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Relict or colonizer? Extinction and range expansion of penguins in southern New Zealand

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Recent human expansion into the Pacific initiated a dramatic avian extinction crisis, and surviving taxa are typically interpreted as declining remnants of previously abundant populations. As a case in point, New Zealand's endangered yellow-eyed penguin (*Megadyptes antipodes*) is widely considered to have been more abundant and widespread in the past. By contrast, our genetic and morphological analyses of prehistoric, historic and modern penguin samples reveal that this species expanded its range to the New Zealand mainland only in the last few hundred years. This range expansion was apparently facilitated by the extinction of *M. antipodes*' previously unrecognized sister species following Polynesian settlement in New Zealand. Based on combined genetic and morphological data, we describe this new penguin species, the first known to have suffered human-mediated extinction. The range expansion of *M. antipodes* so soon after the extinction of its sister species supports a historic paradigmatic shift in New Zealand Polynesian culture. Additionally, such a dynamic biological response to human predation reveals a surprising and less recognized potential for species to have benefited from the extinction of their ecologically similar sister taxa and highlights the complexity of large-scale extinction events.

Keywords: *Megadyptes antipodes*; ancient DNA; New Zealand; palaeontology; Polynesian; extinction

1. INTRODUCTION

Colonization of the Pacific—the 'final frontier' of human expansion—has left a trail of vertebrate extinctions readily discernible from archaeological and palaeontological data (Steadman & Martin 2003), providing an accessible system for revealing anthropogenic impacts on indigenous biota (Hurles *et al.* 2003). Subsistence hunting by early Polynesians is typically implicated in early extinctions (Worthy 1999; Holdaway & Jacomb 2000), and any surviving taxa are usually interpreted as declining remnants of previously abundant populations. With the advent of ancient DNA techniques, we now have a means to test the timing and severity of species and population declines by directly characterizing temporal changes in genetic diversity (Paxinos *et al.* 2002; Shapiro *et al.* 2004; Leonard *et al.* 2007; Valdiosera *et al.* 2008).

In New Zealand, Polynesian expansion southwards (*ca* AD 1280), followed by European colonization (AD 1769 onwards), destroyed much of an indigenous biota that was naive to terrestrial mammalian predators (Higham *et al.* 1999; Wilmshurst *et al.* 2008). At least 41 per cent of the endemic bird species have become extinct, and 35 per cent of those remaining are now classified as threatened (Worthy & Holdaway 2002). The endangered yellow-eyed penguin (*Megadyptes antipodes*), also known as *hoiho*, is one of New Zealand's most publicized threatened species and is the focus of extensive conservation effort, including strong community involvement. The species is considered *taonga* (sacred) by the local Māori, is of high economic importance for local tourism industries and has been ecologically well studied over recent decades. The total population of approximately 7000 individuals breeds on the Subantarctic Auckland and Campbell Islands and the southeast coast of the South Island of New Zealand (Marchant & Higgins 1990; McKinlay 2001; figure 1). Previous analysis of the fossil records and anecdotal evidence suggest that this penguin was more abundant and widespread in the past. Consequently, current management assumes that yellow-eyed penguins on the mainland are a declining remnant of the prehistoric population (Worthy 1997; Moore 2001). The presence of penguin bones in archaeological middens from early Polynesian settlers in New Zealand, ancestors of modern Māori, indicates that penguins were subject to human hunting pressure, but to date this finding has not been considered significant. To test for temporal changes in *M. antipodes* genetic diversity associated with human settlement of New Zealand, we assessed mitochondrial DNA variation of prehistoric, historic and modern samples of yellow-eyed penguin. Based on the results of our genetic analysis, we further performed detailed morphological comparisons between prehistoric and modern *Megadyptes* bones, which lead us to describe a new penguin species that became extinct only a few hundred years ago and revealed the unsuspected recent range expansion of *M. antipodes*.

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2. MATERIAL AND METHODS

(a) *DNA extraction and sequencing*

Yellow-eyed penguin blood samples were collected in 2005–2007 by wing venipuncture of the brachial vein from six different locations throughout the species' breeding range ($n = 15$–20 for each location; M5–M8, M10, M11 in figure 1). DNA was extracted and purified using 40 µg proteinase K in 5 per cent Chelex (Biorad; Walsh *et al.* 1991). An 813 bp fragment of the first hypervariable region of the mitochondrial control region was amplified using primers: L-Man-CR4 (5′-CTGTGCACTGCTTTATGTACGC-3′) and H-Man-CR7 (5′-GTGCATCAGTGTTAAGATGAT TCC-3′). PCRs (15 µl) containing 0.5 µM of each primer, 0.8 mM dNTPs, 1.5 mM $MgCl_2$ and 0.75 U *Taq* polymerase (Mango *Taq*, Bioline, Sydney, Australia) were amplified for 2 min at 94°C, 35 cycles of 20 s at 94°C, 20 s at 50°C and 1 min at 72°C, followed by 10 min at 72°C. Purified PCR products were sequenced with H-Man-CR7.

Historic toe pad samples were obtained from 55 museum specimens collected between 1888 and 1944 across the breeding range of *M. antipodes* and currently held in 15 museum collections worldwide (see table S1 in the electronic supplementary material). Tissue samples were rehydrated by a 24 hour wash in 1 ml 10 mM Tris-HCL (pH 8.0), and DNA was subsequently extracted using the Chargeswitch Forensic DNA Purification Kit (Invitrogen, Carlsbad, CA, USA) or the DNeasy Tissue Kit (Qiagen, Valencia, CA, USA) following manufacturers' instructions. No difference was observed in extraction or amplification success between either of these kits. Two overlapping fragments were amplified using primer pairs L-Man-CR4 (5′-CTGTGCACTGCTTTATGTACGC-3′) and H-Man-CR12 (5′-ACAAACGATACCAACCTATG GG-3′; 299 bp); and L-Man-CR11 (5′-GAGTAATGGTAT GAGGATTAGCTCC-3′) and H-Man-CR14 (5′-CGGGT TGCTGATTTCACGTG-3′; 287 bp), yielding a total of 402 bp. For some samples, a single 444 bp fragment was amplified using primers L-Man-CR4 and H-Man-CR14. Primers H-Man-CR12, L-Man-CR11 and H-Man-CR14 were designed in conserved regions that did not show any polymorphisms in the sequences obtained from modern samples. PCRs (25 µl) containing 0.4–0.8 µM of each primer, 0.8 mM dNTPs, 2.0 mM $MgCl_2$ and 0.5–1.0 U *Taq* polymerase (Mango *Taq*, Bioline) were performed as above with cycles increased to 50. Purified PCR products were sequenced with the same primers used for amplification.

A total of 69 prehistoric *Megadyptes* bones from the South Island and the Auckland Islands, New Zealand, were obtained from museum collections (see table S2 in the electronic supplementary material). Morphological descriptions from Worthy (1997) were used for identification of *Megadyptes* bones. All but two bones (NMNZ S.42156.1 and NMNZ S.42156.2) were indirectly dated to AD 500–1700 based on associated archaeological remains. Independence of individual bones was achieved by sampling either the same bone type within a location or bones from different strata within the archaeological site. Bones were sampled using a hand drill and powdered in a Mikro-Dismembrator S (Sartorius AG, Goettingen, Germany). A total of 50–80 mg of bone powder was decalcified in 2 ml 0.5 M filtered EDTA for 24 hours. DNA was extracted using the DNeasy Tissue Kit (Qiagen) following the manufacturer's instructions with the following modifications: (i) double volumes were used for proteinase K, AL and ATL buffers, and (ii) 2–4 µl of carrier RNA were added to each sample following proteinase K digestion.

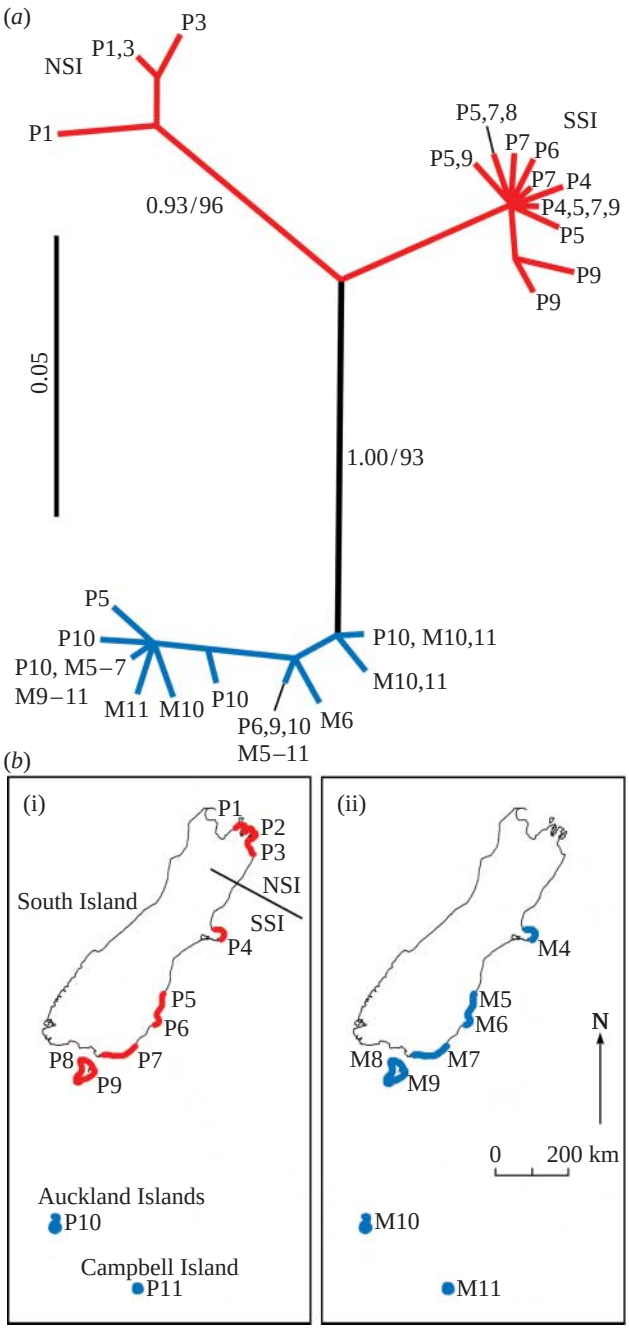

Figure 1. Spatio-temporal genetic relationships and distribution of *Megadyptes* penguins. (*a*) Prehistoric South Island sequences (*M. waitaha* sp. nov.) are shown in red, *M. antipodes* sequences are shown in blue. Numbers on the main branches in the unrooted Bayesian phylogram represent posterior probabilities and ML bootstrap support. (*b*) Maps show the distribution of (i) *Megadyptes* before AD 1500, (ii) *Megadyptes* after AD 1800 on the South Island and subantarctic Campbell and Auckland Islands of New Zealand. Sampling sites are indicated with labels for prehistoric (P1–P11) and modern (M4–M11) samples, and prehistoric sites are further split in northern and southern South Island (NSI and SSI, respectively). The number of samples possessing each haplotype varied between 1 and 94 (see fig. S1 in the electronic supplementary material). It is assumed modern *Megadyptes* inhabited Campbell Island prior to AD 1500, as they do at present, but there is currently no palaeontological evidence to support this.

Samples were amplified for two overlapping fragments as described above. PCRs (25 µl) containing 2 µl of non-diluted or 1 : 10 diluted DNA, 0.8 µM of each primer, 1.0 mM

dNTPs, 2.0 mM $MgSO_4$, 1 mg ml^{-1} BSA/RSA and 0.5–1.0 U *Taq* polymerase (Platinum *Taq* DNA Polymerase High Fidelity, Invitrogen) were performed with 1 min at 94°C, 50 cycles of 15 s at 94°C, 15 s at 55°C and 30 s at 68°C, followed by 10 min at 68°C. Where necessary, 1 µl of the PCR was used as a template for a second PCR to improve amplification success. PCR products were purified and sequenced with the same primers used for amplification. All sequences are deposited in GenBank (accession numbers FJ391944–FJ391968).

Precautions for the analysis of historic and prehistoric DNA were adhered to. Historic sample DNA extractions and PCR set-up were performed inside a UV hood in a laboratory where no contemporary yellow-eyed penguin DNA or vertebrate PCR products have ever been present. Genetic analyses of prehistoric bone samples were all performed at the Australian Centre for Ancient DNA, where extractions and PCR set-up were carried out in a physically isolated, designated ancient DNA laboratory. Contamination was monitored by negative extraction and PCR controls. All historic and prehistoric samples were amplified and sequenced at least twice for both fragments. When conflict was observed among sequences, a third amplification was performed and a majority rule consensus applied (Brotherton *et al.* 2007). Authenticity of prehistoric sequences was further confirmed by extraction replications, cloning and the use of different primers to amplify fragments within the target region as described in the electronic supplementary material.

(b) *Genetic analyses*

Sequences were aligned using SEQUENCHER (Schneider 1998) and analyses were restricted to the 402 bp region sequenced for all specimens. Applying the AIC criterion of MODELTEST (Posada & Crandall 1998), we obtained HKY+I as most appropriate models of evolution for our dataset. Maximum-likelihood (ML) analyses were performed in PAUP* (Swofford 2003). Model parameters were estimated by a heuristic search, with 100 repetitions of stepwise addition. Using the estimated parameters, node support was calculated with 10 000 bootstrap replicates. Bayesian trees were estimated by MRBAYES v. 3.1.2 (Ronquist & Huelsenbeck 2003) in two independent runs, using 20 000 000 generations, sampling every 1000th generation and discarding 25 per cent as burn-in. Convergence diagnostics of Bayesian analyses were explored using TRACER (Rambaut & Drummond 2007) and AWTY (Nylander *et al.* 2008). The topologies of the ML and Bayesian trees were very similar, and therefore only the Bayesian tree is shown in figure 1. The shallow divergence within *Megadyptes* in relation to other penguin species made accurate model selection through MODELTEST and rooting of the trees difficult, and rooted phylogenetic analyses were therefore only performed using a neighbour-joining algorithm with a Kimura-2 distance parameter (see fig. S1 in the electronic supplementary material). Genealogical relationships among samples were reconstructed using a parsimony-based haplotype network with a 94 per cent parsimony criterion in TCS (Clement *et al.* 2000). Observed genetic divergence (*p*-distance) was calculated among clades in PAUP* (Swofford 2003). Haplotype and nucleotide diversity indices were determined using DnaSP (Rozas *et al.* 2003).

(c) *Morphometric measurements and analyses*

Qualitative osteological comparisons were made for coracoid, femur, humerus, tarsometatarsus and tibiotarsus using described terminology from Baumel & Witmer (1993). Morphometric measurements (to the nearest 0.1 mm) of four different bone types (coracoid, femur, humerus and tarsometatarsus) were obtained from genetically analysed specimens (complete bones only), 26 contemporary skeletons (collected 1970–1990) and an additional 47 single bones from prehistoric sites (see the electronic supplementary material for a list of specimens), using Vernier calipers. It was unknown whether prehistoric specimens represented single or multiple skeletons, and each bone type was therefore analysed separately. Difference in average bone length among modern and prehistoric samples was determined using ANOVA followed by *post hoc* analyses (Scheffe) in SPSS v. 16.0. Normality and homoscedasticity assumptions were met and Bonferroni corrections were applied where necessary.

3. GENETIC RELATIONSHIPS

We successfully amplified and sequenced DNA from 100 modern, 43 historic and 42 prehistoric samples. Bayesian, ML and distance analyses all reveal a previously unrecognized and well-supported genetic split among *Megadyptes* samples. Specifically, all South Island specimens from before AD 1500 (sampling sites P1–P9), with the exception of three specimens, form a well-supported distinct genetic group (figure 1; fig. S1 in the electronic supplementary material). Within this group, a further genetic split is observed between the northern (P1–P3) and southern (P4–P9) South Island samples. None of these prehistoric South Island haplotypes is found in the historic or modern samples. On the other hand, all prehistoric Subantarctic sequences (P10 and P11) cluster with the historic and modern yellow-eyed penguins that now inhabit southern New Zealand and the Subantarctic (M4–M11). Currently, *Megadyptes* penguins are absent from the northern parts of the South Island (i.e. north of M4). The haplotype network clearly visualizes the substantial divergence between haplogroups, the relatively close relatedness of haplotypes within each group and the presence of two highly common haplotypes (see fig. S2 in the electronic supplementary material). Genetic divergence between the two identified *Megadyptes* groups was $d=2.24$–4.23% and diversity indices were found to be low for both the prehistoric South Island penguins ($h=0.834$ and $\pi=0.009$) and the group comprising prehistoric subantarctic and modern penguins ($h=0.547$ and $\pi=0.004$). Based on the observed unique genetic composition and the consistent morphological distinctness (presented below) of the prehistoric South Island penguins, we describe these penguins as a new species.

4. SYSTEMATIC PALAEONTOLOGY

Sphenisciformes Sharpe, 1891
Spheniscidae Bonaparte, 1831
Megadyptes Milne-Edwards, 1880
Megadyptes antipodes (Hombron & Jacquinot 1841)
Megadyptes waitaha sp. nov.

(a) *Etymology*

From Waitaha (Māori): the first Polynesian tribe that occupied much of the South Island, New Zealand, before they were displaced by Ngāti Māmoe, who in turn were later dominated by Ngāi Tahu.

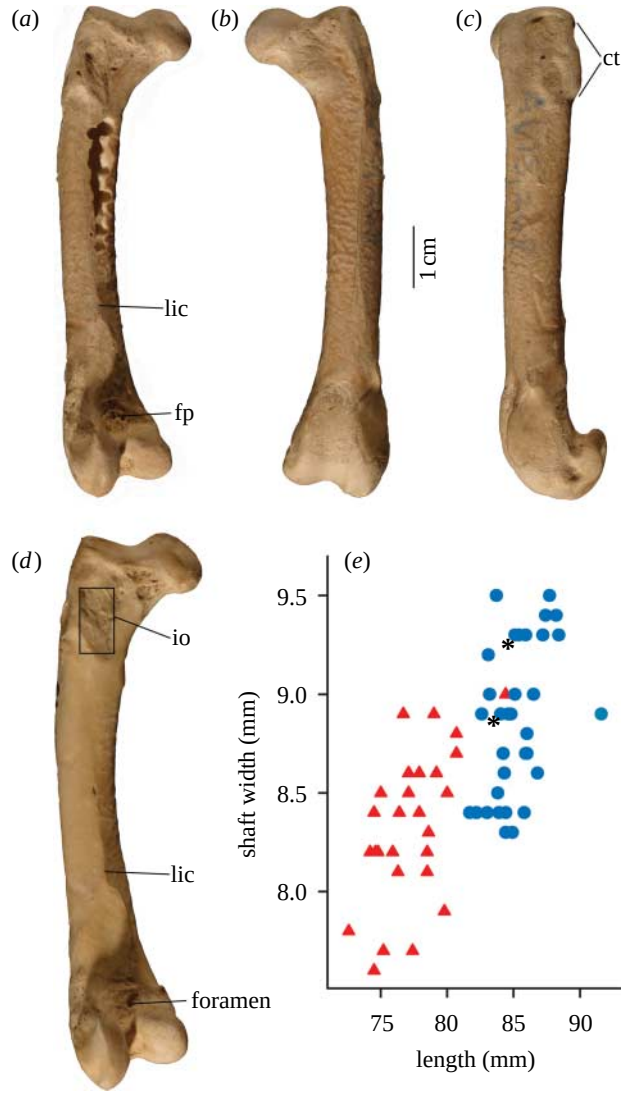

Figure 2. (*a–c*) Holotype left femur of *M. waitaha* (CM AV13269). (*a*) Ventral view; (*b*) dorsal view; and (*c*) lateral view. (*d*) Ventral view of *M. antipodes* femur (CM AV32415). (*e*) Plot showing the size differences of *M. waitaha* and *M. antipodes* femora. Length and width in mm of *M. waitaha* (red triangles) and *M. antipodes* (blue circles) femora. Asterisks indicate two of the three prehistoric South Island samples (i.e. the two femora from P6 to P9 in figure 1) that cluster genetically with *M. antipodes*. The data revealed support the consistent genetic and morphological differences between *M. antipodes* and *M. waitaha*. Anatomical abbreviations: ct, crista trochanteris; fp, fossa poplitea; io, impressiones obturatoriae; lic, linea intermuscular candalis. The ventral view of *M. waitaha* femur (*a*) shows several drill holes resulting from the sampling of the bone.

(b) *Holotype*

Canterbury Museum, CM AV13269 (figure 2), left femur, complete. Measurements of holotype: 77.1 mm length, 8.5 mm shaft width, 18.6 mm proximal width, 16.0 mm distal width.

(c) *Locality and horizon*

CM AV13269 was collected from the dunes along Lake Grassmere, Marfells Beach, Marlborough on the South Island (41°43′21′ S, 174°11′42′ E; site P3 in figure 1), by J. Britton and R. Britton in 1954. Material from these dunes has been widely studied and has been dated to the Late Holocene, between 600 and 1500 years BP (Worthy 1998; Duncan *et al.* 2002).

(d) *Paratypes*

CM AV11995, right femur, complete. CM AV16258Z, right femur, complete. CM AV34941, left femur, complete.

(e) *Referred material*

Referred material includes all specimens from the northern South Island to Codfish and Stewart Island, just south of the South Island, that are listed in table S2 and methods of the electronic supplementary material.

(f) *Diagnosis*

Megadyptes waitaha bones are slender and smaller than those of *M. antipodes* and differ for a range of characters described below. *Megadyptes waitaha* further forms a distinct genetic group based on hypervariable region I (HVI) of the mitochondrial control region. Genetic divergence from *M. antipodes* in HV1 mtDNA is 2.24–4.23 per cent with the following fixed character states (character for *M. waitaha*/character for *M. antipodes*, position corresponding to *Eudyptes chrysocome* mitochondrial genome sequence, GenBank accession number AP009189): T/C (15829), A/G (15855), G/T (15910), T/G (16006) and A/G (16072).

(g) *Description and comparisons*

Megadyptes waitaha bones are distinguished from *M. antipodes* as follows: (i) *femur*: lacks a prominent vascular foramen in the *fossa poplitea*; *linea intermuscular caudalis* more pronounced; *crista trochanteris* shorter and narrower; *impressiones obturatoriae* squarer and more pronounced; *condylus medialis* less robust; (ii) *tibiotarsus*: *crista cnemialis* more pointed; (iii) *tarsometatarsus*: *crista medialis hypotarsi* more flattened; *cotyla lateralis* laterally less prominent; *crista lateralis hypotarsi* less pronounced; medial *foramina vacularia proximalia* more heavily occluded plantaroproximally; medial margin more concave, giving whole bone more slender appearance; (iv) *coracoid*: *facies sternalis* proportionally narrower; dorsal *facies articularis sternalis* less robust; medial process above medial angle less robust; *cotyla scapularis* rounder and smaller; *processus procoracoideus* smaller and less ventrally curved; *processus glenoidalis* more robust; narrower coracohumeral surface (neck) between *processus glenoidalis* and *processus acrocoracoideus*; *foramina procorocoideus* absolutely and relatively larger; (v) *humerus*: *impressio coracobrachialis* proportionally deeper, especially proximally; ventrally located secondary fossa within *fossa pneumotricipitalis* deeper and orientated more anterior-ventrally; *sulcus transversus* dorsal pit relatively deeper; ventral bit shallower; *sulcus tendinis musculus humerotricipitalis* (sesamoid groove) deeper; and the proximal trochlear process caudally bounding the humerotricipital sulcus is more pointed and bent ventrally near tip.

Bones from *M. waitaha* are significantly smaller than bones from *M. antipodes* (figures 2 and 3; table S3 in the electronic supplementary material). There is, however, no size differentiation between *M. waitaha* bones from the northern and the southern South Island of New Zealand (figure 3). The similar size of northern and southern populations of *M. waitaha* occurred over a geographical range greatly exceeding the distance from the South Island

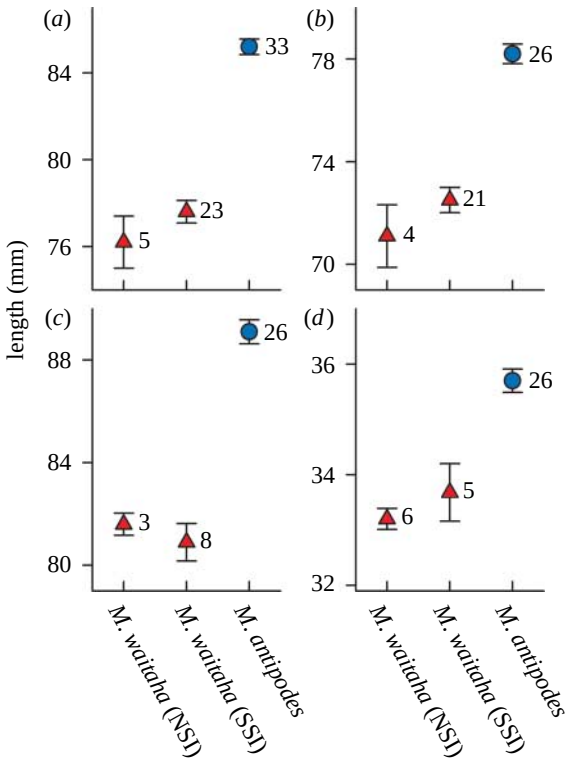

Figure 3. Average length of *M. waitaha* (red triangles) and *M. antipodes* (blue circles) (*a*) femur, (*b*) humerus, (*c*) coracoid and (*d*) tarsometatarsus. *Megadyptes waitaha* bones are divided into southern and northern South Island (figure 1). Error bars are standard error intervals; numbers next to symbols represent sample sizes (*n*). Four separate single factor ANOVAs showed significant differences among the groups: (*a*) $F_{2,58}=91.2$, (*b*) $F_{2,48}=52.2$, (*c*) $F_{2,34}=48.6$, (*d*) $F_{2,34}=18.9$; all $p\leq0.0001$. *Post hoc* analysis (Scheffe) revealed significant differences between *M. antipodes* and both southern and northern *M. waitaha* (all $p\leq0.0015$), but not between southern and northern *M. waitaha*.

to the Subantarctic islands, and thus the geographical distance between the *M. waitaha* and *M. antipodes* populations in prehistoric times.

5. DISCUSSION

(a) *Human-mediated extinction of a new penguin species*

Genetic and morphological analyses reveal a previously unrecognized penguin species in the *Megadyptes* genus. None of the haplotypes of this species are found in any of the historic or modern samples analysed, indicating that *M. waitaha* no longer survives. The presence of its bones in archaeological context implies that its extinction was probably caused by overexploitation (Jones *et al.* 2008). This finding is consistent with the fact that large-bodied species were particularly vulnerable to extinction by hunting in prehistoric New Zealand (Holdaway & Jacomb 2000; Duncan & Blackburn 2004). Indeed, the marked transition from big game (including large penguins) to small game and fish observed in stratified middens reflects the population decline of the larger species within just decades of human settlement (Nagaoka 2001). This previously described 'blitzkrieg' was obviously not only directed against the well-known moa (Diamond 2000), but also against other species such as the overlooked penguin we describe here. It is thus likely that *M. waitaha* became extinct within a few hundred years of human settlement in New Zealand. The recognition of two species in *Megadyptes* reveals an original taxon distribution similar to that of *Eudyptes*, which displays noticeable speciation within the genus (Jouventin *et al.* 2006), including different species inhabiting the South Island and Subantarctic islands of New Zealand.

The phylogeographic split between northern and southern South Island samples of the extinct *M. waitaha* is concordant with biogeographic disjunctions observed around an upwelling zone at latitude 42° S in a number of coastal invertebrate taxa in New Zealand (e.g. Apte & Gardner 2002; Ayers & Waters 2005). This upwelling and associated longitudinal change in currents and water temperature may have also presented a barrier to gene flow for *M. waitaha*. Currently, *M. antipodes* does not breed above 43° S, although occasional vagrants are found as far north as New Zealand's North Island (Marchant & Higgins 1990).

(b) *Recent range expansion of the yellow-eyed penguin*

Our findings demonstrate that yellow-eyed penguins are not a declining remnant of a previous abundant population, but instead went through a recent range expansion following the extirpation of *M. waitaha*. Only three of the prehistoric penguin specimens on the South Island were identified genetically and morphologically as *M. antipodes*. These specimens probably represent non-breeding vagrants from the Subantarctic, as now commonly occurs with *Eudyptes* species. Therefore, it seems almost certain that the entire extant yellow-eyed penguin population on the South Island is derived from a Subantarctic stock.

The rapid replacement of *M. waitaha* by *M. antipodes* suggests that competition between the two species previously prevented *M. antipodes* from expanding northwards. The successful expansion of *M. antipodes* into the South Island, prior to the increase of European settlers and their commensals in the late 1800s and soon after the anthropogenic extinction of *M. waitaha*, may imply that a paradigmatic shift in Māori culture took place. Indeed, it has been suggested that cultural change (including new forms of resource monitoring and conservation) in Māori culture may have developed from the early sixteenth century, possibly forming the basis of modern Māori environmental management (Anderson 2002). Alternatively, the archaeological record shows a marked lack of coastal South Island village sites from the early sixteenth century, in the period following the extinction of big game, suggesting a local temporary reduction of the human population (Anderson & Smith 1996). Environmental changes such as the severe decline in populations of sea lions (*Phocarctos hookeri*), known predators of penguins, might also have facilitated *M. antipodes* colonizing the South Island (Childerhouse & Gales 1998; Lalas *et al.* 2007). We suggest that a similar extinction–colonization process such as that observed in *Megadyptes* might also explain the previously reported arrival of an Australian *Eudyptula minor* lineage in southern New Zealand (Banks *et al.* 2002; Overeem *et al.* 2008).

Ancient DNA analyses are proving to be an extremely valuable tool in wildlife conservation, providing an ability to directly characterize temporal changes

in population sizes and connectivity (reviewed in Leonard 2008). The yellow-eyed penguin provides an unusual case in which prehistoric data support a recent range expansion, instead of the previously assumed decline in numbers. Although the conservation status of South Island *M. antipodes* might be questioned on the basis of these results, the species remains in a vulnerable state with a low total population size, a highly confined breeding range and ongoing threats from the marine and terrestrial environment (Birdlife International 2008). Although the observed range expansion provides evidence of this species's ability to colonize new habitats, the impact of European settlement—such as the introduction of predatory mammals in New Zealand and surrounding islands—might preclude any additional range expansion of *M. antipodes*. As such, the ongoing security of the species would seem to depend largely on the continued health of Subantarctic populations. The New Zealand Department of Conservation's existing policy focuses on the security of a species as a whole, rather than the detailed history of a particular population. Overall, therefore, the yellow-eyed penguin's high conservation status should remain unaffected by our findings.

(c) *Complexity of large-scale extinction events*

Our study reveals a new level of biogeographic and ecological complexity potentially associated with large-scale extinction events that afflicted, for example, the Pacific prehistoric avifauna and North American Pleistocene megafauna. Whereas conventional wisdom suggests that surviving species—like their extinct counterparts—suffered major genetic and ecological declines (Hofreiter 2007), we propose that in some instances native species benefited from the extinction of their ecologically similar sister taxa. For example, we suggest that this extinction–expansion interaction might have had a particularly strong influence on seabird distributions: as numerous colonies went extinct (Steadman 1995), newly vacated habitats would have facilitated rapid range expansion in this highly mobile group of species, as in *Pterodroma nigripennis*, for example (Worthy & Holdaway 2002). Such dynamic anthropogenic processes may turn out to be far more common and important than previously understood.

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