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– ARTICLE –

Ancient DNA Evidence for the Introduction and Dispersal of Dogs (*Canis familiaris*) in New Zealand

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ABSTRACT

When people first arrived in New Zealand around 700 years ago, they brought their dogs (*Canis familiaris*) with them. To investigate the introduction and dispersal of dogs across the country we generated twenty-three new complete, or nearly complete, mitogenomes from ancient DNA from dog teeth sampled from four early archaeological sites in New Zealand and from one archaeological site in the southern Cook Islands. When considered together with fourteen previously reported mitogenomes from the New Zealand colonisation era site of Wairau Bar these sequences reveal a striking lack of mitochondrial genetic diversity in early New Zealand dogs. Our analysis shows that a group of closely-related dogs were brought to New Zealand, probably from an East Polynesian source population, and that these dogs and their offspring were widely dispersed throughout the country during the colonisation process. This pattern is consistent with the current model of rapid colonisation of New Zealand undertaken by highly mobile groups of people.

Keywords: aDNA, dog, kurī, mitogenome, New Zealand, Aotearoa, colonisation, Polynesia, Cook Islands

INTRODUCTION

The colonisation of New Zealand occurred at the terminus of the movement of people across Remote Oceania, a process that began with the appearance of the Lapita Cultural Complex in the uninhabited islands of the southeast Solomon Islands chain some 3,000 years earlier. The easternmost extent of this cultural complex is marked by archaeological sites in Tonga and Samoa (Kirch, 2000). After a pause of around two millenia, people moved out from West Polynesia to rapidly settle the islands of East Polynesia. This colonisation process is again marked by a highly visible archaeological horizon appearing in the previously uninhabited islands of East Polynesia. The Polynesian migrants brought with them a group of domesticated plants and animals that were variously utilised on the new islands they settled. Three domesticated animals, the pig, dog and chicken, along with the commensal Pacific rat (*Rattus exulans*), make up the four animals transported throughout Polynesia.

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The presence of these introduced plants and animals in archaeological sites across the Pacific has prompted the development of molecular genetic approaches to investigate patterns of human mobility, as reflected in these plant and animal proxies. Initially based on patterns of modern animal genetic variation, the approach has been expanded to include archaeological samples (Matisoo-Smith, 2007, 2009; Storey *et al*., 2013). This approach was first applied to the Pacific rat (kiore), where the investigation of Polynesian kiore populations indicated that there were two major spheres of interaction, a northern and a southern sphere, both interacting and most likely originating in central East Polynesia (Matisoo-Smith *et al*., 1998). A later study then addressed questions regarding the links between Polynesia, Lapita, and *R. exulans* populations in Near Oceania and Island Southeast Asia (Matisoo-Smith and Robins, 2004). Subsequent studies have investigated the introduction of dogs to Polynesia (Savolainen *et al*., 2014), the origin of Pacific pigs (Larson *et al*., 2007) and the dispersal of chickens across the Pacific as far as South America (Storey *et al*., 2012). The results obtained from these genetic molecular studies have provided complementary new datasets that can be used by researchers to address questions about the Pacific past.

The dog (*Canis familiaris*) and the kiore were the only two animal introductions successfully established in New Zealand by the first human migrants who arrived in the early fourteenth century AD. Bones and teeth from both species are found in early archaeological sites throughout the two mainland islands, and on some but not all off-

shore islands (Davidson, 1987). The arrival of European explorers, whalers and sealers began a second phase of dog introductions as early as the 1790s. The numbers of these dogs rose quickly as European settlement expanded, to the extent that by the early 1880s the indigenous Māori dog, or kurī, derived from dogs introduced from East Polynesia, no longer existed as a distinct type (Clark, 1995). Archaeological remains now provide the primary means of investigating the origins and early history of Polynesian dogs in New Zealand.

Recent advances in molecular genetic technology and ancient DNA (aDNA) methods are enabling the investigation of genetic variation in archaeological samples with increasing molecular resolution. Savolainen and colleagues (2004) used a small 263 base pair fragment of the mitochondrial genome to investigate the introduction of dogs to the Pacific. On the basis of that study, two ancestral lineages were suggested for Polynesian dogs, Arc1 and Arc2, both observed in sequences from archaeological dog remains from Hawai'i, the Cook Islands, and New Zealand (Savolainen *et al.*, 2004). Our group has more recently sequenced complete mitochondrial genomes (16,500 base pairs) from fourteen dogs from the early Wairau Bar archaeological site in New Zealand (Greig *et al.*, 2015). While only one short fragment haplotype (Arc2) was present in this sample, we were able to identify five distinct complete mtDNA haplotypes. This result suggested that further aDNA work using complete mitogenomes could inform on patterns of dog genetic diversity across New Zealand and the Pacific.

In addition to advances in molecular genetics, ideas about the timing and nature of New Zealand colonisation have also been significantly revised in the last few decades. Excavations at early archaeological sites such as Wairau Bar and Shag River Mouth, combined with refinements in radiocarbon dating, have resulted in a much shortened chronology for colonisation, and the characterisation of the human colonists of the South Island as highly mobile (Anderson and Smith, 1996; Jacomb *et al.*, 2014). Migrants are thought to have departed from an East Polynesian homeland zone where interactions were maintained across several island groups (Walter, 1994, 1996; Walter *et al.* 2017). The development of aDNA techniques now enables us to use more fine-grained genetic markers to investigate the origins and relationships between New Zealand dogs and their links with those of the central East Polynesian homeland.

This study presents the results of an aDNA analysis of complete mitochondrial genomes of twenty-three new specimens from archaeological sites in New Zealand and the southern Cook Islands, dating to the colonisation era of New Zealand. We combine these with fourteen complete mitogenomes previously reported (Greig *et al.*, 2015) to describe and compare the mitochondrial genetic diversity of the early New Zealand dog population, and consider the implications of these results for the current model for New Zealand colonisation and links with the central East Polynesian homeland (Walter *et al.*, 2017).

MATERIALS AND METHODS

Samples and sites

Samples for sequencing were obtained from four archaeological sites in New Zealand: Houhora (Mt Camel), Shag River Mouth, Pleasant River, and Pounawea – all dating from the fourteenth to fifteenth centuries AD (Table 1, Figure 1). In addition to the New Zealand samples, we included two specimens from the Ureia archaeological site on Aitutaki in the southern Cook Island group, dating to a broadly similar period (Allen and Wallace, 2007). Houhora and Shag River Mouth are colonisation era sites that probably date to the first decades of New Zealand settlement. They contain the bones of moa and other extinct birds and artefacts with distinctly East Polynesian stylistic affinities (Anderson *et al.*, 1996; Furey, 2002). Pleasant River and Pounawea also contain artefacts and extinct faunal material indicative of colonisation era occupation (Hamel, 1980; Smith, 1999). As was the case with the Wairau Bar dog assemblage analysed previously (Greig *et al.*, 2015), the large number of dog bones excavated from Houhora and Shag River Mouth enabled specimens of the same element to be selected from each site assemblage, ensuring that each specimen represented a different individual. We can be sure therefore that no dog from these three archaeological sites was sequenced more than once. Both of the samples from Pleasant River and Pounawea comprise a variety of skeletal elements and could potentially have come from the same individual within each site. For our haplotype analysis, we included fourteen complete mitogenomes from Wairau Bar (GenBank Accession Nos. KT168369–KT168382) (Greig *et al.*, 2015). When considered alongside the Wairau Bar site, our sample locations

Table 1. *New Zealand and southern Cook Island archaeological sites and sample information.*

Archaeological Site (Site No.)	Date	Specimens used for analysis
Houhora (N3/59)	Early 14th century (Furey, 2002)	Right mandibular M1 (n=10)
Pleasant River (J43/1 and J43/25)	Late 14th and 15th centuries (Smith, 1999)	Canine (n=1), pre-molar (n=1), molar (n=1)
Pounawea (H47/1)	14th and 15th centuries (Smith and James-Lee, 2010)	Molar (n=3)
Shag River Mouth (J43/2)	Early 14th century (Anderson *et al.*, 1996)	Left maxillary P4 (n=9)
Ureia (AIT-10)	13th to 15th centuries (Allen and Wallace, 2007)	Canine (n=1), pre-molar (n=1)

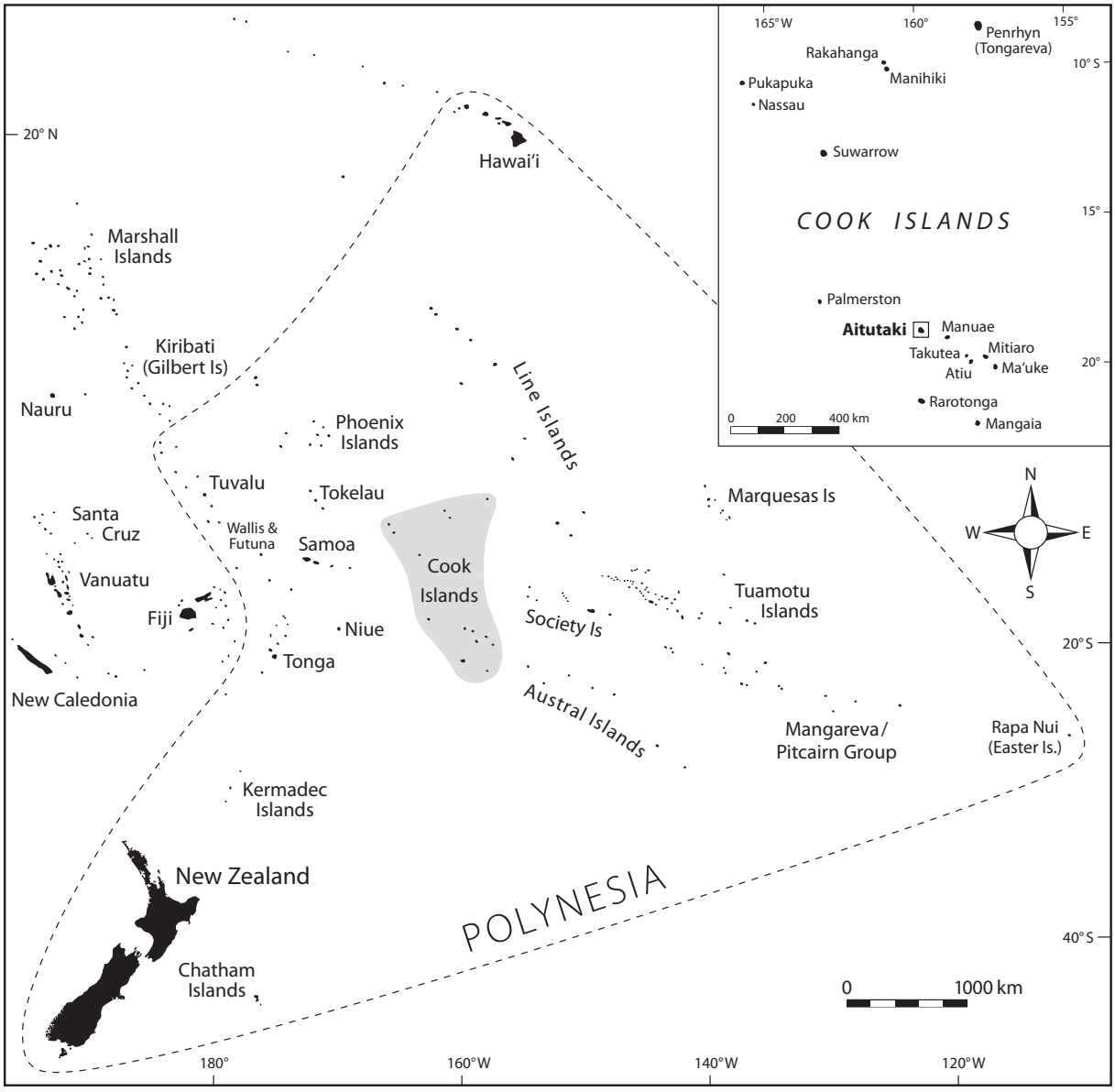

Figure 1: Map of Polynesia, showing New Zealand and the Cook Islands, inset southern Cook Islands.

are geographically spread across the country from the far north to the extreme south (Figure 1).

Houhora (Mt Camel)

The Houhora archaeological site is situated near the tip of the Aupouri Peninsula, just inside the entrance to Houhora Harbour, at the top of the North Island. The site lies on a coastal terrace below high stable dunes at the base of the prominent landmark of Mt Camel. Excavations were carried out in the mid-1960s and early 1970s by archaeologists from the Anthropology Department of the University of Auckland. Although several theses were written about aspects of the excavations, an overall synthesis of the results was not produced for over thirty years (Furey, 2002).

The site contains some ill-defined relatively recent horizons containing European artefacts, and a much better defined context that Furey (2002) interprets as a small village occupied in the early fourteenth century. The site contains artefacts with stylistic affinities to East Polynesian forms, the bones of extinct birds such as moa, and numerous sea mammal bones – all indicative of relatively early settlement. Excavated features and activity areas include artefact manufacturing zones, cooking areas, waste midden dumps, and postholes from structures. On the basis of the quantity of archaeological material excavated, the variety of artefacts, the size and extent of cooking features, and the thickness of the cultural deposit, the site is considered to be a village with year-round occupation, rather than a short duration camp (Furey, 2002: 122). The dog bone

sample used for this study came from excavation areas spread across the site and from layers that are thought to correspond to the earliest occupation levels.

Wairau Bar

Wairau Bar lies at the mouth of the Wairau River, on the northeast coast of the South Island. The site was first formally excavated in the 1950s and 1960s by Canterbury Museum staff, and again more recently in 2009 when the Museum repatriated koiwi tangata (human remains) that had been previously taken from the archaeological site for reburial. Jacomb and colleagues (2014) used aDNA from moa egg shell and Bayesian analysis of radiocarbon dates to develop a high precision chronology for the creation, use and infilling of a large cooking feature that was excavated during the 2009 fieldwork. This showed that the oven had been filled with midden during a single event that took place in the first half of the fourteenth century AD. The specimens used for our previously reported analysis were all excavated from this feature (Greig *et al.*, 2015), and the rapid deposition indicates that the dogs were most likely to be contemporaries, who lived at Wairau Bar immediately prior to their death.

Shag River Mouth

The archaeological site at Shag River Mouth is located just south of Oamaru, on the east coast of the South Island. The archaeological site lies in dunes immediately above the beach at the mouth of the river, and comprises features interpreted as representing a range of structures facing a central activity area, with waste being discarded around the periphery (Anderson *et al.*, 1996). Anderson and Smith (1996) describe the archaeological site as a 'transient village', a settlement established close to rich resources such as seals and moa, occupied briefly, and then abandoned once these resources were depleted. The suite of radiocarbon dates from the excavation show that occupation began in the early fourteenth century AD and spanned 40 to 50 years (Anderson *et al.*, 1996). The sample used for this study was excavated in 1989 from two parts of the site, SM/B and SM/D.

Pleasant River

The archaeological site at Pleasant River comprises a complex of archaeological features spread along the estuarine margins and dunes at the mouth of the river, 20 km south of Shag River Mouth, and about 50 km north of Dunedin. Excavations in 1991–1993 showed the site contained a similar faunal assemblage to Shag River Mouth, however, the stratigraphy, structural features and artefact assemblage were quite different (Smith, 1999). The site contains a wide range of fauna, including moa bones and eggshell, seal, dog, bird, fish and shellfish remains, but lacks evidence of permanent structures and distinct activity areas. Blades and flakes associated with food processing dominate the artefact assemblage.

The radiocarbon chronology suggests a series of short-term occupations spanning several hundred years, but occurring in two phases (Smith, 1999). The first phase of occupation appears to be contemporary with the major settlement at Shag River Mouth, when temporary campsites at Pleasant River may have functioned as satellite settlements of the Shag River Mouth community. The later phase of occupation in the late fourteenth and fifteenth centuries may have been part of a larger and more dispersed settlement system (Smith, 1999). The sample for this study was obtained from Area 1 Layer 2, which dates to around the late fourteenth to early fifteenth century, and is consequently later than the main occupation at Shag River Mouth. Nonetheless, the Pleasant River site still contains a similar faunal assemblage including moa and sea mammals indicative of the colonisation era.

Pounawea

The Pounawea archaeological site, in the Catlins area of coastal Otago in the southern South Island, is located off Manuka Point at the confluence of the Catlins and Owaka Rivers, a few hundred metres from the river mouth. The archaeological site is interpreted as a coastal village, similar to Shag River Mouth, and contains a wide range of fauna including moa and seals, and abundant artefacts with stylistic affinities to other early Māori assemblages (Hamel, 2001). Smith and James-Lee's (2010) review of the site's radiocarbon dates indicates it was occupied between the fourteenth and fifteenth centuries. The location of the site near the river mouth was subject to increasing erosion in the 1970s. A salvage excavation was carried out in 1979 to obtain information about the environment, economy, material culture and any structural remains prior to the loss of the site (Hamel, 1980). Dog bones, including the sample used in this study, were recovered throughout the site.

Ureia, Southern Cook Islands

In addition to the New Zealand samples, two specimens from the southern Cook Islands were analysed. Both come from the Ureia (AIT-10) site on Aitutaki Island where excavations were carried out by Melinda Allen in the 1980s. Dating to between the thirteenth and fifteenth centuries AD (Allen and Wallace, 2007), they are similar in age to the New Zealand dog samples. One specimen comes from an in situ cultural layer (Zone E) associated with postmolds, hearths, pits, and a coral pavement – all indicative of a relatively permanent domestic occupation. In addition to dog, the Zone E fauna includes domesticated pig and chicken, and the commensal Pacific rat. These taxa, along with wood charcoal from breadfruit (*Artocarpus altilis*),

are suggestive of an established agricultural economy. The second dog specimen comes from a deeper, wave-deposited stratum (Zone H) that contains re-deposited cultural materials deriving from an underlying (largely disturbed) cultural layer (Zone J). Radiocarbon dates from occupation Zones E, G and J are essentially indistinguishable, but on stratigraphic grounds the Zone H specimen (MS10326) is the oldest. Although both of the sampled Ureia layers date from relatively early in the Aitutaki cultural sequence, twelfth century dates have been secured from elsewhere on the island, indicating that Ureia is not the initial site of island settlement (Allen *et al*., 2016).

Ancient DNA methods

A total of twenty-seven dog teeth were sampled for this study (Table 1, SI Table 1). All DNA extraction and sequencing library preparation before PCR amplification was carried out at the purpose built Ancient DNA Laboratory at the University of Otago, where stringent procedures are in place to avoid contamination (Knapp *et al*., 2012a). Extraction, library preparation, and raw data processing were undertaken as described in Greig *et al*. (2015). In brief, we carried out silica-based extractions (Rohland and Hofreiter, 2007b), from which sequencing libraries were prepared as described by Knapp and colleagues (Knapp *et al*., 2012b) for Illumina sequencing, with slight modifications. We included an in-solution hybridisation capture step to enrich for target mtDNA (Maricic *et al*., 2010) with slight modifications. Raw sequence reads were processed using a purpose-built in-house pipeline (Greig *et al*., 2015), with alignment performed against the dog mitochondrial reference sequence (NC_002008, Kim *et al*., 1998). Consensus sequences, including insertions and deletions, were generated for each sample that passed quality control measures, and these have been deposited in GenBank (Accession Numbers KU215682–KU215702). In these sequences, non-variant sites that were supported by fewer than three reads were changed to 'Ns'.

We investigated the genetic population structure of the dogs by constructing a median-joining network using Popart (v1.7.1) (Leigh & Bryant, 2015) with default settings. In addition, all ancient haplotypes were aligned to the ancient Polynesian Arc1 and Arc2 short control region fragments (Savolainen *et al*., 2004) using MUSCLE (v3.8.31) (Edgar, 2004) to investigate whether these short haplotypes appear within our dataset.

RESULTS

DNA preservation, sequence recovery and authenticity

Acceptable sequence data was obtained from 23 of the 27 specimens from which libraries were prepared (SI Table 1). Complete mitogenomes were obtained from six of these specimens, with the remaining seventeen specimens having nearly complete coverage (SI Table 1, SI Figure 1). Four specimens failed to generate acceptable consensus sequences (greater than 95% of the reference sequence covered by a read depth of greater than two) and so were discarded from further analyses.

As found in our previous analysis of mitogenomes from the Wairau Bar dogs (Greig *et al*. 2015), the control region generally had a proportionally lower read depth compared with elsewhere in the mitogenome (SI Figure 2). The median average read depth for the twenty three specimens was 29×, varying across specimens from between 1.5× and 423× (SI Table 1). The four discarded specimens had much reduced coverage in comparison with other specimens and also substantially lower read depth. Damage patterns such as short fragment lengths (SI Figure 3) and deamination patterns were consistent with those expected from aDNA (Sawyer *et al*., 2012). Throughout DNA extraction and library preparation, blank extractions were processed alongside samples to provide negative controls. These did not contain any reads mapping to the dog reference genome.

Genetic population structure

The median-joining network (Figure 2) reveals a striking lack of genetic diversity in the sequences from the New Zealand dog specimens, and a close relationship between these sequences and one of the specimens from the southern Cook Islands. The network displays a 'starburst' pattern, with one central node or haplotype, surrounded by other nodes radiating outwards. These starburst patterns generally indicate recent population expansions from a small number of founders (Avise, 2000). The haplotype comprising the central node is shared by over two-thirds of the specimens, and includes representatives from all five New Zealand archaeological sites. In total, only 17 variable sites were observed (SI Table 2) and no clear population structure is evident. Most haplotypes radiating off the central node are separated by only a single point mutation.

There are three branches with terminal nodes that differ from the central haplotype by two or more mutations. One is a sequence from Shag River Mouth. The second branch is from Wairau Bar, which has an intermediate sequence from Shag River Mouth. The third branch is made up of two sequences from the southern Cook Islands, which share a mutation that is not present in the New Zealand sample. In addition, one of these specimens diverges by six mutations from the other, and therefore by seven mutations from the central New Zealand node. Based on stratigraphic information from the Ureia site, the sequence most closely related to the New Zealand central node, MS10326, came from the earlier archaeological stratum.

The short Arc1 and Arc2 haplotypes reported by Savolainen and colleagues (2004) and observed in ancient

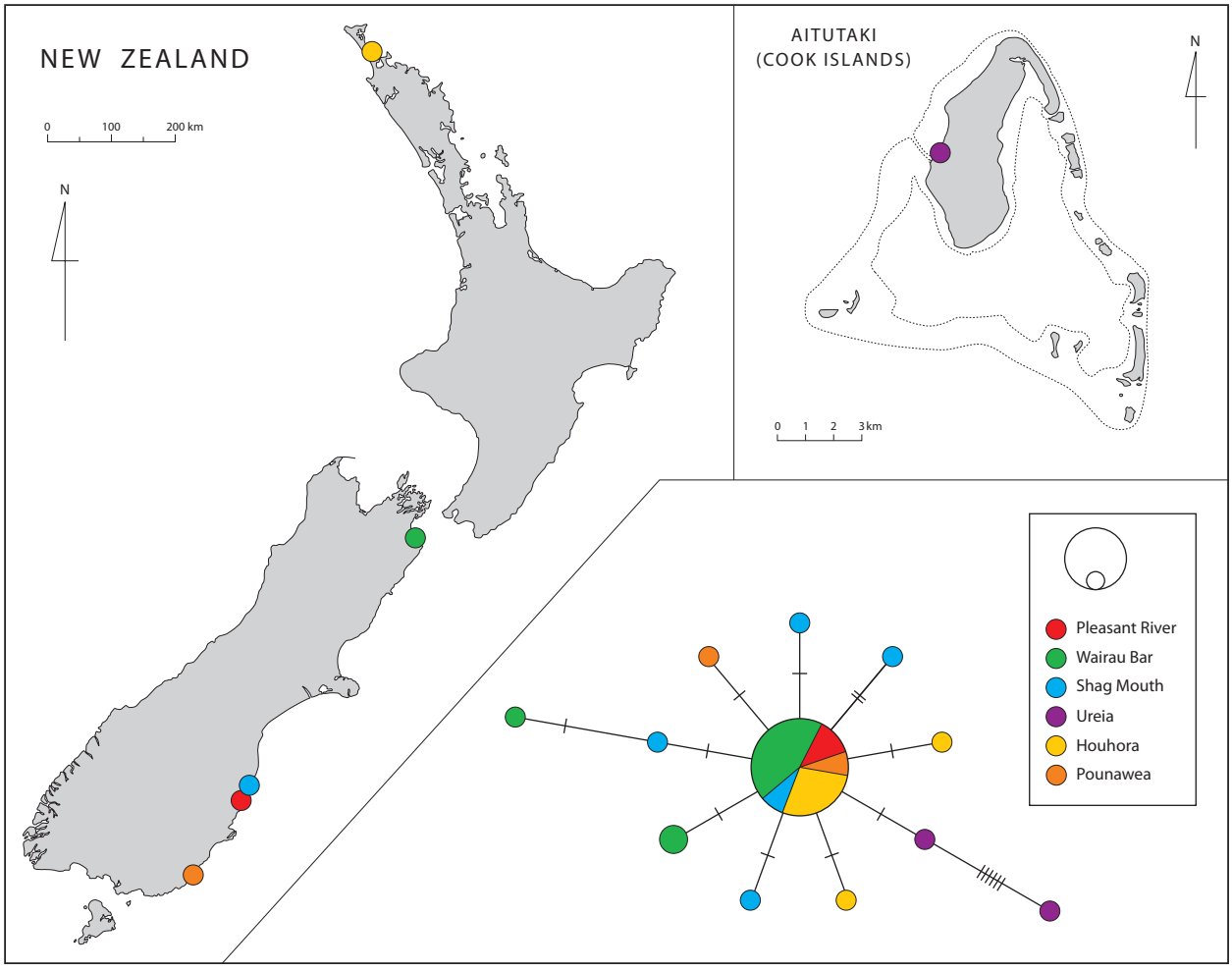

Figure 2. Locations of archaeological sites and median-joining haplotype network of mitogenomes of dogs from New Zealand and the southern Cook Islands. The archaeological sites and network nodes are coloured as shown in the legend, and the number of mutations is shown by hash marks on the branches.

samples from Polynesia are defined by four bases at positions 15630, 15642, 15648 and 15655 (positions given in relation to dog mitochondrial reference sequence NC_002008 (Kim *et al.*, 1998). Only the Arc2 motif (GAGA) is present in the sequences generated in this study (SI Table 2), as in the complete mitogenomes previously reported (Greig *et al.*, 2015).

DISCUSSION

Composition of the founding population

Our analysis of the genetic population structure of the New Zealand dogs, based on samples from sites that span the length of the country, shows that the founding population had extremely limited genetic diversity, with no observable geographic patterning. The genetic structure of the dog sequences included in this study is dominated by one haplotype, which is carried by over two thirds of the dogs sampled. Of the 10 dog specimens that did not carry the founding haplotype, eight differ by only one mutation and two by two mutations. This pattern of limited diversity is the same as observed previously in a smaller sample of dogs from Wairau Bar (Greig *et al.*, 2015).

Although colonisation era sites in New Zealand contain large numbers of dog bones, the mitogenomic homogeneity makes estimating the size of the founding population using molecular genetic methods problematic. The founding human population of New Zealand has been estimated to be high, perhaps involving as many as 200 women or more, based on inferences from modern genetic diversity (Walter *et al.*, 2017; Whyte *et al.*, 2005). Given this estimate, multiple settlement voyages must have been involved (also suggested by oral traditions), raising the possibility that a large number of dogs were brought to New Zealand during the colonisation period. In this scenario, the introduction and establishment of the dog population could potentially have occurred over several

decades and from multiple points. The mitogenomes from the southern Cook Islands suggest otherwise, and this is discussed below.

Origins of New Zealand's first dogs

The sample of dog teeth used for this study was obtained from archaeological contexts dating to the first fifty to one hundred years of dog arrival in New Zealand. Given this short timeframe and estimates of the mutation rate for mitochondrial canid DNA (Pang *et al.*, 2009), it is highly likely that the majority, if not all, of the single point mutations observed in the sample arose prior to this colonisation period. This raises the possibility of identifying the source population for the New Zealand dogs by identifying a location or area where these mutations are also present. Tracking the origin of the New Zealand dog population in this way requires comparative data on the genetic makeup of potential source populations. So far, such data is scarce.

Two short control region haplotypes, Arc1 and Arc2, have been reported in samples from archaeological sites in New Zealand (Arc1 n=3, Arc2 n=10), the southern Cook Islands (Arc1 n=1, Arc2 n=1) and Hawai'i (Arc1 n=2, Arc2 n=2) (Savolainen *et al.*, 2004). However, only one of these haplotypes (Arc2) is observable in the New Zealand and the southern Cook Islands samples we have analysed here. While the distribution of these haplotypes across East Polynesia indicates a shared ancestry for these dogs, they lack the level of discrimination necessary to address inter-island relationships.

The mitogenomes of the two dogs we sequenced from Aitutaki show significantly more diversity than can be determined from the short fragments. These specimens carry two distinct haplotypes, differing from each other by six mutations. In comparison the 35 sequences from New Zealand dogs, derived from five different archaeological sites spread across the country, are only separated from each other by a single or at most two mutations. One of the Aitutaki haplotypes is very similar to the founding New Zealand haplotype though, differing only by one mutation. The diversity observed in the Aitutaki sample of two indicates that there was greater mitochondrial genetic diversity in the central East Polynesian source population, and that the introduction of dogs to New Zealand involved a reduction in genetic diversity.

In contrast to the similarity of the New Zealand dogs' mitogenomic lineages, previous mitogenome analysis of four human burials from Wairau Bar showed that at least three of these individuals were not recently maternally related (Knapp *et al.*, 2012c). Two of the individuals came from burial Group 1 and had similar grave goods thought to be associated with people of high status. These individuals belonged to two different mtDNA haplotypes, indicating the founding populations were unlikely to have originated from a single matrilocal source population. This was the earliest burial group at the site and was also distinctive as stable isotope analysis revealed that these individuals were not local, having had different diets and childhood places of residence from individuals in other burial groups (Kinaston *et al.*, 2013). It is possible that some of these individuals were first generation immigrants, born and raised elsewhere in East Polynesia. The lack of a close maternal genetic relationship was interpreted to mean that the founding human population of New Zealand was derived from a number of different communities within an interaction zone that spanned several islands or archipelagos (Knapp *et al.*, 2012c). This is consistent with the 'Hawaiiki Zone' hypothesis, based on material culture and linguistics, that New Zealand was settled from central East Polynesia, at a time when islands were linked by regular interaction and exchange (Walter, 1994, 1996; Walter *et al.*, 2017).

Molecular genetic analyses of mtDNA variation in modern kiore populations has also shown that the lineages observed in New Zealand populations are highly divergent, indicating that there were multiple introductions (Matisoo-Smith *et al.*, 1998). The New Zealand kiore lineages, and those seen in other East Polynesian populations, are most likely to have been derived from a central homeland region encompassing the Societies and the southern Cook Islands (Matisoo-Smith *et al.*, 1998).

The amount of variation observed in the ancient dog mitogenomes from the southern Cook Islands specimens suggests that, like the people and the rats, the homeland population was genetically diverse. However, the limited variation of the New Zealand dog sequences indicates that the process of introduction may have taken a different form, with only a small subset of the available East Polynesian dog lineages being successfully established in Aotearoa. Alternatively, given that the two southern Cook Islands specimens come from slightly different time periods, the later sequence may represent a further movement of dogs into the homeland region after the cessation of colonising voyages to Aotearoa. The cultural selection of particular dogs for the colonising voyages may have also resulted in a greater reduction of genetic diversity than observed in human and rat founding populations. More samples from critical time periods from the central East Polynesian region are required to test these hypotheses.

Dog dispersal during the colonisation phase of New Zealand

Once established in New Zealand, the lack of mitochondrial genetic diversity of the dogs makes identifying connections between archaeological communities through shared dog mtDNA lineages impossible, as we cannot discriminate between dogs carrying the central haplotype which is present in over two thirds of the specimens sequenced. What we can say, however, from the distribution of dog bone in archaeological sites, is that dogs from the founding population and their descendants were widely dispersed throughout the length and breadth of New Zea-

land during the colonisation era. Given the homogeneity of the mitochondrial lineages, questions about the movement of closely-related dogs between archaeological sites in New Zealand may be better addressed using nuclear DNA markers, if these can be obtained (Greig *et al.*, 2015). Stable isotope analysis may also assist with identifying local versus non-local dogs, as has been demonstrated at Wairau Bar (Kinaston *et al.*, 2013). In that study, the five specimens analysed all possessed strontium values consistent with the local environment, raising the possibility that while humans moved around the colonisation era landscape, once introduced, dogs remained fairly localised. The genetic evidence thus indicates that dogs were widely established throughout the country early in the human settlement period, either with human populations or as items of exchange, while the stable isotope results suggest dog mobility may have subsequently been restricted. Further work is required to investigate whether this isotopic pattern is consistent in dog samples from other archaeological sites.

Introduction and translocation of Oceanic dogs

The mitochondrial make up of New Zealand's first dogs also offers insights into the process of dog introduction across the wider region. The presence of dog bones in archaeological sites in the Pacific is patchy and discontinuous (Greig *et al.*, 2016), and molecular genetic analyses can provide complementary information about the timing and trajectories of dog translocations. The arrival of people and dogs in East Polynesia marks the last leg of a major dispersal by people across the previously uninhabited islands of Remote Oceania. Comparative analysis of the two short haplotypes (Arc1 and Arc2) and the New Zealand mitogenomic lineages with global patterns of modern dog genetic diversity shows that the lineages introduced to East Polynesia at this broad scale are genetically closely related (Savolainen *et al.*, 2004; Greig *et al.*, 2015). The greatest genetic diversity observed in modern dogs occurs in East Asia, which is argued to be the centre of dog domestication (Pang *et al.*, 2009). This implies that during the movement of dogs out of Southeast Asia and across the Pacific there were events, or processes, that resulted in a reduction in genetic diversity. It is unclear where or when this occurs, as we are looking at the endpoint of a process that took several thousand years.

There are several putative scenarios that could explain the decline in dog genetic diversity coincident with their transport across the Pacific:

1. Dog translocation across the Pacific may have been a gradual process that involved a subset of dogs being sequentially taken from the existing populations, resulting in a series of founder effects. This could occur if dogs accompanied people in a series of linked migrations across the region.
2. Alternatively, a single or very limited movement involving a small number of dogs at a critical point or points in time could have resulted in a major reduction in genetic diversity, such as what we see in the settlement of New Zealand. This may have also happened in Island South East Asia or in West Polynesia.
3. Finally, selection for favourable traits may have also contributed to a reduction in overall genetic diversity. In nineteenth century New Zealand, for example, dog skin cloaks were associated with people of chiefly rank, dog hair tassels were used to adorn weapons and other items of material culture, and white dog hair was particularly valued (Colenso, 1877); fur colour and length may have been desirable traits that were selected for by people in the past.

In apparent contradiction to the decline in mitochondrial genetic diversity, the starburst pattern of the haplotype network for the New Zealand and southern Cook Islands mitogenomes indicates a recent population expansion from a small number of founders (Avise, 1987). This phenomena may be associated with a key period in the dispersal process, signaled in the archaeological record by the significant increase in numbers of dog bone in Near Oceania and the sudden appearance of dog bones in Polynesian archaeological sites beginning around 2,000 years ago (Greig *et al.*, 2016). More work is required to document the molecular genetic composition of dog populations at key places and time periods, and investigate the nature of dog translocations in relation to models for human migrations and exchange networks in the Pacific.

CONCLUSION

The arrival of people and dogs in New Zealand marks one of the last legs of a major dispersal across the previously uninhabited islands of Remote Oceania. Our study of mitogenomes from dogs from New Zealand and the southern Cook Islands has revealed the strikingly limited mitochondrial diversity of dogs sampled from the New Zealand colonisation era. While this genetic uniformity constrains our ability to investigate interactions between human communities at this time, the presence of dog remains in early archaeological sites across the country supports the widespread dispersal of dogs during the colonisation process. The mitogenomes of dogs from the southern Cook Islands also indicates that there may have been greater mtDNA diversity in the central East Polynesian dog population. Our mtDNA results provide new insights into the process of dog translocation and establishment, which contrast with the outcomes of genetic studies of human migration and kiore introductions to New Zealand. Future studies of kurī incorporating nuclear markers have the potential to discriminate between individual dogs in the closely-related New Zealand population, and

may enable new questions to be addressed. These could include investigating possible selective pressures operating during the processes of migration and colonisation, and elucidating differences in the recruitment processes for human migrants and dogs. Given the rapid extinction of kurī that followed European arrival, our aDNA study has been especially valuable in revealing the genetic signatures of introduction and dispersal in dogs that would not otherwise be known.

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References

Allen, M.S. & Wallace, R. 2007. New evidence from the East Polynesian gateway: Substantive and methodological results from Aitutaki, southern Cook Islands. *Radiocarbon,* 49:1163–1179.

Allen, M.S., Morrison, A.E., Lorrey, A.M., Zhao, J-X. & Jacobsen, G.E. 2016. Timing, magnitude and effects of late Holocene sea level drawdown on island habitability, Aitutaki, Cook Islands. *Archaeology in Oceania*, 51(2):108–121.

Allo, J. 1971. The dentition of the Māori dog of New Zealand. *Records of the Auckland Institute and Museum,* 8:29–45.

Anderson, A. & Smith, I. 1996. The transient village in southern New Zealand. *World Archaeology,* 27: 359–371.

Anderson, A.J., Allingham, B. & Smith, I.W.G. (eds.) 1996. *Shag River Mouth: The Archaeology of an eEarly Southern Māori Village,* Canberra: ANH Publications.

Anderson, A.J. & Clark, G. 2001. Advances in New Zealand mammalogy 1990–2000: Polynesian dog or kuri. *Journal of the Royal Society of New Zealand,* 31:161–163.

Avise, J.C. 2000. *Phylogeography: The History and Formation of Species,* Cambrdige, MA., Harvard University Press.

Clark, G.R. 1995. The Kuri in prehistory: a skeletal analysis of the extinct Māori dog. Unpublished MA Thesis, University of Otago.

Clark, G.R. 1997. Anthropogenic factors and prehistoric dog morphology: a case study from Polynesia. *Archaeology in Oceania,* 32:124–130.

Colenso, W. 1877. Notes, chiefly historical, on the Dog of the ancient New Zealanders. *Transactions and Proceedings of the Royal Society of New Zealand,* 10: Article X, pp.135–155.

Davidson, J.M. 1984. *The Prehistory of New Zealand,* Auckland, Longman Paul.

Drummond, A.J., Rambaut, A., Shapiro, B. & Pybus, O.G. 2005. Bayesian coalescent inference of past population dynamics from molecular sequences. *Molecular Biology and Evolution,* 22:1185–1192.

Edgar, R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research,* 35:1792–1797.

Furey, L. 2002. *Houhora: A Fourteenth Century Māori Village in Northland,* Auckland, Auckland War Memorial Museum.

Greig, K., Boocock, J., Prost, S., Horsburgh, K.A., Jacomb, C., Walter, R. & Matisoo-Smith, E. 2015. Complete Mitochondrial Genomes of New Zealand's First Dogs. *PloS one,* 10: e0138536.

Greig, K. 2017. Tracking dogs across the Pacific: An archaeological and ancient DNA study. Unpublished PhD Thesis. Department of Anthropology and Archaeology, University of Otago, Dunedin, New Zealand.

Greig, K., Walter, R. & Matisoo-Smith, E. 2016. Dogs and people in Southeast Asia and the Pacific. In: Oxenham, M. & Buckley, H. (eds.) *The Routledge Handbook of Bioarchaeology in Southeast Asia and the Pacific Islands*. Oxon, Routledge. pp.462–482.

Hamel, G. 1980. Pounawea: the last excavation. Unpublished report to NZ Historic Places Trust, Wellington, New Zealand.

Hamel, J. 2001. *The Archaeology of Otago,* Wellington, Department of Conservation.

Jacomb, C., Holdaway, R.N., Allentoft, M.E., Bunce, M., Oskam, C.L., Walter, R. & Brooks, E. 2014. High-precision dating and ancient DNA profiling of moa (Aves: Dinornithiformes) eggshell documents a complex feature at Wairau Bar and refines the chronology of New Zealand settlement by Polynesians. *Journal of Archaeological Science,* 50:24–30.

Kim, K.S., Lee, S.E., Jeong, H.W. & Ha, J.H. 1998. The complete nucleotide sequence of the domestic dog (*Canis familiaris*) mitochondrial genome. *Molecular Phylogenetics and Evolution*, 10:210–220.

Kinaston, R.L., Walter, R.K., Jacomb, C., Brooks, E., Tayles, N., Halcrow, S.E., Stirling, C., Reid, M., Gray, A.R., Spinks, J., Shaw, B., Fyfe, R. & Buckley, H.R. 2013. The first New Zealanders: patterns of diet and mobility revealed through isotope analysis. *PloS one,* 8:e64580.

Kirch, P.V. 2000. *On the Road of the Winds: An archaeological history of the Pacific Islands before European contact,* Berkeley, University of California Press.

Knapp, M., Clarke, A.C., Horsburgh, K.A. & Matisoo-Smith, E.A. 2012a. Setting the stage - building and working in an ancient DNA laboratory. *Annals of Anatomy,* 194:3–6.

Knapp, M., Stiller, M. & Meyer, M. 2012b. Generating barcoded libraries for multiplex high-throughput sequencing. *Ancient*

DNA*: Methods and Protocols*, pp. 155–170.

Knapp, M., Horsburgh, K.A., Prost, S., Stanton, J.-A., Buckley, H.R., Walter, R.K. & Matisoo-Smith, E.A. 2012c. Complete mitochondrial DNA genome sequences from the first New Zealanders. *Proceedings of the National Academy of Sciences,* 109: 18350–18354.

Larson, G., Cucchi, T., Fujita, M., Matisoo-Smith, E., Robins, J., Anderson, A., Rolett, B., Spriggs, M., Dolman, G., Kim, T.-H., Thuy, N.T. D., Randi, E., Doherty, M., Due, R.A., Bollt, R., Djubiantono, T., Griffin, B., Intoh, M., Keane, E., Kirch, P., Li, K.-T., Morwood, M., Pedriña, L.M., Piper, P.J., Rabett, R.J., Shooter, P., Van Den Bergh, G., West, E., Wickler, S., Yuan, J., Cooper, A. & Dobney, K. 2007. Phylogeny and ancient DNA of Sus provides insights into neolithic expansion in Island Southeast Asia and Oceania. *Proceedings of the National Academy of Sciences of the United States of America,* 104: 4834–4839.

Leach, B.F. 1979. Excavations in the Washpool Valley, Palliser Bay. *In:* Leach, B.F. & Leach, H.M. (eds.) *Prehistoric Man in Palliser Bay.* Wellington: National Museum of New Zealand Bulletin, pp. 67–136.

Leigh, J.W. & Bryant, D. 2015. Popart: full-feature software for haplotype network construction. *Methods in Ecology and Evolution*, 6 (9): 1110–1116.

Maricic, T., Whitten, M., & Pääbo, S. 2010. Multiplexed DNA Sequence Capture of Mitochondrial Genomes Using PCR Products. *PloS one*, 5 (11): e14004.

Matisoo-Smith, E., 2007. Animal translocations, genetic variation and the human settlement of the Pacific. In: Friedlander, J.S. (ed.) *Genes, language and culture history in the southwest Pacific*, pp. 157–170.

Matisoo-Smith, E. 2009. The Commensal Model for human settlement of the Pacific 10 Years on – What can we say and where to now? *The Journal of Island and Coastal Archaeology,* 4: 151–163.

Matisoo-Smith, E. & Robins, J. 2009. Mitochondrial DNA evidence for the spread of Pacific rats through Oceania. *Biological invasion*s, 11 (7): 1521–1527.

Pang, J.F., Kluetsch, C., Zou, X.J., Zhang, A.B., Luo, L.Y., Angleby, H., Ardalan, A., Ekström, C., Sköllermo, A., Lundeberg, J. and Matsumura, S., 2009. mtDNA data indicate a single origin for dogs south of Yangtze River, less than 16:300 years ago, from numerous wolves. *Molecular Biology and Evolution*, 26 (12): 2849–2864.

Rohland, N. & Hofreiter, M. 2007. Comparison and optimization of ancient DNA extraction. *Biotechniques,* 42: 343–352.

Savolainen, P., Leitner, T., Wilton, A.N., Matisoo-Smith, E. & Lundeberg, J. 2004. A detailed picture of the origin of the Australian dingo, obtained from the study of mitochondrial DNA. *Proceedings of the National Academy of Sciences of the United States of America,* 101: 12387–12390.

Sawyer, S., Krause, J., Guschanski, K., Savolainen, V. & Paabo, S. 2012. Temporal patterns of nucleotide misincorporations and DNA fragmentation in ancient DNA. *Plos one,* 7 (3): e34131.

Smith, I. 1999. Settlement permanence and function at Pleasant River Mouth, East Otago, New Zealand. *New Zealand Journal of Archaeology,* 1999: 27–79.

Smith, I.W. G. 1981. Mammalian fauna from an Archaic site on Motatapu Island, New Zealand. *Records of the Auckland Institute and Museum,* 18: 95–105.

Smith, I. and James-Lee, T. 2010. Data for an Archaeozoological Analysis of Marine Resource Use in Two New Zealand Study Areas (Revised edition). Otago Archaeological Laboratory Report Number 7.

Storey, A.A., Athens, J.S., Bryant, D., Carson, M., Emery, K., Defrance, S., Higham, C., Huynen, L., Intoh, M., Jones, S., Kirch, P.V., Ladefoged, T., Mccoy, P., Morales-Muñiz, A., Quiroz, D., Reitz, E., Robins, J., Walter, R. & Matisoo-Smith, E. 2012. Investigating the global dispersal of chickens in prehistory using ancient mitochondrial DNA signatures. *PloS one,* 7: e39171.

Storey, A.A., Clarke, A.C., Ladefoged, T., Robins, J. & Matisoo-Smith, E. 2013. DNA and Pacific commensal models: Applications, construction, limitations, and future prospects. *The Journal of Island and Coastal Archaeology,* 8: 37–65.

Walter, R. 1994. The Cook Islands – New Zealand connection. In: Sutton, D.G. (Ed.). *The Origins of the First New Zealanders.* Auckland, Auckland University Press, pp. 220–229.

Walter, R. 1996. What is the East Polynesian 'Archaic'? A view from the Cook Islands. In: Davidson, J., Irwin, G., Leach, B.F., Pawley, A. & Brown, D. (eds.) *Oceanic Culture History: Essays in Honour of Roger Green.* Dunedin: New Zealand Journal of Archaeology Special Publication, pp. 513–529.

Walter, R., Buckley, H., Jacomb, C. and Matisoo-Smith, E., 2017. Mass Migration and the Polynesian Settlement of New Zealand. *Journal of World Prehistory*, 30 (4): 351–376.

Whyte, A.L. H., Marshall, S.J. & Chambers, G.K. 2005. Human Evolution in Polynesia. *Human biology,* 77: 157–177.