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## ***Something Old, Something New: Do Genetic Studies of Contemporary Populations Reliably Represent Prehistoric Populations of Pacific *Rattus exulans*?***

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*Abstract* Through our research focusing on genetic studies of both ancient and extant commensal animals in the Pacific for addressing issues of population origins and mobility in the region, we have been able to process a large number of archaeological faunal remains that we can compare to modern samples from the same islands. These comparisons shed light on and provide specific evidence for *Rattus exulans* population change through time. This information may provide a model for understanding human populations in the region and will illustrate the complexities of using data obtained from modern populations to infer prehistoric relationships. Two case studies are presented here—analyses of modern and archaeological populations of *R. exulans* from both Chatham Island and New Zealand. These two cases provide very different pictures regarding the relationship between the archaeological and the extant populations.

Much of the research conducted by our laboratory has focused on genetic variation in Pacific commensal animals. It has been argued that by constructing the molecular phylogenies of the animals that ancestral Pacific peoples transported as they settled the Pacific, we can identify the pathways taken by the human populations (Matisoo-Smith 1994; Allen et al. 1996; Allen et al. 2001). Our initial work focused on mitochondrial DNA (mtDNA) variation in extant populations of the Pacific rat, *Rattus exulans*, found throughout most of Polynesia (Matisoo-Smith et al. 1998). While that approach was very successful, it was recognized that there might be limitations to studies of extant populations. We recognized the strong likelihood that we might be missing particular lineages from the past due to stochastic lineage extinction. In certain locations in the Pacific, for example Easter Island and the main islands of New Zealand, *R. exulans* are no longer present due to competition with the later-introduced European species of rat, *R. rattus* and *R. norvegicus* (in New Zealand, populations of *R. exulans* remain on a few small offshore islands). Alternatively, the lineages present in modern populations may be severely reduced due to recent population bottlenecks or other selective fac-

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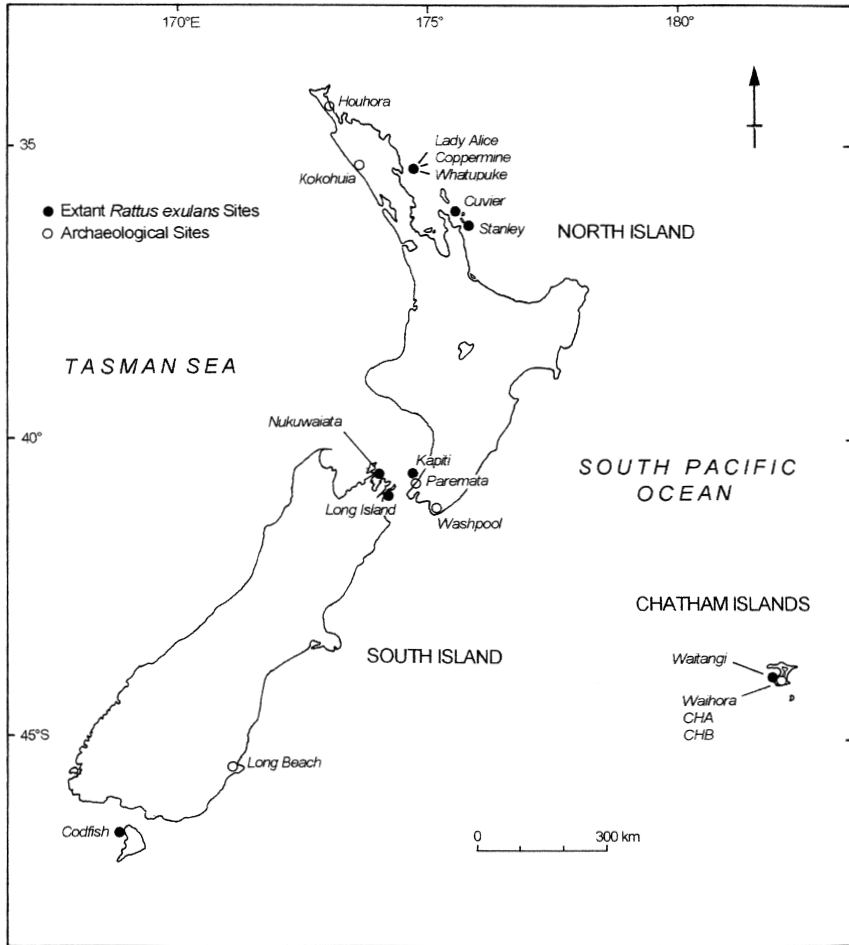
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tors. In order to address these issues, we applied a diachronic approach and began work on ancient DNA variation in archaeological remains of *R. exulans* and other Polynesian commensal animals, the dog and pig. As a result of these studies, we have now sequenced several hundred *R. exulans* samples recovered from archaeological excavations from throughout the Pacific. Comparison of ancient and modern *R. exulans* populations can perhaps provide a new kind of model that can be applied to studies of human settlement. By looking at how well modern *R. exulans* collections represent prehistoric populations, we may have a model for addressing the question: How informative are genetic studies on the contemporary indigenous populations for understanding the population history of Southeast Asia and Oceania?

While a few studies of ancient DNA of Pacific human populations have been conducted and have provided valuable information about prehistoric populations (Hagelberg and Clegg 1993; Hagelberg et al. 1994), there are numerous difficulties in working with ancient human DNA in the Pacific. In addition to all of the standard “contamination” issues inherent in all ancient human DNA studies, the issue of destructive analyses of human remains is a huge ethical dilemma in the Pacific, particularly in Polynesia. While the analysis of commensal animal remains is not totally without its own ethical issues, the destruction of faunal material for genetic studies is generally less controversial than dealing with human remains. In addition, faunal remains are often plentiful in archaeological middens, allowing for extensive sampling of populations through time and space. This is particularly the case for *R. exulans* remains throughout the Pacific.

Our first comparison between extant and ancient populations of *R. exulans* focused on material recovered from Chatham Island during archaeological excavations conducted in the mid 1970s by Douglas Sutton. The Chatham Island material was chosen specifically because analyses of extant Chatham Island rats showed that they were a monophyletic group within Polynesian rats, with limited mtDNA variability. All of the extant rat sequences possessed a single nucleotide polymorphism (SNP) not found in any other Polynesian *R. exulans* population (Matisoo-Smith et al. 1998). In order to determine how well the genetic variation of the extant population reflected the prehistoric population, we amplified and sequenced the SNP-containing region in a total of 15 archaeological samples from three archaeological sites on the southwest coast of Chatham Island (Matisoo-Smith et al. 1999). The three sites (see Figure 1)—Waihora (C240/283), the main occupation site, and CHA (C240/681) and CHB (C240/680), satellite sites to Waihora—all date to approximately 450 years BP, and currently represent some of the earliest archaeological evidence on the island (Sutton 1985).

All 15 archaeological samples sequenced possessed the unique Chatham SNP, and showed little other variation, either with each other or when compared to the modern sequences. The direct relationship between the two populations, ancient and extant, separated in time by approximately 450 years, was clearly demonstrated. This result—of limited mtDNA variation in the Chatham Island *R. exulans* populations—is unusual when compared to other *R. exulans* populations



**Figure 1.** Distribution of extant and prehistoric *Rattus exulans* sites in New Zealand and the Chatham Islands.

in Polynesia. Most other island populations show much higher levels of mtDNA variation. For example, gene diversity ( $h$ ) as calculated by Nei (1987:179) for Chatham Island *R. exulans* populations was 0.54, which was significantly lower than the value for New Zealand, which was 0.985, and the value for Raoul Island in the Kermadecs, which was 0.90 (Matisoo-Smith et al. 1999).

It has been argued that the lack of mtDNA variation on Chatham Island is suggestive of a single or extremely limited introduction with little postintroduction prehistoric contact (Matisoo-Smith et al. 1999). This scenario is consistent with Irwin's (1992) suggestion that the Chatham Islands (Chatham and Pitt Islands constitute the Chatham Islands) were particularly isolated in terms of pre-

historic voyaging. This was due primarily to their geographic location in a westerly zone of subtropical and sub-Antarctic convergence, which produces severe and dangerous weather conditions, making prehistoric voyaging to or from the Chathams particularly difficult (Levison et al. 1973). This geographic isolation and resulting limited contact with the Chatham Islands has resulted in a relatively simple *R. exulans* population history. In a case such as this, analysis of genetic variation in extant populations is a relatively good representation of the prehistoric variation on the island. This, however, is a rather rare situation. It appears that a much more complex history is common on other larger and geographically more accessible islands like New Zealand.

In the initial analysis of mtDNA variation in extant New Zealand *R. exulans* populations, 34 haplotypes were identified from the 50 samples collected. *R. exulans* are extinct on the main islands of New Zealand, and exist only on a limited number of small offshore islands. Samples were collected from nine offshore islands from around both the North and South Islands of New Zealand (see Figure 1, dark circles). This high level of variation was interpreted as being the result of multiple prehistoric introductions of rats to the islands (Matisoo-Smith et al. 1998). The phylogenetic analyses suggested that most of the samples were closely related to samples collected in the southern Cook and Society Islands. We recognized, however, that given that the extant populations of *R. exulans* were found only on offshore islands, we did not know how representative these populations were of the mainland New Zealand populations. While the extant samples exhibited significant levels of variation, this could be an underestimation of the prehistoric variability in New Zealand.

Analyses of mtDNA variation in archaeological remains of *R. exulans* collected from prehistoric occupation sites on the North and South Islands of New Zealand provide very interesting information when compared to modern population sequences. A total of 33 bone samples from Houhora (N6/4), Kokohuia (O06/317), Washpool Midden (N168/22), Paremata (N160/50), and Long Beach (S164/20) were processed. All ancient DNA (aDNA) samples were processed in a dedicated aDNA lab, with negative extraction controls and other aDNA protocols as described previously (Matisoo-Smith et al. 1997; Höss and Pääbo 1993). Extraction was followed by polymerase chain reaction (PCR) amplification in a dedicated aDNA PCR machine and direct automated sequencing using primers EGL 8 & 9 (Matisoo-Smith et al. 2001). These sequences were aligned, and a total of eight phylogenetically informative sites were identified and are shown in Table 1. All of the archaeological sites are relatively early for New Zealand, dating between 800 and 500 years BP (Davidson 1984; Leach et al. 1997).

While many of the archaeological samples analyzed were very similar to samples collected from the extant populations on offshore islands, we also found sequences suggesting that at least one very different *R. exulans* population was present on the New Zealand mainland in early prehistoric sites. In total, five distinct haplotypes were identified. All of the extant samples from New Zealand were similar to the consensus East Polynesian sequence, as was much of the ar-

**Table 1.** Phylogenetically Informative Sites in 175 bp of *R. exulans* mtDNA Sequence from NZ Archaeological Samples

	Variable Site							
	1	2	3	4	5	6	7	8
Reference Number <sup>a</sup>	15641	643	657	660	676	692	700	719
NZ1—all 5 sites and E.P. consensus	C	T	C	A	C	C	C	C
NZ2—Houhora and Paremata	C	T	C	A	C	C	A	C
NZ3—Washpool and Paremata	C	T	T	A	C	C	A	C
NZ4—Washpool and Kokohuia	A	C	T	A	T	C	A	C
NZ5—Houhora and Paremata	C	T	T	T	T	T	A	T

a. Reference numbers 15641–15719 from Gadaleta et al. 1989.

archaeological material from mainland North Island and the samples from the Long Beach site (S164/20) on the South Island. This haplotype is identified in Table 1 as NZ1. Some archaeological samples, however, produced very different results. These samples have a number of SNPs that are not found in the extant samples from New Zealand or any other extant populations sampled previously from East Polynesia. Similar “non–East Polynesian” sequences (e.g., the NZ4 lineage) were also identified in some archaeological material from the Emily Bay site on Norfolk Island. A phylogenetic analysis of the Norfolk and New Zealand samples identified two distinct groups: one clade with the East Polynesian consensus sequence (NZ1) and the NZ2 lineage, along with some of the Norfolk samples, and a second clade that included the NZ3 and NZ4 lineages and closely related Norfolk samples (Matisoo-Smith et al. 2001). We have since identified the NZ5 lineage in archaeological material from Houhora and Paremata, which contains three new polymorphic sites (sites 4, 6, and 8 in Table 1).

It is not surprising that the New Zealand situation regarding genetic variation is much more complex than that of the Chatham Islands, in both extant and archaeological samples. What was surprising however, was the fact that the haplotypes NZ3, and particularly NZ4 and NZ5, were so different from the extant samples.

There has been much debate regarding the Polynesian discovery and colonization of New Zealand. Most evidence suggests that New Zealand was successfully settled from Central East Polynesia, and colonization was probably the result of multiple events (Sutton 1994; Murray-MacIntosh et al. 1998). The results of the mtDNA analyses of extant New Zealand *R. exulans* populations were thoroughly consistent with this scenario (Matisoo-Smith et al. 1998). The main and on-going debate, however, focuses on the issue of the possibility of presettlement contact with New Zealand (see, for example, Holdaway 1996, Anderson 1996, and Hedges 2000). While the earliest settlement sites date to around 800 BP, there is increasing evidence that suggests that humans may have been in contact with New Zealand much earlier. Holdaway (1996) provides evidence of *R. exulans* remains in natural predator deposits on both the North and South Island that date to

around 1800 BP, as much as 1000 years earlier than the oldest archaeological settlement sites in New Zealand. Given that *R. exulans* is not native to New Zealand, and could only reach the archipelago with humans, this result would suggest that humans did make contact with New Zealand earlier than the date at which it was successfully settled by Polynesians. People were moving into Remote Oceania (the region east of the Solomon Islands) by 3500 BP and were in New Caledonia, an archipelago less than 1500 kilometers northwest of New Zealand, by 3000 BP (Kirch 1996). Irwin (1992:147) shows that not only are voyages from New Caledonia to New Zealand possible, they are among some of the safest easterly voyages from New Caledonia. Norfolk Island lies halfway between New Caledonia and New Zealand, and Norfolk shares the “non–East Polynesian” haplotypes with New Zealand. It is therefore possible that the initial contact with New Zealand did not actually come from Polynesia, but more westerly locations, and was then later followed by contact and successful settlement from the traditional “homeland region” of Central East Polynesia. Further research on archaeological material from West Polynesia, and more western locations like New Caledonia and Vanuatu, may shed light on this possible “western” connection.

From the results of the comparisons of ancient and extant *R. exulans* populations in the two case studies of New Zealand and Chatham Island, we see two very different pictures. In the case of Chatham Island, the analysis of extant populations provides a reliable indication of the prehistoric variability. The Chatham Islands are relatively isolated and have had a comparatively simple and limited contact history. New Zealand, on the other hand, is a different matter. Analyses of extant populations, while showing high variability and multiple lineages, still do not identify significant lineages that were present in prehistory. This result is not too surprising given that the extant New Zealand *R. exulans* samples come from isolated remnant populations on offshore islands.

The main reason we began studying mtDNA variation in *R. exulans* was to try to identify the colonization and contact pathways traveled by the people who carried the rats. Our ultimate interests are humans and human behavior. As with the initial rat model, the result presented here can also be useful for the study of human genetic variation and implications for studies of prehistoric settlement. If we are to apply the *R. exulans* situation as a model for human populations in Southeast Asia and the Pacific, we would expect to see a situation much more like New Zealand than the Chatham Islands. Most aboriginal populations in the region today are isolated remnant populations on islands that have had complex contact histories. This would be particularly the case for islands like the Philippines, Taiwan, and Indonesia—some of the proposed homeland regions for Pacific populations.

The results of our *R. exulans* studies may also provide an indicator of the likelihood of genetic variation in island populations. While we currently have no continental data with which to compare our results, the precariousness of island living, particularly in the early stages of settlement, would undoubtedly lead to a high probability of local extinctions. Factors such as island size, elevation, natu-

ral resources, climate, and isolation would clearly affect extinction rates and the likelihood of later recolonization. These factors could be combined with the genetic data to model their various effects on genetic variation seen in both archaeological and extant populations.

The results presented here will come as no surprise to those familiar with the complexity of Pacific and Southeast Asian prehistory. By sampling contemporary populations, we are likely to be missing significant information about the past populations. This means that we need to be very careful when interpreting patterns of genetic variation in these regions today and making statements about population origins and prehistoric mobility.

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