

Patterns of colonisation and the "thrifty" genotype in Pacific prehistory

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The seemingly distinctive markers of Polynesian biology - serologic, molecular, anatomical, and developmental - have been argued to have emerged from the special circumstances of colonisation and early settlement of the region. Models point to the microevolutionary impact of mortality selection while voyaging, small founding group size forcing bottlenecks, and subsequent relative isolation of groups introducing heterogeneity through genetic drift within Polynesia. These ideas have drawn on a melange of ideas about the colonising experience to construct evolutionary narratives, including that of the "thrifty" genotype in Polynesia. The substantial problem is that there previously has been no independent theory of colonisation and inter-island contact for the region. We critically examine which microevolutionary forces would have impacted prehistoric Polynesians in terms of an independent navigational theory of colonisation, and map out the expected biological/ evolutionary sequelae. This theory suggests that Remote Oceania was settled by directed return voyages, that the tempo of population expansion was probably rapid, that voyaging continued after settlement, that whereas episodes of colonisation were directed to safety, subsequent inter-group voyages followed the pattern of mutual inter-island accessibility. The implication is that mortality selection would not have been the predominant force shaping the Polynesian genotype; the development of survival sailing strategies were designed to remove these very risks. This makes it unlikely that the specific experience of Polynesian colonisation would promote an efficient insulin mechanism, and so explain, for example, the high incidence of Type II diabetes mellitus in contemporary Polynesian groups.

Introduction

First proposed in 1962 by James Neel, the concept of the "thrifty" genotype has been posed as an evolutionary explanation for the high prevalence of diabetes mellitus in many populations, but most particularly in native Americans and Pacific islanders in modernising settings^{1,2}. The proposition is that periods of acute nutritional stress generated a selective advantage for an "efficient" insulin metabolism. In Polynesia, these stresses have been posed to be provided during a risky and selectively costly maritime colonisation process³.

Polynesia, the geographic region that encompasses one sixth of the earth's surface (Fig 1), has long been recognised as a rare and telling arena for studying human microevolution⁴. It was settled rapidly and recently, and there is a startling biological homogeneity, given the enormous space over which the component populations are distributed. Further, the chronology of settlement is comparatively precise with the exception that two alternative chronologies are proposed, and debated, for East Polynesia. These are conditions under which microevolutionary scenarios, such as that posed to explain "thrifty" genetics in Polynesia, can be best tested. In the Polynesian case, this assessment has been difficult because, as we will describe in the background section, we have been stumped in linking cause-and-effect, and used untested assumptions about the nature of voyaging to drive interpretations of biological history. What we have needed is a distinct body of organised ideas about the nature of

Polynesian colonisation that can allow us to better interpret biological history in the region that is particularly explicit about the process of colonisation and population founding. This is because assessments of genetic diversity between human groups do not provide any obvious or automatic explanations of population history. In this paper we present a systematic and independent navigational theory of colonisation, map the anticipated evolutionary sequelae of this pattern to see if the selection-bottleneck-drift narrative is warranted against likely voyaging and settlement strategies, and present the implications of this model for the thrifty genotype hypothesis as it has been applied to Polynesian populations.

Background

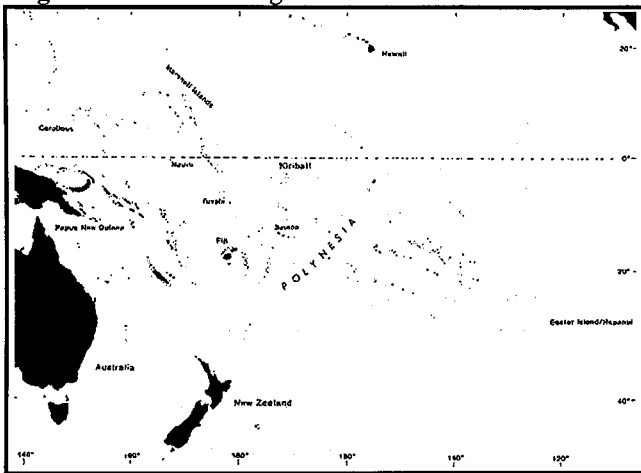
Although the exact source(s) of the Polynesian ancestors remain(s) unidentified, molecular studies-including of mtDNA lineages⁵ and globin gene variability⁶ - confirm a genetic history of Asian immigrants having admixed with non-Austronesians in Near Oceania, around the northern coast of Papua New Guinea, resulting in a complex colonising genotype(s). A roughly similar pattern is evinced in linguistic and archaeological data. Current debates focus on the speed with which the later Asian

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migrants moved through the area, and (consequently) the degree of admixture, both prior to and following initial colonisation of Polynesia^{7,8}.

Figure 1. The Pacific region.



There are several aspects of Polynesian population biology that have been posed as defining. For skeletal biologists, these have been relatively short lower limbs, tall and muscled skeleton^{9,10}, characteristically pentagonal and brachycephalic head form with wide cranial base angle (over 140 degrees), high frequencies of "rocker" jaw¹¹, femoral and humeral bowing, (possibly) oval shaped fovea capita, tibial and talar squatting facets¹², and reduced frequencies of shovelling on incisors¹³. Molecular and serological markers of Polynesian populations have been: near fixity in the nine base-pair deletion in region V of mtDNA¹⁴; lack of diversity in HLA; low frequency of *aaa* globin gene variant; an absence of A1 blood type with relative absence of type B¹⁵; and an almost startling lack of overall genetic variation, such as within the (non-coding) D-loop region of mtDNA¹⁶. Polynesian groups in non-industrial settings may also display precocious development and, maybe, relatively low age at menarche.¹⁰ None of these markers are specific to Polynesians, although they are generally regarded as defining because they are displayed at considerably different frequencies to other Oceanic groups, particularly those in West and East Micronesia and Near Oceania.

These characteristically Polynesian population traits (serological, molecular, developmental or anatomical) have often been argued, like "thrifty" genotypes, to have emerged from the particular circumstances of colonisation and early settlement of the region, in that they would create and enforce opportunities for microevolutionary change. There has emerged in the literature a seeming trilogy of microevolutionary explanations for the emergence of the Polynesian pheno/genotype, all related to notions of the relationship between the colonising and settling experience and the evolutionary sequelae that would emerge under such conditions. The basic scenario invoked is: selection through mortality and bottlenecking during colonization, followed by genetic drift through relative isolation. (Mutation is rarely invoked as an explanation because the time-scale since colonisation, less

than two millennia, provides insufficient time for the accumulation of new mutations².)

For example, in developing an explanation for the anatomical markers of the Polynesian skeletal phenotype, Houghton has posed that the crucial evolutionary force was selection through mortality, where only the better adapted would survive to settle new islands, so to be ancestral to contemporary Polynesians:

The large and muscular body form that is still evident in Polynesia, and which on a growing archaeological record was widespread through the western Pacific in prehistory, is an appropriate adaptation to the island environment. The body form arose within the Pacific as a consequence of the selective pressures of voyaging and small-island environments¹⁷.

This is based on the notion that the sea is a dangerous environment, and that while sailing technology of the proto-Polynesians is acknowledged to have been sophisticated, the process of colonisation across ocean is seen as inherently risky, by sheer force of distance and the changing nature of the nautical climate. Under such a scenario, Houghton argues that Polynesian body form evolved a cold climate form- a stocky, large body that would be better suited to the conservation of heat during voyages in which people were exposed to the elements.

Houghton, however, also acknowledges genetic drift as an integral force in the evolution of the Polynesian form, noting that selection combined with the "inevitable" processes of genetic drift in this world of islands,... provides sufficient explanation for the large range of human morphological variation¹⁸ (emphasis ours). The assumption of the inevitability of bottlenecking during colonisation and subsequent drift through isolation in producing the Polynesian form is implicit in virtually all the regional scholarship. The seeming homogeneity of Polynesian biology is often posed as *a priori* evidence of founder effect due to small founding group size. For example in the globin gene system, low frequency of *aaa*-chromosomes in Eastern Polynesians are argued to result from founder effect, with overall globin gene data suggesting "...considerable genetic drift and founder effects during the colonization of Polynesia"¹⁹.

The assumption of relative population isolation providing the mechanism for genetic drift is also widely acknowledged, even accepted. In the classic model of Kirch and Green²⁰, the implicitness of this process in Polynesian population history is used to develop complex models of linguistic/ biological/ socio-cultural divergence within Polynesia. That is, following an homogenising process at colonisation of the region, that the contemporary and more recent prehistoric Polynesian form has subsequently *diverged* within Polynesia from a more standardised ancestral form. Kirch draws on this thread with reference to social behaviour:

Since colonizing parties of Polynesians were small, and therefore representative of only a portion of the cultural-behavioral variability inherent in the 'mother' population, something akin to the 'founder effect' known to

geneticists...may have operated to produce rapid change in island populations (emphasis added)²¹.

More specifically with reference to biology, Green poses that the current phenotypic forms in Near Oceania have been diverging from the forms that were ancestral to Polynesians, experiencing more genetic divergence than the Polynesians and "...that a lot of this change is due to gene flow from near Oceania as far as Fiji in the last 2500 years, which did not affect the more isolated populations of...Polynesia"⁸. Especially in Eastern Polynesia, the initial burst of colonisation was followed by relative isolation (with selection/ adaptation in specific island environments), so that genetic divergence increased through time away from a more homogenous founding gene pool. He says:

There is no evidence for cultural, biological or linguistic replacement, but only of gradual evolution of speakers of a Polynesian language with a Polynesian culture and physical phenotype out of their immediate predecessors. It was from ancestral Polynesian populations of West Polynesia that those of East Polynesia (and later the Outliers) derive. In East Polynesia, *because of genetic isolation, drift through small founding population size, and natural and cultural selection* an unusual physical form in the Mongoloid population radiation occurred (emphasis added)⁵.

It is, arguably, in interpreting genetic data that this vague model of selection-bottleneck-drift has been most explicitly invoked. One of the most explicitly developed examples of this is Flint *et al*, who argue on the basis of data from six DNA minisatellites, that the lack of gene diversity in Polynesians compared to Melanesians is a product of this specific pattern of settlement history²²:

... our knowledge of the colonization of Polynesia suggests it probably involved bottlenecks. In addition to...geographic bottlenecks, colonization is estimated to have cost approximately half a million lives... Furthermore, once settled, island populations are known to have suffered catastrophic diminution in size... The minisatellite data, revealing a low gene diversity in Polynesia, would appear to confirm...the process of settling so many small and well-separated islands in so short a time, the Polynesians have become relatively homogenous. ...*The most likely explanation for low genetic diversity in Polynesia is that colonization involved small numbers of settlers passing through numerous bottlenecks* (emphasis ours).

Interestingly, they maintain this conclusion despite their observation that genetic diversity in these Polynesian DNA minisatellites was less than they expected, and less than that seen, for example, within highland Papua New Guineans and Australian Aborigines.

Such models, placing primacy on selection during colonisation, and the role of founder effect and subsequent drift on the creation of the Polynesian form, are based

(variously) on a trilogy of assumptions about the nature of the colonisation and settlement of the region: that voyaging was risky, that founding populations were small, and that after colonisation Polynesian populations were relatively isolated. These ideas about the origins of Polynesian biological distinctiveness have drawn on a melange of ideas about the nature of the colonising experience to construct evolutionary narratives. The substantial problem is that, while a reliable chronological framework has been developed, there has been no independent navigational theory of Pacific colonisation and inter-group contact. This is perhaps most obviously the case with respect to how founder effect has been built into narratives about population history in Polynesia. For example, Green recognises:

...there currently seems to be a consensus that 'initial colonization was always by small propagules'.... This agreement stems not from estimates derived from the archaeological evidence of founder and settlement period sites in tropical Polynesia..., as from the various voyaging and colonisation models employed by pre-historians, which often tend to incorporate findings from the simulation studies of demographers²³.

The Independent Colonisation Model²⁴

Through Island Southeast Asia and western Melanesia as far as the end of the Solomons was a sheltered 'voyaging corridor' of large, often intervisible islands separated by short water gaps. This was a zone of Pleistocene colonisation which occurred in the period approximately 50,000-30,000 years ago. Beyond this corridor, in a region known as Remote Oceania, islands generally become further apart and smaller and their natural resources more attenuated. The difference was sufficient to arrest further colonisation for some 25,000 years, until deep-sea explorers had developed maritime technology and exploration strategies which allowed them to search offshore and survive.

Further east, between West and East Polynesia and, in Micronesia, the Marianas and the islands lying to the east, there is a biogeographic distinction between the islands of the continental Western Pacific and the smaller volcanically-based ones on the Pacific Plate, to the east of the 'Andesite' line. Continental islands are often more diverse in geology, flora and fauna than oceanic islands, which may be high volcanic islands or low-lying and often short of good soils and fresh water. The most extreme examples being atolls which are fringes of coral above an underwater volcano.

Some 3500 years ago, two distinct episodes of maritime colonisation, characterised by two distinct archaeological signatures, spread into western Micronesia and Island Melanesia. The latter was associated with an entity known as Lapita which, while materially distinctive, is nevertheless ambiguous in cultural, linguistic and biological terms. However, when this entity spread beyond the Solomons into the Remote Pacific, it represented an integrated navigational system. Lapita in Fiji/West Polynesia is identified as ancestral to subsequent

Polynesian peoples and cultures. However, whether it carried the full inventory of information which was to develop into Polynesian is a question which must be raised.

Colonisation was obviously deliberate because canoes carried the domesticated plants and animals and the people needed to establish breeding populations. Moreover computer simulations which consider real winds and currents proved that the major voyages did not happen at random but were the result of directed navigation. But while this much was clear, much remained that was unknown and in particular the strategies of exploration which were used as the first Pacific navigators penetrated an unknown ocean.

Sailing between known and unknown islands has its risks, but sailing into an empty ocean can be fatal. Some earlier theories of Pacific colonisation preferred many explorers to die at sea, but there is nothing to show that Pacific explorers were careless with their lives. Their options were to search and find, to search and die, or to search and return. From the practical point of view, a non-suicidal sailor the best strategy goes a long way to explaining why the thrust of Pacific exploration was against the easterly trade winds. Without a doubt, it is safest to sail first in the direction which is normally upwind because one can expect the fastest trip back. The hard way is really the easy or safe way and this simple paradox is one of the keys to explaining the trajectory of human settlement. Practically every radiocarbon date in the remote Pacific supports the view that colonisation went first against the prevailing winds and only then across and down them.

Sailing upwind also provides the means to find the way home by latitude sailing. This was evidently developed during the settlement of Polynesia and simply involves using the altitude of one's origin island, while still upwind of it, and then running with the wind along the latitude. Experimental evidence shows that the error in estimating latitude without instruments is matched by the ability to detect the presence of land from offshore by observing bird behaviour and other signs.

A second point to be made about latitude sailing is that it is possible to make mistakes in dead-reckoning, to lose track of one's position and still get back. This was more than just a safeguard in prehistory. One could safely continue to search upwind with the knowledge of what lay behind. It meant that upwind exploration could virtually escape from navigational limits. Given the immensity of the Pacific Ocean we now have an insight into how it might have been explored. The ultimate limit of early voyages into the east was set by the human body and spirit almost without navigational constraint.

To sail with some safety across the prevailing winds requires a knowledge of islands to leeward of the starting island, in case that cannot be reached on the return journey. Sailing downwind, on the other hand, usually requires returning by a different route. The circumstances of exploration changed in the remote Pacific as geographical knowledge was added to navigational knowledge, and the range of feasible options increased. Increasing experience and skill were needed to manage

the long exploratory probes eventually made into different and more difficult weather systems on the high-latitude extremities of Polynesia, and to South America.

The broad pattern of settlement is that deep-sea colonisation began after 3500 years ago with the spread of Lapita through the islands of Melanesia to reach Fiji, Tonga and Samoa by 3000 BP (before present), or before. The evidence is that the ancestral people concerned were few in number and travelling fast. They carried a portable economy of plants and animals, and engaged in long-distance exchange. Available radiocarbon dates now indicate that the Marquesas Islands in far East Polynesia may have been settled soon after 0 AD, although not in association with Lapita. It is likely earlier sites will be found among closer groups such as the Cooks and Societies. By about 500 AD settlement reached Hawaii, distant Easter Island and probably South America. Cool and more difficult sailing conditions delayed settlement south of the tropics, but by about A.D.1000, colonists reached New Zealand.

Voyaging did not end with settlement. The evidence is that inter-island voyaging continued and, once the location of islands was known, navigators were freed from the constraints of survival sailing strategies. Thereafter, the frequency of communication was affected by accessibility more than safety. Variables such as distance and size of island target were invoked.

Implications for the thrifty genotype hypothesis

To summarise the aspects of this model that have particular relevance for interpretations of biological history, this theory suggests that Remote Oceania was settled by directed return voyages, that the tempo of population expansion was probably rapid, that voyaging continued after settlement, that whereas episodes of colonisation were directed to safety, subsequent inter-group voyages followed the pattern of mutual inter-island accessibility. Given this explicit model of prehistory in the region, we can better anticipate the possible role of microevolutionary forces for a thrifty genotype sequelae in Polynesia.

Under this model of population movement and contact, opportunities for mortality selection were subdued; mortality selection during voyaging was minimised by the very nature of navigational strategies, designed as they were to minimise these specific risks. In essence, nothing about Polynesian biology particularly suggests the heavy hand of directional selection during the colonisation process, or even subsequently while settled on Polynesian islands. This is not only because of the lack of opportunities, but because many features of Polynesian biology do not appear as forms of traits that would be selected for/against in such a scenario. Further, implicit in this model of exploration, settlement and post-settlement contact is that founding populations were likely to be multiple, and relatively diverse in source and timing.

This model provides a very different explanation of why Polynesian biology appears relatively genetically homogenous. Since genetic divergence, including through drift, requires isolation, conceptualising prehistoric Polynesian groups as coming into regular contact with

each other provides a reasonable explanation for the lack of genetic diversity found in Polynesians. While opportunities for drift are implicit in island sequences, given the often devastating impact of natural disasters on small island groups, they would tend to occur at different locations at different times. But the force of gene flow would counteract the changes in gene frequencies promoted by drift in specific island groups. The homogeneity of the Polynesian biology could result from population contact and the associated reduction in opportunity for differentiation and inter-group heterogeneity. That is, the evolutionary history of Polynesians may actually be characterised by genetic convergence rather than divergence.

In summary, navigational expectations make it difficult to suggest that the specific experience of Polynesian colonisation would promote an efficient insulin

mechanism, and so explain, for example, the high incidence of Type II diabetes mellitus in contemporary Polynesian groups. Given this voyaging theory, we propose that the (proto) Polynesian phenotype was not a product of the colonisation of the region because opportunities for selection were subdued and the founding populations may have been initially externally reinforced and subsequently admixed. Second, the independent model of Pacific colonisation conservatively favours the idea that "thrifty" genotypes, including that shared by Polynesians, had an evolutionary origin/basis considerably more ancient than the period of initial and subsequent voyages of settlement in the Pacific region. This fits with the suggestion that "thrifty" genotypes may be virtually pan-species, with a small number of (predominantly Northern European-derived) populations having more recently experienced selection for a "non-thrifty" genotype.

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