THE IDENTIFICATION OF FOSSIL *EUDYPTES* AND *MEGADYPTES* BONES AT MARFELLS BEACH, MARLBOROUGH, SOUTH ISLAND

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ABSTRACT

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Distinguishing characters separating bones of *Eudyptes pachyrhynchus, E. robustus, E. sclateri* and *Megadyptes antipodes* are described. The bones of large penguins from fossil and midden deposits at Lake Grassmere, Marlborough, South Island, New Zealand are studied, and only *E. pachyrhynchus* and *M. antipodes* are present. Bones of *Megadyptes* from northern South Island locations are significantly smaller than those of extant southern populations, and thus vary in a similar way to populations of *Eudyptula minor* in these areas. The fossil bones of *Megadyptes antipodes* indicate the present range of the species is a relict one, and the frequent inclusion of this species in middens suggests that the decline is due to human disturbance.

KEYWORDS: Fossil - bird - penguins - *Eudyptes* - *Megadyptes* - New Zealand - Holocene.

INTRODUCTION

Several penguin species breed on the coastline of mainland New Zealand, and several more are occasional visitors (Turbott 1990). Most widespread and abundant of the breeding species is the Blue Penguin *Eudyptula minor*, which lives all around the North, South, and Stewart Islands and Chatham Islands. Two species of considerably larger penguins breed in much more restricted ranges. The Yellow-eyed Penguin *Megadyptes antipodes* breeds on Canterbury, Otago and Southland coasts, Stewart Island, Campbell Island and Auckland Islands (Marchant & Higgins 1990), and is considered to be one of the rarest species of penguins with between 5930 and 6970 birds in 1988-89 (Moore 1992). The population remaining on the Canterbury and Otago-Southland coasts accounts for only a few of these. Stragglers have been recorded up to Cook Strait (Turbott 1990). Nesting in South Westland, Fiordland, Stewart Island and surrounding islands is the Fiordland Crested Penguin *Eudyptes pachyrhynchus*. Stragglers have been recorded as far north as the Bay of Islands (Turbott 1990). The population of *E. pachyrhynchus* is small with less than 2000 pairs (McLean & Russ 1991, Russ *et al.* 1992, McLean *et al.* 1993, Studholme *et al.* 1994, McLean *et al.* 1997).

On New Zealand's subantarctic islands other species of *Eudyptes* are found. The Snares Crested Penguin *E. robustus*, closely related to *E. pachyrhynchus*, has a population of about 20,000 pairs (Turbott 1990), and is reported regularly on southern beaches. The Erect-crested Penguin *E. sclateri* breeds in large numbers on the Antipodes and Bounty islands, and in smaller numbers on Campbell Island and on Disappointment Island in the Auckland Group. It is regularly reported as a visitor to eastern South and North islands (Turbott 1990).

The following species are rare visitors to the New Zealand mainland (Turbott 1990, Heather & Robertson 1996): Emperor Penguin *Aptenodytes forsteri* one record; King Penguin *A. patagonicus* three records; Northern Gentoo Penguin *Pygoscelis papua* five records; Adelie Penguin *P. adelie* two

records; Eastern Rockhopper Penguin *Eudyptes chrysocome filholi* rare; Moseley's Rockhopper Penguin *E. chrysocome moseleyi* one record; Royal Penguin *E. chrysolophus schlegeli* rare visitors.

In the Holocene fossil record and from Polynesian middens the following large penguins were listed by Scarlett (1979) *Eudyptes pachyrhynchus, E. sclateri*, and *Megadyptes antipodes*. *Eudyptes pachyrhynchus* was the most often listed and from sites covering the largest geographic range. *M. antipodes* was only listed for sites between Otago and Southland and had the fewest records.

A survey of the archaeological literature shows that *E. pachyrhynchus* has been recorded from at least 40 sites (Canterbury Museum Av register, Anderson 1982, Butts 1978, Davidson 1978, Hamel 1977, Leach 1979, Leach & Leach 1980, McGovern-Wilson 1986, McGovern-Wilson *et al.* 1996, Mason & Wilkes 1963; Millener 1981; Scarlett 1979, Sutton & Marshall 1980, Trotter 1970, 1975, 1980, Wilkes & Scarlet 1963, 1967); *E. sclateri* 16 sites (Barber 1994, Hamel 1977, Higham 1968, Leach 1979, McGovern-Wilson 1986, Scarlett 1979); *E. robustus* 3 sites (McGovern-Wilson 1986, McGovern-Wilson *et al.* 1996); *E. chrysocome* 2 sites (Hamel 1977); *Megadyptes antipodes* 12 sites (Dawson & Yaldwyn 1952, McGovern-Wilson 1986, McGovern-Wilson *et al.* 1996, Scarlett 1979, Trotter 1967). Most recently the following were recorded from the Shag Mouth archaeological site in North Otago, *M. antipodes* (minimum number of individuals 17), *Eudyptes pachyrhynchus* (7), *E. robustus* (1), *E. sclateri* (9) (McGovern-Wilson *et al.* 1996). None of these records was associated with justification of species determinations.

Identifying the 'big penguin' species present was part of a re-evaluation of the Marfells Beach / Lake Grassmere fauna from natural sand dunes and midden origins (Worthy in prep). An initial examination of the bones of recent species showed that they were often very similar in form and overlapped in size. Therefore, a detailed examination of recent skeletons was undertaken to identify specific differences useful for the identification of the fossil material. This paper reports those results and the identifications of 'big penguins' from Marfells Beach, Lake Grassmere, Marlborough.

METHODS

I assumed that those species recorded as rare vagrants in New Zealand would be unlikely in the fossil or midden record, therefore, only *Megadyptes antipodes*, *Eudyptes pachyrhynchus*, *E. sclateri*, and *E. robustus* were studied. Recent skeletal specimens were examined at the Canterbury Museum, Museum of New Zealand Te Papa Tongarewa, and Otago Museum. Species identity of these recent specimens was verified by checking the cranial morphology, as each species was very distinct in this regard. In some cases, mainly beach specimens, the stated identifications were found to be incorrect. Specimens are listed with the identifications I accepted.

All the *E. robustus* recent skeletal material examined came from The Snares, and is assumed to be correctly identified, but it is acknowledged that other *Eudyptes* species are rare visitors to that group. Most of the *E. pachyrhynchus* skeletons were from storm cast birds around the New Zealand mainland - there are only two from nesting grounds - so I have necessarily accepted their identifications as correct after excluding the possibility of them being *E. sclateri* and *M. antipodes* using the characters described below.

Bones of the rare visitors of other genera are unlikely to be confused with those of the common visitor species or resident species as the *Aptenodytes* species are much bigger. The *Pygoscelis* species have a markedly different cranial morphology to that of *Eudyptes* and *Megadyptes*, with a wide rim bordering the orbit lateral of the supraorbital depressions, and while the femur (one of the most commonly found fossil elements) have the form of *Eudyptes* (see below), their bones are in the size range of *E. sclateri*. It is possible the bones of *Eudyptes chrysocome filholi*, which are on

average smaller penguins than *E. pachyrhynchus*, would go undetected, but their presence would not impair the detection of *Megadyptes*.

Measurements of the recent specimens were made with dial callipers to 0.01 mm and rounded to 0.1 mm. Summary statistics were prepared (Table 1) and the significance of the difference in the means assessed with *t*-tests (Table 2).

As the principal bones found in fossil and midden deposits are femora, tibiotarsi, tarsometatarsi and coracoids, specific differences were sought in mainly these elements.

ABBREVIATIONS AND DEFINITIONS

New Zealand institutions: MNZ, Museum of New Zealand Te Papa Tongarewa, Wellington (formerly National Museum of New Zealand); CM, Canterbury Museum, Christchurch; OM, Otago Museum, Dunedin. When listing specimens only the first number in a series from an institution is prefixed with letters denoting the institution and the collection, e.g. CM Av. Succeeding numbers in a series separated by commas can be assumed to have the same prefix.

In the specimen list M = male, F = female, ? = unknown sex. When listing material, bones are sometimes identified as left (L) or right (R) elements. If L or R is prefixed by 'p' or 'd', this means 'proximal' or 'distal' part of the element. For example, pR femur means proximal right femur.

MNI (minimum number of individuals) was determined for each taxon at each site from the most frequent skeletal element (maximum of left or right side only) in the sample.

NOMENCLATURE

I follow the nomenclature including higher taxonomy given in the Checklist of the Birds of New Zealand (Turbott 1990). Anatomical nomenclature follows that advocated by Baumel *et al.* (1993), but after the first reference simple English translations are used.

SPECIMENS EXAMINED

Species are listed by their institution and catalogue number and their sex (M, F, ?) is indicated.

Eudyptes sclateri: OMAv1909 M, Av1331 F; MNZ 1441 ?, 668-S ?, 669-S ?, 670-S ?, 672 ?, 11217 M, 23160 M, 23578 ?, 24704 ?; CM Av9748 ?, Av9749 F, Av10303 F, Av12361 ?, Av12407 ?, Av12692 ?, Av30245 ?, Av36600 ?, Av36768 ?.

Eudyptes pachyrhynchus: OMAv820 F, Av825 ?, Av963 M, Av964 M, Av965 F, Av966 F, Av967 F, Av1336 ?, Av4172 ?, Av4175 ?; CM Av5434 ?, Av32402 ?, Av32414 ?, Av32500 ?; MNZ 9126 F, 11230 ?, 13308 ?, 13592 ?, 17176 ?, 19309 ?, 22934 ?, 24426 M, 24427 M, 24428 F, 24429 ?, 24513 ?, 24514 M, 24546 M, 24549 ?.

Eudyptes robustus: OMAv1178 ?; CM Av23567 ?, Av25351 ?, Av25353 ?, Av36113 ?,Av36663 ?; MNZ 1270 ?, 1271 ?, 1272 ?, 23672 F, 23723 ?, 23724 ?, 23735 ?, 23736 M, 23737 ?, 23741 ?, 23746 ?, 23754 ?, 23755 ?, 23758 ?, 23673 F.

Megadyptes antipodes: OM Av948 M, Av949 ?, Av950 ?, Av951 F, Av983 M, Av984 M, Av987 M, Av988. M, Av990 M, Av994 ?, Av997 M, Av1004 F, Av1012 F, Av1180 ?; MNZ 631 ?, 715 ?, 930 ?, 11242 ?, 13593 ?, 15176 ?, 18335 ?, 19308 ?.

RESULTS

OSTEOLOGICAL COMPARISONS OF RECENT SPECIMENS

Figure 1 shows crania of *Megadyptes antipodes*, *Eudyptes pachyrhynchus*, *E. sclateri*, and *E. robustus* in dorsal and in lateral views. They differ markedly, particularly in bill morphology, as follows: *Megadyptes* has a slender premaxilla that has little depth and little lateral expansion of the rostrum maxillare; *E. pachyrhynchus* has the shortest skull with a relatively short bill in which the rostrum maxillare is markedly wider than the os nasale, and the premaxilla is relatively deep; *E. sclateri* has the longest skull in the genus, and is characterised by the lack of lateral expansion of the rostrum maxillare which is the same width as the os nasale, and whose depth is less than in *E. pachyrhynchus*; *E. robustus* is like *E.*

Table 1. Summary statistics of measurements (mm) for large resident and common visitor penguin species in New Zealand. FemL is femur length, FemS is femur lateromedial shaft width, TibL is tibiotarsus greatest length, TmtL is tarsometatarsus length, TmtP is tarsometatarsus proximal width, TmtD is distal width of the tarsometatarsus, HumL is the humerus length.

Eudyptes robustus

	FemL	FemS	TibL	TmtL	TmtP	TmtD	HumL
Mean	69.92	6.93	113.07	29.36	14.73	19.35	64.85
Std Dev.	2.12	0.33	3.63	1.10	0.67	1.00	2.15
Minimum	66.43	6.3	107.1	27.35	13.48	16.7	61.42
Maximum	74.47	7.66	120.48	31.3	15.7	20.8	68.06
Count	21	21	18	18	18	18	18
CV	3.04	4.71	3.21	3.76	4.58	5.18	3.31

E. pachyrhynchus

	FemL	FemS	TibL	TmtL	TmtP	TmtD	HumL
Mean	71.86	7.23	114.09	30.02	15.20	19.75	66.10
Std Dev.	2.62	0.54	3.15	1.23	0.60	0.77	2.13
Minimum	65.6	6.5	107.27	27.28	13.62	18.1	61.33
Maximum	75.91	8.9	119.8	32.5	16.2	21.1	69.9
Count	28	28	28	28	28	28	29
CV	3.65	7.41	2.76	4.10	3.97	3.91	3.22

E. sclateri

	FemL	FemS	TibL	TmtL	TmtP	TmtD	HumL
Mean	78.80	8.12	126.21	31.60	17.03	22.00	74.07
Std Dev.	2.07	0.49	2.08	1.05	0.70	1.52	1.72
Minimum	76.1	7.35	123.5	29.8	16	19.8	71.7
Maximum	82.25	9.2	130.8	33.7	18.9	26.88	77.9
Count	20	20	19	19	19	19	19
CV	2.62	6.09	1.65	3.32	4.09	6.91	2.33

Megadyptes antipodes

	FemL	FemS	TibL	TmtL	TmtP	TmtD	HumL
Mean	84.61	8.79	130.36	35.03	18.37	22.94	77.27
Std Dev.	1.57	0.28	2.77	0.84	0.59	0.61	1.07
Minimum	81.4	8.3	125.44	33.15	17.3	21.96	75.8
Maximum	87.6	9.22	135.2	36.5	19.3	24.3	79.8
Count	22	22	21	20	20	20	20
CV	1.86	3.17	2.12	2.39	3.22	2.67	1.39

pachyrhynchus in having a markedly expanded rostrum maxillare, but has a deep stout premaxilla. Figure 2 shows the mandibles in lateral view. They differ principally in relative height as follows: *Megadyptes* has a very shallow mandible; *E. sclateri* has

Table 2. Example *t*-test results for comparison of the means for femur length (upper right quadrants) and humerus length (lower left quadrants) for *Eudyptes* species and *Megadyptes antipodes*. Results given as *t*-statistic, df, probability level (P>0.05 = NS, P< 0.05 = *, P<0.01 = **, P<0.001 =***).

	E. pachyrhynchus	*E. robustus*	*E. sclateri*	*M. antipodes*
E. pachyrhynchus		2.852, 47, **	-10.257, 45, ***	-21.333, 45, ***
E. robustus	1.957, 36, NS		-13.574, 39, ***	-25.688, 37. ***
E. sclateri	-14.240, 44, ***	-14.360, 33, ***		-10.186, 35, ***
M. antipodes	-24.109, 44, ***	-22.165, 24, ***	-6.912, 30, ***	

the deepest mandibles and in which depth decreases continuously towards the tip; mandibles of both *E. robustus* and *E. pachyrhynchus* are alike in being shallower than those of *E. sclateri* but markedly deeper than those of *Megadyptes*, and which have half of their anterior portion with parallel dorsal and ventral borders. These features do not distinguish skulls of *E. robustus* from those of *E. pachyrhynchus* but together they differ markedly from *Megadyptes* and *E. sclateri*.

Size of each species was assessed by the measurements given as summary statistics in Table 1. *E. pachyrhynchus* average slightly larger than *E. robustus* in measurements of the femur, tibiotarsus, tarsometatarsus and humerus, but the differences are weakly or not significant (Table 2). *E. sclateri* is significantly bigger than *E. pachyrhynchus* and *E. robustus* in all measurements with little or no overlap in range, as seen for example in Figure 3. Bones of *Megadyptes* are significantly longer than those of *E. sclateri*.

DISTINGUISHING FEATURES OF POST-CRANIAL ELEMENTS

Femora Femora of all *Eudyptes* species share similar morphology. No consistent differences other than larger size of *E. sclateri* are found. However, in addition to being larger, femora of *Megadyptes* have three features that distinguish them from those of *Eudyptes*: 1, in ventral view there is a distinct groove passing laterally from under the *trochanter femoris* (Fig. 4) which is absent or much reduced in *Eudyptes*; 2, in lateral view there is a marked constriction of the shaft immediately anterior to the *epicondylus lateralis* creating the effect of a groove passing anterodorsally over the bone. Femora of *Eudyptes* have no such groove, which is very obvious in fossil material. 3, on the lateral surface of the *trochanter femoris* there is a centrally placed depression proximally which is much deeper and distinct in *Megadyptes* than it is in *Eudyptes*.

Tibiotarsi Tibiotarsi (Fig. 5) of *Eudyptes* have no differences unrelated to size and considerable intraspecific variation. Tibiotarsi of *Megadyptes* apart from being usually longer than even those of *E. sclateri*, have more expanded distal ends caused in part by a narrower least shaft width, their tendinal bridges are relatively shorter, the caudal part of the lateral condyle is developed more proximally than the medial condyle (equal in *Eudyptes*), and the distal part of the fibular crest is rotated somewhat caudally so that the anterior shaft surface at this point is rounded (flatter in *Eudyptes*).

Tarsometatarsi Tarsometatarsi (Fig. 6) of *Eudyptes* species have few differences unrelated to size. Those of *Megadyptes* are longer but also differ from those of *Eudyptes* as follows: 1, the *foramina vascularia proximalia* are larger; 2, in caudal view the *trochlea metatarsi II* has sub-parallel lateral and medial margins (in *Eudyptes* the lateral margin of this trochlea is much shorter than the medial margin so that the trochlea as a whole tends to be pointed); 3, the *crista lateralis hypotarsi* slopes distally to the shaft (ends abruptly in a diagonal ridge in *Eudyptes* that overhangs the lateral proximal vascular foramen); 4, the *tuberositas m. tib. cranialis* is round and directed craniolaterally in *Megadyptes* but larger, more oval in shape, and directed either anteriorly or laterally in *Eudyptes* species.

Coracoids Coracoids (Fig. 7) of *Eudyptes* are all of similar form and differ from those of *Megadyptes* as follows: 1, the

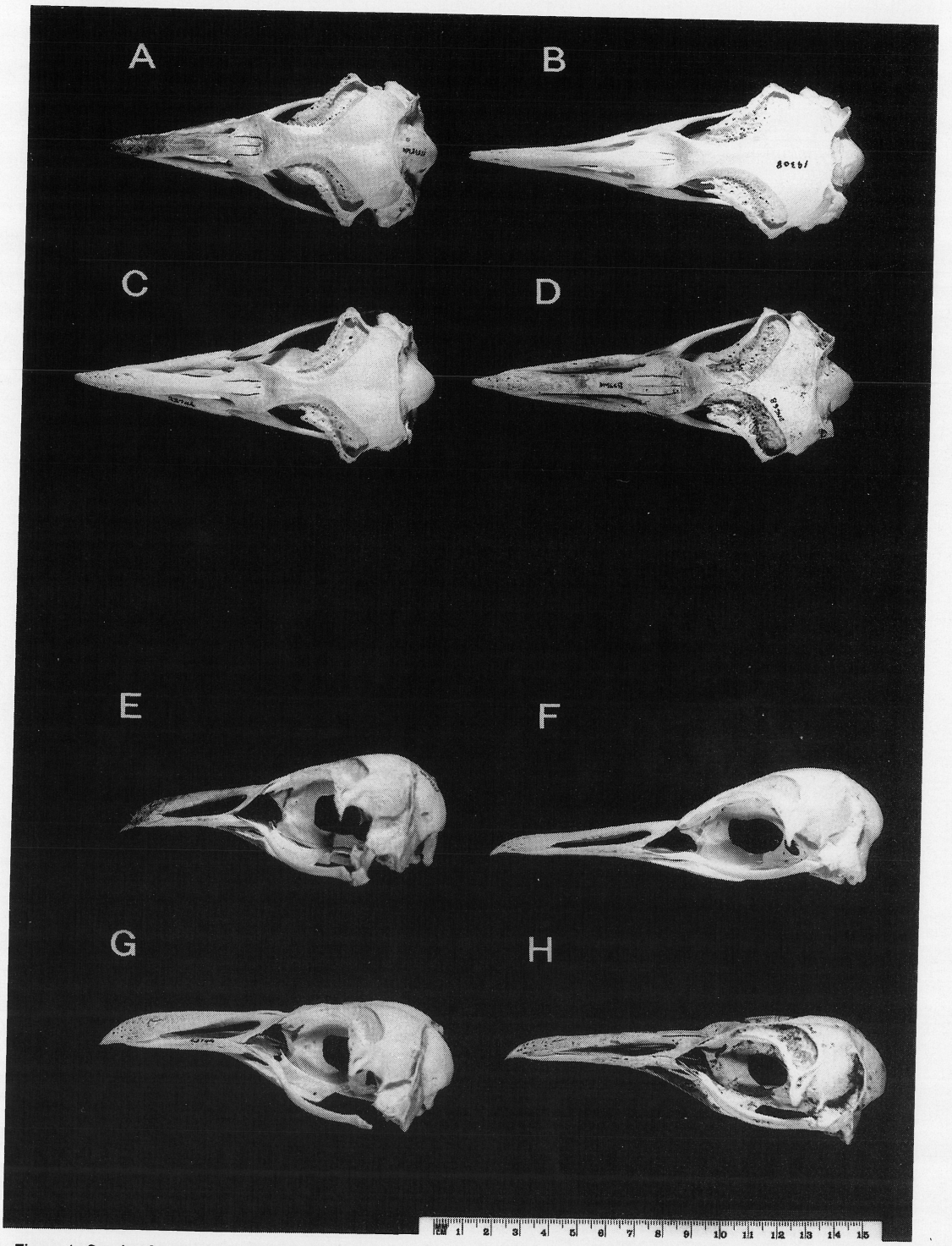

Figure 1. Crania of penguins in dorsal view (A-D) and lateral view (E-H). A,E *Eudyptes pachyrhynchus* MNZ 24513; C,G *E. robustus* MNZ 23746; B,F *Megadyptes antipodes* MNZ 19308; D,H *E. sclateri* MNZ 668.

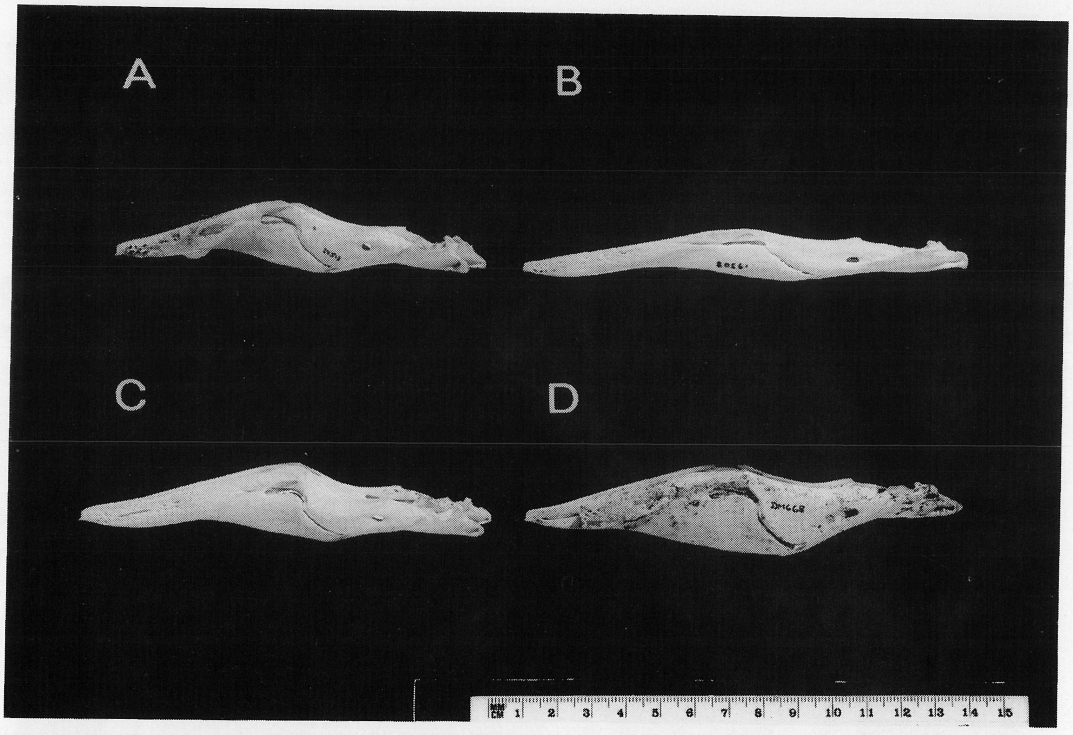

Figure 2. Mandibles of penguins in lateral view. A, *Eudyptes pachyrhynchus* MNZ 24513; B, *Megadyptes antipodes* MNZ 19308; C, *E. robustus* MNZ 23746; D, *E. sclateri* MNZ 668.

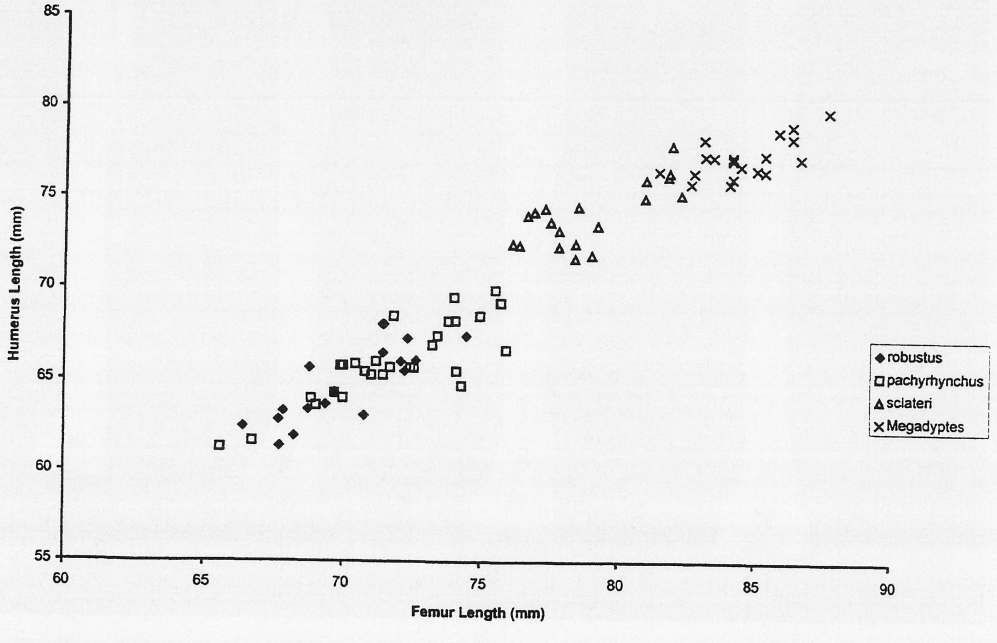

Figure 3. Graph plotting femur length against humerus length for various penguin species illustrating similar proportions of these elements but differing size of the species.

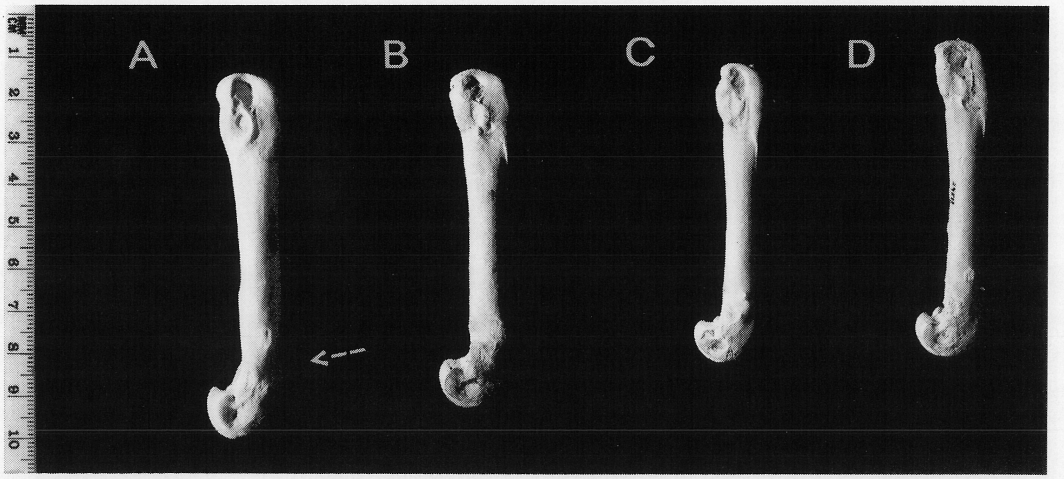

Figure 4. Femora of penguin species in lateral view. A, *Megadyptes antipodes* MNZ 19308; B, *E. sclateri* MNZ 668; C, *E. robustus* MNZ 23746; D, *Eudyptes pachyrhynchus* MNZ 24513. The arrow points to the marked constriction of the distal lateral part of *Megadyptes* femora.

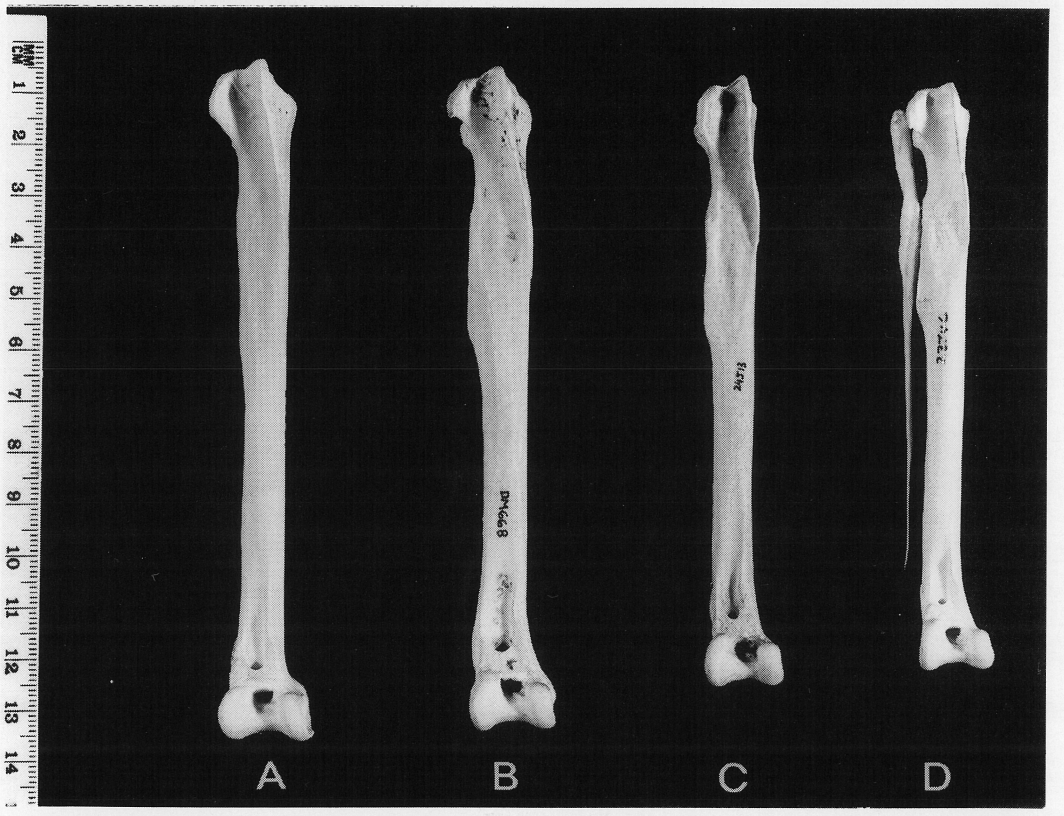

Figure 5. Tibiotarsi of penguin species in anterior view. A, *Megadyptes antipodes* MNZ 19308; B, *E. sclateri* MNZ 668; C, *Eudyptes pachyrhynchus* MNZ 24513; D, *E. robustus* MNZ 23746.

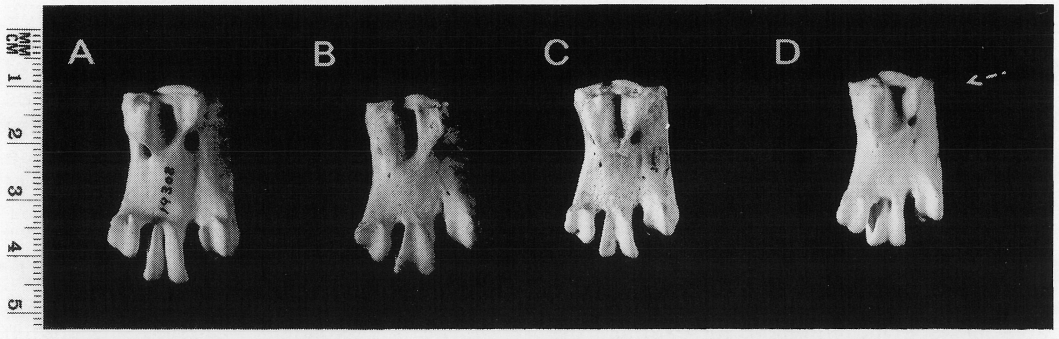

Figure 6. Tarsometatarsi of penguin species in posterior view. A, *Megadyptes antipodes* MNZ 19308; B, *E. sclateri* MNZ 668; C, *Eudyptes pachyrhynchus* MNZ 24513; D, *E. robustus* MNZ 23746. Arrow points to the lateral hypotarsal ridge that ends abruptly in an angular ridge above the foramen in *Eudyptes* spp.

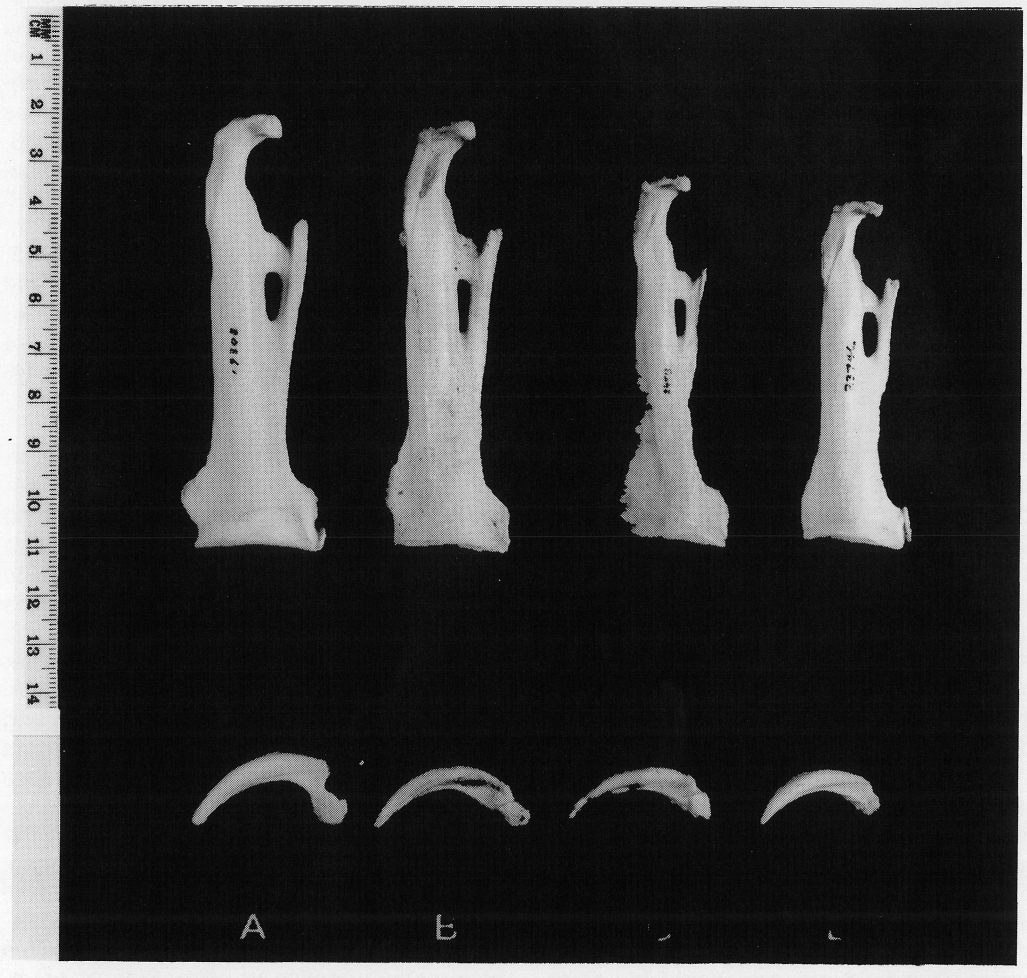

Figure 7. Coracoids of penguin species showing ventral view (top) and sternal articulation (bottom). A, *Megadyptes antipodes* MNZ 19308; B, *E. sclateri* MNZ 668; C, *Eudyptes pachyrhynchus* MNZ 24513; D, *E. robustus* MNZ 23746. Arrow points to the highly characteristic constriction in *Megadyptes*.

acrocoracoid in *Eudyptes* is directed more ventrally and tapers toward the tip, whereas, in *Megadyptes* it is oriented more medially and has parallel sides (in ventral view); 2, the sternal end viewed in the articular plane has a short 'neck' between the *facies artic. sternalis* and the *angulus medialis* in *Eudyptes* compared to a longer and constricted neck in *Megadyptes*.

Humeri Humeri (Fig. 8) of *Eudyptes* species are similar in shape with considerable intraspecific variation, for example the proximal edge of the *sulcus lig. transversus* after it passes from the cranial surface ventrally to lie proximal to the bicipital fossa (*fossa pneumotricipitalis*) may either converge on the fossa or pass above it separated by a wide groove. However, a useful difference in humeri morphology is the form of the bicipital fossa in ventral view: the proximal margin in *Eudyptes* forms a symmetric ∩ shape whereas in those of *Megadyptes* this is skewed towards the caudal surface.

IDENTIFICATION OF FOSSILS

Using the characters described above, bones from either sand dunes or midden origin from Marfells Beach, Lake Grassmere, Marlborough in the Canterbury Museum previously labelled as *Eudyptes sclateri*, *E. pachyrhynchus* and *Megadyptes antipodes* were reidentified (Appendix 1). Bones from this site in the MNZ, that had been collected in 1948 and 1951 by E. W. Dawson, are also listed. Study of the most diagnostic elements such as the humerus and femur made it readily apparent that only two taxa were present: the larger has all the characters of *Megadyptes antipodes* and the smaller is a small *Eudyptes* species that is referred on geographic parsimony grounds to *E. pachyrhynchus* rather than to *E. robustus*. The recognition of two size classes in the fossils allows referral of morphologically undiagnostic elements (ulna, radius, carpometacarpus, some worn specimens) to one of these taxa by their size.

For *E. pachyrhynchus* 67 bones representing 9 individuals are identified, compared to 58 bones of 8 individuals for *Megadyptes*. Another 6 bones of appropriate size, but lacking diagnostic characters are probably *Megadyptes*. No bones of *E. sclateri* are in the sample. Measurements of these fossils (Table 3) show that the bones referred to *Megadyptes* are larger than those referred to *Eudyptes*, but on average are smaller ($P<0.01$) than recent specimens of *M. antipodes* (Table 4).

DISCUSSION

The Fiordland Crested Penguin *Eudyptes pachyrhynchus* is verified as part of the Marfells Beach fossil fauna. However, occurring in approximately equal numbers are larger bones that were previously identified as Erect-crested Penguin *E. sclateri*. All diagnostic specimens of this large penguin are Yellow-eyed Penguin *Megadyptes antipodes*. At least two of the *Megadyptes* bones from Marfells Beach (CM Av 14068, 14317) have the equivalent osteological maturity of *E. robustus* specimens collected after dying on their first swim in the ocean. In these birds (CM Av23567, 25351, 25353, 36663) the bones had reached full size and the leg bone symphyses are fused but retained surface porosity. The fossil bones of the fledglings are, therefore, likely to be derived from breeding colonies in the immediate vicinity.

All the bones examined in the Canterbury Museum, that had been previously referred to *E. sclateri*, are *Megadyptes*: no fossil or midden records of this species are sustainable (T. H. Worthy, unpubl. data). In addition, I have found bones of *Megadyptes* in dunes at Delaware Bay, Whangamoa River mouth and a site a few hundred metres east of Mussel Point, Marfells Beach. Therefore, as Darby and Seddon (1990) and Moore (1992) have suggested, these data indicate that the species was much more widely distributed in the past.

The smaller size of the bones from the northern South Island compared to recent specimens from Otago deserves some comment. The extant populations of Yellow-eyed Penguin have little or no discernible geographic variation in either size or plumage characteristics (Darby & Seddon 1990), but are comprised of larger birds than the

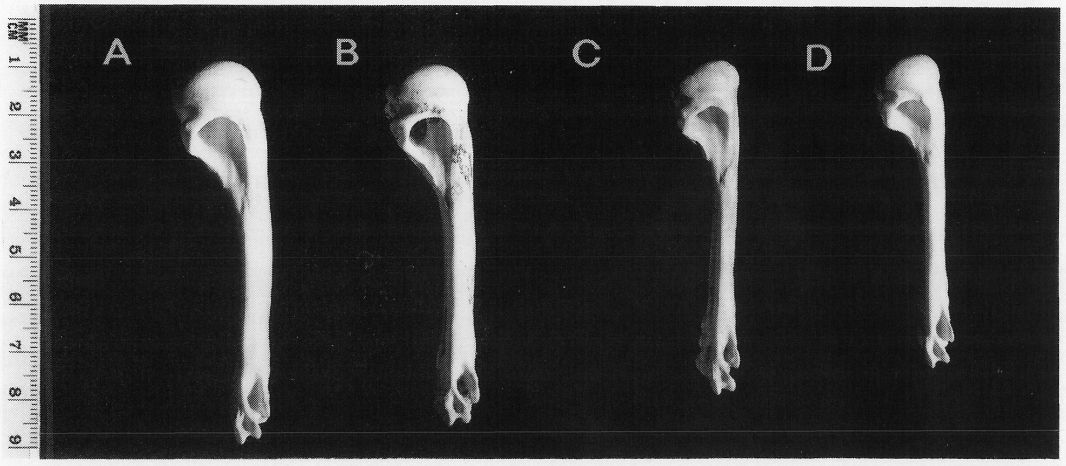

Figure 8. Humeri of penguin species in medial view. A, *Megadyptes antipodes* MNZ 19308; B, *E. sclateri* MNZ 668; C, *Eudyptes pachyrhynchus* MNZ 24513; D, *E. robustus* MNZ 23746.

fossils from the northern South Island. This size difference rules out the possibility that these northern fossils are derived from southern birds moving north after breeding as they are known to do (Darby & Seddon 1990). If humans had extirpated the northern populations then a similar fate may have befallen the southern populations, raising the possibility that the extant Otago and Southland populations are derived from recent colonisations from Campbell Island. However, the populations in the two areas have discrete genetic differences (Darby & Seddon 1990), which are unlikely to have evolved in the few hundred years available, so I conclude that there were discrete size differences between the northern and southern populations on the South Island.

Populations of Blue Penguins *Eudyptula minor* show significant geographic size variation. This variation is not a simple clinal trend as described by Meredith and Sin (1988). The most southern birds and west coast birds on the South Island, unstudied by Meredith and Sin (1988), are smaller than central eastern South Island birds, but thereafter in a northwards direction the mean size of birds declines significantly (Kinsky & Falla 1976; Meredith & Sin 1988). The scale of this size decrease is 4.5, 6.2, 13.7% (flipper length, head length, tarsal diagonal length measurements) between Onawe Peninsula (30 km southeast of Christchurch) and Cook Strait (derived from data in Meredith & Sin 1988). The size difference between Marfells Beach fossils and extant southern birds range from 8.5 - 9.5% (Table 4) and is thus comparable to variation in extant Blue Penguins.

The bones of large penguins from Marfells Beach and other northern South Island sites that have the discrete characters of *Megadyptes* are significantly smaller than extant counterparts, but as such variation is seen in Blue Penguins, it is acceptable to refer the fossil *Megadyptes* to *M. antipodes*.

The recent observations of population decline in this species along the Otago - Southland coasts (Darby & Seddon 1990) are, therefore, only the final chapter in a much longer history of decline. The loss of the northern populations in particular has probably resulted in a marked loss of genetic diversity in the species. The fact that *Megadyptes antipodes* is found in the middens at Marfells Beach, and many other sites around the country indicate Maori ate it. Their present vulnerability to mammalian predation, specific breeding habitat requirements and intolerance of disturbance (Darby & Seddon 1990), indicate their vulnerability to human impacts of predation and land clearance, and so it is likely that the species' decline is wholly due to the impact of humans.

The decline of the Yellow-eyed Penguin

Table 3. Summary statistics for length measurements (mm) of fossil penguin bones from Marfells Beach listed in Appendix 1. tmt is tarsometatarsus, cmc is carpometacarpus. Length data for specimens of *Megadyptes* from dunes at Delaware Bay and south of Mussel Point, Marlborough are given to show they are of similar size to the Marfells Beach specimens.

Eudyptes pachyrhynchus

	femur	tibiotarsus	tmt	humerus	ulna	radius	coracoid
Mean	73.39	114.73	29.98	66.67	48.55	46.65	77.85
Std Dev.	3.18	3.56	1.47	1.76	1.20	2.47	2.25
Minimum	68.7	108.9	26.8	65	47.7	44.9	74.5
Maximum	79.4	118.7	31.3	69.0	49.4	48.4	80.1
Count	9	7	9	7	2	2	5
CV	4.34	3.10	4.92	2.64	2.48	5.31	2.89

Megadyptes antipodes

	femur	tibiotarsus	tarsus	humerus	ulna	radius	cmc	coracoid
Mean	76.75	119.24	31.72	70.53	55.90	52.48	41.42	81.07
Std Dev.	1.94	3.98	1.41	3.22	1.73	2.05	1.07	2.52
Minimum	74.4	115.0	28.7	62.2	53.9	50.4	39.8	77.5
Maximum	80.1	125.0	33.9	74.4	56.9	55.2	42.6	84.2
Count	6	5	14	13	3	4	5	7
CV	2.52	3.34	4.44	4.56	3.10	3.90	2.59	3.11
Sth Mussel Point	72.3, 72.8, 77.6		33.5					
Delaware Bay	74.0		32.1		54.5, 52.2			80.0

Table 4. *t*-tests of the significance in the difference of the means (mm), assuming unequal variances, for lengths of selected long bones between Marfells Beach and recent *Megadyptes* specimens.

	Femur		Tibiotarsus		Tarsometatarsus		Humerus	
	Marfells	Recent	Marfells	Recent	Marfells	Recent	Marfells	Recent
Mean	76.75	84.61	119.24	130.36	31.72	35.03	70.53	77.27
Variance	3.755	2.473	15.863	7.669	1.983	0.699	10.348	1.155
Count	6	22	5	21	14	20	13	20
df	7		5		19		14	
t Stat	-9.153		-5.912		-7.878		-7.294	
P(T<=t) two-tail	3.82E-05		0.001973		2.1E-07		3.95E-06	

is, therefore, very similar to that of the King Shag *Leucocarbo carunculatus* which Worthy (1996) showed was widespread in New Zealand in the latest Holocene. This evidence shows that coastal marine birds as well as terrestrial species were extirpated from various regions of New Zealand by human impact.

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Appendix 1. Specimen lists of large penguins from Marfells Beach, Lake Grassmere, in the Canterbury Museum and the Museum of New Zealand. They are arranged firstly by species, and secondly by whether or not the specimen was found and checked. Abbreviations are: fem is femur, tt is tibiotarsus, tmt is tarsometatarsus, cor is coracoid, hum is humerus, rad is radius, cmc is carpometacarpus, pmx is premaxilla, vert is vertebra, innom is innominate or iliac plate, acet is acetabular region of pelvis, phal is phalange.

Eudyptes pachyrhynchus
Checked specimens: CM Av10945, L tmt; 10976, pmx; 11169, R fem; 11170, dR tt; 11568, R tt; 11992, L fem; 11993, L tt; 12085, R cor; 12122, L ulna; 12308, L tmt; 12537, anterior sternum; 12538, 2 vert, R fem, R tt , R tmt, pmx; 12861, L tt; 14632, L rad; 14633, R rad; 14678, L ulna; 14726, L fem; 14803, L tmt; 16445, R cor; 17871, dL tt, R ulna, L fem; 33704, dL fem; 14214a-c, R tmt, L cor, pL hum; 14879 a b, 2L tmt; 15179a, R fem; 9653a, L tmt, L hum.
MNZ unreg (EWD colln 1951) - 2L1R fem, 2L1R cor, LR hum, 5L2R1pL1dL tt, LR tmt;
MNZ unreg (EWD colln 1948) - 2L fem, 2L1R cor, 2L2R hum, R tt, R tmt, syn.

Unlocated / unchecked specimens: CM Av 12462, L rad L ulna; 12998, R cmc; 16315, 1R cor; 16820, 1pL tt, pt L innom; 17386, 1L fem, 1dL tt, 1 phal; 31010, 1R ulna;

Eudyptes sclateri
Unchecked / unlocated specimen: CM Av10615, 1 tt.

Megadyptes antipodes
Checked specimens: CM Av 9654, LR tmt, R hum; 10942, L tt; 10943, R cor; 10944, L tmt; 11083, L tmt; 11540, L hum; 11551, L hum; 11718, L tmt; 11987, R hum; 11989, R fem; 11995, R fem; 12082, R hum; 12083, R hum; 12121, R cmc; 12123, dR L cor; 12265, L cor; 12535, R fem; 12987, L tt; 12988, L ulna; 13269, L fem; 13653, R cor; 13973, L tmt; 14068, R tmt; 14316, R tt; 31039, dL fem; 33723, 1R cor; 36465, L ulna; 11589a, L tt; 14679 b, R ulna; 14879 c, L ulna; 15179b, R tmt; 9653b, R ulna, R rad.
MNZ unreg (EWD colln 1951) - RL fem, RL cor, L tt, 3L3R tmt, 2R1L hum;
MNZ unreg (EWD colln 1948) - syn, sL fem, L cor, 3L2R hum.

Unchecked / unlocated specimens:
CM Av10170, L rad; 14317, R tt.

Probable *Megadyptes antipodes*
CM Av 11550, L hum; 11988, L cmc; 11990, L rad; 12999, R cmc; 16344, L hum.

Unidentifiable 'Big penguin'
CM Av 11543, R acet; 11569, L rad; 11663, sacrum; 11677, pt furcula; 11715, sacrum; 11991, L pt fur; 12084, pL hum; 12460, sacrum; 12461, pt sacrum juv; 12536, 1 vert; 12989, R acet; 14067, axis vert; 14436, vert; 14894, axis vert; 26524, R cmc, dL tt; 26566, 5 vert; 33657, 2 thoracic vert; 33785, 5 vert; 11589b, juv R tt; 11716a, dR scap; 14214d, M3.1; 14679 a c d , L acet, 2 vert; 15179 c-g, 3 vert, 2 phal; 33798a, 2 phal.

MNZ unreg (EWD colln 1951) - R scap, syn, pL cor, pt stern, pt cran, LR M2.1, R cmc;
MNZ unreg (EWD colln 1948) - 2R1L cmc, 2R1L ulnae, 2L1R rad, LR pt furcula, dR tt.