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Former presence of a parakeet (*Cyanoramphus* sp.) on Campbell Island, New Zealand subantarctic, with notes on the island's fossil sites and fossil record

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Abstract One significant late Holocene deposit of bird and other fossils was discovered during a brief survey of potential fossil sites on subantarctic Campbell I, New Zealand. The bones recovered included the first specimen of a *Cyanoramphus* parakeet from the island. Preliminary ancient DNA analysis of the parakeet bone confirmed its generic identification and may ultimately facilitate the re-introduction of a taxon that most closely resembles the genetic make-up of the extinct population. Some implications of the fossil record and value of the fossil sites are discussed.

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INTRODUCTION

Management and restoration of the New Zealand subantarctic islands, the environments of almost all of which have been degraded by human activities over the past 2 centuries (Johnstone 1985), depend ultimately on knowledge of the original faunas and floras, and some understanding of the ecological processes that produced and supported them. Although land-bird faunas of the islands of the Southern Ocean and subantarctic waters in general are characteristically depauperate, their true diversity has been obscured by cryptic extinctions in the early decades of European presence (Miskelly 2000). In addition, the diversity and abundance of breeding seabirds, although still comparatively high, were certainly higher in the recent past, before extirpations during the sealing and whaling periods.

Present land-bird faunas of the subantarctic consist mainly of representatives of the most vagile species from the closest large landmasses. Ducks, rails, and small passerines of open habitats dominate (Holdaway *et al*. 2001). Of the island groups south of New Zealand (Fig. 1), excluding The Snares, which are biologically closer to the islands surrounding Stewart I, and the barren Bounty Is, ducks have colonised all but the Antipodes, rails have been recorded from all but the Antipodes and Campbell, and pipits (*Anthus* spp.) are known from all but Macquarie I. The Macquarie I rail (*Gallirallus macquariensis*) and duck (*Anas* sp.) became extinct in the 19th century (Marchant & Higgins 1993; Holdaway *et al.* 2001), and the Campbell I duck (*Anas nesiotis*) and pipit

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(*Anthus novaeseelandiae aucklandica*) were confined to small islets while Norway rats (*Rattus norvegicus*) were on the main island. The rats were eliminated from Campbell I in July 2001; the pipit has since recolonised from its refugia (Thompson *et al.* 2005), and the duck has been re-introduced (McClelland & Gummer 2006).

Two other groups of terrestrial birds have also colonised the New Zealand subantarctic successfully. New Zealand snipe (*Coenocorypha*) are now known from all the islands except the Bounty group and Macquarie. *Coenocorypha aucklandica perseverance* survived on Jacquemart Islet (19 ha) after apparent extinction on the main island, but since its discovery in 1997 (Judd 1998; Miskelly 2000; Miskelly & Baker 2009) and the elimination of rats, it has started to recolonise the southern end of Campbell I (Barker *et al.* 2005; Miskelly & Baker 2009).

Parakeets of the genus *Cyanoramphus* colonised 3 (Antipodes, Auckland, Macquarie) of the 5 major southern island groups: although The Snares have forest and are within sight of Stewart I, parakeets have never bred there in historical times, but 3 vagrants were seen in 1974/1975 (Miskelly *et al.* 2001). No parakeets had been reported from Campbell I before 2006 (Turbott 1990).

In the late 18th century, *Cyanoramphus* parakeets were found from New Caledonia to the Society Is, and south to Macquarie I, an immense area of ocean from the tropics to the subantarctic. Alone among the larger islands, Campbell apparently lacked parakeets and rails. Their apparent absence has been a biogeographic puzzle (Miskelly 2000) given the apparent ease with which they have colonised islands elsewhere, and the presence of populations to the northeast (Antipodes), northwest (Aucklands), and southwest (Macquarie) (Fig. 1).

Introduced rodents, cats (*Felis catus*), rabbits (*Oryctolagus cuniculus*), and ungulates (King 1990) changed the vegetation and eliminated and reduced populations of both terrestrial and marine birds (Holdaway *et al.* 2001), and other organisms, on most islands before systematic biological surveys began. Early written records have filled some gaps in knowledge of the original biotas, but many remain. However, unlikely as it seems from their climate and mainly volcanic geology, subantarctic islands do have useful fossil records of Quaternary age. For example, Olson & Jouventin (1996) described an extinct duck from Amsterdam I (southern Indian Ocean), and further analysis revealed a substantial record of the pre-human avifauna (Worthy & Jouventin 1999). In the New Zealand region, there is a substantial amount of recent and probable fossil material from the Auckland Is in the Museum of New Zealand Te Papa Tongarewa collections. Taylor (2000a: 305) pointed out the value of a study of material from Sandy Bay, Enderby I, "to determine the former abundance of breeding sea birds on this island prior to human settlement and the introduction of mammals". Farther north, the fossil record from the Chatham Is has been particularly valuable in documenting the former diversity and distribution of birds. Bones were collected from dune systems as early as the 19th century, and at intervals since. There are large collections in Canterbury Museum and at the Museum of New Zealand, and significant progress has been made for the smaller islands (Tennyson 2004; Tennyson & Millener 1994).

Recovery and analysis of fossil materials will be important in developing a full inventory on other island groups (Barker *et al.* 2005). van Tets (1980) reported on significant recent deposits from skua middens on Campbell I, but did not mention any material that was substantially older than the time of collection. The reported presence of recently-deposited bones at Norton Stream, Sandy Bay (within Northwest Bay) and of limestone outcrops in Northwest Bay and elsewhere suggested that older deposits could be present (van Tets 1980). Here we document the first record of a *Cyanoramphus* parakeet from Campbell I from a site under a rock outcrop, report the first stage of a DNA analysis of its relationships, and discuss the other remains in the site and comment on the site's heritage significance.

METHODS

Potential fossil sites were investigated by JMT on 12, 14, and 16 Sep 2004. Most were beneath rock overhangs on the ridges at the head of Perseverance Harbour. The consolidated dune sands at Norton Stream were inspected on 15 Sep, but no test pits were dug because of potential disturbance to vegetation and the sediments themselves. Site locations were established using a Garmin® 12XL global positioning system receiver.

A test pit was excavated in one site. Friable sediments, where present, were passed through a 1 mm sieve. The bones recovered were retained in labelled plastic re-sealable plastic bags and identified by RNH by comparison with material in the reference collections in Canterbury Museum, Christchurch. Measurements were taken by vernier callipers, to 0.01 mm, rounded to 0.1 mm. The material, including fragments of newspaper and other cultural material, has been accessed to the collections of the Canterbury Museum. For the birds, the minimum number of individuals represented was calculated as the sum of the commonest ipsilateral element for each taxon, and represented as number of elements of taxon/number of individuals. Nomenclature follows that of the 1990 Checklist (Turbott 1990).

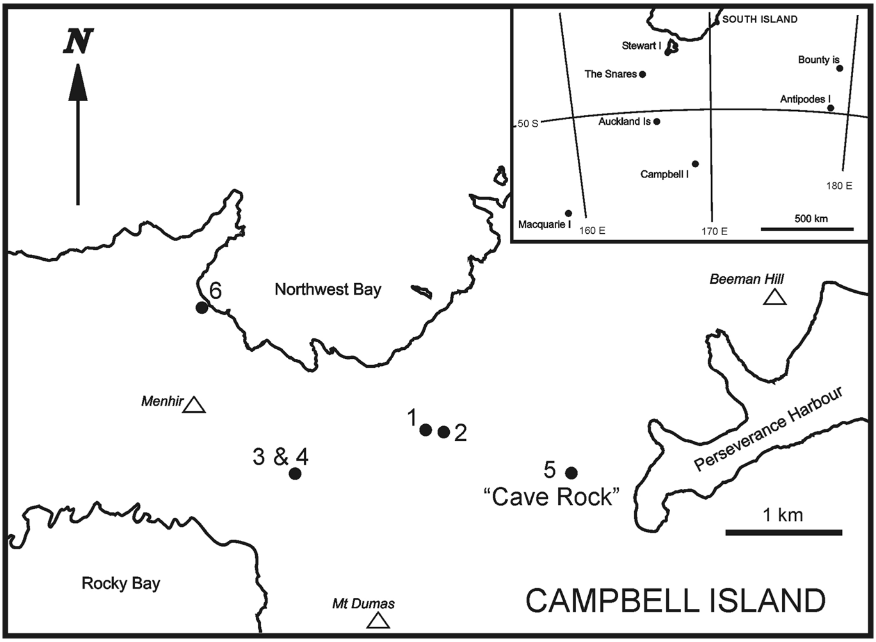

Fig. 1. Location of potential palaeontological sites investigated on Campbell I, Sep 2004. Sites 1-6: Site 5, small alcove next to "Cave Rock" shelter; Site 6, Norton Stream dune system. The inset map shows the location of island groups mentioned in text.

DNA analysis

DNA was extracted from a small piece of the parakeet coracoid in a dedicated ancient DNA laboratory where no work on *Cyanoramphus* or other parrots had been conducted before. The methodology of the DNA extraction methods has been described elsewhere (Bunce *et al.* 2003; Bunce *et al.* 2005). Briefly, the bone fragment was ground to a powder, decalcified and incubated at 55°C overnight in a digest buffer (25mM Tris, 1% SDS, 10mM DTT, 10mM PTB, 5mM $CaCl_2$ and Proteinase K). Two phenol and one chloroform extractions were conducted and the aqueous phase passed over a microcon (Millipore®) and washed with water several times to remove inhibitors. PCR reactions were carried out as described in Willerslev *et al.* (2003) using the primers 12SAFH1753 5′- CTGGGATTAGATACCCCACTAT-3′ and 12SHRb1985 5′-CCTTGACCTGTCTTGTTAGC-3′ that were previously able to amplify *Cyanoramphus* from sediments (Willerslev *et al.* 2003). The resulting PCR product (*c.* 280 bp in length) was direct sequenced in both orientations using BigDye® version 1.1 (Applied Biosystems®) and analysed on a 3130 genetic analyzer (Applied Biosystems®). The lack of data on *Cyanoramphus* on GenBank, despite publication of the DNA sequences (Boon *et al.* 2001), precluded further analysis of the Campbell Is sequences. We also note that during sequencing we detected multiple nuclear copies of mtDNA: we suspect that this has complicated molecular analyses of *Cyanoramphus* to date.

RESULTS

Study site

Site 5 "Cave Rock" (52° 33′ 31.4″ S 169° 07′ 26.9″ E) (Fig. 1) The site investigated was in a small alcove to the left (viewed from the entrance) of the main shelter, which is a cave-like overhang in a basalt outcrop, and very sheltered and dry. The alcove is beneath a smaller overhang, facing in the same direction as the main shelter, towards the southeast. The alcove also contained a dry, sheltered area, in which a test pit (*c.* 300 × 400 mm) was dug to *c.* 900 mm deep on Sep 14. The first 600 mm were excavated through sediment consisting largely of sheep (*Ovis aries*) droppings; a few fossil bones were retrieved from this layer without sieving. For 100 mm below the primary layer of sheep droppings, the sediment contained an admixture of droppings. Three bones were recovered from this layer; by 700 mm depth the sediment was soil with a significant component of small stones.

This lowest layer was excavated to 200 mm into material showing no signs of sheep droppings, and three identifiable bones and some shards were recovered by sieving. The layer extends to an unknown but apparently significant depth below the level reached in the test pit.

Other potential sites investigated

Five other sites were investigated briefly. No suitable deposits were found in the time available and without the use of climbing equipment. Locations of the sites are given in Appendix 1.

Fig. 2. A, internal (left) and **B**, external (right) views of left coracoid of *Cyanoramphus* sp., Site 5, Campbell I; cranial end of bone (arrowed) used in DNA analysis. **C**, Cranial view of left humerus of immature sooty shearwater (*Puffinus griseus*) Site 5, Campbell I; arrows indicate predator damage to pectoral and brachial crests. **D**,Two right humeri of diving petrel (*Pelecanoides* sp.), Site 5, Campbell I; Scale bar is 10 mm.

Systematic palaeontology
Nine bird fossils, attributed to 3 species, and several elements of 1 species of mammal are reported here. Fossils were recovered only from the test pit in Site 5. The fossils, stratigraphic locations, and identifications are listed in Table 1.

Class Aves
Order Procellariiformes
Sooty shearwater *Puffinus griseus*
Material: (2/1) 1 left humerus (imm: length 110.6, proximal width 19.2, shaft width 6.6 mm, distal width 14.0, Av 39476) (Fig. 2C); 1 right femur (immature: length 38.1, proximal width 9.0, shaft width 4.5, distal width 7.9, Av 39477).
Remarks: The pectoral crest of the left humerus has a notch consistent with damage caused by a predator's beak engaged in removing the pectoral muscle. The damage is characteristic of that inflicted by a hawk (Accipitridae) (Worthy & Holdaway 2002), which suggests the former presence of a raptor on Campbell I. The bones are adult-sized but immature and indicate the presence of breeding birds nearby.

Diving petrel *Pelecanoides* sp.
Material: (3/3) 2 right humeri (both adult Av 39478, Av 39479: length 43.7, 44.9; proximal width 8.7, 9.3; shaft width 3.1, 3.3; distal width 6.7, 6.9) (Fig. 2D); 1 furcula (imm.), Av 39480.
Remarks: The presence of both adult and immature bones indicates the presence of breeding birds near the site. Diving petrels have not previously been reported breeding on the main island. Murphy & Harper (1921) believed that both *P. urinatrix chathamensis* and *P. urinatrix exsul* breed on the Auckland Is. This, and minor plumage and considerable size differences, led them to consider *P. exsul* to be a separate species. The humeri from Site 5, Campbell I are longer and more robust than those listed by Worthy (1998, table 2) for *P urinatrix chathamensis* from the Chatham Is and Stewart I, but they are similar to measurements given for *P. urinatrix urinatrix* and *P. urinatrix exsul* by Worthy & Jouventin (1999, appendix 7). These bones cannot be assigned to a particular specific or subspecific taxon of *Pelecanoides* without genetic analysis.

Sp. inident.
Material: sternal rostrum, Av 39481; pedal phalanx, Av 39482 (length 12.3, proximal width 3.4, distal width 2.4; 1 cervical vertebra, Av 39483).
Remarks: Both the sternal fragment and the pedal phalanx are from petrels, but no attempt was made to identify them to species from the very limited material. The vertebra probably represents a medium-sized petrel.

Order Psittaciformes
Parakeet *Cyanoramphus* sp.
Material: (1/1) 1 left coracoid, Av 39471 (adult: length 20.6+ to medial angle, anterior end damaged; width of sternal facet 6.3; shaft width 2.4) (Fig. 2A,B).
Remarks: The coracoid is the first evidence for the former presence of a *Cyanoramphus* parakeet on Campbell I (Barker *et al.* 2005; Holdaway 2005). It is possible, although unlikely, that it represents a vagrant: the rarity of fossil sites and of the low likelihood of representation of anything but a common species in those sites, suggests that the bone represents a resident population. Whether more than one taxon of parakeet occupied the

Table 1. Fossil material from test pit at Site 5 (Cave Rock), Campbell I.

Level	Sediment	Taxon	Common name	Element	1990 Checklist	Age
0-600 mm	Sheep dung	*Ovis aries*	Sheep	Various		
0-600 mm	Sheep dung	*Puffinus griseus*	Sooty shearwater	Left humerus		Juvenile
0-600 mm	Sheep dung	*Puffinus griseus*	Sooty shearwater	Right femur		Juvenile
0-600 mm	Sheep dung	*Pelecanoides* sp.	Diving petrel	Right humerus	*Pelecanoides urinatrix exsul*	Adult
0-600 mm	Sheep dung	*Pelecanoides* sp.	Diving petrel	Furcula	*Pelecanoides urinatrix exsul*	Juvenile
0-600 mm	Sheep dung	*Felis catus?*	Mammal (cat?)	Rib		
600-700 mm	Sheep dung/gravel/soil	*Pelecanoides* sp.	Diving petrel	Right humerus	*Pelecanoides urinatrix exsul*	Adult
600-700 mm	Sheep dung/gravel/soil	*Ovis aries*	Sheep	Bone fragment		
600-700 mm	Sheep dung/gravel/soil	Aves	Bird	Cervical vertebra		
700-800 mm	Gravel/soil	Petrel	Petrel	Sternal rostrum		
800 mm	**Gravel/soil**	***Cyanoramphus* sp.**	**Hochstetter's? parakeet**	**Left coracoid**		**Adult**
800 mm	Gravel/soil	Petrel?	Petrel?	Pedal phalanx		
800 mm	Gravel/soil	?		4 bone shards		

island, as on the Antipodes, can be answered only by further investigation of fossil deposits, aided by an approach that combines DNA and morphological analysis.

The DNA extracts from the sample of bone (Fig. 2A) yielded a single amplification from the 12S mitochondrial gene. In ancient DNA analysis it is often advisable to clone amplification products to detect both contamination, or DNA damage, or both. However, in this instance, where a simple species identification was required, the direct sequence was of sufficient quality and length for the purpose. The sequence obtained from the Campbell I coracoid was compared directly to the sequence of the New Zealand red-crowned parakeet (*C. novaezelandiae*) and to the *Cyanoramphus*-like sequence obtained from soil sediments from the Clutha River (Willerslev *et al*. 2003), which is the only other fossil sequence attributed to that taxon available at present. An alignment of the sequence data is shown in Fig. 3 and unambiguously placed the bone in the genus *Cyanoramphus*, which is consistent with the generic identification based on bone morphology. Species determination on skeletal material is problematic in *Cyanoramphus* (Worthy & Holdaway 1994) and further diagnosis of species and sub-species is not currently possible with this genetic marker.

Class Mammalia
Cat (*Felis catus*)
Material: 1 rib?, Av 39484; 1 desiccated corpse, not collected.
Remarks: The dried body of a cat was found beneath a piece of rotten sacking, on top of the layer of sheep dung, at the junction of the shelter wall and roof.

Sheep (*Ovis aries*) Wool and a fragment of sheep bone (Av 39485) were found in the layer of sheep dung. No remains of cattle (*Bos taurus*) were seen.

DISCUSSION

Miskelly (2000), Barker *et al.* (2005) and Miskelly & Baker (2009) have highlighted the apparent rapidity of the extinction of terrestrial birds on Campbell I after the arrival of Europeans in the early 19th century. The first human visitors were engaged in exploitative industries, and their ships were home to predatory mammals. The first wave of extinctions removed the land birds from all but the least accessible of the surrounding islets (Miskelly 2000). Then the seabirds were depleted, both the surface-nesters as food and sale items for humans, and the burrow-nesters as food for rats. The combined effects of herbivory, fire, and the reduction and ultimate removal of significant populations of burrow-nesting petrels altered the vegetation to the extent that only a subset of the

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                   1          11         21         31         41         51
                   |          |          |          |          |          |
redcrowned         GCCTAGCCCT AAATCTTGAT GTCTC--ACA CACAAACATC CGCCCGAGAA CTACGAGCAC
campbell_Island_   .......... .......... .....TC... .......... .......... ..........
Clutha_sediment    .......... .......... .....ATG.. .......... .......... ..........

                   61         71         81         91         101        111
                   |          |          |          |          |          |
redcrowned         AAACGCTTAA AACTCTAAGG ACTTGGCGGT GCCCTAAACC CACCTAGAGG AGCCTGTTCT
campbell_Island_   .......... .......... .......... .......... .......... ..........
Clutha_sediment    .......... .......... .......... .......... .......... ..........

                   121        131        141        151        161        171
                   |          |          |          |          |          |
redcrowned         ATAACCGATA CTCCACGATA CACCCAACCA CTTCTTGCCA AAACAGCCTA CATACCGCCG
campbell_Island_   .......... .......... .......... .......... .......... ..........
Clutha_sediment    .......... A......... .......... .......... .......... ..........

                   181        191        201        211
                   |          |          |          |
redcrowned         TCGC?AGCCC ACCTCCA??G AGAGCACAAC AGTGAGCT
campbell_Island_   ....C..... .......-T. .......... ........
Clutha_sediment    ....C..... .......-T. .......... ........
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Fig. 3. Alignment of DNA sequences of the 12S mitochondrial gene for New Zealand red-crowned parakeet (*Cyanoramphus novaezelandiae*) (Willerslev *et al.* 2003), the parakeet bone from Campbell I, and parakeet DNA extracted from sediments from a site beside the Clutha River, South I, New Zealand (Willerslev *et al.* 2003). For the Campbell I and Clutha sediment fossil sequences, only differences in bases from the red-crowned parakeet sequence are shown.

primitive associations now survive, as fragments on the surrounding islets. The damage to populations of terrestrial invertebrates also has probably altered the rate and mode of detrital decomposition, and nutrient cycling (Smith & Steenkamp 1992; Zavaleta 2002), with unknown but potentially significant consequences for the ecosystem.

Miskelly (2000) and Holdaway *et al.* (2001) predicted the presence of a parakeet on Campbell I on biogeographic grounds, a prediction confirmed by the discovery of a fossil parakeet coracoid below the "sheep" layer in Site 5. The discovery shows the importance of further analysis of the avian fossil record on the island, and the predictive power of biogeography in the New Zealand archipelago. Miskelly (2000: 132) noted that Robert McCormick, surgeon on the *Erebus* and *Terror* expedition, which visited Campbell I in 1840, "specifically mentioned that he did not meet with a single land bird" on Campbell I. The land birds potentially present would have been Campbell I teal, the subantarctic pipit, and the Campbell I snipe. To that list can now be added the parakeet, which should have been conspicuous. Miskelly (2000) concluded that rats, which were abundant in 1868 (Armstrong 1868, cited in Miskelly 2000), had been introduced by at least 1828. Given the time needed for a rat population to expand after colonisation, and then to exterminate at least 4 species of terrestrial birds as well as large populations of several species of sea birds, it is likely that rats were introduced at the time of the very earliest European contacts with the island, perhaps at first contact. That, it must be assumed, could even have been before the official discovery date of 1810.

Boon *et al.* (2001) proposed that the extant population of "red-crowned" parakeets on the Antipodes is conspecific with the extinct population on Macquarie I. However, Scofield (2005) has shown that the specimen in Canterbury Museum attributed to *C. erythrotis* and used by Boon *et al.* (2001) actually came from Antipodes I, and so the relationship of the 2 populations remains unresolved. Without authentic DNA sequences from the surrounding island groups, it is difficult to infer anything regarding the genetic structure of *Cyanoramphus* in this region. We are undertaking further research into their relationships, particularly with respect to the Macquarie I form using material certainly from that island. The ability to PCR amplify a 280bp sequence of the Site 5 bone (a large fragment for ancient DNA work) suggests the environment on Campbell I may be generally conducive to DNA survival. It raises the possibility of further profiling of bones and perhaps of sediments (Willerslev *et al*. 2003).

The genetic profiling of past *Cyanoramphus* populations from these islands should be considered before moves are taken to re-establish colonies. The former presence of a second species of parakeet on Campbell I, even *C. unicolor*, should not be discounted. Campbell I lies between, and is roughly equidistant from, Antipodes I and Macquarie I, and the islands share a similar treeless landscape, so if the populations of "red-crowned" parakeets on those groups are conspecific as proposed by Boon *et al.* (2001), it would be reasonable to suggest that the Campbell I bird was part of a southern radiation. If they can be grouped at the species level, the earlier available name is *Cyanoramphus erythrotis*, the type specimen being from the population formerly on Macquarie I (Taylor 1979). Boon *et al.* (2001) refer to the surviving Antipodes I population as Reischek's parakeet (*C. erythrotis hochstetteri*), but we follow Holdaway *et al.* (2001) in using Hochstetter's parakeet as the name for the species. However, it is more likely that each group was colonised independently, and possibly at different times.

Boon *et al.* (2001) suggested that the ancestor of Hochstetter's parakeet colonised the Antipodes and Macquarie I about 30,000 years ago, after the arrival of the Antipodes I parakeet (*Cyanoramphus unicolor*) and before the coldest stage of the Otiran Glaciation (*c.* 22,000-19,000 years ago). If so, suitable habitat must have survived on both these southern islands (and also on Campbell I) throughout the period of the Last Glacial Maximum. However, our results suggest that the status of the southern parakeets is not known well enough at present, so interpretation of the sequence of colonisation events is premature.

Taylor (1979) attributed the extinction of the Macquarie I parakeet to predation by feral cats and the introduced weka (*Gallirallus australis*). Cats had a major effect because introduced rabbits provided food for them during the seasons when petrels were not breeding, which allowed the cat population to remain high. Such a scenario is not tenable for Campbell I, where the land birds went extinct before cats were introduced (Miskelly 2000). Norway rats alone must have been responsible for the parakeet's extinction on Campbell I. Hence, the eradication of Norway rats opens the way for the establishment of a replacement population. Based on the foods of populations on other southern island groups listed in Higgins (1999), the present vegetation of Campbell I could sustain a population of parakeets, particularly once the invertebrate populations begin to recover from the effects of rat predation. For Hochstetter's parakeet, at least, and perhaps for *C. unicolor*, there is a clear potential for the establishment of another population, on Campbell I. Both are presently confined to a single island and are therefore vulnerable to introduced predators. Antipodes I is isolated and visited rarely, so predators could be present and damaging bird populations for some time before being detected. Taylor (1979) makes the important point that the mouse (*Mus musculus*) population on Antipodes I would provide potential prey for cats if they are ever introduced there.

Other birds

The presence of the *Cyanoramphus* bone suggests the possibility that other species may formerly have been part of the Campbell I fauna (Barker *et al.* 2005). Bailey & Sorensen (1962) noted that the sooty shearwater is common at sea off Campbell I, and also attempts to nest on the main island (Taylor 2000a). No young or fledglings were observed when Norway rats were present (Bailey & Sorensen 1962); the lack of successful nesting was blamed on rat predation. The species is smaller (*c.* 800 g) than either of the two species – grey petrel (*Procellaria cinerea*, *c.* 1000 g); white-chinned petrel (*Procellaria aequinoctialis*, *c.* 1300 g) that survived longest (Bailey & Sorensen 1962). Jacinda Amey (DoC Southland Conservancy File SUB 30 vol2) noted some active burrows in 2000-2001 and the species' tenuous survival until rat eradication probably reflected its former great abundance on the main island, or attempts to colonise from colonies on other islands.

The damage to the juvenile sooty shearwater humerus, particularly the sharp incision in the brachial crest, is a characteristic result of harrier feeding behaviour (Worthy & Holdaway 2002), which suggests that the Australasian harrier (*Circus approximans*) either visited or was resident on Campbell I. Barker *et al.* (2005) also raised the possibility of New Zealand falcons having been present in the past, when there was a rich variety of both terrestrial and oceanic birds as prey. It is possible that a falcon inflicted the bone damage. Falcons are known to wander to Campbell I (Bailey & Sorensen 1962), and the population on the Auckland Is is much closer than the nearest harriers breeding on Stewart I. However, harriers are regular vagrants to the Auckland Is (PM, *pers. obs.*).

Diving petrels, identified as "subantarctic diving petrels" (*Pelecanoides urinatrix exsul*) by Turbott (1990) and Taylor (2000a), are seen commonly at sea near Campbell I. They once bred on Campbell I (Taylor 2000a), but until the rats were eradicated they nested only on adjacent islets and rock stacks (Bailey & Sorensen 1962; Taylor

2000a). The species bred on the highest parts of the main island before Norway rats were introduced. Diving petrel colonies are often assumed to be strictly coastal, but *Pelecanoides u. urinatrix* bred at altitudes up to *c.* 800 m and nearly 30 km from the coast in North Canterbury (Worthy & Holdaway 1995). The birds may have been brought to Site 5 by a raptor, although there are no predation marks on the bones.

The successful recolonisations by snipe (Miskelly & Barker 2009) and pipit (Thompson *et al.* 2005) and the history of colonisation by both indigenous and introduced birds suggest that other taxa, including *Cyanoramphus* parakeets, may eventually establish or re-establish breeding populations on Campbell I in the absence of rats. Vagrants from adjacent groups regularly reach Campbell I, as illustrated by the presence of a New Zealand bellbird (*Anthornis melanura*) for several years after the rat eradication (PM, *pers. obs.*), and a group of (possibly Auckland I) banded dotterels at the northern end of Campbell I, again after the eradication (Peter Moore, *pers. comm.* to PM).

Mammals

Cats were introduced to Campbell I during the period of continuous occupation (based on farming and whaling) from 1895 to 1931. Veitch (1985) gave the year of introduction as 1908, but it may have been as late as 1916 (Dilks 1979; Kerr & Judd 1978). By 1985, they were said to be "in low numbers" and "do not seem to affect remaining bird life" (Veitch 1985). Veitch (1985) also noted that breeding petrels were rare, and smaller species were absent. Dilks (1979) recorded mainly insects and Norway rats in scats of Campbell I cats, but one scat contained material from a "prion-sized seabird" and others included the remains of introduced passerines, but apparently not the subantarctic pipit. That a small petrel appeared in the samples Dilks examined, suggests that birds often attempted to breed on the main island but fell prey to cats and rats. This is likely to have applied also to terrestrial species (Barker *et al*. 2005) whose rarity meant that remains were very unlikely to appear in scat samples.

Cats were declared extinct on Campbell I after 2 targeted searches, by Derek Brown and Scott Theobald in Feb 1999, and by Sandy King in Aug 1999. No cats had been seen on the island since the 1980's, when Graeme Taylor saw sign at "Cave Rock" (Moore 1997), and their continued existence was questioned. With the demise of the rat population in 2001, any cats remaining would have lost their staple diet (Dilks 1979). The rapid recovery of the pipit population on the main island after their rapid recolonisation (Thompson *et al.* 2005) and the appearance of snipe (Barker *et al*. 2005) indicate that cats are indeed extinct on Campbell I. The dried individual found in Site 5, near where cat sign was last seen, may have been the last survivor. Stable isotopic analysis of skin and bone samples could indicate whether seabirds were a significant component of its diet.

The thick layer of sheep droppings formed a useful time marker for the fossil deposit. Sheep were introduced to the island in 1895 (Dilks & Wilson 1979). Material from beneath the layer of droppings can be assumed, in the absence of evidence for bioturbation or other disturbance, to predate 1895. Sheep were removed from the northern part of the island in 1970, after a fence had been erected across the narrowest part, west from Tucker Cove at the head of Perseverance Harbour. Sheep were not eliminated from the southern section, where Site 5 (Cave Rock) is situated, until 1991 (Taylor 2000b) or 1992 (Moore 2004). They had been in very low numbers in the "Mt Honey Block" which includes Cave Rock, after 1984 when a second fence was built from Capstan Cove to Mt Dumas. The few (?<10) sheep in the block were on the slopes of Mt Honey and there would not have been enough near Cave Rock to have influenced the deposit (PM, *pers. obs*.). Wool and bone in the deposit presumably reflect the random death of individuals in the shelter of the rock before 1992.

No evidence of cattle was found at any of the sites investigated. Taylor *et al.* (1970) reported they were confined to *c.* 500 ha of the south-western part of the island, so they are unlikely to have influenced the environment near Site 5. The last beast was shot in 1984 (Taylor 2000b).

Importance of fossil deposits

The information derived from the fauna from Site 5, Campbell I underlines the value of palaeobiological surveys of islands. Further surveys and excavations are likely to yield a greater diversity of remains and provide more information on the pre-human vertebrate fauna but should only be attempted by qualified personnel. It is important to note that taphonomic analysis of the remains revealed the presence of a species that has not yet been found as a fossil on the island. The presence of immature bones can provide breeding records which will help establish the original resident fauna and so allow the progress of ongoing natural and managed restoration of the ecosystem to be assessed. There are other large caves and overhangs on Campbell I; some at least could contain significant fossil deposits. Site 5 or one of the other sites could contain evidence for other "lost species", given that neither the teal nor the snipe is presently known from fossils although both were present on the island. A rail and perhaps another species of parakeet might be expected.

Implications for interpretation of the Campbell I ecosystem

The fossil record confirms that the history of the vegetation of Campbell I has to be interpreted in the light of the former presence of high numbers of large and small burrow-nesting petrels and shearwaters. Much more has been written on the effect of grazing mammals (e.g., Taylor *et al.* 1970; Dilks & Wilson 1979, references therein) than on the seabirds but both have played major roles in the development of the present soils and biota of the island. The losses of both terrestrial and marine birds have been so great on islands such as Campbell I, that their former roles, and in particular those of seabirds, can be significantly under-appreciated. For example, surveys of the soils (Campbell 1981) and vegetation (Meurk *et al.* 1994; McGlone 2002) barely mention seabirds at all (and then only surface-nesting species), despite their effects on both (e.g., Gillham 1956, 1961; 1963; Burger *et al.* 1978; Smith 1978; Frost 1979). Research on islands suggests that the birds would have been major determinants of vegetation cover and composition (Burger *et al.* 1978; Anderson & Polis 1999; Mulder & Keall 2001; Bancroft *et al.* 2005a, b; Croll *et al.* 2005).

"Cave Rock" as a heritage site

The rockshelter containing Site 5 is not included in Palmer & Judd's (1981) summary of archaeological and historical sites on Campbell I. The presence of the remains of old newspaper and magazine fragments and the remnants of sackcloth accords with tradition that the overhang was used both as a place of refuge for the Coast Watching parties during World War II and as a shelter by musterers during the pastoral phase of the island's history (Dingwall & Gregory 2004) and suggest that "Cave Rock" merits the same level of heritage recognition as other such sites on the island. This is especially so given its dual nature as an historic site and the only place known at present to contain faunal remains recording the pre-human biota.

The main shelter at "Cave Rock" is likely to contain further evidence of human occupation. The possible presence of such deposits should be taken into account if the site is investigated for the fossil fauna. However, an excavation should not be attempted by an archaeological team alone. Natural deposits require a different expertise and any future excavation should be done by a team with both palaeontological and archaeological expertise.

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Appendix 1. Other sites investigated on Campbell I.

Site 1 (52° 33′ 19.1″ S 169° 06′ 20.2″ E) (Fig. 1)
Site 1, in a basalt outcrop on the ridge between Northwest Bay and Perseverance Harbour, was visited by JMT on 12 Sep 2004. The outcrop stands above the ridge level, and contains several sheltered ledges, most of which were not accessible without rock-climbing equipment. Several large puddles nearly surrounded the base of the outcrop. At the south-western end, a sheltered ledge contained a reddish soil but this was only *c.* 5-10 cm deep above the rock surface and no fossils were found.

Site 2 (52° 33′ 21.2″ S 169° 06′ 31.7″ E) (Fig. 1)
This site was in an outcrop 230 m down the eastern side of the ridge leading to Camp Stream, and was also investigated on 12 Sep. A semi-sheltered ledge on the north-western face of the outcrop contained damp soil similar to that in Site 1 and no fossils.

Sites 3 & 4 (52° 33′ 31.4″ S 169° 07′ 26.9″ E) (Fig. 1)
These sites were at opposite ends of a long basalt outcrop on the eastern face of the ridge separating Capstan Cove and Middle Bay, *c.* 20 m above the "Top Track" which follows from "Cave Rock" to Northwest Hut. The outcrop faces northeast and Site 3 was under an overhang at the southern end. From a distance it appeared to have suitable sediment, but closer inspection revealed that it was a fibrous, peaty soil with standing water. Site 4, at the northern end, was similar.

Site 6 Norton Creek, Sandy Bay (Fig. 1)
Bones have been recovered previously from "dunes" in this area, but they were of recent origin, perhaps from a skua midden. A visit by JMT on Sep 15 revealed no suitable places for excavation. The area is mostly blanketed by thick peat, with scattered stones exposed in the creek banks. Where sediment layers were exposed, they were composed of a consolidated aeolianite. The vegetation is predominantly tussocks of *Poa litorosa* and lower herbs, and the area is surrounded by *Dracophyllum scoparium* scrub. There were *c.* 80 northern giant petrels (*Macronectes halli*) resting on the beach, and at least 7 brown skuas (*Catharacta skua*) were seen. There were also many Hooker's sea lions (*Phocarctos hookeri*) in the area, but no count was made.