs were probably also on Onetahi until recently (Sachet and Fosberg 1983), and a pair of dogs remain on Onetahi and regularly swim across to Honuea (pers. obs.). In this paper we record the distribution of *R. exulans* and *R. rattus* on Tetiaroa and describe how introduced rats interact with the extant seabird community. Genetic analyses are used to verify the species and population structure of invasive rats.

METHODS

In July 2009, we visited each motu (Table 1) and determined the species of rat present through a combination of observation and snap-trapping (Victor Professional) by the Société d'Ornithologie de Polynésie. Identification of rats in the field used morphological traits, particularly the dark stripe of fur on the outer hind feet, which is present on *R. exulans*, but absent from *R. rattus*. Sex, body-weight, head-body length, tail length and reproductive condition were all recorded, and a 5mm tail or paw tissue sample stored in 70% ethanol for genetic analyses. In January 2010, motu where we had not previously trapped rats were revisited and ten waxtags (Pest Control Research) were placed overnight in order to verify previous negative trapping results.

Table 1 Distribution of rat species on Tetiaroa. TN = trap nights.

Motu	Size	R. rattus	R. exulans	TN
Onetahi	73.8	✔	✔	30
Honuea	28.0	✔ *	✔	45
Tiaraunu	163.4	✔ *	✔ *	50
Tauini	6.7	✔ *	✔	10
Auroa	3.9	✔ *	✔	15
Hiraanae	34.0	✔ *	✔	25
Oroatera	81.4	✔	✔	10
Aie	2.4	–	✔	40
Reiono	21.4	–	✔ *	50
Tahuna Rahi	0.5	–	–	20
Tahuna Iti	5.9	–	✔	75
Rimatuu	88.3	–	✔ *	65
Total	509.7	7	11	435

* indicates samples from motu included in Structure genetic analysis

Genomic DNA was extracted using a high salt extraction. Cytochrome c oxidase subunit 1 (COI) was amplified using the following primers (Meyer 2004): dgLCO-1490 (5'-3') GGT CAA CAA ATC ATA AAG AYA TYG G, and dgHCO-2198 (5'-3') TAA ACT TCA GGG TGA CCA AAR AAY CA using standard PCR protocols. Six microsatellite markers characterised for *R. norvegicus* but suitable for other *Rattus* species were used: D19Mit2, D7Rat13, D15Rat77, D10Rat20, D20Rat46, D16Rat81 (Jacob *et al.* 1995). Each forward locus primer was tailed with M13 at the 5' end and a nested PCR was performed which included a fluorescent dye-labeled M13 primer (Schuelke 2000). PCR was performed in 10 µL volumes, containing 1 µg DNA, 0.1 µM of the M13-tagged primer, 0.1 µM of the other primer, and 0.1µM of the fluorescent dye-labeled M13 primer, and 0.2 µM of each dNTP, 1 unit *Taq* polymerase, and 1X reaction buffer with 1.5 mM MgCl$_2$. For each locus, annealing temperature was at 55°C for 30 cycles, followed by 10 cycles at 50°C to incorporate the fluorescent dye in the PCR product. PCR products were

run on an ABI 3730 (Applied Biosystems). Amplification size was scored using GENEMAPPER v.4.

We used STRUCTURE v.2.3.1 (Pritchard *et al*. 2000) to identify the number of clusters, *k*, for both species of *Rattus*. We only included motu where more than one rat was caught. We implemented the admixture model without priors of sampling location, with correlated allele frequencies and a burn-in of 50,000 and MCMC chain of 200,000, with five iterations for each of $k = 1, …, m + 1$ (*m* = the total number of motu in the analysis). For each motu we used ARLEQUIN v.3.1 (Excoffier *et al*. 2005) to estimate F_{ST} with 1000 permutations to estimate p-values. Microsatellite variation across the atoll was displayed visually with a principal components plot of the log posterior genotype probabilities (Russell et al. 2010). All motu with five or more captures were deemed reference populations, so each individual has a multi-dimensional coordinate consisting of its log posterior genotype probability for each reference population..

To investigate possible source populations for the recently arrived *R. rattus* we obtained tissue samples from four other major atolls in the Society Islands (atoll, sample size; Tahiti, 2; Moorea, 2; Huahine, 1; Raiatea 4) and compared these with four individuals from Tetiaroa. Complete cytochrome b (cyt b) was amplified using primers L14723 (5'-ACC AAT GAC ATG AAA AAT CAT CGT T-3') and H15915 (5'-TCT CCA TTT CTG GTT TAC AAG AC-3'), and in addition we amplified a further 758bp at the 3' end of the cyt b gene comprising two tRNAs and a partial D-Loop region (Tollenaere *et al*. 2010). Polymerase chain reactions (PCR) were performed in a 25 μL total volume containing: 2 μL of extracted DNA, 0.5ul of each primer (10pm/ul), 200 μM of each dNTP, 1 ul BSA (10mg/ml), and 1.25 U of FastStart Taq DNA Polymerase in the appropriate 1x Buffer with $MgCl_2$ (Roche Diagnostics). Samples were subjected to an initial denaturation at 95 ºC for 4 min, followed by 35 cycles of denaturation at 94 ºC for 45 s, annealing at 55 ºC for 45 s, and extension at 72 ºC for 1 min, with a final extension phase at 72 ºC for 10 min.

All Tetiaroa tissue specimens are lodged as part of the "Moorea Biocode project" (JR-2009-01 to JR-2009-78) (Check 2006).

Seabird distribution for each motu was determined from presence of the most abundant species, generally on the lagoon side, in July 2009.

RESULTS

Rats were detected on all motu except Tahuna Rahi (Table 1). On Aie and Tahuna Iti rats were not trapped but were subsequently verified at low density with waxtags and presumed to be *R. exulans* based on seabird presence and rats present on neighbouring motu. *Rattus exulans* inhabited all rat-invaded motu, whereas *R. rattus* were only found on the north-west chain. *Rattus exulans* were often observed throughout the day on motu with and without *R. rattus*, while *R. rattus* were never observed. Only one juvenile *R. exulans* was trapped on Onetahi as the concurrent rat eradication program during our trapping had substantially reduced rat numbers, while *R. rattus* were neither trapped nor observed on Onetahi but had been previously recorded. In January 2010, *R. rattus* and

R. exulans were both widespread though not abundant on Onetahi. *R. exulans* were observed in abundance in the late afternoon on Hiraanae and Oroatera but were not trapped. Morphologically *R. exulans* were within the normal range but *R. rattus* were particularly large (Table 2). All three colour forms of *R. rattus* were found. Most rats caught were reproductively active adults, as indicated by enlarged testes in males and uterine scars and/or embryos in females. At least 18% of rats trapped were missing part of their tails, but with no clear pattern regarding sex or species.

Genetic samples were obtained from all rats trapped and were used to verify species and the extent of gene-flow across key water barriers (Fig. 2). COI barcoding results were compared to sequences of *Rattus* species available on Genebank. *Rattus exulans* on Tetiaroa aligned with those from the Pacific region (Robins *et al*. 2008), and *R. rattus* aligned with those from French Polynesia and the Pacific region (Robins *et al*. 2007). In our STRUCTURE analysis, we only included motu where more than one rat was caught (*m* = 3, *n* = 35 for *exulans*, *m* = 5, *n* = 36 for *rattus*). Our three sufficiently sampled *R. exulans* motu were isolated from one another (> 1.5 km), well outside the known swimming range of *R. exulans* (Russell *et al*. 2008). STRUCTURE found relatively equal support for $k = 1$ or 3. Support was marginally stronger for $k = 3$ but with much greater variances on estimated probabilities, which increasing simulation length did not alter. F_{st} values for *R. exulans* were significantly different among all three motu (Table 3). *Rattus rattus* were sufficiently sampled from five adjacent motu (< 500 m), predominantly around two major adjacent water-crossings, within the known swimming range of *R. rattus* (Russell *et al*. 2008). STRUCTURE found equal support for all of $k = 1,…,6$. F_{st} values for *R. rattus* averaged less than 0.1 between motu, and were generally significantly different only between motu not adjacent to one another
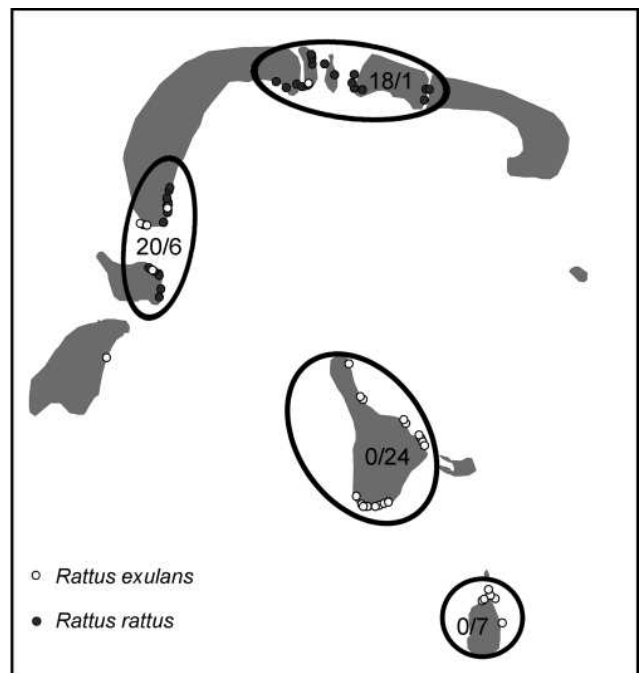
Fig. 2 Trapping locations and genetic sample sizes (excluding Onetahi) for rats on Tetiaroa.

Table 2 Average morphological measurements of adult *Rattus exulans* and *R. rattus* on Tetiaroa.

Species	Sex	n	Weight (g)	Head-body length (mm)	Tail length (mm)
R. exulans	M	10	77 (53-97)	150 (126-162)	163 (151-176)
	F	13	61 (48-70)	139 (114-149)	150 (132-163)
R. rattus	M	9	240 (200-308)	214 (202-228)	243 (215-268)
	F	14	192 (133-272)	206 (194-221)	233 (210-257)

Table 3 Fst values (3 d.p.) between Honuea, Reiono and Rimatuu for *Rattus exulans*.

F_{st}	Honuea	Reiono	Rimatuu
Honuea	0		
Reiono	0.120*	0	
Rimatuu	0.141*	0.167*	0

* significant at $p < 0.01$ (1000 permutations).

(results not shown). Allelic diversity was markedly different between the two species. Across the atoll, *R. exulans* loci were characterised by long consecutive runs of two base pair microsatellite repeats, although any given motu would have a subset of these allele lengths. The mean number of alleles per locus globally was 9.2 (range 4 – 16). In contrast, across the atoll, *R rattus* loci were characterised by limited allelic diversity, and any given motu would include most of the globally available allelic diversity. The mean number of alleles per locus globally was 4.4 (range 3 – 6). Principal components analysis of microsatellite log posterior genotype frequencies among individuals
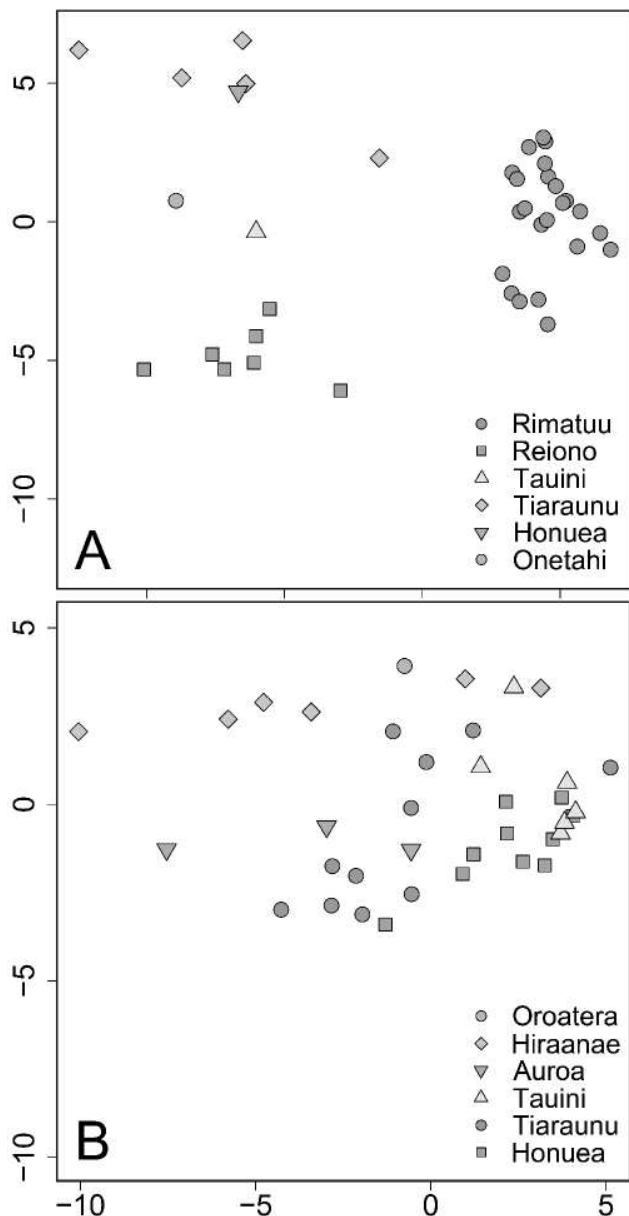
supported our Structure results, with evidence of strong differentiation in *R. exulans* populations (Fig. 3a), but only weak differentiation in *R. rattus* populations (Fig. 3b). *Rattus rattus* did tend to align along the direction of their invasion front originating at Onetahi, with neighbouring motu at the lower right and more distant motu at the upper left (Fig. 3b), possibly coinciding with patterns in genotype frequency drift from serial founder events. Only one cyt b/D-loop haplotype was found among the 13 rats from five different atolls in the Society Islands (Genbank sequence HQ588111).

Colonies of small seabirds such as noddies (*Anous stolidus*) and terns (*Onychoprion fuscatus* and *Thalasseus bergii*) were only found on small motu where *R. exulans* was the only species of rat present (Fig. 4). Larger seabirds such as frigatebirds (*Fregata minor* and *F. ariel*) and boobies (*Sula leucogaster* and *S. sula*) could breed in the presence of either species of rat (Fig. 4). For all seabirds, every reproductive stage (adults incubating eggs, juveniles and small chicks) was present, except for the small number of *Onychoprion lunatus* for which we only noted the presence of two juveniles. Since most of these species breed all-year round, numbers may differ at other times of the year.
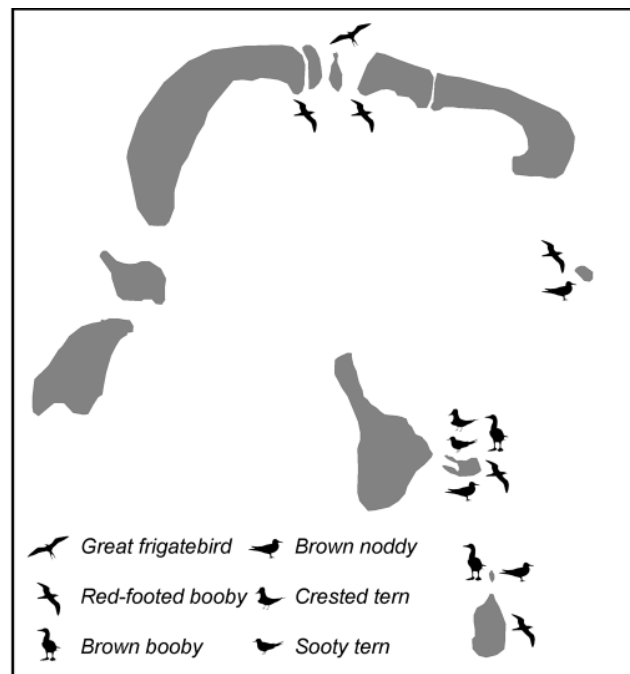
Fig. 4 Distribution of abundant seabirds on Tetiaroa (2009).

DISCUSSION

Dominance of *R. exulans* by *R. rattus* has been widespread on islands of the Pacific (see Atkinson 1985). The relatively recent arrival of *R. rattus* on Tetiaroa provides an excellent opportunity to study how the process of domination proceeds. *Rattus rattus* successfully established in the presence of *R. exulans*, although how much of a detrimental effect this has had on incumbent *R. exulans* populations remains an open question. On Tetiaroa, *R. exulans* persist on even very small motu with *R. rattus*. In contrast, on McKean Island (49 ha) in the Phoenix Islands, a 2001 invasion of *R. tanezumi* appears to have completely replaced the incumbent population of *R. exulans* (Pierce *et al*. 2006). On Tetiaroa, the invasion by *R. rattus* over *R. exulans* has little positive benefits for the wider island community given that *R. rattus* is the more damaging invasive species (Jones *et al*. 2008). In New Zealand, *R. rattus* dominates over *R. exulans* and populations only co-exist on islands larger than 100 ha (Russell and Clout

Fig. 3 Principal component analysis of log posterior genotype probability between individuals of (a) *Rattus exulans* and (b) *R. rattus*. Motu of capture has been overlaid.

2004), although data are lacking for smaller islands, and mis-identification may be possible. In the tropics, however, introduced rats appear able to co-exist on smaller islands, and with less negative effect upon one another.

Our genetic results are constrained by small sample sizes, which limits our inferences. Nonetheless, the patterns of allelic diversity, sequential pair-wise mutations, and clustering in *R. exulans* are congruent with the hypothesis of a single historically large and diverse population (k = 1), either prior to introduction to Tetiaroa or on Tetiaroa but with regular gene-flow between motu. More recently, *R. exulans* on different motu have become isolated (k = 3), and the patterns of allelic diversity we observed are generated by a combination of genetic drift and our sample sizes, where in either case allelic diversity becomes a subset of the original global population. This change in dynamics is likely to have arisen when heavy use of the atoll by Polynesians ceased around the start of the 20th century. The limited allelic diversity in *R. rattus* suggests only a small number of founders, although probably more than one (the 'single pregnant female' hypothesis; Miller *et al*. 2010). Presuming *R. rattus* arrived in Onetahi and then subsequently invaded the north-west chain through isolated invasion events, we would expect to see a signature of sequential founder events (Clegg *et al*. 2002). However, given the rapid invasion of the entire north-west chain in the 1970s, only weak evidence for sequential founder events, and poor discrimination among the number of clusters, it is most likely that *R. rattus* form a single meta-population with regular gene-flow by swimming across the north-west chain. The entire north-west chain must be considered as a single eradication unit for *R. rattus* (Robertson and Gemmell 2004, Abdelkrim *et al*. 2005).

Despite a small channel crossing (tens of metres), *R. exulans* are apparently absent from Tahuna Rahi. This is likely a result of the complete inundation of the previously larger Tahuna Rahi prior to its reformation as the current nearby smaller motu (e.g. Sachet and Fosberg 1983). On Tahuna Rahi, the absence of rat gnaw on pandanus (*Pandanus tectorius*) and coconut (*Cocos nucifera*) nuts was a good indicator of rat absence, although it was not guaranteed when rats were also at low density such as on Aie or Tahuna Iti. *Rattus rattus* on Tetiaroa were particularly large, and with relatively short tails compared to body length. Both species of rat most likely benefit from the abundance of fallen coconuts that they open, and the presence of enhanced nutrient inputs under large seabird colonies.

Identifying a local source population for the recent *R. rattus* invasion of Tetiaroa was not possible due to a lack of haplotype variation among introduced *R. rattus* of the Society Islands. This lack of variation is most likely a consequence of the sequential invasion of *R. rattus* across the Pacific, meaning genetic diversity was already relatively homogeneous once *R. rattus* arrived in eastern-most French Polynesia. Populations of *R. rattus* in the Society Islands are likely to share a common single invasion ancestry.

Tahuna Iti is a stronghold for breeding seabirds, resilient to *R. exulans* which have probably been present for some time (Thibault 1976). Seabirds on Tahuna Iti are jointly threatened by *R. rattus* invasion and human disturbance from eco-tourism operating from Papeete since the late 1980s. The vegetation on the five smaller islets (< 10 ha) has important value as these islands were not heavily planted in coconut trees. Reiono and Tahuna Iti have the highest ecological value for their intact flora and avifauna respectively. Eradicating *R. exulans* from Reiono should allow seabirds to recolonise, creating an 'insurance policy' against seabird disturbance on Tahuna Iti, and mitigating disturbance in other parts of the atoll. The risk of rats reinvading the rat-free Reiono and Tahuna Rahi unit is low given their isolation (1150 m).

Although Tetiaroa appears generally pristine due to uninhabitation, the ecosystem is degraded by introduced species. Introduced rats limit the distribution of seabirds, where Tetiaroa is their last stronghold in the Society Islands. Introduced plant species on Onetahi and Rimatuu are naturally spreading (Sachet and Fosberg 1983, Butaud 2006). New invasions continue, such as a small but growing number of red-vented bulbuls (*Pycnonotus cafer*) observed on Tahuna Iti and Rimatuu in the last few years (Butaud 2006), and a pair of common mynas (*Acridotheres tristis*) observed on Onetahi in January 2010. In both cases colonisation was likely by self-dispersal from Tahiti or Moorea. Eradication of small populations of plants and birds before they become established should be considered a priority management action. Other species are likely arriving unnoticed (e.g. insects). Ongoing biosecurity quarantine and surveillance is required.

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