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Report

Native American Y Chromosomes in Polynesia: The Genetic Impact of the Polynesian Slave Trade

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Since Thor Heyerdahl asserted that Polynesia was first colonized from the Americas (Heyerdahl 1950), geneticists have sought—but have not found—any evidence to support his theories. Here, Native American Y chromosomes are detected on the Polynesian island of Rapa. However, this, together with other odd features of the island's Y-chromosomal gene pool, is best explained as the genetic impact of a 19th century Peruvian slave trade in Polynesia. These findings underscore the need to account for history before turning to prehistory and the value of archival research to understanding modern genetic diversity. Although the impact of the Atlantic slave trade on the distribution of modern genetic diversity has been well appreciated, this represents the first study investigating the impact of this underappreciated episode on genetic diversity in the Pacific.

The reconstruction of Polynesian ancestry through archaeology and linguistics has indicated clear affinities with populations to the west, in island Southeast Asia. The first settlement of the islands of remote Oceania ~3,000 years ago was accomplished by carriers of the Lapita culture with clear antecedents in the islands of Near Oceania, first settled ~30,000 years earlier (Kirch 1999). The languages spoken in remote Oceania are closely related and clearly belong to the diverse family of Austronesian languages spoken throughout island Southeast Asia (Blust 1999). Despite these convincing lines of evidence for Polynesian origins to the west, several more minor aspects of pre-European Polynesian culture appear to have American origins. The most definitive of these is the presence of the sweet potato (Yen 1974) and bottle gourd (Green 2000). The distribution of these plants requires some prehistoric contact between Polynesians and Native Americans. Most prehistorians favor a return Polynesian voyage to South America to explain this phenomenon, although a one-way voyage by Native Americans cannot be ruled out.

The genetic evidence has strongly supported a western ancestry for Polynesians, with all loci studied thus far indicating a proximal biological origin for Pacific populations in island Southeast Asia (Serjeantson and Hill 1989; Sykes et al. 1995; Hurles et al. 2002). Although most genetic lineages can be traced exclusively to the west, some mtDNA types are shared by Polynesian and Native American populations. However, these types are also found in intervening continental Asian populations and occupy basal positions in phylogenetic analyses, thus supporting the hypothesis that they represent mutual retention of ancestral Asian sequences (Bonatto et al. 1996). Other researchers are not convinced by these analyses and insist there is still room for limited prehistoric gene flow between these populations (Cann and Lum 1996). The paternally inherited Y chromosome provides a useful tool to explore this issue by virtue of the presence of a lineage (Q3) in Native Americans that is both predominant and American-specific. This lineage is defined by the derived state of the DYS199 binary marker and is typically found at frequencies of 70%–100% in South America (Underhill et al. 1996; Tarazona-Santos et al. 2001). We have detected this lineage on the Polynesian island of Rapa as part of our expansion upon previous investigations into the origins of Oceanic peoples (Hurles et al. 2002), and here we discuss alternative

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hypotheses for the arrival of these lineages on this isolated Polynesian island.

Rapa lies within the Austral group in Eastern Polynesia. Its population is well documented to have suffered an extreme reduction from an initial size of ~2,000 to only 120 by the mid-1860s (McArthur 1968). Genetic evidence for this bottleneck has been sought previously within extant diversity at autosomal minisatellites (Martinson et al. 1993) but has not been found, which is surprising.

Twenty-seven individuals from the island of Rapa were typed by use of Y-chromosomal markers. The available genealogical records for these individuals document grandparental origins and allow the exclusion of related individuals and those with non-Rapan paternal ancestry. Given the small size of the population of the entire island, it is not surprising that this reduces the number of unrelated, autochthonous paternal lineages to 16.

These 16 Y chromosomes from Rapa were analyzed by use of 10 binary markers, seven microsatellites, and the minisatellite MSY1. All markers were typed as described elsewhere (Hurles et al. 2002), and a lineage summary is shown in table 1 (full haplotype data are available from the authors). Only 10 of these chromosomes belong to typically Polynesian lineages. Of the remainder, two chromosomes belong to the distinctively Native American lineage described above (the derived state of DYS199 was confirmed by sequencing). The final four chromosomes belong to the P*(xQ3,R1a) lineage, which is found at appreciable frequencies in Europe and the Americas but not in Southeast Asia (Hurles et al. 1998). On the basis of the multiallelic marker haplotypes, three of these chromosomes appear to have European origins, whereas the fourth appears Native American in origin. Whereas these three putatively European-derived microsatellite haplotypes are found in a database (Y-STR Haplotype Reference Database) of >11,000 European haplotypes with an average of 20 matches, the putatively Native American-derived haplotype has no matches at all in the database but is identical to one of the other Native American chromosomes on Rapa. Thus, this Polynesian population contains substantial levels of both European (3/16) and Native American (3/16) male-mediated admixture. The microsatellite haplotype diversity among both of these sets of chromosomes is such that neither set could descend from a single recent founder. Two of these admixed chromosomes, one European and one Native American, belong to individuals born before 1940 whose paternal grandfathers were of Rapan origin. An average male generation time of 32 years, derived from the genealogical records, indicates that these admixed chromosomes probably entered the population before 1900. Although unrecorded nonpaternity in the past two generations might be an alternative explanation, we do not observe any nonpaternities among the individuals known to be related, which includes carriers of both Polynesian and admixed Y chromosomes, and so deem this unlikely.

Studies of many different genetic loci show a cline of decreasing diversity throughout the Pacific in order of date of first settlement, which broadly follows a west-to-east distribution (Martinson et al. 1993). However, once the 6 admixed chromosomes are removed, the 10 typically Polynesian (Hurles et al. 2002) Y chromosomes

Table 1

Y-Chromosomal and Mitochondrial HVS-1 Haplotypes Found among Rapans with Nonredundant Rapan Ancestry

Lineage and Haplotype	Number	Defining Mutations	Geographic Location
Y Chromosome[a]:			
P*(xQ3,R1a)	3	M9, DYS257	European[b]
P*(xQ3,R1a)	1	M9, DYS257	Native American[b]
Q3	2	M9, DYS257, DYS199	Native American
C	5	RPS4Y	Remote Oceania, Near Oceania, Eastern Indonesia[c]
K*(xM,N,P)	4	M9	Remote Oceania, Near Oceania, Island Southeast Asia[c]
K*(xM,N,P)	1	M9	Remote Oceania[c]
MtDNA[d]:			
"Polynesian Motif"	14	16189, 16217, 16247, 16261	Remote Oceania, Near Oceania, Eastern Indonesia
B4a	1	16189, 16217, 16261	Remote Oceania, Near Oceania, South East Asia, and a single Native American
Q	3	16129, 16144, 16148, 16223, 16241, 16265C, 16293, 16311, 16343	Central Polynesia

[a] Y-chromosomal haplotypes named according to the YCC consensus nomenclature.

[b] Assigned on the basis of alternative MSY1 modular structures and matches in the Y-STR Haplotype Reference Database (see text).

[c] Sublineage affiliation refined on the basis of unique MSY1 modular structures (Hurles et al. 2002).

[d] Mitochondrial mutations are all transitions compared with the Cambridge Reference Sequence, except an A→C transversion at 16265.

exhibit greater diversity than is expected from their geographical position (fig. 1) and demographic history.

The Y-chromosomal pool of this isolated island thus possesses three unusual features that require explanation: (i) European admixture, (ii) Native American admixture, and (iii) greater-than-expected Polynesian diversity. These features could be the result of several unrelated historical or prehistorical episodes, which are considered below.

First, male-biased European admixture has been noted on a number of other Oceanic islands (Hurles et al. 1998; Underhill et al. 2001), most likely reflecting a cumulative effect from the 19th century onward. It is possible that the Rapan European Y chromosomes are in this category. However, the isolated nature of this island means that there were only a handful of European visitors during the 19th century and no evidence for long-term settlement by large numbers of males. Second, the Native American lineages could represent the residue of an initial settlement by a Native American population, who were subsequently joined by Polynesians, as envisaged by Thor Heyerdahl. Third, the higher-than-expected Rapan paternal lineage diversity could result from an unusually large founding population or several colonization events from diverse source populations.

If the above hypotheses for the presence of Native American and highly diverse Polynesian paternal lineages are correct, they should be testable using data from other genetic loci, such as mtDNA; we might expect to find Native American maternal lineages and high Polynesian maternal lineage diversity.

We generated sequence data from segment I of the hypervariable D-loop of the mitochondrial genome in 28 individuals from Rapa. Excluding related individuals and those with known non-Rapa maternal ancestry gave 18 unrelated, autochthonous sequences. Three different haplotypes were found among these 18 sequences (summarized in table 1), and their global distribution was examined using a database of >13,000 sequences with precise sampling locations (Röhl et al. 2001). All three lineages are commonly found in other Polynesian populations and have ancestry to the west, in Eastern Indonesian and Near Oceania (Redd et al. 1995; Sykes et al. 1995; Tommaseo-Ponzetta et al. 2002). The sole haplotype match in the Americas was for the B4a haplotype, in North America, from a Pima Indian. The population specificity of this match means that it is likely to result from a recent recurrent mutation on a basal haplotype in the Americas.

Thus, there is no evidence for any Native American contribution to the maternal lineages of Rapa, implying that the Native American paternal lineages are not the

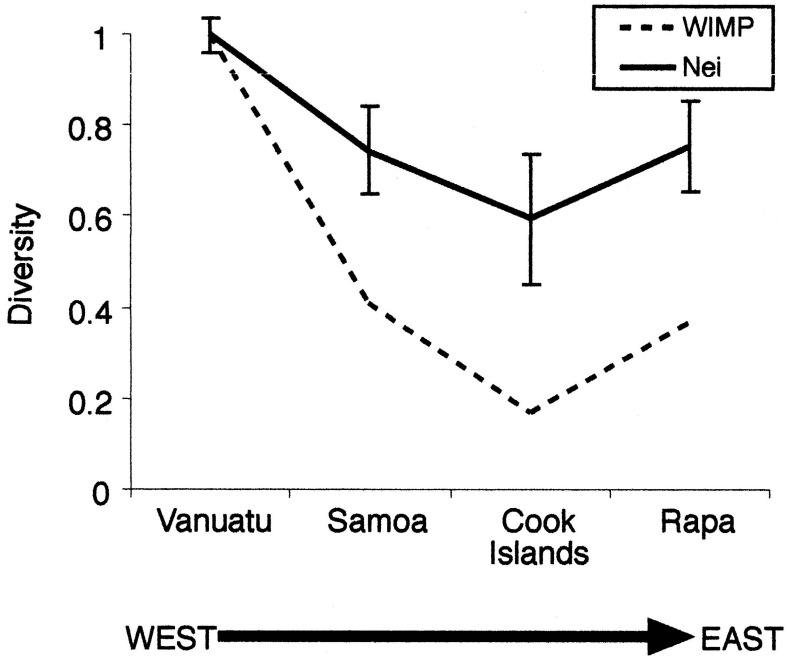

Figure 1 Diversity among four Pacific populations, ordered according to settlement timing. Two different normalized diversity measures are used to show greater-than-expected diversity among genuine Polynesian Y chromosomes in Rapa (calculated using Arlequin 2.0). Nei's estimator of diversity, together with standard errors, was calculated on the population frequencies of lineages defined elsewhere using binary and multiallelic markers (Hurles et al. 2002). The second measure is the weighted average of intralineage mean pairwise (WIMP) differences between microsatellite haplotypes (Hurles et al. 2002).

residue of an ancient settlement. It could be suggested that the absence of Native American mtDNA lineages is a result of their loss through drift after an ancient settlement. However, the Native American paternal lineages were not lost, despite the population bottleneck during the 1864 epidemic being at least fivefold more severe for paternal than maternal lineages. In addition, unlike paternal lineage diversity, the diversity among Rapan maternal lineages is not elevated (fig. 2), which is inconsistent with the settlement hypothesis considered above, and instead suggests that a male-biased process contributed these additional lineages.

Since explanations for the unusual features of Rapan Y chromosomes owing to independent events were clearly inadequate, archival research was undertaken to ascertain whether any historical episode might provide a better explanation. This research revealed that the population crash in 1864 resulted from an epidemic of either dysentery or smallpox, following the repatriation of infected Polynesians from Peru. This repatriation represents the final act of a Peruvian slave trade perpetrated throughout Polynesia during 1862–1863, which was halted under international pressure but not before certain islands had been depopulated by up to 80%. The entire episode cost the lives of ~6,000 Polynesians (Maude 1981). Only 1 of the 33 slave ships was ever captured, when forewarned Rapans overpowered the crew of the *Cora* in January 1863. Some of the crew were sailed to Tahiti for trial, but five remained on Rapa. At the time, the origins of four of these five crew members were recorded in the French-language Pacific newspaper, *Messager de Tahiti.* Three were of Chilean origin, and one came from Mexico (*Messager de Tahiti* 1863). Although all had Hispanic names, by the 1860s, many Native American laborers had adopted such names, and substantial admixture between European and indigenous populations had already occurred. Thus, it is likely that these five men carried both European and Native American genes. Had they contributed to succeeding generations of Rapans, we would expect to see both European and Native American lineages in the extant population.

It is striking that the sole Oceanic island on which these admixed lineages are found together is also the sole island on which a Peruvian slave ship was captured and the crew assimilated into the population. The likelihood that both the European and Native American Y chromosomes were introduced to the island before the 20th century, together with the fact that only a handful of contacts between Rapans and outside populations occurred before this time, leads us to propose that the admixed chromosomes are likely to derive from this stranded crew. The current appreciable frequency of these lineages on Rapa, despite their small initial numbers, is due to their arrival on the island immediately prior to the population crash, which only 20 adult males are thought to have survived (Green 1864). The crew's contribution may have been amplified by a greater resistance of the marooned sailors to the epidemic, which devastated the Polynesians.

The aim of repatriation was to return the surviving Polynesian slaves to their home islands. The majority of the transported slaves had already died as a result of the poor working conditions and novel disease environment (Maude 1981). The *Barbara Gomez* set out with 470

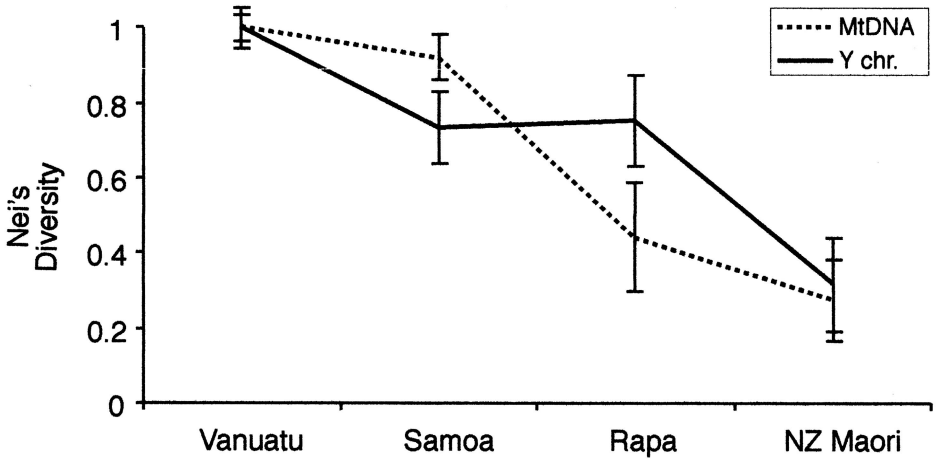

Figure 2 Normalized diversity in paternal and maternal lineages among four Pacific populations, ordered according to settlement timing. Nei's estimator of diversity and standard errors were calculated as described elsewhere (Hurles et al. 2002). New Zealand Maori Y-chromosomal data come from Underhill et al. (2001). Mitochondrial data are taken from Lum et al. (1994), Redd et al. (1995), Lum et al. (1998), Murray-McIntosh et al. (1998), and Lum and Cann (2000), as described in Röhl et al. (2001). There is no representative mtDNA diversity data set from the Cook Islands.

liberated slaves from numerous Polynesian islands, but 439 succumbed to disease on the voyage and were thrown overboard. After dropping 15 of the remainder at Rapanui (Easter Island), the captain abandoned the remaining slaves on Rapa, irrespective of their previous origin (Maude 1981). Missionaries' papers and journals (Green 1865; Saville 1871) and other records (Stokes 1930) document these Polynesians as contributing significantly to the Rapan gene pool: for example, by 1921, one repatriated slave counted a quarter of the island's population among his descendants (Stokes 1930). Their relative resistance to the disease that caused the epidemic, as witnessed by their survival of the voyage, may have enhanced the slaves' chances of surviving the ensuing epidemic on Rapa. The diverse origins of the ancestors of modern Rapans explain why the previous attempt to demonstrate the impact of the population bottleneck on minisatellite diversity was unsuccessful, and the fact that all but one of the repatriated slaves that contributed to succeeding generations was male (Stokes 1930) explains our detection of increased paternal but not maternal lineage diversity.

The combined analysis of both maternal and paternal lineage diversity on the island of Rapa reveals that the most likely explanation for the joint presence of European and Native American admixture and the higher-than-expected paternal lineage diversity is the impact of the abortive Peruvian slave trade and its immediate consequences. Consequently, this first finding of Native American paternal lineages in Polynesia gives no insight into the nature of prehistoric contact between Polynesians and Native Americans.

The present study emphasizes the need to account for events in history before turning to prehistory: the genetic impact of this brief but deadly slave trade on other Polynesian islands has yet to be ascertained.

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Electronic-Database Information

URLs for data presented herein are as follows:

Arlequin, http://lgb.unige.ch/arlequin/ (for population genetics data analysis)

Y Chromosome Consortium, http://ycc.biosci.arizona.edu/nomenclature_system/frontpage.html (for Y-chromosome haplogroup tree and nomenclature)

Y-STR Haplotype Reference Database, http://ystr.charite.de/index_gr.html (for a searchable database of Y-chromosomal microsatellite haplotypes in >50 European populations)

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