Prehistoric Mobility in Polynesia: MtDNA Variation in Rattus exulans from the Chatham and Kermadec Islands

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ONE SIGN OF HUMAN ARRIVAL on Pacific Islands is the presence and ecological impact of commensal plants and animals that are not capable of independent dispersal (Flenley 1989; Kirch and Ellison 1994; Kirch et al. 1991; McGlone et al. 1994). Recent research on the Pacific Rat, *Rattus exulans*, suggests that DNA-based phylogenies of extant populations can provide a model for prehistoric human mobility in the Pacific region (Matisoo-Smith 1996; Matisoo-Smith et al. 1998; Roberts 1991). *Rattus exulans* was transported intentionally by ancestral Polynesians, who valued it as a food source, and its remains are found in early archaeological layers throughout Polynesia. This rat cannot swim more than a few meters in open ocean (Spenneman and Rapp 1989), and its behavior and habitat preferences suggest it was an unlikely stowaway (Matisoo-Smith 1994; Williams 1973). Like other rodent species, *R. exulans* has a rapid generation turnover and, with little competition for resources, viable populations establish quickly and grow rapidly (Holdaway 1999). Although European contact and exploration in the Pacific resulted in the introduction of two more rat species (*R. rattus* and *R. norvegicus*), hybridization among these three species does not occur.

Though a *R. exulans*-based model of monitoring prehistoric Polynesian voyaging has been questioned on grounds of intentionality of transport and the possibility of dispersal and evolution of the rat without human intervention (Anderson 1996; Langdon 1995), testing the model depends not on a priori assumptions but on evaluation of the patterns of variation uncovered by genetic analyses. However, synchronic patterns of variation are always open to multiple interpretations as to the historical processes that produced them, as has been demonstrated in the human mtDNA out-of-Africa debate (Brown 1980; Cann et al. 1987; Vigilant

et al. 1991). (For an in-depth discussion of mtDNA, see Cann [1988] and for ancient DNA see Hagelberg [1993] and Richards and Sykes [1995]). One way to constrain the number of possible interpretations is to introduce a diachronic genetic perspective through the analysis of ancient DNA (Krings et al. 1997).

The study described in this article focuses on an analysis of genetic variation of 15 archaeological and 8 modern samples of *R. exulans* from the Chatham Islands. These samples are compared with 7 modern samples from Raoul Island, in the Kermadecs, and 50 modern samples from New Zealand. By combining the genetic perspectives afforded by ancient and modern samples, a clearer under-standing of the population history of Chatham *R. exulans* can be obtained, which in turn can be interpreted in light of other information available on the prehistory of that island group. In addition, a more thorough understanding of the Chatham situation is useful in interpreting a contrasting genetic pattern observed in the Kermadec Islands and New Zealand.

The Chatham Islands lie approximately 950 km due east of the South Island of New Zealand (Fig. 1). The group consists of two main islands, Chatham Island and Pitt Island, and several smaller uninhabited islands. They lie in a westerly zone of subtropical and sub-Antarctic convergence and are regularly exposed to frontal low-pressure systems, making the islands a difficult and dangerous location to travel to and from (Levison et al. 1973). The date of Polynesian discovery of the Chathams is unknown, but estimates vary from A.D. 800–1000 (Sutton 1985) to around A.D. 1450 (Anderson 1994; Irwin 1992; McFadgen 1994; McGlone et al. 1994). Archaeological and linguistic evidence supports a New Zealand origin for Chatham Island colonists (Clark 1994; Sutton 1985).

The Kermadec Islands lie approximately 1000 km northeast of New Zealand, nearly halfway between New Zealand and Tonga. The four islands were unin-habited when Europeans first arrived in 1788 (Johnson 1995), but there is clear evidence in the form of archaeological sites, and the presence of *R. exulans*, that the two largest islands, Macauley and Raoul, were each colonized at least once by Polynesians. It was initially suggested that first settlement occurred around A.D. 960 from Central East Polynesia (Anderson 1980), with a later settlement from New Zealand (Leach et al. 1986). However, more recently, a thirteenth or fourteenth century A.D. settlement date is favored (Higham and Johnson 1996; Spriggs and Anderson 1993 : 210).

Though basically equidistant from New Zealand, the Chathams and the Ker-madecs differ dramatically in their latitudinal position, accessibility, and in their predicted role in East Polynesian prehistory (Irwin 1992). The Kermadecs have been described as a possible stepping-stone group (Irwin 1992 : 111) for voyages between Central East Polynesia and New Zealand, whereas the Chathams are typically seen as the end of the line in prehistoric Polynesian voyaging. If the dis-tribution and phylogenies of *Rattus exulans* act as markers of human movement (Matisoo–Smith et al. 1998), then the different contact and settlement histories of the Kermadecs and Chathams should be reflected in the level and patterns of variation in their *R. exulans* populations. Results from a previous study involving an analysis of 395 base pairs (bp) of the mtDNA control region from 132 extant Polynesian *R. exulans* samples indicate that this is the case. Phylogenetic analyses consistently placed the Chatham samples in a monophyletic group, while the Kermadec samples were by contrast highly variable (Matisoo–Smith et al. 1998).

The extent to which contemporary patterns of genetic variation reflect prehis-
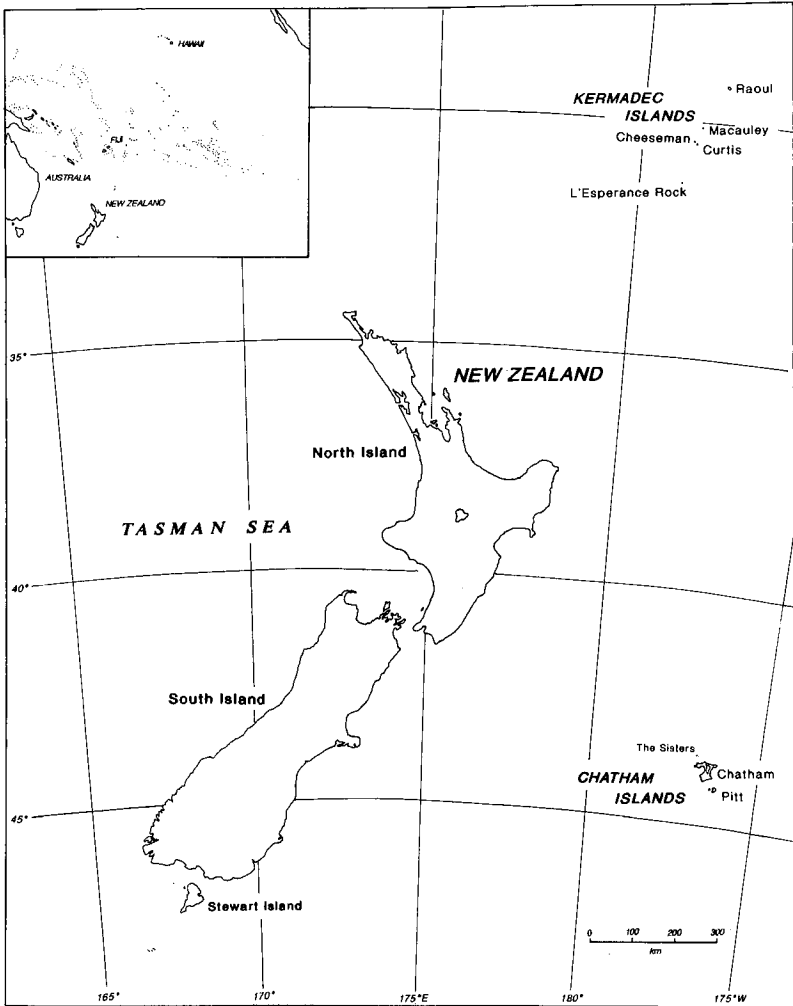
Fig. 1. Location map of New Zealand, the Chatham Islands, and the Kermadec Islands.

toric human mobility or other factors cannot be determined directly from modern samples collected within a circumscribed geographic area. For example, the lack of variability in the contemporary Chatham Island *R. exulans* populations may not simply reflect a limited history of contact; it could be the result of a recent population crash on the island—an effective genetic bottleneck that dramatically reduced variability. This can only be tested by introducing a diachronic perspective, through analyses of well-provenanced archaeological samples. In contrast, although highly unlikely given the current theories regarding the timing of human presence in the region, a high level of variation, as seen in the Kermadecs, could theoretically be the result of in situ evolution, indicating a long history of occupation rather than multiple introductions. These two possibilities can be dis-

entangled by looking at the patterns of mtDNA variability (using distance and diversity measures) within populations.

In this article we compare mitochondrial variation in archaeological *R. exulans* samples from the Chatham Islands with contemporary samples from the Chathams, the Kermadecs, and New Zealand. We show that the lack of variation in the Chatham population is consistent with an early limited introduction of rats, limited in-situ evolution, and postcolonization isolation. This result allows further interpretation of the high levels of diversity in other Pacific *R. exulans* populations, such as those from the Kermadecs and New Zealand.

MATERIALS AND METHODS

Archaeological bone samples (femora and mandibles) were obtained from *R. exulans* collections excavated from three sites on Chatham Island during the mid-1970s by Douglas Sutton. Occupation of this coastal region (Fig. 2) centered on the permanently occupied Waihora settlement. Petrel colonies were exploited during summer and autumn seasons at sites such as CHA and CHB, and a nearby seal colony provided a stable resource base. The sites date to approximately 450 B.P. (Sutton 1985, in press).

Bone samples were removed to a laboratory where no previous *Rattus* DNA studies had been carried out. Bones were sanded with sterile, fine-grained sandpaper to remove the immediate surface, then placed in a sterile mortar, which was then frozen at −80 °C for at least one hour. Each bone sample was ground to a powder and placed into a sterile 2-ml tube. Disposable gloves and working surfaces were used throughout the procedure to prevent cross-contamination. Ground samples weighed between 0.07 and 0.14 g. DNA extractions were conducted as previously described (Matisoo-Smith et al. 1997). An extraction control, containing no bone powder, was processed with each extraction performed.

A 200-base-pair (bp) fragment of the mtDNA control region (bases 15355–15555) in the complete *R. norvegicus* mtDNA sequence (Gadaleta et al. 1989) was amplified using the following primers:

EGL7-H   5-TGA TAA CAC AGG TAT GTC C-3

EGL4-L   5-CCA CCA TCA ACA CCC AAA G-3

Both PCR and extraction controls, to which no DNA was added, were amplified with each set of reactions in order to identify possible contamination. On all occasions, both strands of the 200-bp-PCR product were directly sequenced using an Applied Biosystems 373A Sequencing System in a dye terminator reaction using the above primers (EGL 4 and 7).

All stages of sample preparation, PCR amplification, and post-PCR laboratory work were conducted in physically separate laboratories, and with dedicated ancient DNA equipment and reagents. In a subsample of the archaeological samples described in this article, a more variable region of the D-loop was amplified and sequenced. Slight variability in all five samples was observed, confirming the lack of cross-contamination of samples during DNA extraction (Matisoo-Smith et al. 1997). After the initial digestion stage of the extraction, aliquots of each sample were prepared and archived. These aliquots were used when initial extractions
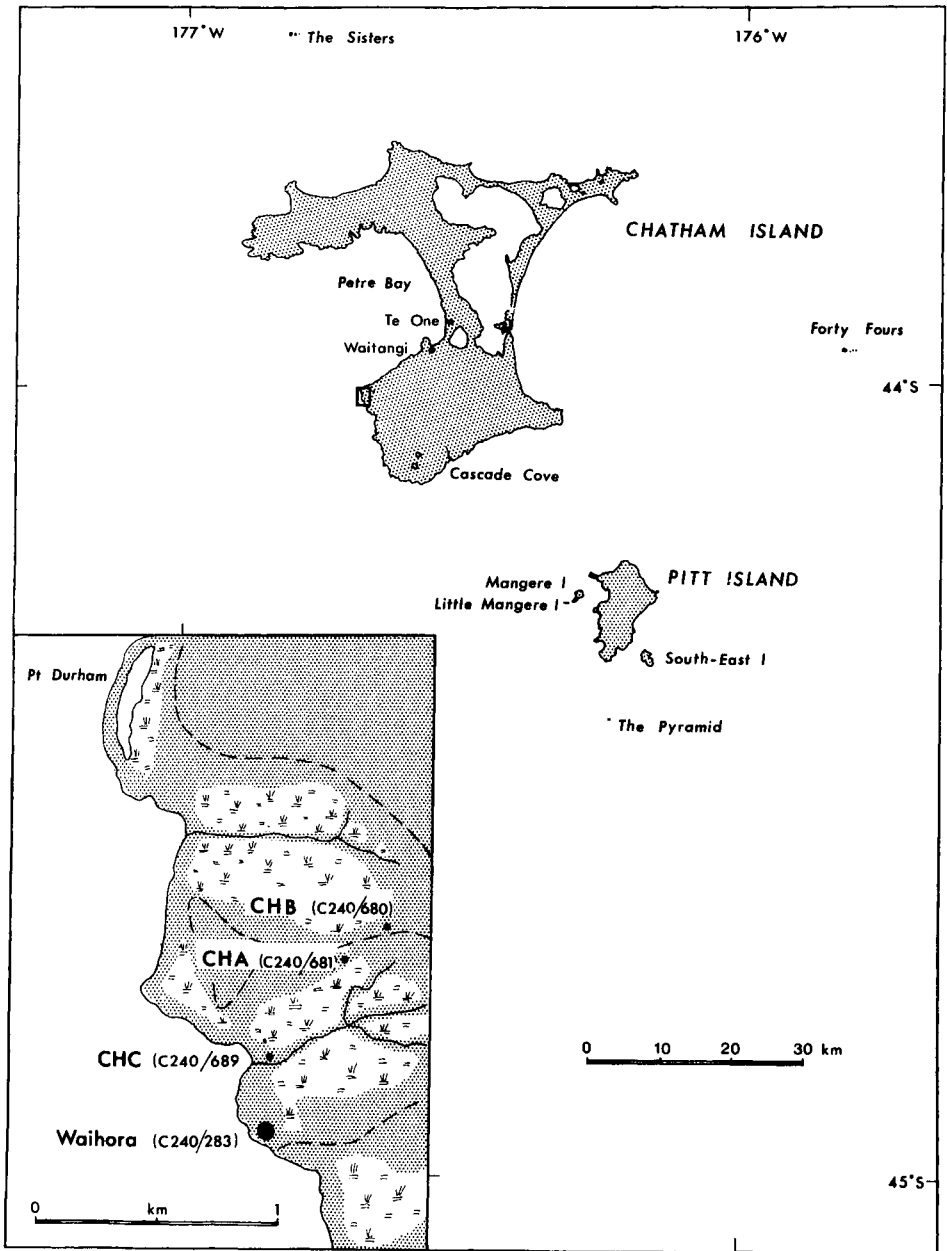
Fig. 2. Map of the Chatham Islands. Inset shows sites from which archaeological *Rattus exulans* material was obtained.

were unsuccessful or showed signs of contamination. Eventually DNA was amplified and sequenced from 15 of 16 samples attempted. Comparative sequences from modern *R. exulans* tissue samples from Chatham Island, Raoul Island, and New Zealand were extracted, amplified, and sequenced as described previously (Matisoo-Smith et al. 1998).

Diversity was calculated for lineage frequency variation within each population using Nei's (1987) equation:

$$h = (1 - \Sigma x^2)n/(n - 1)$$

Distance analyses were performed (Kimura two-parameter), and phylogenies were constructed by the neighbor joining method using PHYLIP, Version 3.57c (Felsenstein 1993).

RESULTS

Sequences for 15 archaeological samples, five samples from each of the three Chatham Island sites, were obtained and are shown, compared with modern *R. exulans* sequences, in Figure 3. The archaeological samples (samples 590-7 through 669-7) exhibit very little mtDNA variability and differ from the modern Chatham sequence at only one position—a deletion at position 67 in the modern Chatham sample. There is one variable position in the archaeological Chatham material, a deletion at position 133, which is found in all five of the samples from the CHA site and in two samples from Waihora.

All Chatham Island archaeological samples possess a unique Chatham Island point mutation. This change from Adenine to Guanine (A to G) at position 106 (base 15508 in the reference sequence from Gadaleta et al. 1989) was previously identified in all eight modern samples from the Chatham Islands and is not present in any of 124 other Polynesian *R. exulans* samples analyzed previously (Matisoo-Smith et al. 1998).

According to Tajima (1990), in geographically isolated populations, genetic diversity, or diversity, will be low where migration rates are low and higher in populations where migration rates are high. Estimated diversity *(h)* was calculated for lineage diversity in New Zealand, Raoul, and Chatham Island *R. exulans* populations and is shown in Table 1. The New Zealand samples were the most variable, with 34 mtDNA lineages identified from 50 samples sequenced, and a diversity value of 0.985. Of the eight modern rat samples collected from Chatham Island, only two were unique mtDNA sequences, differing at only one position. Diversity for modern Chatham Island lineages was estimated at 0.43, slightly lower than the 0.54 in the archaeological samples. By contrast, extant samples from Raoul Island have a very different signature. Of seven samples analyzed, four were unique sequences, and these differed at 12 positions. Diversity for Raoul (0.90) was much more similar to the New Zealand value.

A neighbor joining tree for all extant New Zealand, Kermadec, and Chatham Island samples is shown in Figure 4. Where the Chatham Island samples are monophyletic, the distance between the Raoul samples suggests at least two phylogenetically distinct populations on the island. Similarly, New Zealand *R. exulans* origins appear to be multiple and phylogenetically distinct.

DISCUSSION

This study clearly demonstrates an ancestor-descendant relationship between Chatham Island *Rattus exulans* living 450 years ago and those living on the island today. This finding has significant implications for Chatham Islands prehistory and

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                          10        20        30        40        50
                           .         .         .         .         .
Chatham        AGTACATAAAATGACATAGGACATTAAAACATTTATGTATATCGTACATT
590-7          .................................................
591-7          .................................................
592-7          .................................................
593A-7         .................................................
594A-7         .................................................
642-7          .................................................
643-7          .................................................
646-7          .................................................
647-7          .................................................
651-7          .................................................
665-7          .................................................
666-7          .................................................
667-7          .................................................
668-7          .................................................
669-7          .................................................
Huahine38      ...........................A..........G....C....
Hawai'i3       ..C...-...G......................................
Aitutaki4      .................................................
Stanley-NZ     .................................................

                          60        70        80        90       100
                           .         .         .         .         .
Chatham        AATTTATCTACCCCAAGCATATAAGCATGTAATATAAGTCAATGTATTAA
590-7          .................................................
591-7          .................................................
592-7          .................................................
593A-7         .................................................
594A-7         .................................................
642-7          .................................................
643-7          .................................................
646-7          .................................................
647-7          .................................................
651-7          .................................................
665-7          .................................................
666-7          .................................................
667-7          .................................................
668-7          .................................................
669-7          .................................................
Huahine38      .................................................
Hawai'i3       .................-...............................
Aitutaki4      ..........................-....................G
Stanley-NZ     ...............................................-.

                          110       120       130       140       150
                          ↓1        .         .  ↓2       .         .
Chatham        GACATGATATTTAAACTCAACTAGAAATCCACGATAACATGAATATTCTC
590-7          .....................................-........-....
591-7          .....................................-........-....
592-7          .....................................-........-....
593A-7         .....................................-........-....
594A-7         .....................................-........-....
642-7          .....................................-........-....
643-7          .....................................-........-....
646-7          .....................................-........-....
647-7          .....................................-........-....
651-7          .....................................-........-....
665-7          .....................................-........-....
666-7          .....................................-........-....
667-7          .....................................-........-....
668-7          .....................................-........-....
669-7          .....................................-........-....
Huahine38      .....A.......CT..................-T.T.....
Hawai'i3       .....A...........................................
Aitutaki4      .....A...........................................
Stanley-NZ     .....A...........................................
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Fig. 3. Aligned mtDNA D-loop sequences of modern Chatham Island *R. exulans* (reference sequence), archaeological samples from Chatham Island (samples 590-7 through 594A-7 from CHA, samples 642-7 through 651-7 from Waihora, and samples 665-7 through 669-7 from CHB), and modern samples from Huahine (Society Islands), Hawai'i, Aitutaki (Southern Cook Islands), and Stanley Island (off of the North Island, New Zealand). (.) signifies accordance with the reference sequence. (−) signifies a deletion. [1] identifies the Chatham Island marker (position 106) and [2] identifies Chatham Island variable site (position 134).

TABLE 1. SAMPLE NUMBERS AND ESTIMATES OF DIVERSITY FOR NEW ZEALAND,
KERMADEC, AND CHATHAM ISLAND *R. EXULANS* SAMPLES

POPULATION	*n*	NO. OF HAPLOTYPES	*h*
New Zealand	50	34	0.985
Raoul Is.	7	4	0.90
Chatham Is., modern	8	2	0.43
Chatham Is., archaeological	15	2	0.54

settlement. All of the Chatham Island rats analyzed, ancient and modern, possess a unique mutation—the A to G transition—not yet observed in any other *R. exulans* population. Given that the archaeological rats we analyzed came from relatively early sites in the Chatham archaeological sequence, the founding ancestral population almost certainly also possessed this mutation. Therefore, the identification of this "marker" in archaeological *R. exulans* remains in some location other than the Chatham Islands will be a strong indicator of the ancestral population and could identify the possible region(s) of origin of colonizing canoes. Based on current archaeological and linguistic evidence, we predict that the most likely place to find this is in archaeological deposits on the East Coast of central New Zealand. We are currently testing archaeological samples from this region.

The mtDNA of Chatham *R. exulans* is clearly derived from a single, or very limited, number of mtDNA lineage(s)—this supports the concept of post-colonization isolation of the group. It is possible that there may have been continuing contact between the Chathams and other parts of Polynesia during the prehistoric period, but rats were not transported in later voyaging canoes or, upon introduction, they were excluded by rats already present on the island. In such a case the rat phylogenies would not be a true reflection of human interaction. However, the continuous contact scenario for the prehistoric Chatham Islands is not consistent with current evidence from other fields (Clark 1994; Sutton 1985, in press). The Chatham Islands were, of course, subject to extensive contacts during the historic period because they were a site for major whaling operations, and the islands are visited regularly today (King 1989). These contacts resulted in the introduction of new species of rats, but apparently no new *R. exulans* lineages have been introduced. This is consistent with the ethnographic and natural historical assumptions (Matisoo-Smith 1994) of the rat-based model of Pacific settlement and suggests that such historic introduction was also unlikely elsewhere in the Pacific.

The demonstration of an ancestor-descendant relationship between Chatham Island archaeological and modern *R. exulans* allows us to interpret the differing levels of variation seen in Polynesian rat populations from locations with a similar duration of human contact—for example, the Kermadecs and New Zealand. Compared with the Chathams, *R. exulans* from New Zealand and the Kermadecs exhibit substantially higher mtDNA diversity values. Similarly, phylogenetic analyses (Matisoo-Smith et al. 1998) indicate highly divergent lineages for these populations within the Polynesian context. It is increasingly accepted that the settlement of New Zealand was the result of multiple settlement events (e.g., see discussions in Sutton [1994]), and this is consistent with the high level of di-
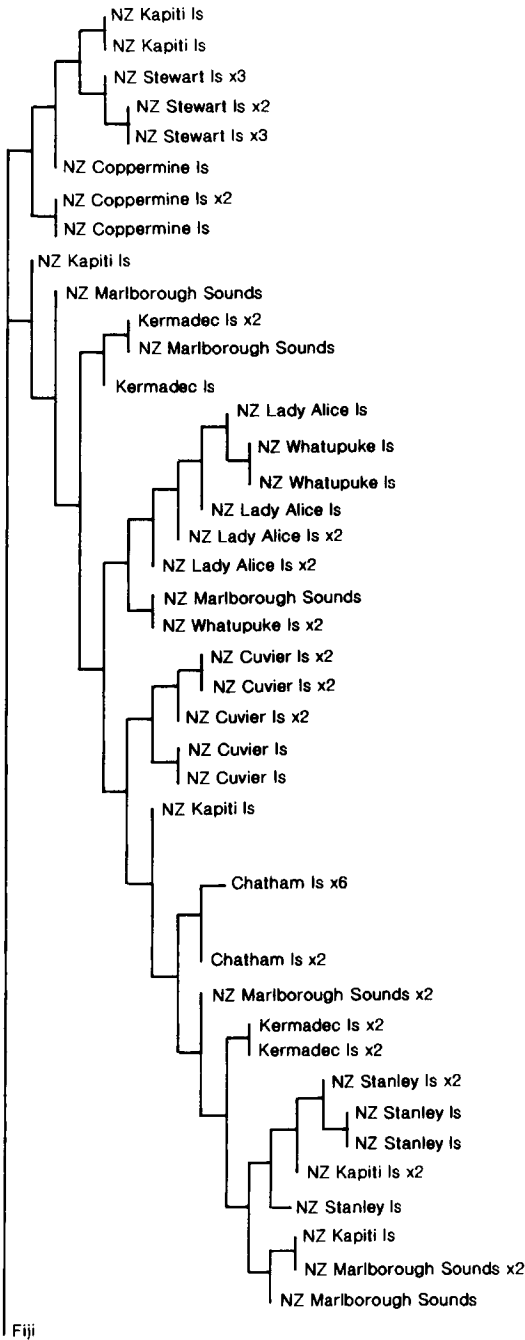
NZ Kapiti Is
NZ Kapiti Is
NZ Stewart Is x3
NZ Stewart Is x2
NZ Stewart Is x3
NZ Coppermine Is
NZ Coppermine Is x2
NZ Coppermine Is
NZ Kapiti Is
NZ Marlborough Sounds
Kermadec Is x2
NZ Marlborough Sounds
Kermadec Is
NZ Lady Alice Is
NZ Whatupuke Is
NZ Whatupuke Is
NZ Lady Alice Is
NZ Lady Alice Is x2
NZ Lady Alice Is x2
NZ Marlborough Sounds
NZ Whatupuke Is x2
NZ Cuvier Is x2
NZ Cuvier Is x2
NZ Cuvier Is x2
NZ Cuvier Is
NZ Cuvier Is
NZ Kapiti Is
Chatham Is x6
Chatham Is x2
NZ Marlborough Sounds x2
Kermadec Is x2
Kermadec Is x2
NZ Stanley Is x2
NZ Stanley Is
NZ Stanley Is
NZ Kapiti Is x2
NZ Stanley Is
NZ Kapiti Is
NZ Marlborough Sounds x2
NZ Marlborough Sounds
Fiji

Fig. 4. Neighbor joining tree, using Kimura 2 parameter correction, for Kermadec (n = 7), New Zealand (n = 50), and Chatham Island (n = 8) modern *Rattus exulans* samples based on 438 base pairs of mtDNA D-loop sequence, with a sample from Fiji included as an outgroup. Numerals following location names represent the number of individuals with identical sequences.

versity (0.985). Although Holdaway's (1996) suggestion that rats were in New Zealand 2000 years ago provides a longer time frame than more conservative estimates of 600 to 800 years, the Chatham ancient rat results suggest that it is unlikely that New Zealand lineages are the result of in situ evolution from a single introduction.

The most recently suggested date for Polynesian settlement of Raoul Island is around A.D. 1250 (Spriggs and Anderson 1993); however, a still earlier date of A.D. 960 has been rejected by Spriggs and Anderson on the basis of their chronometric hygiene strategy. Regardless of which date is accepted, the timing of initial human occupation of Chatham Island and Raoul is broadly similar. We cannot, however, completely reject the possibility of earlier introductions of rats to Raoul by humans who left no other identified evidence of their presence, but to date no evidence suggests this for the Kermadecs. Mutation rates would be expected to be the same for both Raoul and Chatham Island populations, so, given strict isolation of founding populations, we would expect to see approximately the same degree of diversity within each population. We do not. Therefore, the high degree of variability seen in modern Raoul Island *R. exulans* must, as in New Zealand, be assumed to be the result of introduced variation.

Introduced variation can be the result of either (a) the single introduction of a large number of rats from a region of high variability or (b) multiple introductions from a region or regions with highly variant *R. exulans* lineages. In terms of a single introduction, in order for such a high degree of variation to exist in one population, the place of origin would, again, either have to be ancient or have to encompass a large region of regular interaction. The concept of a large Polynesian homeland region is often suggested (Irwin 1992; Kirch 1986), and the debate about the timing of initial settlement of East Polynesia is ongoing. However, any single introduction event would still require transport of a large number of totally unrelated rats at one time.

Because of lineage extinction, mtDNA trees are constantly self-pruning in that certain lineages are lost while others proliferate (Avise 1994). *Rattus exulans* populations in a temperate climate are far from stable—they are regularly affected by seasonal population crashes (Roberts and Craig 1990). This would dramatically reduce the levels of variation, particularly over 800 years. Though the computation of specific numbers of introduced female rats cannot be estimated here, given a small number of founding females (e.g., <100), the probability of survival of two or more founding lineages in a population over 800 generations is low (Avise et al. 1984), and indeed, the diversity values for the ancient Chatham Island rats (0.54) are higher than those of the modern rats (0.43), indicating a loss of variation over time. If it is unlikely that hundreds of unrelated rats are introduced at one time, then in order to explain the high degree of variation, we are left with option (b): multiple introductions from a region or regions with highly variant *R. exulans* lineages.

The number of variant *R. exulans* lineages present in modern Kermadec samples is significantly different from the pattern seen in the Chathams and, given the same relative time frame for human contact, is suggestive of multiple introductions. Introductions of *R. exulans* during the historic period by European sailing vessels seem unlikely. Raoul Island has had limited contact during the historic period (Johnson 1995), significantly less than the Chatham Islands. Evidence suggesting no historic introduction of *R. exulans* to the Chathams makes this explanation for variation on Raoul improbable. The concept of multiple prehistoric Polynesian contacts with Raoul is consistent with computer voyaging simulations (Irwin 1992; Irwin et al. 1990), archaeology (Leach et al. 1986), and Maori migration traditions (Smith 1900; Te Rangi Hiroa 1949), and this concept now

seems the most likely explanation for the highly variable mtDNA lineages found in the Raoul Island rats.

SUMMARY AND CONCLUSIONS

The application of a diachronic approach, focusing on DNA variation in extant and archaeological *R. exulans* samples from the Chatham Islands, provides a clearer understanding of the population history of these rats. This allows a better interpretation of the patterns of variation identified in modern *R. exulans* populations. The lack of mtDNA variation shown in Chatham Island populations does not appear to be the result of a recent population crash, but it is consistent with the concept that the island received only a single introduction of rats and was isolated in prehistory. The New Zealand and Raoul rats have highly variable mtDNA and appear to be the result of multiple introductions. Therefore, the differing patterns of genetic variation in *R. exulans* populations from Chatham and Raoul Islands are consistent with their hypothesized roles as end-of-the-line and stepping-stone islands.

The animal-human relationship is receiving increasing attention by archaeologists and prehistorians (Clutton-Brock 1989; O'Connor 1997), and with this attention come not only a better understanding of concepts such as domestication and commensalism, but also new approaches to familiar problems. The results of this study exemplify the value of genetic studies of commensals both for understanding Pacific prehistory and for modeling human population mobility in general.

ACKNOWLEDGMENTS

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ABSTRACT

Irwin (1992) has suggested that island accessibility in the Pacific, in terms of latitude and safety of return voyaging, for example, affects their degree of contact with other islands and their role in Pacific prehistory. We present results of mtDNA variation in both ancient and modern populations of the Pacific Rat (*Rattus exulans*), an animal that was transported by humans as they settled the Pacific islands. We argue that the varying levels of genetic diversity in *R. exulans* populations on Pacific islands will to some degree reflect the level of prehistoric human contact with those islands, and thus will be tied to island accessibility. A high level of mtDNA variation is reported for the Kermadec Island *R. exulans* populations, but there is marked lack of variation in Chatham Island rats. This is consistent with predictions based on the relative degrees of accessibility of the Kermadecs and the Chathams. High levels must be the result of either multiple introductions by humans or in situ evolution over an extended time frame; however, lack of variation could conceivably be the result of recent population crashes, and may therefore not be reflective of low levels of human mobility. Analysis of mtDNA from archaeological *R. exulans* samples shows a direct link between ancient and modern populations on Chatham Island. This result (1) confirms relative prehistoric isolation of Chatham Island; (2) allows for rejection of the in situ evolution explanation for New Zealand and Kermadec levels of variation; and (3) supports the use of *Rattus exulans* mtDNA variation as an assessment for accessibility and contact of prehistoric Pacific populations. KEY-WORDS: *Rattus exulans*, mtDNA, ancient DNA, prehistory, Polynesia.