Proc. Natl. Acad. Sci. USA
Vol. 95, pp. 15145–15150, December 1998
Anthropology

Patterns of prehistoric human mobility in Polynesia indicated by mtDNA from the Pacific rat

(*Rattus exulans*/population mobility)

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Communicated by R. C. Green, University of Auckland, Auckland, New Zealand, October 14, 1998 (received for review July 20, 1998)

ABSTRACT **Human settlement of Polynesia was a major event in world prehistory. Despite the vastness of the distances covered, research suggests that prehistoric Polynesian populations maintained spheres of continuing interaction for at least some period of time in some regions. A low level of genetic variation in ancestral Polynesian populations, genetic admixture (both prehistoric and post-European contact), and severe population crashes resulting from introduction of European diseases make it difficult to trace prehistoric human mobility in the region by using only human genetic and morphological markers. We focus instead on an animal that accompanied the ancestral Polynesians on their voyages. DNA phylogenies derived from mitochondrial control-region sequences of Pacific rats (*Rattus exulans*) from east Polynesia are presented. A range of specific hypotheses regarding the degree of interaction within Polynesia are tested. These include the issues of multiple contacts between central east Polynesia and the geographically distinct archipelagos of New Zealand and Hawaii. Results are inconsistent with models of Pacific settlement involving substantial isolation after colonization and confirm the value of genetic studies on commensal species for elucidating the history of human settlement.**

The history of the settlement of Remote Oceania and the subsequent population dispersal has been the subject of debate and research for over a century. Over the last 30 years, work in a variety of disciplines, including archaeology, human skeletal biology, cultural anthropology, linguistics, and human genetics, has led to a vast increase in our understanding of this important historical problem, but a number of questions remain unanswered.

Archaeological evidence of human occupation of the western Pacific (Near Oceania) dates from at least 40,000 years before present (BP). The eastern extreme of this initial human presence reached the Solomon Islands by ≈30,000 BP. After 3,500 BP, sophisticated maritime technology enabled human expansion beyond this region of initial settlement and eastwards into Remote Oceania, as far as Tonga and Samoa. This latter process was associated variously with (*i*) an archaeological entity sometimes referred to as the Lapita cultural complex, (*ii*) ancestral Polynesian populations, and (*iii*) the introduction of Austronesian languages to Remote Oceania. Humans first arrived in western Polynesia (Tonga and Samoa) earlier than 3,000 BP. Subsequently, the settlement of central and east Polynesia began, by conservative estimates, by 1,500 BP. It concluded with the colonization of New Zealand early in this millennium, followed by its offshore satellites, the Chatham Islands, soon afterward (1).

Recent genetic research focusing on Polynesian populations has contributed significantly to our understanding of the ultimate origins of this last major human migration. Studies of globin gene variation (2) and mtDNA lineages of modern Polynesians (3, 4) and studies of ancient DNA from Lapita-associated skeletons (5) may indicate that some degree of admixture with populations in Near Oceania occurred as more remote biological ancestors left Southeast Asia and passed through Near Oceania. An alternative hypothesis is that the biological ancestors of these groups were one of a number of diverse populations residing within the Bismarck Archipelago of Melanesia (6). However, analysis of genetic variation amongst Polynesian populations has provided little evidence regarding the settlement of the Polynesian triangle itself. The relatively recent and rapid settlement process involving genetic bottlenecks (7) was undoubtedly a contributing factor leading to the remarkable linguistic, cultural, and biological homogeneity found in Polynesian populations (8). It has been suggested that this lack of variation may also be the result of a network of communication and contact that was in place throughout Polynesia during the period of settlement, continuing in some regions until European contact (9). However, the level and degree of contact throughout Polynesia, particularly in the geographic extremes of Hawaii, New Zealand, and Easter Island, is still a matter of debate (10). In this report, we present an alternative approach to the problem of Polynesian settlement and mobility, focusing on genetic variation in the Pacific or Polynesian rat (*Rattus exulans*) an animal that traveled with the ancestral Polynesians and other Austronesian-speaking peoples throughout Remote Oceania.

The ancestral Polynesians carried with them, in their colonizing canoes, a number of plant and animal species including the dog, pig, chicken, and the Pacific rat (*R. exulans*). Skeletal remains of this commensal rat have been found in early archaeological layers throughout Remote Oceania. Its ubiquitous distribution, which ranges from the Andaman Islands off of Southeast Asia to Easter Island and from Hawaii to Stewart Island in New Zealand, is suggestive of intentional transport (11, 12) possibly as a food item (13, 14). However, unintentional transport at some times cannot be discounted. This rat cannot swim more than a few meters in open ocean (15). However, the possibility that it traveled as a stowaway in prehistoric canoes cannot be excluded. In common with other rodent species, *R. exulans* has a rapid generation turnover (16) and apparently accumulates mutations faster than its human counterparts (17). Moreover, the islands of the Pacific east of Tikopia lacked a terrestrial mammalian fauna before the arrival of humans. It is very likely, therefore, that after introduction, viable rat populations were established quickly.

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Abbreviation: BP, years before present.

Data deposition: The sequences reported in this paper have been deposited in the GenBank database (accession no. AF104120–AF104211).

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Although European colonization brought with it the introduction of two more rat species (*Rattus rattus* and *Rattus norvegicus*) no hybridization between these three species has been known to occur. It follows that a phylogenetic analysis of populations of *R. exulans* provides an ideal model for tracing episodes of prehistoric human movement in Polynesia, which may include exploration voyages, colonization events, unsuccessful human colonization attempts, and postcolonization contacts. Ultimately, this evidence will provide an indication of degrees of interaction between the various archipelagos within the Polynesian triangle.

MATERIALS AND METHODS

Animals were trapped with basic snap-type rat traps. Heart, liver, and tail samples were removed and stored either in liquid nitrogen or in at least 2× their volume of 70% EtOH. Total genomic DNA was extracted from liver tissue by using standard phenol/chloroform methods (18).

A 480-bp (base pair) fragment of the hypervariable mitochondrial control region was PCR amplified with primers designed for *Rattus* mtDNA (bases 15,354–15,834; ref. 19). PCR amplifications were performed in 50-μl reaction volumes containing 1 unit of *Taq* DNA polymerase (Perkin–Elmer/Cetus), buffer (10 mM Tris, pH 8.3/50 mM KCl/1.5 mM $MgCl_2$), 0.2 mM each of dATP, dCTP, dGTP, and dTTP (Pharmacia), 0.5 μM each primer, and 2 μg of target DNA. After an initial denaturing at 94°C for 2 min, samples were run on a PHC-2 thermo-cycler for 36 cycles (Techne Laboratories, Princeton). Each cycle consisted of denaturation at 94°C for 1 min, annealing at 55–58°C for 1 min, and extension at 72°C for 1 min. A final extension of 5 min at 74°C followed, and samples were cooled to 4°C. Control samples to which no DNA was added were processed with all amplifications to check for contamination.

The PCR products were electrophoresed in a 2% agarose gel and, after staining with ethidium bromide, excised from the gel, placed in a Spin-X filter unit (Costar), and processed as per the manufacturer's instructions. The DNA was precipitated by addition of 0.2 vol of 10 M ammonium acetate and 2.5× the total vol of cold 90% EtOH. The resulting pellet was dried in a vacuum dryer and resuspended in 10 μl of distilled H_2O. PCR products were sequenced with an Applied Biosystems 373A DNA Sequencing System in a dye terminator reaction, at the Centre for Gene Technology, University of Auckland.

We analyzed 94 unique *R. exulans* DNA sequences, consisting of 432 bp of the mitochondrial control region. Distance analyses were performed by using MEGA, version 1.01 (20), with a sample from Halmahera (Moluccas Islands) as an outgroup to root the tree. Kimura two-parameter, Jukes and Cantor, and γ-distance matrices were generated, and phylogenies were constructed with the neighbor-joining method (21). All three methods produced identical trees; 500 bootstrap replicates were conducted, and all splits/partitions with 5% or more support (of which there were 272) were saved for use in further statistical tests as explained below.

RESULTS AND DISCUSSION

The resulting neighbor-joining tree is shown in Fig. 1. As yet, there are no general procedures available for testing the reliability of trees with such a large number of sequences when levels of intraspecific genetic variation are inevitably low, despite the fact that clear signals may be present in the data. Current methods of analyzing bootstrap results are commonly used for assessing the reliability of trees but are not appropriate for such data (22). However, a slightly relaxed version of the traditional analysis of bootstrap results has been reported (23). The problem with traditional bootstrap analysis is that it does not compensate for the exponentially increasing number of possible internal branches ($\approx 2^{n-1}$) as the number of sequences (n) increases. For four taxa, traditional bootstrap analysis tests just one of three alternatives. For 94 sequences, it allows only 91 of $\approx 9.90 \times 10^{27}$ possibilities. In essence, traditional bootstrap analysis tests all aspects of the tree structure simultaneously, even though there may be many stable local features. In a study of intraspecific variation, traditional bootstrap values inevitably will be low, regardless of the reliability of the overall structure of the tree. The improvement, the nearest-neighbor bootstrap (23), is used to test whether the optimal tree is stable locally, because it allows two rearrangements around every internal branch of the tree. This method is still a very conservative test; in this study, it allowed only 273 (3×91) internal branches of 9.90×10^{27}.

An example of nearest-neighbor bootstrap on the tree in Fig. 1, involving a Society Island sequence (Societies 4) is as follows. Societies 4 joins the optimal tree after three other Society Island samples, Societies 1, 2 and 3. The simple bootstrap support for this group of four sequences is 51.1%. The sample Societies 5 is the next deepest sequence in this tree. In the trees from the bootstrap samples, Societies 4 is found at either of the next two deepest positions (with or immediately deeper than Societies 5) in another 40% of samples, giving a total 91.2% support for Societies 4 being at one of three adjacent positions in the tree. Similarly, Societies 4 could move one step into the other three Society Islands sequences, Societies 1, 2 and 3. Overall, this result means that the position of Societies 4 is "locally stable." In the bootstrap samples, it can readily move one position in the tree, but it does not appear suddenly at quite different locations. This local stability criterion is a useful measure for a data set with a large number of closely related sequences. By working through the tree presented in Fig. 1 in this manner, we found that it was indeed locally stable.

Thus, given that its structure is well supported, the tree provides a valuable starting point for testing a range of specific hypotheses regarding the degree of interaction throughout Polynesia. Of particular interest is evidence of the degree of contact between central east Polynesia (the Southern Cook Islands and Society Islands) and the geographically marginal archipelagos of Hawaii and New Zealand, as well as between mainland New Zealand and the Chatham Islands.

An East Polynesian "Homeland". The Society Islands and Southern Cook Islands samples occupy the deepest branches (Group I) on the tree in Fig. 1 and are also dispersed throughout the tree, which is what would be expected with an "ancestral" population. It is interesting to note that the Samoan sample also falls into this group, as would be predicted based on the archaeological and linguistic evidence that suggests a west Polynesian origin for east Polynesian populations.

The close relationships between the *R. exulans* sequences of the Cook and Society Islands suggest a broad central east Polynesian interaction sphere encompassing the Southern Cook and Society Islands, and there is no evidence in the tree for a dispersal center restricted to any particular archipelago or east Polynesian "homeland" (24, 25). Rather, it seems that there was a large "homeland region," central to a number of interaction spheres, as suggested in Fig. 2. This view is highly consistent with ethnobotanical evidence (26), voyaging simulations (25), and accumulating archaeological evidence (27).

Isolation of the Chatham Islands. One of the most obvious features on the tree is the monophyletic nature of the five unique Chatham Islands sequences. These samples show closest affiliation to a Society Islands sequence from the island of Tahiti (Societies 9) but are part of a larger group consisting of five New Zealand samples from Cuvier Island (NZ 12–16), located off the east coast of the North Island. Archaeological evidence and linguistic evidence suggest that the Chatham Islands were settled from New Zealand and isolated soon after settlement. The result described here is consistent with this

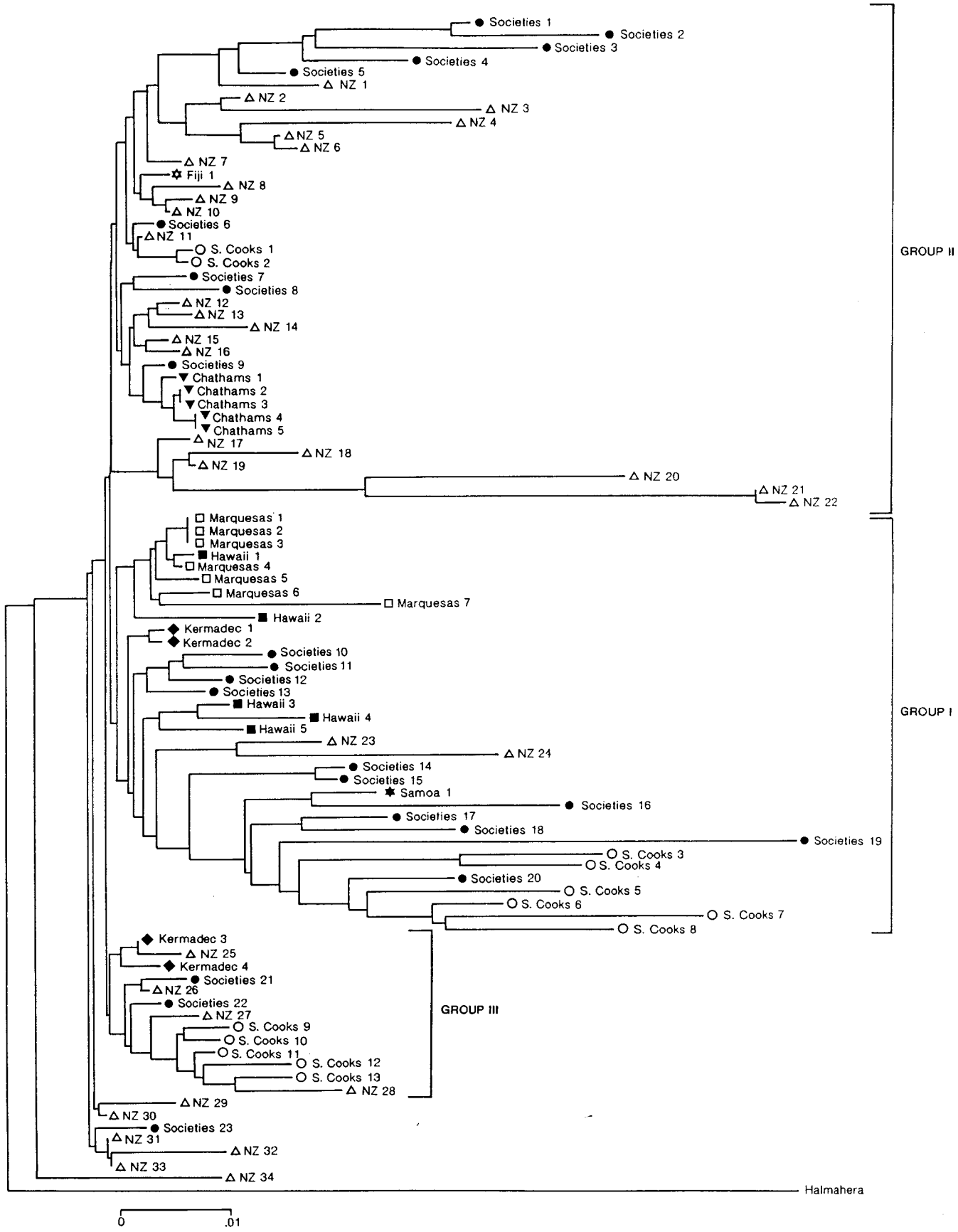

FIG. 1. Neighbor-joining tree. Branches are drawn to scale, with the bar scale representing percentage of divergence.

scenario. To test the validity of the monophyletic nature of the Chathams, we used theorem one from Carter *et al.* (28) and calculated that the chance of a group of five sequences forming a monophyletic group within 89 other distinct sequences is

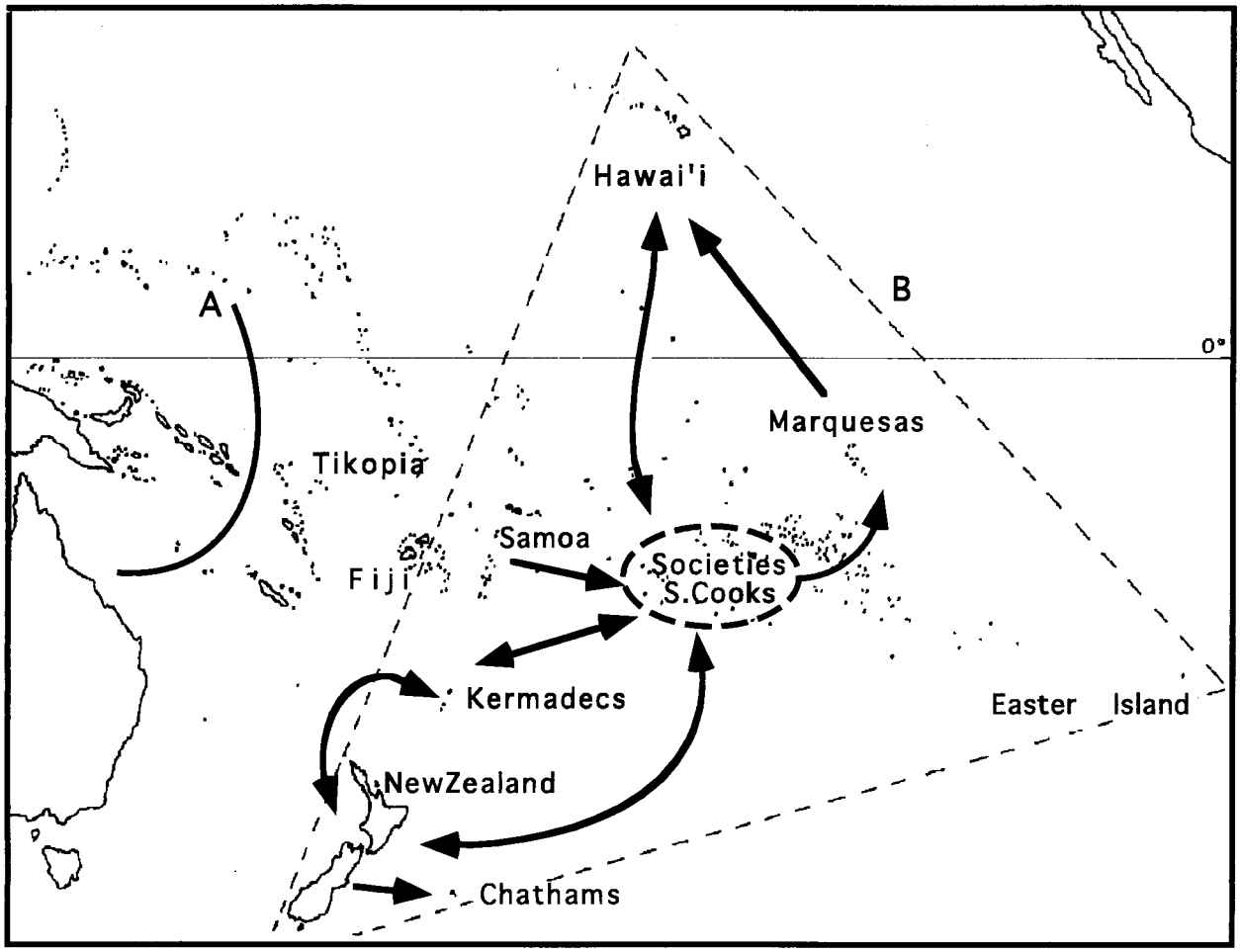

FIG. 2. Map of Polynesia. Line *A* identifies delineation between Near and Remote Oceania and *B* shows the Polynesian Triangle. Bold arrows show a likely sequence of colonization and contact in prehistoric Polynesia. These sequences are based on interpretations from the mtDNA phylogenies of *R. exulans*. Samples included in the analyses were collected from Fiji ($n = 1$ from Waya), Samoa ($n = 1$ from Manua), the Cook Islands [$n = 13$ from Rarotonga (S. Cooks 12), from Aitutaki (S. Cooks 2, 3, 4, 6, and 11), from Takutea (S. Cooks 7, 9, and 10), and from Atiu (S. Cooks 1, 5, 8, and 13)], the Society Islands [$n = 23$ from Tahiti (Societies 6, 9, 11, 13, 18, and 21), from Raiatea (Societies 4, 5, 7, 8, 14, 15, 16, 17, 19, 20, and 22), and from Huahine (Societies 1, 2, 3, 10, 12, and 23)], the Marquesas ($n = 7$ from UaHuka), Hawaii [$n = 5$ from Hawaii (Hawaii 1–3 and 5) and from Oahu (Hawaii 4)], the Kermadecs ($n = 4$ from Raoul), New Zealand [$n = 34$ from off shore islands of the east coast of the North Island (NZ 7–10, 12–24, 28, and 34), from Kapiti Island off the west Coast of the North Island (NZ 2, 3, 11, 26, 27, and 32), from Marlborough Sounds (NZ 1, 25, 29, 30, 31, and 33), and from Stewart Island (NZ 4, 5, and 6)], and the Chatham Islands ($n = 5$ from Chatham Is.). The sample from Halmahera (Moluccas Islands) was used as an outgroup to root the tree.

highly unlikely (1.0×10^{-7}). Thus, there is strong support that the monophyletic nature of the Chathams represents a "real" event. This outcome is most easily explained as the result of isolation of the Chatham Islands after a single or very limited introduction of *R. exulans*, probably from New Zealand.

Isolation of the Marquesas. It is interesting to note the location of the Marquesan samples within the section of the tree containing the deepest lineages. The seven Marquesan samples are monophyletic, with one Hawaiian sample imbedded within them. A Marquesan–Hawaiian connection has long been suggested based on linguistic data (29) and more recently on biological grounds (30). However, archaeological models often include the Marquesas group in the central east Polynesian homeland region (24). The monophyletic nature of the Marquesan *R. exulans* samples suggests isolation of that group, similar to the situation described for the Chatham Islands; the isolation of the Marquesas is inconsistent with the view that they were central in east Polynesian interaction and contact.

Discounting the five Chathams sequences, which we already have shown to be a monophyletic group, there are 89 "independent" sequences with which to test the monophyly of the Marquesas Islands. The likelihood of this group of 8 samples (7 Marquesan and 1 Hawaiian) forming, by chance, a group just one additional step from the 81 other sequences is 0.374×10^{-10}. Thus, as is the case for the Chatham Islands, the monophyly of the Marquesas–Hawaii group is supported strongly. This result supports the idea that the Marquesas Islands were a more marginal island group of east Polynesia, as initially suggested by Burrows (31) and more recently by Irwin (32), and not a central part of the larger homeland region discussed above. It also provides evidence of a directional connection from the Marquesas to Hawaii for the introduction of *R. exulans*.

Multiple Contacts with Hawaii. In addition to the Hawaiian–Marquesan link, a range of evidence suggests that there are also links between Hawaii and the region of the Society and Southern Cook Islands (33). Similarly, there seem to be non-Marquesan lineages in the Hawaiian *R. exulans* populations—the closest sequences on the tree being Society Island samples. Given the relatively short period of human occupation of Polynesia, it is difficult to attempt any direct chronological interpretation of *R. exulans* dispersal based on mtDNA variation from extant populations (e.g., the application of a "molecular clock"). Therefore, although there may have been multiple introductions of the Polynesian rat from the Marquesas and the Society and Southern Cook Islands, we are unable

to determine whether there were more than one effective human colonization or whether this variation may represent later contact, as archaeological evidence suggests (34). Our results clearly suggest that the Hawaiian archipelago was not isolated completely after initial human arrival.

Multiple and Possibly Early Contacts with New Zealand. The result of the neighbor-joining analysis strongly suggests that the New Zealand *R. exulans* populations are most closely related to Southern Cook, Kermadec, and Society Islands populations. This result corroborates the strong indications of archaeology, language, and culture (35). However, it has been argued recently that people may have arrived in New Zealand and introduced *R. exulans* by 1,800 BP, nearly 1,000 years before any evidence of successful human settlement (36). The fact that two New Zealand samples (NZ 23 and 24) appear within the deep branches of the "ancestral" Group I sequences from the Society and Cook Islands is not inconsistent with an early introduction of *R. exulans* to New Zealand. Similarly, the unusually long branch lengths for New Zealand samples NZ 20, 21, and 22 may represent evidence of an earlier introduction. Also, the Fiji sample is most closely related in the tree to New Zealand samples in Group II. A New Zealand–Fiji connection is inconsistent with archaeological, linguistic, and cultural evidence; however, it is not inconsistent with the suggestion that rats may have been introduced to New Zealand from some more westerly location before the successful human settlement from central east Polynesia. Regardless of the timing of the introduction events, it is clear that New Zealand *R. exulans* populations are highly divergent and are unlikely to be the result of a single introduction as has been suggested by some (37, 38).

Recent analyses of mtDNA variation in New Zealand Maori (39) conservatively suggest that a minimum number of 50–100 founding females was required to explain the diversity observed in modern Maori populations. These results are also consistent with multiple canoe voyages to New Zealand. To confirm the diverse structure of the New Zealand *R. exulans* populations, we sought any support for the monophyly of the New Zealand samples by looking for any splits or partitions in the bootstrap results that included all 34 New Zealand sequences. There were none. In other words, there is no support for a monophyletic New Zealand *R. exulans* population. Therefore, it is highly likely that the prehistoric settlement of New Zealand was the result of multiple contacts with at least the central Southern Cook and Society Islands group and the Kermadecs and possibly with other locations west of the Polynesian triangle.

The Kermadec Islands: A Stepping Stone for New Zealand. Today, the Kermadec Islands fall under the jurisdiction of New Zealand. The four islands that make up the group lie ≈800–1,000 km northeast of New Zealand, nearly half way between New Zealand and Tonga. Although uninhabited when Europeans arrived, there is clear archaeological evidence that the islands were colonized at least once by Polynesians (40). Obsidian artifacts of New Zealand origin have been found on Raoul Island, the northern-most and largest of the Kermadecs (41). Irwin (32) suggests, based on voyaging simulations, that the Kermadecs, like Norfolk Island to the east, were settled around the same time as New Zealand and that such islands could have been used as "staging posts" and occupied multiple times during periods of interaction between New Zealand and the rest of central east Polynesia.

The four unique Kermadec samples come out in two distinct groups on the tree. Samples Kermadec 1 and 2 group with the deepest central east Polynesian samples in Group I, and Kermadec 3 and 4 are part of a Southern Cook, Kermadec, and New Zealand cluster, Group III, that also includes a Society Islands sample. To test the diversity in the Kermadecs, we applied a test similar to that used for the New Zealand samples, asking the question: is there any tendency for the four distinct Kermadec sequences to come out together in a single group? When we searched all of the 272 bootstrap partitions with at least 5% support, we found that the smallest group in which all four sequences were included consisted of 80 sequences. This strongly suggests that the Kermadec populations are the result of multiple introductions. Genetic diversity among rats from the Kermadecs supports their role as intermediary islands in two-way and multiple voyaging between the New Zealand archipelago and the tropics, as stated in Maori traditions (42) and suggested by archaeological evidence (41).

CONCLUSION

This study of mtDNA variation in *R. exulans* populations from a number of Pacific islands supports the following hypotheses. (*i*) Colonization of the islands of east Polynesia and subsequent contact occurred from a broad central region that included at least the Southern Cook and Society Islands, but the Marquesas Islands probably should not be considered a part of this central region to the same degree. (*ii*) A minimum of two introductions of the rat into Hawaii supports suggestions of postsettlement human contact with central east Polynesia. (*iii*) New Zealand's prehistoric colonization and contact history included multiple visits from the Southern Cook and Society Islands region and the Kermadecs and may have included earlier exploratory visits and/or unsuccessful colonization attempts. (*iv*) Intermediary and stepping-stone islands (e.g., the Kermadecs) have a significant role in colonization and subsequent voyaging. (*v*) Relative accessibility and isolation among islands influence colonization and interaction histories.

All of these conclusions are generally consistent with patterns predicted by Pacific voyaging simulations (31). More specifically, our conclusions suggest the rejection of a number of key points in what has been referred to as the "orthodox" model of Polynesian settlement (24), namely, the concept of the Marquesas Islands as the primary east Polynesian homeland or dispersal center. Perhaps more importantly, the results presented here strongly suggest that multiple contact, to a greater or lesser degree, rather than isolation was the general pattern in Polynesian prehistory, particularly in the central region. Geographically remote islands and archipelagos such as Easter Island and, perhaps to a lesser degree, the Marquesas and Hawaiian Islands may have featured less prominently in the central contact sphere or may have dropped out of contact at earlier points in time. The major exception to this pattern of multiple contact seems to be the Chatham Islands, which were most likely isolated by their latitudinal location (31).

mtDNA sequences from *R. exulans* prove to be valuable genetic markers for tracing the migration routes and movement of the first humans entering the remote Pacific, because the species was intentionally transported by them. In addition, the high levels of genetic variation make it an ideal study animal for issues of recent evolutionary events. Studies of other commensal plants and animals would provide valuable evidence to help elucidate the historical question of human population origins and interactions in the Pacific. Such studies could involve larger sample sizes of *R. exulans*, including samples from Melanesia, Micronesia and Southeast Asia, and analyses of mtDNA variation in *R. exulans* remains from archaeological sites throughout the Pacific, including samples from Lapita sites. These types of approaches might be applied usefully in other studies of human population mobility as well.

We thank Dr. Tim Lovegrove, Mr. Gerald McCormack, Ms. Judith Künzlé, Dr. Becky Cann, Dr. Terry Hunt, Ms. Sandra Anderson, Ms. Simone and Mr. Conor Holmes, and many scientists from the New Zealand Department of Conservation for sample collection. We thank Mme. Maeva Navarro and the staff of the Musée de Tahiti et des Îles for assistance in French Polynesia. Our thanks to Ms. Joan Lawrence for Fig. 1, and Dr. Allen Rodrigo and Mr. Brad Haami for their input,

discussions, and comments on this project. For their valuable comments on this manuscript, we thank Dr. Thegn Ladefoged, Mr. Peter Ritchie, Prof. Vince Sarich, and the anonymous referees. Funding for this research was provided by the University of Auckland Research Fund, the Skinner Fund of the Royal Society of New Zealand, and the New Zealand Lottery Science Fund.

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