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What was on the Menu? Avian Extinction in New Zealand

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ABSTRACT

The North and South Islands of New Zealand had 129 taxa of resident birds in the Late Holocene. Thirty-three of these became extinct during the prehistoric period (about 900 to 200 BP) and six more since. At least another 30 species are rare on the main islands or restricted to inshore islands. All extinct taxa are present and usually common in Late Holocene fossil deposits.

Data are compiled from 177 archaeological sites containing avifauna; the number of sites in which each taxon is present is tabulated. Only 28% of sites are in the North Island. Archaeological techniques to date have sampled small bird species poorly; 56 (43%) resident taxa have been recovered from fewer than six sites. Few sites have been investigated with a prime purpose of obtaining a representative sample of the associated fauna. This is reflected in the fact that moa, whose remains were most obvious in sites, were recovered from 103 sites (58%), far more than any other taxon. Despite these biases, the data indicate that predation by humans was a significant factor in the majority of Late Holocene avian extinctions in New Zealand. Thirty-four extinct species are known from Māori sites. The five extinct species as yet unknown from the archaeological record are either recently described species whose bones are likely to have been wrongly identified, or small, non-harvested species whose extinction is probably a result of predation by the Pacific Rat *Rattus exulans*.

The frequency of extinct species in archaeological sites as a whole does not indicate which species were preferentially targeted. Analysis of synchronous natural and archaeological faunas from Marfell's Beach suggests that most species there were taken in the proportions in which they were found in the natural environment. This suggests that extinction was not the result of massive over-hunting of the extinct taxa alone. Rather, in addition to habitat destruction, most extinctions can be related to the inability of 'K-selected' species to withstand the 'new' predation pressure humans introduced. Such extinctions probably took place over several centuries. Although the impact of rats on the smaller vertebrates cannot be over-estimated, it is concluded that harvesting was instrumental in the loss of most now extinct birds.

Keywords: NEW ZEALAND, ARCHAEOLOGICAL AVIFAUNA, EXTINCT SPECIES, SPECIES FREQUENCY, EXTINCTION CAUSE.

INTRODUCTION

Moa (Aves: Dinornithiformes) were first revealed to the scientific world by Sir Richard Owen in November 1839 (Owen 1839) and within a few years he had described several species (Owen 1844). The contemporaneity of man and moa was soon established, and shortly thereafter Gideon Mantell attributed the extinction of the moa to predation by man

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(Mantell 1848a, 1848b, 1848c, 1851). Therefore, essentially from the onset of studies of New Zealand's extinct birds, contemporaneity with man was known, and the causal effect of humans in their extinction assumed. Throughout last century, the causal effect of humans was generally accepted (e.g., Haast 1879: 430). The main debate was not so much whether humans hunted the moa, but whether the moa hunters were different from the Maori.

Over the next century, the evidence for human hunting of moa and other extinct birds accumulated. Some sites were vast: the Waitaki River Mouth site was 51 ha when first surveyed in 1951, but erosion of the coastline had probably already reduced it from about 120 ha. Anderson (1989a) estimated that the remains of between 5000 and 8000 birds were present in this site alone. Archaeological sites with moa bones were recorded throughout New Zealand. In 1969, Ron Scarlett addressed the New Zealand Archaeological conference in Dunedin about the bird species recorded from archaeological sites and concluded that "the Polynesian population of these islands found almost every bird and animal edible" (Scarlett 1979). At least 16 extinct species other than moa were noted from few, but widespread, sites around New Zealand.

In the 30 years since Scarlett presented his paper on this topic, the only comprehensive examination of the role of man in extinctions in New Zealand was by Cassels (1984). He showed that all Holocene extinctions in New Zealand took place after the arrival of humans and were therefore linked to human presence, but he provided no quantitative analysis. He recorded 13 moa, 16 other endemic taxa and 5 taxa very close to Australian forms that became extinct. He also listed three taxa he considered of doubtful validity. Many more data are now available, and there have been considerable changes to the understanding of New Zealand's extinct fauna in species composition and especially in nomenclature².

In this paper, the impact of human predation on the whole avifauna is examined. All available published and some unpublished faunas from as many archaeological sites as possible are analysed. The frequency of each species (extinct and extant) in the sum of all sites is determined for each of the North and South Islands, thus providing a very basic comparison. This allows certain fundamental questions to be addressed. Are extinct species over-represented in the archaeological record compared to extant species? If so, the probability that specific hunting of extinct taxa led to their extinction should be examined.

² The accepted number of moa species is now 11, not 13 (Millener 1982; Worthy 1988a, 1988b, 1989, 1994). The New Zealand black swan is indistinguishable from *Cygnus atratus* (Worthy 1998a) and is considered an indigenous population that was exterminated in prehistoric times, then re-established following reintroduction. *Pelecanus* bones from New Zealand are indistinguishable from the Australian *P. conspicillatus* and are considered to represent stragglers from Australia. They are listed here as they have been considered a distinct New Zealand species in the past.

Cassels (1984) listed *Porphyrio porphyrio*, *Halcyon sancta*, *Gallirallus philippensis* and *Ninox novaeseelandiae* as species that are rare in archaeological sites and that lack fossil records. Fossils of *H. sancta* have been found in coastal cave deposits in the eastern South Island, but similar deposits where this species (which prefers coastal habitats among natural ecosystems) could be found are unknown elsewhere (unpublished data). *Gallirallus philippensis* is fossil in Otira Glacial deposits in Honeycomb Hill Cave, South Island (Worthy and Mildenhall 1989) and Holocene deposits at Lake Poukawa (Horn 1983). *Ninox novaeseelandiae* is widespread in fossil deposits, and is in equal frequency to *Sceloglaux albifacies* (Worthy and Holdaway 1993, 1994, 1996). Of the four species, only *P. porphyrio* has been verified as absent from the fossil record in prehuman deposits, and so is accepted as a recent colonist (Worthy and Holdaway 1996).

What else might have contributed to extinction? Answers to these questions will shed light on the extinction process.

For most sites, only presence/absence data were available. Where information on frequency was given, small sample sizes usually meant that it was not very meaningful. It was generally not possible to assess the relative frequency of a taxon in different sites or to obtain a real assessment of species diversity within individual sites. However, Marfells Beach in Marlborough is an important exception. It has a very large and diverse midden fauna and, in addition, is unique in that it is the only known site in New Zealand where an essentially contemporaneous and large natural fauna was deposited (Worthy 1998a). It was therefore the only place where meaningful-sized and contemporary archaeological and natural faunas could be compared. Elsewhere, areas with large archaeological sites and faunas, for example on the Otago and South Taranaki coasts, lack contemporary fossil faunas, and where large fossil faunas are known, for example Tokerau Beach, significant bone-bearing middens are absent. The Marfells Beach faunas allowed unique examination of the question: were any extinct species being hunted preferentially?

METHODS

INCLUSION OF SITES

Archaeological sites were included in this survey if lists of associated avifauna were found in the literature. A few sites were added after direct examination of museum catalogues or collections. Data from 177 sites are included (Appendix 1), but a major bias is that only 49 of these are in the North Island. This fact accounts for most of the perceived rarity of North Island species. Faunal assemblages from each archaeological site were treated as one, with data from all sub-units in a site amalgamated³. Site layers, or other sub-units, were not differentiated, as the question being addressed was "was a species present in a site?" and the occupation period of most sites is believed to have been short.

The literature mentions only one or two species from a number of sites, yet many more are probably present in undescribed collections. Mussel Point, Marlborough, is a case in point. Only three species are listed, yet many more are present in the undescribed material in the Canterbury Museum. Similarly, the Wairau Bar fauna is undescribed and could be expected to approach that of Marfells Beach in diversity, yet only 17 species are recorded in the literature. I have not included data from Native Island in Paterson Inlet on Stewart Island, as the fauna is derived from natural dunes 1000–3500 years old (Worthy 1998b) rather than the adjacent midden.

CRITERIA FOR ACCEPTANCE OF A SPECIES IN THE RECORD

Only where a taxon was identified to species was the record used, with the exception of cryptic species, for example big kiwi in the South Island, or *Cyanoramphus* sp. Thus,

³ Redcliffs was treated as one site, with the fauna from the Hamilton's section, the Sewer Trench and the School Section combined, as Trotter's plan of the area suggests these are subsets of one large site.

records of *Phalacrocorax* sp. or *Anas* sp. were ignored, as previous authors used these names for shags and ducks in general, and such specimens may have been from several genera. The species accepted in either the fossil or archaeological record of the North or South islands and their associated near-shore islands are tabulated in Appendix 2. This list was based upon that of Millener (1990), with additions or deletions as described by Worthy and Holdaway (1993, 1994, 1995, 1996) and Worthy (1993, 1997a, 1998c).

NOMENCLATURE

The nomenclature given in the *Checklist of the Birds of New Zealand* (Turbott 1990) was followed, with modifications at the specific level as detailed in Worthy and Holdaway (1993). I therefore list *Cnemiornis calcitrans* and *Aptornis defossor* as distinct South Island species, and *Fulica prisca* as distinct from the Chatham Island *Fulica*. *Anas chlorotis* is recognised as a species, distinct from its flightless relatives on Auckland and Campbell Islands. This follows Oliver (1955), and is supported by a study of the morphology of the Australasian teal group (Livezey 1990), and as recognised in Marchant and Higgins (1990). I do not accept that the extinct New Zealand crow is generically distinct from *Corvus*, neither do I consider that the extinct New Zealand owl nightjar is generically distinct from *Aegotheles*, and so I list the New Zealand species in these genera. I follow Trewick (1996) in recognising that the South Island takahe is a distinct species from the North Island takahe, and so takahe are referred to by their original specific names *Porphyrio hochstetteri* [A. B. Meyer 1883] and *P. mantelli* [Owen 1848] respectively. *Leucocarbo chalconotus* is treated as a subspecies of *Leucocarbo carunculatus* as they are osteologically indistinguishable (Worthy 1996). This nomenclature is shown relative to that used by Cassels (1984) in Table 1.

TABLE 1

LIST OF SPECIES KNOWN TO HAVE BECOME EXTINCT DURING THE HOLOCENE ON THE NEW ZEALAND MAINLAND AND ITS NEAR-SHORE ISLANDS

The species listed by Cassels (1984) are given to facilitate comparison. Time of extinction is indicated as either P: prehistoric or H:historic.

Cassels 1984 (extinct prehistorically)	Cassels status	Extinct Species NZ mainland (1997)	Extinct time
<i>Megalapteryx didinus</i>	NZ	<i>Megalapteryx didinus</i>	P
<i>Megalapteryx benhami</i>	NZ		
<i>Anomalopteryx didiformis</i>	NZ	<i>Anomalopteryx didiformis</i>	P
<i>Anomalopteryx oweni</i>	NZ		
<i>Pachyornis elephantopus</i>	NZ	<i>Pachyornis elephantopus</i>	P
		<i>Pachyornis australis</i>	P
<i>Pachyornis mappini</i>	NZ	<i>Pachyornis mappini</i>	P
<i>Euryapteryx geranoides</i>	NZ	<i>Euryapteryx geranoides</i>	P
<i>Euryapteryx curtus</i>	NZ	<i>Euryapteryx curtus</i>	P
<i>Emeus crassus</i>	NZ	<i>Emeus crassus</i>	P
<i>Dinornis struthoides</i>	NZ	<i>Dinornis struthoides</i>	P
<i>D. torosus</i>	NZ		
<i>D. novaezealandiae</i>	NZ	<i>D. novaezealandiae</i>	P

<i>D. giganteus</i>	NZ	<i>D. giganteus</i>	P
		<i>Puffinus spelaeus</i>	P
<i>Pelecanus conspicillatus novaezealandiae</i>	Aust	<i>Pelecanus conspicillatus</i>	
<i>Dupetor flavicollis</i>	Aust	<i>Ixobrychus novaezealandiae</i>	H
<i>Cygnus sumnerensis</i>	NZ	<i>Cygnus atratus</i>	P ¹
<i>Cnemiornis calcitrans</i>	NZ	<i>Cnemiornis calcitrans</i>	P
<i>Cnemiornis gracilis</i>	NZ	<i>Cnemiornis gracilis</i>	P
<i>Euryanas finschi</i>	NZ	<i>Euryanas finschi</i>	P
<i>Malacorhynchus scarletti</i>	NZ	<i>Malacorhynchus scarletti</i>	P
<i>Mergus australis</i>	NZ	<i>Mergus australis</i>	P
<i>Biziura lobata</i>	Aust	<i>Biziura delautouri</i>	P
<i>Oxyura australis</i>	Aust	(<i>Aythya/Malacorhynchus</i>)	
<i>Circus eylesi</i>	NZ	<i>Circus eylesi</i>	P
<i>Circus teauteensis</i>	NZ		
<i>Harpagornis moorei</i>	NZ	<i>Harpagornis moorei</i>	P
		<i>Coturnix novaezealandiae</i>	H
<i>Capellirallus karamu</i>	NZ	<i>Capellirallus karamu</i>	P
? <i>Gallirallus minor</i>	NZ	(<i>Gallirallus australis</i>) ²	
? <i>Gallirallus insignis</i>	NZ	(<i>Gallirallus australis</i>) ³	
<i>Gallinula hodgeni</i>	NZ	<i>Gallinula hodgenorum</i>	P
? <i>Gallirallus hartreei</i>	NZ	(<i>Gallinula hodgenorum</i>)	
		<i>Porphyrio hochstetteri</i>	
<i>Porphyrio mantelli</i>	NZ	<i>Porphyrio mantelli</i>	P
<i>Fulica chathamensis</i>	NZ	<i>Fulica prisca</i>	P
<i>Fulica atra</i>	Aust		
<i>Aptornis otidiformis</i>	NZ	<i>Aptornis otidiformis</i>	P
		<i>Aptornis defossor</i>	P
		<i>Sceloglaux albifacies</i>	H
<i>Megaegotheles novaezealandiae</i>	NZ	<i>Aegotheles novaezealandiae</i>	P
		<i>Xenicus longipes</i>	H
		<i>Traversia lyalli</i> ⁴	H
		<i>Pachyplectes yaldwyni</i>	P
		<i>Pachyplectes jagmi</i>	P
		<i>Dendroscansor decurvirostris</i>	P
		<i>Heterolocha acutirostris</i>	H
		<i>Turnagra capensis</i>	H
<i>Palaeocorax moriorum</i>	NZ	<i>Corvus moriorum</i>	P

1. Reintroduced historically.
2. *Gallirallus minor* has long been unofficially considered indistinguishable from *G. australis*. Holdaway and Worthy (1997) presented data showing *G. minor* to be an unsustainable taxon.
3. Worthy (1998c) has found the 'type' of *G. insignis* and relegated it to synonymy of *G. australis*.
4. Species extinct globally in historic times but extinct on the mainland during prehistory.

This use of nomenclature, therefore, necessitates many changes from the source material. The specific determinations given in the source material are, of necessity, accepted, unless I have checked them. In Appendix 1, 'THW' indicates that I have checked the material. In addition, I have examined much of the moa material, including all that listed in Barber (1994), and from Paremata, Makara, Foxton, Kaupokonui, Ohawe, and Opua (Worthy 1990:

Appendix 4). Other bones in collections have also been re-identified. For example, the goose from Pounaweia became an eagle. Thus, the listings are based on the sum of all investigations; lists for each site are available upon request.

The effect of identification errors is minimised in this study by using only presence/absence data, for so long as one bone of the species is correctly identified other errors will not affect the incidence of the species. In my experience, most errors represent shuffling within taxa. Only relatively few errors will result in the inclusion of species not present in the assemblage, and in this regard any species represented by one or few bones is suspect (see comments below, and the goose/eagle above). The following comments on specific groups are pertinent.

Penguins: The bones of penguins are notoriously difficult to identify to species. In addition to the species listed in Appendix 2, three others have been listed in archaeological faunas, all without supporting reasons. *Eudyptes robustus* was recorded from three sites in Otago (McGovern-Wilson 1986; Anderson *et al.* 1996), but bones of this species have the same size range as, and are otherwise indistinguishable from, those of *E. pachyrhynchus* (Worthy 1997b). *Eudyptes chrysocome* was listed from two South Otago sites, but as the long bones of this species are only on average smaller than *E. pachyrhynchus*, and otherwise indistinguishable, I consider it probable the bones concerned are small specimens of *E. pachyrhynchus*. *Eudyptes sclateri* was recorded from 14 South Island and 2 North Island sites. However, all such bones were identified by R.J. Scarlett, who identified as *E. sclateri* virtually all penguin bones that were bigger than those of *E. pachyrhynchus*. When I re-examined all bones so identified in the Canterbury Museum, all were found to be *Megadyptes antipodes* (Worthy 1997b). As a result I do not accept the records for these three species. At least 12 sites have *E. sclateri* and not *M. antipodes* listed from them, so at these sites the large penguin bones are tentatively referred to *Megadyptes*.

Apteryx sp.: *Apteryx australis* is listed for the North Island, but in the South Island, *A. australis* and *A. haastii* are combined as one taxon because their bones cannot be reliably distinguished.

Rails: Many of the archaeological records of *Gallirallus philippensis* are likely to be in error. Records I have checked, e.g., Shag Mouth, Marfells Beach and Hawksburn, were all found to be wrong, and were invariably *Coturnix*, so the number of sites in which *G. philippensis* occurs is almost certainly an over-estimate.

Ducks: Non-recognition of rare taxa is a problem in this group. *Mergus*, *Malacorhynchus*, and *Biziura* have rarely been considered as potentially part of the fauna and their bones have been unrecognised in the past; for example, the bone identified as *Aythya* in the Shag Mouth site (Anderson *et al.* 1996) was *Mergus*. I have, in addition, also recently identified *Mergus* bones from dunes on Native Island and Delaware Bay, and the archaeological site on Ponui Island. Bones of the smaller ducks, *Anas chlorotis*, *A. gracilis*, *A. rhynchotis*, and *Aythya novaeseelandiae*, have often been found to be incorrectly identified, e.g., in the Ototara site. Some records must be re-evaluated: for example, the record of three small duck taxa from the 'oyster lens' at the Sunde site is based on the improbable event of each being represented by elements not duplicated by the other taxa. As a generality, I suspect that when duck specimens are re-examined *A. gracilis* will be found to be over-represented and *A. chlorotis* under-represented by the totals in Appendix 2.

Waders: Bones of this group are also difficult to identify, and this is compounded by a lack of appropriate reference material in many collections. For example, reference skeletons of *Charadrius obscurus* and *Thinornis novaeseelandiae* are few, yet these are among the

most likely species to be encountered, as they were resident taxa. Numerous errors were found when checking the Marfell's Beach fauna.

Petrels: The identification of petrels and their allies is also notoriously difficult. I suggest that the identifications of all the species apparently represented in just one site are suspect pending re-examination, particularly as all are or were non-resident species. In addition, the records of *Halobaena* seem improbable and deserve re-examination.

RESULTS

A compilation of data from Turbott (1990), Millener (1990), Worthy and Holdaway (1993, 1994, 1996), and Worthy (1997a, 1998c) resulted in a list of 129 taxa that were formerly resident in the North and South Islands or their near-shore islands in the Late Quaternary. Another 22 species known from the fossil or archaeological record that are or were non-breeding visitors (vagrants) were added to this total. Appendix 2 lists these species and also whether they were found in the fossil and archaeological record. The 39 resident birds that became extinct in the late Holocene are all known as Holocene fossils.

The faunas from 177 archaeological sites (Appendix 1) were studied, and the number of sites in which a given taxon was found was tabulated for each of the North and South Islands (Appendix 2). I arbitrarily placed the species in groups that reflected progressive categories of abundance: those not in any site, 1–5 sites, 6–10 sites, 11–20 sites, 21–50 sites and >50 sites. Seventeen resident species (13.2%) were not represented in any site. Thirty-six (27.9%) were present in only 1–5 sites; 19 (14.7%) in 6–10 sites; 26 (20.2%) in 11–20 sites; 22 (17.0%) in 21–50 sites, and 9 (7.0%) in >50 sites (Fig. 1).

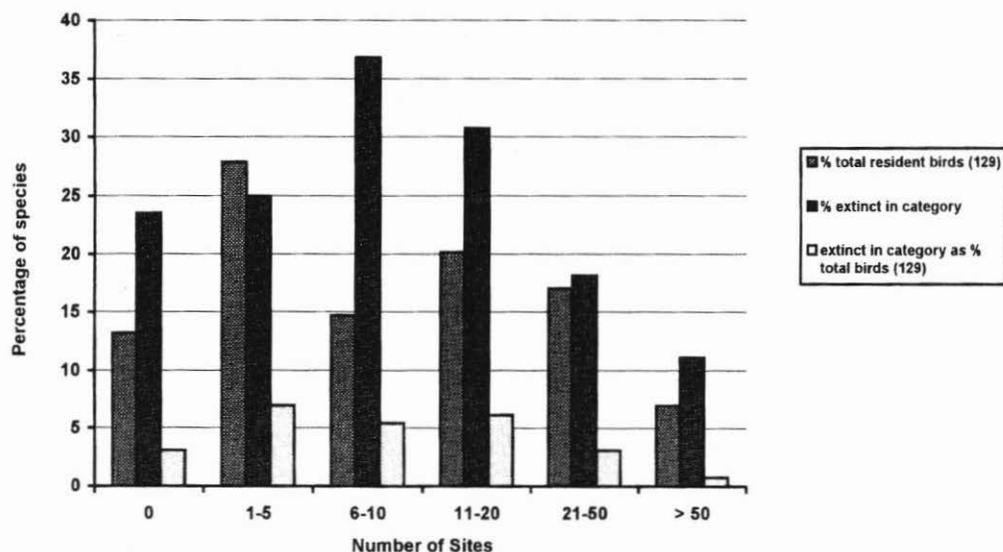


Figure 1: A graph of the frequency of the 129 formerly resident New Zealand species in archaeological sites. For example, about 13% of former residents have not been recorded in any site. The five extinct species in this category represent 3% of the total species, and 29% of the number of species not recorded from a site.

Apart from the recently recognised alpine moa *Pachyornis australis* (Worthy 1989), *Puffinus spelaesus*, and two small wrens, all other prehistorically-extinct species were found in at least one archaeological site. *Puffinus spelaesus* has only recently been described (Holdaway and Worthy 1994) and only one archaeological faunal sample (Heaphy River) is available from within its former breeding range. It is likely that bones recorded as *Puffinus assimilis* from the Heaphy River Site are this species. The wrens are minute, easily overlooked taxa, probably not eaten by people.

A majority of species were found in one to five sites, so it is not surprising that the greatest number of prehistorically-extinct species were in this category. The nine prehistorically-extinct taxa represent 25% of the resident birds in the category (Fig. 1). This is the expected frequency if no biases were present, as prehistorically-extinct taxa represent 25% of the total resident species. The extinct species that were found in 1–5 sites fall into several groups. a) very rare species: *Biziura* and *Ixobrychus* (both constrained to specific habitats rarely sampled in the fossil record), *Harpagornis* (large predators can be expected to be rare); b) rare and difficult to identify (therefore probably under-represented because of identification errors): *Malacorhynchus*, *Gallinula*; c) North Island species (for which the number of sites was only 28% of the total): e.g., *Heteralocha acutirostris*, *Aptornis otidiformis*, *Cnemiornis gracilis*; d) small and hence easily overlooked taxa; e.g., *Pachyplechus yaldwyni*, *Aegotheles*. These small taxa include rails, waders and, in particular, the passerines.

It is unlikely that most previous excavations used wet-sieving with fine mesh (<3 mm), which is necessary to detect most small taxa. Similarly, large samples of the bird fauna are necessary to facilitate the detection of rare and/or small taxa. In this respect, the 1996–97 excavations at Kakanui were instructive (M. Weisler and T. H. Worthy, unpublished data). In 1996, among 134 identifiable bird bones, 15 taxa were recorded. From the 1997 excavation, a further 326 bird bones were identified; 18 species, 8 of which had not been found in 1996, were recorded from the 6.4 mm sievings; 18 species were also recorded from the 3.2 mm sievings, of which 11 (mainly passerines) were not recorded in 1996 or from the 6.4 mm sieved material of 1997. These data clearly show that detection of small or rare species is reliant on large sample size and use of fine mesh during screening.

Seven extinct species were found in 6–10 sites, more than the number predicted from the faunal average of 25%. They include species rare in natural sites, e.g. *Mergus*, *Circus eylesi*, *Cnemiornis calcitrans*, *Aptornis defossor*, and North Island taxa such as *Capellirallus karamu* and *Porphyrio mantelli*. The only surprising extinct species in this category is *Euryanas finschi* which was found in only eight archaeological sites, but is abundant in Holocene sites, especially in eastern regions.

Eight extinct species were found in 11–20 sites, again more than was predicted from the faunal average of 25%. They were all large species and included six species of moa, *Fulica prisca* and *Cygnus atratus*.

The four extinct species found in 21–50 sites include three more moa and *Corvus moriorum*. The latter may reflect the coastal distribution of many archaeological sites, as this species was only found in coastal regions.

The taxa that were present in more than 50 sites and therefore appeared to be the most significant in the Maori diet included one extinct species, the moa *Euryapteryx geranoides*, and the extant *Puffinus gavia/huttoni*, *Eudiptula minor*, *Stictocarbo punctatus*, *Gallirallus australis*, *Hemiphaga novaeseelandiae*, *Nestor meridionalis*, *Cyanoramphus* sp., and *Prosthemadera novaeseelandiae*.

Procellariiforms were present in few sites with the notable exceptions of *Diomedea cauta*, *Puffinus griseus*, *P. gavia/huttoni*, and *Pelecanoides urinatrix*. The northern species, e.g., *Puffinus carneipes*, *P. bulleri*, *P. assimilis*, *Pterodroma pycrofti*, and *P. macroptera*, are probably under-represented because of lack of archaeological samples from their range. *Morus serrator* is in few sites. The present increase in populations of this species is probably related to increased availability of small fish, now that commercial fishing has removed their predators (kahawai, mackerel, etc.).

Although this was primarily a survey of the number of sites each species was found in, I noted that in only two sites did the frequency of bones of a species other than moa suggest it was a targeted prey. At both Tiwai Point and Old Neck, *Puffinus griseus* was disproportionately highly represented. At Old Neck, bones of this species accounted for about 48% of the 5388 bones I checked (Worthy 1998b). Anderson (1997) presented data showing that the historical importance of mutton-birding was not revealed in the prehistoric archaeological faunas and suggested that large scale mutton-birding on the southern islands was possibly a recent phenomenon.

The godwit (*Limosa*) was present in only two sites and the knot (*Calidris*) in only one. The data do not support public claims that these species were important dietary components.

Ten of the 11 moa species have been found in archaeological sites. As noted above, the exception, *Pachyornis australis*, has only recently been recognised (Worthy 1989). Its bones have probably been unrecognised in faunas, although few sites are known from within its natural high-country range. Moa were recorded from 103 (58%) sites, although specifically unidentifiable material was all that was present in 15 of these. Sites where indeterminate fragments of moa bone were the only avifauna recorded were not included in this survey, and their addition could only increase the proportion of sites with specifically unidentifiable material. In 20 (11%) sites, only moa were recorded. It is noteworthy that although moa are only 11 of 33 prehistorically extinct taxa, they dominate the assemblages of extinct taxa found in more than 10 sites.

The presence of pukeko (*Porphyrio p. melanotus*) in few sites is consistent with a recent arrival of this species in New Zealand.

The data in Appendix 2 are summarised in Table 2, where North and South Island faunas are separated into extinct and extant subsets, and further categorised by body size. Species were listed as small if smaller than ducks or *Puffinus* species. Large species were moa, *Cygnus*, *Aptornis*, *Harpagornis* and *Cnemiornis*. All intermediate-sized taxa were listed as medium. This table clearly shows the effect of the small number of North Island sites available (49): most species, small and large, extant or extinct, are found in five or fewer sites.

These data were then consolidated so that size categories were reduced to 'small' and 'medium plus large', and frequency in sites limited to '0-5 sites' or '>5' to enable a Chi² analysis. The null hypothesis that size and extinction status make no difference to representation in sites is rejected for both the North and South Island data: North Island: Chi² = 11.99, significant at about 0.1%; South Island: Chi² = 16.16, significant at better than 0.1%. For both the North and South Island data sets, large species are over-represented among extinct taxa found in six or more sites. Among extant taxa found in 0-5 sites, small species are over-represented, whereas medium-large species are under-represented.

In summary, as Figure 1 suggests, extinct species are over-represented in sites and these extinct species are mainly the medium to large taxa. Small taxa are under-represented.

TABLE 2
A SUMMARY OF REPRESENTATION OF BIRD SPECIES
CATEGORISED BY SIZE IN ARCHAEOLOGICAL SITES

For example, 10 species in the North Island fauna were found in 1-5 sites, and 2 of these were small, 5 medium and 3 large.

NORTH Is		Size	Small	Medium	Large	Sum
	No. of sites					
Extinct	None	1	2	1	4	
	1-5	2	5	3	10	
	6-10	1	1	3	5	
	11-20	0	1	4	5	
	21-50	0	0	0	0	
Extant	None	11	8	0	19	
	1-5	22	23	0	45	
	6-10	7	7	0	14	
	11-20	0	8	0	8	
	21-50	2	4	0	6	
Totals		46	59	11	116	

SOUTH Is		Size	Small	Medium	Large	Sum
	No. of sites					
Extinct	None	2	2	1	5	
	1-5	2	5	1	8	
	6-10	0	0	4	4	
	11-20	0	2	5	7	
	21-50	0	0	2	2	
	>50	0	0	0	0	
Extant	none	14	9	0	23	
	1-5	11	8	0	19	
	6-10	8	9	0	17	
	11-20	3	11	0	14	
	21-50	6	9	0	15	
	>50	0	4	0	4	
Totals		46	59	13	118	

MARFELLS BEACH

Marfells Beach is west of Cape Campbell in Clifford Bay at the northeastern extremity of the South Island. The fossil and archaeological faunas from sites in dunes that formed on a gravel ridge between Lake Grassmere and the sea at the eastern end of the beach have recently been reassessed (Worthy 1998a). The analysis of the Marfells Beach fauna was based on 8435 checked specimens from a minimum of 982 individuals in 95 taxa, of which 89 were native. The dunes and hence the fossil fauna post-date the formation of the lake (McFadgen *et al.* 1996) and thus are younger than 1500 years old. The archaeological fauna was of typical Archaic composition with many extinct species and therefore was probably between 800 and 500 years old.

In geological terms, these two faunas were contemporary and invited a direct comparison, as both were deposited in the same small area of dunes. I assumed that the birds in the natural fauna lived in the immediate vicinity and died in proportions that reflected their living frequencies in the environment. Obvious exceptions to this were the seabirds, which could be explained as storm-cast individuals. Although this mainly affected petrels and shearwaters, which were absent from the middens, the large number of *Eudyptula minor* in the dunes is probably due to this factor. The other necessary assumption to make for this comparison is that similar-sized species had equal chance of being preserved and subsequently discovered. Thus, I consider it valid to compare the frequencies of *Gallirallus australis* and *Anas superciliosa*, but not that of *Gallirallus australis* with small waders.

Bearing these limitations in mind, I asked whether the species present in the midden were found in the same proportions in the natural fauna. This is a valid question, as the comparison is with the same species, so biases due to species-specific factors apply equally. If species are not in equal proportion, and a given species is 'over-represented' in the midden, I suggest that this reflects selection of that species on the part of the early inhabitants of the site. Whether this selection was because the species was a prized food or because it was easier to kill can only be guessed at in the case of extinct taxa. In any case, it is irrelevant to the result that more of such species were taken, so was not considered further. If a species was under-represented, we might likewise infer that it was either avoided or could not be caught. To address this question, I used only those species found in the midden, so the compared natural fauna was a subset of the whole. However, all the species so excluded were either rare small waders or seabirds whose presence in the dunes could be explained as the result of beach-wreck. A χ^2 test indicated that the midden and dune faunas were significantly different (Table 3). The source of the differences was detected by examining the relative frequency of each species (%MNI) across deposit types.

TABLE 3
ANALYSIS OF SPECIES KNOWN FROM THE MARFELLS BEACH MIDDENS
COMPARED TO THEIR FREQUENCY IN THE NATURAL DUNE DEPOSITS

The composition of the faunas from the midden and the dunes differs significantly ($\chi^2 = 156.579$, $df=44$, $P<0.0001$). The species that contribute to this difference are those whose %MNI differ markedly. These are indicated in the column headed 'Differ': '+' means that species is over represented in the midden, '-' means that species is under represented in the midden. Only a few species are present in the middens at a frequency other than that predicted from the natural fauna. Those that became globally or locally extinct in the prehistoric period are in bold letters.

	Midden	Dune	Midden	Dune	Differ
	MNI	MNI	%MNI	%MNI	
<i>Euryapteryx geranoides</i>	1	4	0.48	0.61	
<i>Emeus crassus</i>	5	3	2.38	0.46	+
<i>Apteryx australis</i>	1	4	0.48	0.61	
<i>Apteryx</i> sp. juv	1	1	0.48	0.15	
<i>Poliocephalus rufopectus</i>	2	2	0.95	0.31	
<i>Pterodroma cookii</i>	1	1	0.48	0.15	
<i>Puffinus griseus</i>	1	3	0.48	0.46	
<i>Puffinus gavia/huttoni</i>	2	35	0.95	5.38	
<i>Eudyptula minor</i>	3	88	1.43	13.52	-
<i>Eudyptes pachyrhynchus</i>	1	9	0.48	1.38	
<i>Megadyptes antipodes</i>	4	8	1.90	1.23	
<i>Phalacrocorax melanoleucos</i>	1	1	0.48	0.15	
<i>Phalacrocorax varius</i>	2	6	0.95	0.92	
<i>Phalacrocorax carbo/variatus</i>	1	7	0.48	1.08	
<i>Leucocarbo carunculatus</i>	6	12	2.86	1.84	
<i>Stictocarbo punctatus</i>	47	60	22.38	9.22	+
<i>Cygnus sumnerensis/atratatus</i>	12	30	5.71	4.61	
<i>Tadorna variegata</i>	23	42	10.95	6.45	
<i>Malacorhynchus scarletti</i>	1	1	0.48	0.15	
<i>Anas superciliosa</i>	5	13	2.38	2.00	
<i>Anas chlorotis</i>	8	25	3.81	3.84	
<i>Anas gracilis</i>	1	2	0.48	0.31	
<i>Aythya novaeseelandiae</i>	14	12	6.67	1.84	+
<i>Mergus australis</i>	5	5	2.38	0.77	
<i>Biziura delautouri</i>	1	2	0.48	0.31	
<i>Circus eylesi</i>	4	5	1.90	0.77	
<i>Harpagornis moorei</i>	1	2	0.48	0.31	
<i>Coturnix novaeseelandiae</i>	1	14	0.48	2.15	

<i>Gallirallus australis</i>	3	42	1.43	6.45	-
<i>Porphyrio porphyrio</i>	2	1	0.95	0.15	
<i>Porphyrio hochstetteri</i>	1	1	0.48	0.15	
<i>Fulica prisca</i>	22	11	10.48	1.69	+
<i>Haematopus unicolor</i>	1	3	0.48	0.46	
<i>Larus dominicanus</i>	1	8	0.48	1.23	
<i>Larus scopulinus/bulleri</i>	1	9	0.48	1.38	
<i>Sterna striata</i>	2	4	0.95	0.61	
<i>Hemiphaga novaeseelandiae</i>	5	33	2.38	5.07	
<i>Strigops habroptilus</i>	1	6	0.48	0.92	
<i>Nestor meridionalis</i>	5	29	2.38	4.45	
<i>Cyanoramphus</i> spp.	5	61	2.38	9.37	-
<i>Anthus novaeseelandiae</i>	1	5	0.48	0.77	
<i>Prothemadera novaeseelandiae</i>	2	16	0.95	2.46	
<i>Philesturnus carunculatus</i>	1	9	0.48	1.38	
<i>Turnagra capensis</i>	1	2	0.48	0.31	
<i>Corvus moriorum</i>	1	14	0.48	2.15	
sum	210	651	100.00	100.00	

The midden fauna indicates that, while at least 43 taxa were exploited (Table 3), only 4 were taken by the early Marfells Beach inhabitants in relative abundances that were markedly greater than those in which they were present in the natural fauna. These were *Emeus crassus*, *Stictocarbo punctatus*, *Aythya novaeseelandiae*, and *Fulica prisca*. Little confidence can be placed in the difference in relative abundances of *Emeus crassus* because of the small sample sizes involved, but the remaining three species were apparently favoured food.

Only three species were markedly more abundant in the dunes. Of these, the abundance of *Eudiptula minor* could be explained as the result of beach-wrecked birds. The abundance of *Gallirallus australis* in the dune deposits may be explained as the result of the prehistoric hunters having avoided this species in favour of the larger *Fulica prisca*. The apparent greater abundance of *Cyanoramphus* sp. in the dunes probably reflects the lack of adequate sieving techniques in the recovery of fauna from the archaeological deposits. Most of the few bones found in the dunes were the highly distinctive premaxillae, so this species was probably significantly under-represented in both faunas. The overwhelming conclusion reached by this analysis was that most species were present in the midden in the frequency in which they appeared naturally in the environment. Despite this apparently unfocused hunting strategy, the data clearly show that many species now extinct in the region were living there in the very latest Holocene. They became extinct following human intervention.

DISCUSSION

It has long been known that a substantial proportion of the New Zealand fauna became extinct following the arrival of humans in New Zealand (e.g., Oliver 1955; Cassels 1984; Holdaway 1989; Atkinson and Millener 1991; Bell 1991). Knowledge of the composition of the original avifauna has changed continuously and is still in a state of flux; thus while many extinct species have long been known, the proportion that they represent in the original resident avifauna varies with the numbers of species accepted. One of the latest commentators was Millener (1990), who listed all the species known from either extant, fossil, or archaeological records. He stated

Of the 33 avian species known to have become extinct during the Polynesian period, the remains of at least 30 (including 11 moa species) have been found in association with Archaic Maori occupation sites. However, it seems that for none of them can extinction be attributed solely to direct hunting. (Millener 1990: 99)

There is an apparent typing error here, as the number of species should read 43 not 33 (see Millener's Table 4), but this larger total includes 7 from the Chatham Islands. If these exclusively Chatham species are excluded, 36 are left. Despite recent taxonomic changes resulting in the removal of taxa formerly considered distinct New Zealand species, such as pelican and swan, the data presented here show that the situation is actually worse than was portrayed by Millener: a minimum of 39 of the 129 formerly resident species became extinct on the New Zealand mainland alone.

For ease of comparison with other studies, for example Cassels (1984), and because this is a natural group arguably most likely to be impacted upon by people, the analysis can be restricted to the 93 land and freshwater birds (Appendix 1). Among Pelecaniformes only *Phalacrocorax carbo*, *P. sulcirostris*, and *P. melanoleucos* are considered resident freshwater birds. *Pelecanus conspicillatus* is excluded, as it is a vagrant species. Among the Ciconiiformes *Egretta sacra* has a mainly coastal distribution, so is excluded. Perhaps unconventionally, among the Charadriiforms, both *Haematopus* sp., *Himantopus*, both *Charadrius* sp., *Thinornis*, *Anarhynchus*, *Sterna albostrata* and *Coenocorypha* are accepted as land/freshwater species, as all spend or spent a significant amount of time inland. *Anas rhynchotis*, *Circus approximans*, and *Porphyrio porphyrio* are excluded as post-colonisation arrivals.

Thirty-two land and freshwater species, representing 34% of this fauna, became extinct in the prehistoric period; a further six became extinct in the historic period, giving a total of 38, or 41% of the original land and freshwater fauna. However, the situation is very much worse than these numbers indicate, as all those taxa listed with R in Appendix 1 are rare and declining in abundance on the mainland, or are already extinct there, surviving only on offshore islands. Thirty such taxa are listed, which is probably an underestimate of threatened species, as populations of other *Apteryx* species, *Nestor meridionalis*, *Cyanoramphus* spp., and *Eudyptes pachyrhynchus* are all declining. So, does the incidence of species in archaeological sites reflect these extinctions?

All moa species were extinct by 300–400 years ago; thereafter they are not found in middens (Anderson 1989a). Their case needs to be considered separately from that of other birds. This is because their large size has made them easily found and therefore as a group they have been recorded in far more sites than any other group. This is also illustrated by the fact that only moa were recorded in 20 sites, whereas in very few sites was only a single species of small bird recorded. In reality, if this bias in collection was not operating, the

minimum number of individual moa would be far less than the sum of other birds. For example, there were 25 individual moa in the Shag Mouth excavation, compared to 510 other birds (Anderson *et al.* 1996). Similarly, at Marfells Beach the MNI of moa was much less than that of other birds. Moa of one or other species were hunted and eaten in all districts. The significance of moa in the diet of early Polynesians is probably related to their availability; and while the fossil record does not help to elucidate former moa densities, the archaeological record probably does. In most districts, sites contain only a few individual moa and these were not the main prey, either in terms of numbers of animals killed or in relative biomass, as Davidson (1979) and Anderson (1989a) observed. The main exceptions to this generalisation are the sites that had catchments of grassland-shrubland-forest mosaics, such as those in Canterbury and Otago, and Kaupokonui in South Taranaki. Anderson (1989b) drew a useful analogy with densities of emu populations, which are maximal in areas with rainfall 300–700 mm and decrease either side of this range, and predicted that moa densities would be greatest in drier eastern regions. In these areas the characteristic moa species (*Pachyornis mappini* in South Taranaki, *Pachyornis elephantopus*, *Emeus crassus*, and *Euryapteryx geranoides* in the eastern South Island) were certainly hunted in significantly greater numbers than the species found in closed forest communities, so must have been more common. But Anderson (1989b) concluded that 'overkill' had not occurred, even for these species where there is evidence of specific or focused moa-hunting in sites such as Kaupokonui, Waitaki Mouth, Hawksburn and Rakaia River.

The extinction of animals has often been blamed on 'overkill', a popular term to describe the results of extreme over-hunting that rapidly made animals extinct. The various papers in Martin and Klein (1984) were a landmark in the debate between the overkill advocates and those who preferred climatic changes as the cause of extinctions. In New Zealand, the extinction of moa has long been accepted as the result of hunting (Owen 1844; Cassels 1984; Trotter and McCulloch 1984; Anderson 1989a). However, the important word in the above definition of overkill is 'rapid' — how fast is rapid? If the American extinction event at the end of the Holocene took 400 years, this would appear very rapid, viewed from our perspective 10,000 years later. But in New Zealand this same 400-year period may represent half of our prehistory. The extinction of moa was not caused by the sort of massive slaughter that killed the American bison or passenger pigeons, which is what the term 'overkill' conjures. This blitzkrieg model of overkill requires a rapidly expanding population of hunters who make prey extinct as they are encountered. However, as shown above, Anderson (1989b) could find no evidence in New Zealand of the extinction front that such a model would predict. Rather, initial settlement and exploitation of moa was widespread in New Zealand, and exploitation occurred over a 400-year period (Anderson 1989a, 1991), by the end of which all moa were extinct. Yet this was still overkill, as too many were killed for the populations to persist.

Within some areas, extinction of the local populations may have been very much more rapid, perhaps as little as the 50–100 years advocated by Anderson *et al.* (1996). This would certainly be the case for the shrubland-preferring species such as *Euryapteryx geranoides* and *Pachyornis mappini*. The Holocene record shows that these species occupied the dunes along the Wairarapa coast (Worthy 1990), while only a few hundred metres inland, closed forest was the home of *Anomalopteryx didiformis* and *Dinornis novaezealandiae*. The small narrow available area of coastal habitat would have made the shrubland-preferring species extremely vulnerable. The early settlers on the Wairarapa coast could have removed this moa fauna in 5–10 years and left very little evidence.

Thus both the frequency in sites of moa and other species and the Marfells Beach data suggest that birds were generally not hunted in a frequency in excess of their initial abundance in the environment. The data do not support massive overkill in a short space of time, as would be predicted by the blitzkrieg model. There are few exceptions. Notably, there is compelling evidence from just two sites that *Puffinus griseus* was a targeted species. This is the now widely sought after 'muttonbird'. It is known to have been an important food source historically, yet the archaeological record does not reveal this significance (Anderson 1997). The data suggest that *Stictocarbo punctatus* and *Aythya novaeseelandiae* were also targeted species at Marfells Beach. In the case of *Stictocarbo* this is supported by the site frequency data, as this species was found in many sites; in contrast, *Aythya* was recorded from few sites. Perhaps the requirement of *Aythya* for deep still water limited the places where it was available. However, where it was available, it was the preferred species, as at Ototara, where five anatid species accounted for 16 out of a total of 38 individuals, and 7 of them were *Aythya* (Worthy 1998c).

The extinct coot, *Fulica prisca*, was targeted at Marfells Beach, yet in the site frequency data there is little indication that it was a preferred species. Again, habitat is probably all-important. *Fulica prisca* seems to have had a preference for riparian habitats in drier eastern regions (Worthy and Holdaway 1996) and few sites are adjacent to such places. Of the 16 species that became extinct prehistorically either regionally or totally at Marfells Beach, only *Fulica prisca* was specifically targeted as prey. The logical conclusion to be drawn from these observations is that the relative frequency of a given species in all sites does not really indicate whether or not it was a preferred prey. Rather, such data probably reflect how widely available these species were. Of the 9 species found in more than 50 sites, only one is extinct. The others were widely distributed and abundant when Europeans arrived.

Generally it is not possible to determine if a species was sought after, as one needs the juxtaposition of archaeological and natural sites to determine if it was present in greater frequencies in the former than in the latter. However, the data, poor as they are, reveal that in both the North and South Islands, medium to large extinct species are over-represented in sites, supporting the generalisation that such species were sought after. Some species, such as some moa, were undoubtedly sought after in the areas where they had local concentrations, as was *Fulica prisca* at Marfells Beach. The significant thing about the site frequency data is that they show that virtually all extinct taxa were hunted prehistorically.

Many species did become extinct and for some, like the former resident population of *Cygnus atratus*, there is no evidence that they were preferentially sought from the environment – they were common in Lake Grassmere, but were not more so in the Marfells Beach middens. So why are they extinct? Three factors are important: 1, habitat loss or modification reduced or removed a species habitat; 2, habitat preferences probably gave some species heightened susceptibility; 3, the biology of some species made them intolerant of predation.

It is widely accepted now that following colonisation of New Zealand by Polynesians there was widespread clearance of forests by burning (McGlone 1983, 1988, 1989). This affected the drier eastern forests to a much greater extent than wetter western ones, and therefore largely removed the habitat of the suite of species that preferred the mosaics of forest, shrubland and grasslands. These species included *Aptornis* sp., *Cnemiornis* sp., *Euryanas finschi*, *Harpagornis moorei*, *Fulica prisca*, and *Gallinula hodgenorum*, which are all extinct (Worthy and Holdaway 1993, 1996). Some such species probably had narrow preferred habitats, for example *Cnemiornis calcitrans* and *Fulica prisca*, so presenting smaller initial populations constrained to specific areas. The extinct population of *Cygnus* probably

succumbed because only limited areas of acceptable habitat were present. In prehistoric New Zealand, waterways were largely oligotrophic and the water-plant flora was very limited, with the result that suitable forage was probably restricted to the estuarine areas of *Zostera* seagrass beds and a few shallow lakes. Combine the loss of habitat with a formerly narrow ecological preference and the fact that most of these birds were large and flightless and it is apparent that such species would have been very susceptible to predation and can be expected to have become extinct more rapidly than other species.

However, for most species the extinction process probably took centuries and some, such as *Aegotheles novaezealandiae* and some moa species (e.g., *Anomalopteryx didiformis* and *Dinornis novaezealandiae*), preferred to live in areas where habitats remained largely unmodified (Worthy and Holdaway 1993, 1994). The 32 terrestrial and freshwater species that became extinct in the prehistoric period did so as the result of at least 600 years of adjustment to the presence of Polynesians, kiore (*Rattus exulans*) and dogs. This drawn out time frame of the extinction event is important to understanding the process. The survival into the historic period of population remnants of many species that were otherwise widely reduced also illustrates the extended process of extinction. For example, by European colonisation, *Strigops habroptilus* had been markedly reduced from what the fossil record shows was one of the most common and widely distributed birds in New Zealand to remnant populations in the North Island and to wetter western areas in the South Island. For this species, loss of habitat was probably a minor factor, as it preferred the wet rimu forests of the west that survived intact until European times. The effects of human predation and, most importantly, kiore predation of the chicks and eggs caused the decline. Similarly, it is little more than an accident that *Traversia lyalli* survived into the European era. In the latest Holocene, it was widespread in the North and South Islands, from sea-level to the subalpine zone. Its extinction is certainly due to this small flightless wren's susceptibility to predation by the kiore. The kiore, alone, is responsible for the extinction of several frogs, larger lizards, and several small flightless birds, such as other wrens, snipe and the smaller petrels (Atkinson 1978; Whitaker 1978; Holdaway 1989; Bell 1991; Towns and Daugherty 1994). I conclude that the demise of many prehistorically-extinct taxa probably took place over a period of at least 400 years, and that others, such as *Strigops habroptilus*, the kakapo, were still in the downward spiral preceding extinction when Europeans came on the scene.

As this extinction event was slow and probably not entirely the result of habitat loss, it is necessary to consider what factors of biology caused the extinct or endangered species to be or have been more susceptible to the effects of predation by either people or kiore. This differing extinction potential is probably best explained by differing reproduction potential. *Stictocarbo punctatus* faced massive targeted predation throughout New Zealand, yet survived. It is a marine species adapted to periodic massive deaths caused by uncertain food availability and periodic storms, and rapid increases in population are possible (Doherty and Bräger 1997). Similarly, *Aythya* was demonstrably a targeted species yet survived. It is flighted, so can disperse readily but, most importantly, it lays numerous eggs. In contrast, many of our endangered species still surviving in New Zealand are K-selected species, which breed only after several years' adolescence, do so infrequently, and produce few offspring. They tend to be long-lived. But such a breeding strategy makes them susceptible to a new predation pressure. In a number of years that will vary with differences in age at first breeding, life expectancy, etc., they will ultimately become extinct. Perhaps the most extreme example among the surviving species is *Strigops habroptilus*, which is also one of the most endangered. It breeds late in life, maybe once every five years, and then only lays two eggs.

In summary, the data suggest that, coming on top of background levels of natural mortality for which these animals were adapted, the levels of predation by humans or kiore and the habitat changes people induced were what drove many species to extinction. It was not a blitzkrieg event but something much more insidious, as progress towards extinction was probably not even discernible during the course of a human lifetime, but nevertheless just as terminal.

The fact that we are still monitoring declines in the range and abundances of many native species indicates they are still adjusting to the impact of Europeans and their associated introduced species, which is limited to less than 200 years. As some species had not reached a balance after 400–600 years of association with only Polynesians and kiore, this should not be a surprise. We would be naive to think that our present fauna is in any sort of balance with all the new factors recently introduced, such as the new range of mammalian predators (cats, rats, mustelids), mammalian browsers (goats, deer), and new insects (e.g., vespid wasps). It is probable that in another 400 years, most if not all the 30 endangered taxa will join the 6 that are listed as extinct historically. If some survive it is likely that they will do so only because their populations are managed by man; that is, they are not self-sustainable in the new regime. The impact of Europeans on the New Zealand fauna has been vastly greater than that of Polynesians — it just has not been completed yet.

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Appendix 1. List of archaeological sites

Site numbers are those of the New Zealand Archaeological Association Site Recording Scheme. THW: personal checking by author. CM: Canterbury Museum. MNZ: Museum of New Zealand. AMNH: American Museum of Natural History.

Site	Moa	Site No.	References
84 Landscape Rd		R11/66	Millener 1981a
Ahuriri, Waitaki River	Y	H39/12	Ambrose 1970
Anapai	Y	N25/59	Barber 1994
Andersons Bay	Y	I44/172	Scarlett 1974
Appleby		N27/118	Barber 1994
Auckland Point	Y	O27/49	Barber 1994
Avoca Point	Y	O31/30	Trotter 1980
Awamoa	Y	J41/3	McDonnell 1889; Trotter 1970
Awamoko			Duff 1977: 362
Awaroa Inlet		N26/18	Barber 1994
Awaroa Inlet		N26/214	Barber 1994
Breaksea Sound		BSS/1	McGovern-Wilson 1986
Bromley		M36/12	Scarlett 1979
Bushface 2, Hawkes Bay	Y		CM catalogue
Cannibal Bay		H46/28	Hamel 1977; McGovern-Wilson 1986
Cascade Cove 3		B45/28	McGovern-Wilson 1986
Cascade Cove Island		Fiordland	McGovern-Wilson 1986
Chalky Island		Fiordland	McGovern-Wilson 1986
Church Gully		M36/11	Challis 1995
Coal Creek	Y	G43/51	Anderson and Ritchie 1984
Cooper Island		Fiordland	McGovern-Wilson 1986
Dashing Rocks	Y	K39/1	Scarlett 1979; Mason and Wilkes 1963
Delaware Bay	Y	O27/15	Barber 1994
Duckworth Midden	Y	B44/1	Scarlett 1979
False Island	Y	H47/6	Scarlett 1974
Flock Hill		L34/2	Challis 1995
Foxtan	Y	S24/3	Millener 1981a
Gooseneck Bend	Y	H39/16	Ambrose 1970
Gowan Rockshelter		M34/5	Worthy and Holdaway 1996
Hahei	Y	T11/326	Millener 1981a
Hamiltons Shelter No 3		H39/4	Challis 1995
Hampden Beach	Y	J42/31	Trotter 1967c
Harataonga	Y	T08/5	Davidson 1979; Law 1972; Spring-Rice 1963
Haulashore Island		O27/56	Barber 1994
Hawksburn	Y	G42/13	THW
Heaphy River Mouth	Y	L26/1	Wilkes and Scarlett 1963; 1967
Hinahina		H47/2	Hamel 1977
Hoopers Inlet	Y	I44/13	Munro 1960
Hotwater Beach, Layers 3b, 4, 5	Y	T11/115	Davidson 1979
Houhora	Y	N03/59	Scarlett 1979; Millener 1981a
Huriawa (Areas A & B)		I43/1	McGovern-Wilson 1986
Hurunui River Mouth	Y	O33/11	Challis 1995
Ikirangi Bay	Y	M37/35	Challis 1995
Italian Creek		G42/197	Ritchie 1982
Kaiararo Stream		J41/7	Trotter 1970

Kaikais Beach	Y	I44/127	Scarlett 1974
Kaka Point, Port Molyneux	Y	H46/10	Scarlett 1974
Kakanui	Y	J42/4	THW (1996 + 1997)
Katiki		J42/19	Trotter 1967a
Kaupokonui	Y	P21/3	Buist 1963; Foley 1980
Killermont No 2	Y	H39/19	Challis 1995
Kings Rock	Y	G47/51	Hamel 1977; Scarlett 1974
Kohika		V15/80	Nichol 1988
Lagoon Flat	Y	O32/31	McCulloch and Trotter 1975
Lake Mangakaware site 1		S15/16	Peters 1971
Lake Ngaroto		S15/9	Millener 1981a
Lee Is		D41/4	Anderson and McGovern-Wilson 1991
Lee Is No 1		D41/5	Anderson and McGovern-Wilson 1991
Lee Is No 2		D41/7	Anderson and McGovern-Wilson 1991
Little Papanui	Y	J44/1	Scarlett 1974; McGovern-Wilson 1986
Long Beach	Y	I44/23	McGovern-Wilson 1986; Dawson and Yaldwyn 1952; Scarlett 1974
Long Island (all layers)		Fiordland	McGovern-Wilson 1986
Long Point South		G47/73	Hamel 1977
Mahia Peninsula		Y20/30	Jeal 1987
Makara	Y	R27/3	McFadgen ms; Yaldwyn 1959; moa THW
Mapoutahi Pa		I44/7	Anderson and Sutton 1973; McGovern-Wilson 1986
Marfells Beach	Y	P29/2	THW; Scarlett 1979
midden		S24/20	Butts 1982a
midden		S24/26	Butts 1982a
Moa Bone Point Cave	Y	M36/77	Scarlett 1972, 1974, 1979; Duff 1977
Moawhango Dam			Millener 1981a
Monck's Cave		M36/47	CM; Challis 1995
Moturua Island	Y	Q05/682	Millener 1981a
Muhunua West midden		S25/46	Butts 1982b
Murdering Beach		I44/127	McGovern-Wilson 1986
Mussel Point #2 (500 m south)	Y		THW
Mussel Point, Lake Grassmere	Y	Q29/1	Millener 1981b; Scarlett 1974
Native Island	Y		EXCLUDED - ALL FAUNA IS OF NATURAL ORIGIN (Worthy 1998b)
Needles Point	Y	P29/8	Orchiston 1977
Nenthorn	Y	I43/51	Easdale and Jacomb 1986
Ngararahae Bay	Y	R17/80	Wilkes 1995
Ohawe	Y	Q21/75	Buist 1960, 1962; Millener 1981a
Old Neck	Y		Scarlett 1979; reanalysis THW
Olivers	Y	O31/30	Scarlett 1974
Omimi	Y	I44/1	McGovern-Wilson 1986
Opito Bay, Parkers Midden	Y	T10/160	Davidson 1979; Jolly and Murdoch 1973
Opito Bay, Skippers Midden	Y	T10/161	Scarlett 1979
Opua Moa Hunter Site	Y	P20/10	Fyfe 1988; moa TWH
Otokia Mouth, Brighton	Y	I44/5	Anderson 1982
Ototara	Y	J42/2	THW; Trotter 1965
Owens Ferry	Y	F41/66	Ritchie and Harrison 1981
Oyster Island	Y	N27/120	Barber 1994
Paekakariki midden			MNZ
Panau		N36/72	C. Jacomb pers. comm.

Papanui Beach		J42/47	McGovern-Wilson 1986
Papatowai	Y	G47/50	Hamel 1977; Scarlett 1974
Paradise Cave		M36/32	Challis 1995; Millener 1988
Paremata	Y	R26/122	Scarlett 1979; Sinclair 1977; Davidson 1978a; Dawson 1962
Pareora River Mouth	Y	J39/29	Challis 1995
Patons Rock Cave	Y		CM catalogues
Picnic Point Middens		G47/68	Hamel 1977
Pleasant River	Y	J43/1	Teal 1975: 29; Smith 1999
Ponui Island	Y	S11/20	Nicholls 1963; M. Taylor pers. comm.
Port Craig (PC/1 - PC/4)			McGovern-Wilson 1986
Port Jackson	Y	S09/53	Davidson 1979; Millener 1981a
Pounaweia	Y	H47/1	Scarlett 1974; Hamel 1977; McGovern-Wilson 1986
Puketapu Pa	Y	Q19/157	Millener 1981a
Puketoi	Y	H42/3	Murison 1872; Hector 1872
Purakanui		I44/21	McGovern-Wilson 1986
Rakaia River Mouth	Y	L37/4	Trotter 1972; moa AMNH, THW
Redcliffs	Y	M36/24	Trotter 1967b; 1975
Ringaringa			Knight 1970
Riverton (Areas A-C)		D46/35	Leach and Leach 1980
Rockfall II, Central Otago	Y	G41/453	Ritchie 1982; Ritchie and Harrison 1981
Rocky Hill Rockshelter	Y		CM catalogues, THW
Ross's Rocks		I43/22	McGovern-Wilson 1986
Rotokura	Y	O27/1	Butts 1978; Barber 1994
Sandhill Point (SHP/1)		C46/31	McGovern-Wilson 1986
Sandhill Point (SHP/2)		C46/31	McGovern-Wilson 1986
Sandhill Point (SHP/3)		C46/31	McGovern-Wilson 1986
Saraha Gully	Y	T10/167	Scarlett 1979; Davidson 1979
Seacliff	Y	I43/4	Scarlett 1974; Blake-Palmer 1956
Shag Mouth (1988 excav)	Y	J43/2	Anderson <i>et al.</i> , 1996; THW
Shepherds Creek II	Y	H39/6	Scarlett 1979
Slipper Island	Y	U12/5	Rowland 1978
Slipper Island	Y	U12/9	Rowland 1978
Smuggler's Cove		Q07/83	Anderson 1997
Southport 1			McGovern-Wilson 1986
Southport 10			McGovern-Wilson 1986
Southport 11			McGovern-Wilson 1986
Southport 4			McGovern-Wilson 1986
Southport 5			McGovern-Wilson 1986
Southport 7			McGovern-Wilson 1986
Southport 9			McGovern-Wilson 1986
Station Bay, Motutapu Island		R10/31	Davidson 1978b
Sunde Site, Motutapu island	Y	R10/25	Scott 1970; Millener 1981a
Tahunanui	Y	O27/21	Millar 1964, 1971; Barber 1994
Tai Rua	Y	J42/1	Trotter 1965, 1979; McGovern-Wilson 1986
Taiaroa Head		J44/3	McGovern-Wilson 1986
Tairua	Y	T11/62	Smart <i>et al.</i> 1962; Davidson 1979; Rowland 1977
Takahe Valley	Y		O'Regan 1992
Takamatua		N36/93	Trotter 1973
Takou Bay	Y		Millener 1981a

Tautuku North	Y	G47/65	Hamel 1977
Tautuku Point	Y	G47/64	Hamel 1977
Te Awamate Pa		S23/71	Cassels <i>et al.</i> 1988; THW
Te Ika-a-maru Bay		Q27/30	Davidson 1976
Te Ika-a-maru Bay	Y	Q27/36	Davidson 1976
Te Rangatapu/Waingongoro	Y	Q21/32	Millener 1981a
Te Rangatapu/Waingongoro	Y	Q21/76	Buist 1960, 1962; Canavan 1962
The Glen	Y	O27/13	Barber 1994
Timpendean	Y	M33/11	Worthy and Holdaway 1996
Tiwai Point	Y	E47/13	Sutton and Marshall 1980; Hamel 1969
Tokoroa Moa Hunter Site	Y	T16/1	Law 1973
Tumbledown Bay	Y	N37/12	Challis 1995; Duff 1977; CM
Twilight Beach		M02/162	Millener 1981a
Waianakurua River Mouth	Y	J43/22	Anderson 1979
Waiiau River Mouth	Y	O33/4	Challis 1995
Waihao River Mouth	Y	J40/32	Challis 1995
Waiheke Island		R11/1311	Millener 1981a
Waimataitai	Y	J42/38	Trotter 1965; McGovern-Wilson 1986
Waipara Cliffs cave midden		N34/4	CM
Waipara Cliffs Midden		N34/4a	CM
Wairau Bar	Y	P28/21	Falla 1942; Simmons 1968; Scarlett 1972, 1974; Millener 1981b
Waitaki River Mouth	Y	J41/56	Scarlett 1974
Wakanui Creek	Y	L37/8	Scarlett 1974; Millener 1981b
Wakapatu		D46/38	Higham 1968
Warrington (Masons site L1-4)		I44/194	McGovern-Wilson 1986
Warrington A		I44/177	McGovern-Wilson 1986
Washpool Midden	Y	S28/49	Leach 1979
Whakamoenga Cave	Y	U18/4	Hosking 1967; Leahy 1976
Whalers Bay Cave		O31/12	Scarlett 1979
Whangamata	Y	T12/2	Davidson 1979
Whiritoa	Y	T12/500	Davidson 1979
Whittles Rockshelter #2	Y		CM catalogues
Woolshed Flat	Y	I40/27	Trotter 1966

Appendix 2. List of birds known by fossil or archaeological records from the North and South Islands of New Zealand, modified from Millener (1990).

Those known as fossils are marked with Y. The number of archaeological sites each species is recorded from is totalled for each of the North and South Islands. Sites on Stewart Island and nearby islands are included in South Island; sites on islands off the North Island are included in North Island. Status: probable non-resident species are marked with a V and land and freshwater species with L/F. Extinct: P = extinct in prehistoric period; H = extinct in historic period; R = rare and endangered on mainland or restricted to offshore islands. A dash (-) indicates that the species is not known from that island. In the South Island list, species marked with an * are present in the dunes at Marfell's Beach but were not specifically reported from middens there, and are not included in the totals.

The list includes data from 177 sites, of which 103 have moa bone, although often it was not specifically identified.

Order	Status	Fossil	Species	Extinct	N.I.	S.I.	Total
Dinornithiformes	L/F	Y	<i>Megalapteryx didinus</i>	P	-	12	12
	L/F	Y	<i>Anomalopteryx didiformis</i>	P	9	13	22
	L/F	Y	<i>Pachyornis elephantopus</i>	P	-	14 *	14
	L/F	Y	<i>Pachyornis australis</i>	P	-	0	0
	L/F	Y	<i>Pachyornis mappini</i>	P	14	-	14
	L/F	Y	<i>Euryapteryx geranoides</i>	P	14	49	63
	L/F	Y	<i>Euryapteryx curtus</i>	P	18	-	18
	L/F	Y	<i>Emeus crassus</i>	P	-	30	30
	L/F	Y	<i>Dinornis struthoides</i>	P	9	9	18
	L/F	Y	<i>D. novaezealandiae</i>	P	8	6	14
	L/F	Y	<i>D. giganteus</i>	P	12	11	23
Apterygiformes	L/F	Y	<i>Apteryx australis</i>		14	-	14
	L/F	Y	<i>Apteryx australis/haastii</i>		-	13	13
	L/F	Y	<i>Apteryx owenii</i>	R	10	6	16
Podicipediformes	L/F	Y	<i>Poliocephalus rufopectus</i>		2	1	3
	L/F	Y	<i>Podiceps cristatus</i>		3	2	5
Procellariiformes		Y	<i>Diomedea exulans/epomophora</i>	R	5	6	11
	V	Y	<i>Diomedea bulleri</i>		1	8	9
	V	Y	<i>Diomedea cauta</i>		7 +?3	24	31
							+?3
	V	?Y	<i>Diomedea chrysostoma</i>		1	1	2
	V		<i>Diomedea melanophrys</i>		0	1	1
	V		<i>Phoebetria palpebrata</i>		0	1	1
		Y	<i>Procellaria parkinsoni</i>	R	0	0	0
		Y	<i>Procellaria westlandica</i> ⁴	R	0	0	0
	V		<i>Procellaria aequinoctialis</i>		0	2	2
	Y	<i>Pterodroma macroptera</i>	R	6	0	6	
	Y	<i>Pterodroma inexpectata</i>	R	2	14	16	

⁴This species has recently been found in a site at Punakaiki, and is apparently known from other unpublished sites in that area.

	Y	<i>Pterodroma cookii</i>	R	4	6	10
	Y	<i>Pterodroma pycrofti</i>	R	0	0	0
V	Y	<i>Pterodroma lessonii</i>		0	0	0
V	Y	<i>Pterodroma leucoptera</i>		0	0	0
V		<i>Pterodroma brevirostris</i>		1	0	1
V		<i>Pterodroma nigripennis</i>		0	1	1
	Y	<i>Puffinus griseus</i>		6	23	29
	Y	<i>Puffinus spelaeus</i>	P	-	0	0
	Y	<i>Puffinus gavia/huttoni</i>	R	18	45	63
	Y	<i>Puffinus bulleri</i>	R	1 +?1	0	1 +?1
	Y	<i>Puffinus assimilis</i>	R	3 +?1	2	5 +?1
	Y	<i>Puffinus carneipes</i>	R	3	0	3
V	Y	<i>Puffinus tenuirostris</i>		1	4	5
V	?Y	<i>Halobaena caerulea</i>		1	3	4
V	Y	<i>Daption capense</i>		1	0	1
	Y	<i>Pelecanoides urinatrix</i>	R	8	32	40
	Y	<i>Oceanites nereis</i>	R	0	0	0
V	Y	<i>Oceanites oceanicus</i>		0	0	0
	Y	<i>Fregetta tropica ssp</i>	R	0	0	0
	Y	<i>Pelagodroma marina</i>	R	1	9	10
V	Y	<i>Macronectes</i>		3	4	7
		<i>halli/giganteus</i>				
	Y	<i>Pachyptila turtur</i>	R	9	27	36
V	Y	<i>Pachyptila salvini</i>		0	0	0
	Y	<i>Pachyptila vittata</i>	R	4	14	18
Sphenisciformes	Y	<i>Eudyptula minor</i>		32	52	84
	Y	<i>Eudyptes pachyrhynchus</i>		5	36	41
	Y	<i>Megadyptes antipodes</i>	R	0	14	14
				+?2	+?11	+?13
Pelecaniformes	Y	<i>Morus serrator</i>		4	1	5
V	Y	<i>Pelecanus conspicillatus</i>		2 ?+1	0 *	2
						?+1
L/F	Y	<i>Phalacrocorax melanoleucos</i>		10	17	27
L/F		<i>Phalacrocorax sulcirostris</i>		1	0	1
L/F	Y	<i>Phalacrocorax carbo</i>		9	14	23
	Y	<i>Phalacrocorax varius</i>		4	23	27
	Y	<i>Leucocarbo carunculatus</i>	R	0	35	35
	Y	<i>Stictocarbo punctatus</i>		13	55	68
Ciconiiformes	L/F	Y	<i>Egretta alba</i>	3	2	5
			<i>Egretta sacra</i>	0	?1	0 +
						?1
	L/F	Y	<i>Botaurus poiciloptilus</i>	1	0	1
	L/F	Y	<i>Ixobrychus novaezelandiae</i>	P	1	0
						1
Anseriformes	L/F	Y	<i>Cygnus atratus</i>	P	5	15
	L/F	Y	<i>Cnemiornis calcitrans</i>	P	-	10
	L/F	Y	<i>Cnemiornis gracilis</i>	P	1	-
	L/F	Y	<i>Tadorna variegata</i>		4	22
	L/F	Y	<i>Eurynas finschi</i>	P	3	5 *
						8

	L/F	Y	<i>Malacorhynchus scarletti</i>	P	0	1	1
	L/F	Y	<i>Hymenolaimus malacorhynchos</i>		4	5	9
	L/F	Y	<i>Anas superciliosa</i>		15	31	46
	L/F	Y	<i>Anas chlorotis</i>	R	11	16	27
	L/F	Y	<i>Anas gracilis</i>		2	11	13
		Y	<i>Anas rhynchotis</i>		6	10	16
	L/F	Y	<i>Aythya novaeseelandiae</i>		6	5	11
	L/F	Y	<i>Mergus australis</i>	P	2	4	6
	L/F	Y	<i>Biziura delautouri</i>	P	0	1	1
Falconiformes	L/F	Y	<i>Falco novaeseelandiae</i>		7	20	27
		Y	<i>Circus approximans</i>		4	10	14
	L/F	Y	<i>Circus eylesi</i>	P	3	4	7
	L/F	Y	<i>Harpagornis moorei</i>	P	-	5	5
Galliformes	L/F	Y	<i>Coturnix novaezealandiae</i>	H	10	34	44
Gruiformes	L/F	Y	<i>Gallirallus philippensis</i>		6	9	15
	L/F	Y	<i>Gallirallus australis</i>		23	51	74
	L/F	Y	<i>Capellirallus karamu</i>	P	6	-	6
	L/F	Y	<i>Porzana tabuensis</i>		1	0	1
	L/F	Y	<i>Porzana pusilla</i>		1	0	1
	L/F	Y	<i>Gallinula hodgenorum</i>	P	4	1 *	5
		Y	<i>Porphyrio porphyrio</i>		4	6	10
	L/F	Y	<i>Porphyrio mantelli</i>	P	7	-	7
	L/F	Y	<i>Porphyrio hochstetteri</i>	R	-	9	9
	L/F	Y	<i>Fulica prisca</i>	P	2	11	13
	L/F	Y	<i>Aptornis otidiformis</i>	P	4	-	4
	L/F	Y	<i>Aptornis defossor</i>	P	-	10 *	10
Charadriiformes	L/F	Y	<i>Haematopus ostralegus finschi</i>		0	7	7
	L/F	Y	<i>Haematopus unicolor</i>		2	6	8
	L/F	Y	<i>Himantopus novaezealandiae</i>	R	0	0	0
	L/F	Y	<i>Charadrius bicinctus</i>		1	3	4
	L/F	Y	<i>Charadrius obscurus</i>		3	2	5
	L/F	Y	<i>Thinornis novaezealandiae</i>	R	0	2	2
	L/F	Y	<i>Anarhynchus frontalis</i>		2	0	2
	V	Y	<i>Numenius phaeopus</i>		0	0	0
	L/F	Y	<i>Coenocorypha aucklandica</i>	R	1	5 *	6
	V	Y	<i>Calidris canutus</i>		1	0	1
	V	Y	<i>Limosa lapponica</i>		2	1	3
	V	Y	<i>Stercorarius parasiticus</i>		0	0	0
	V	Y	<i>Catharacta skua</i>		1	0	1
		Y	<i>Larus dominicanus</i>		17	32	49
		Y	<i>Larus scopulinus/bulleri</i>		7	21	28
	L/F	Y	<i>Sterna albobriata</i>		1	6	7
		Y	<i>Sterna striata</i>		3	9	12
		Y	<i>Sterna nereis</i>		0	0	0
		Y	<i>Sterna caspia</i>		3	0	3

Columbiformes	L/F	Y	<i>Hemiphaga novaeseelandiae</i>		26	54	80
Psittaciformes	L/F	Y	<i>Strigops habroptilus</i>	R	12	17	29
	L/F	Y	<i>Nestor meridionalis</i>		34	50	84
	L/F	Y	<i>Nestor notabilis</i>		0	1	1
	L/F	Y	<i>Cyanoramphus</i> spp.		22	39	61
Cuculiformes	L/F	Y	<i>Eudynamis taitensis</i>		0	0	0
	L/F	Y	<i>Chrysococcyx lucidus</i>		0	0	0
Strigiformes	L/F	Y	<i>Ninox novaeseelandiae</i>		5	8	13
	L/F	Y	<i>Sceloglaux albifacies</i>	H	1	14	15
Caprimulgiformes	L/F	Y	<i>Aegotheles novaeseelandiae</i>	P	1	0	1
Coraciiformes	L/F	Y	<i>Halcyon sancta</i>		1	0	1
Passeriformes	L/F	Y	<i>Acanthisitta chloris</i>		1	1	2
	L/F	Y	<i>Xenicus longipes</i>	H	0	0	0
	L/F	Y	<i>Xenicus gilviventris</i>		0	0	0
	L/F	Y	<i>Traversia lyalli</i>	H	0	1	1
	L/F	Y	<i>Pachyplichas yaldwyni</i>	P	-	1	1
	L/F	Y	<i>Pachyplichas jagmi</i>	P	0	-	0
	L/F	Y	<i>Dendroscansor decurvirostris</i>	P	-	0	0
	L/F	Y	<i>Anthus novaeseelandiae</i>		3	9	12
	L/F	Y	<i>Bowdleria punctata</i>		0	2+?1	2+?1
	L/F	Y	<i>Mohoua albicilla</i>		1+?1	-	1+?1
	L/F	Y	<i>Mohoua ochrocephala</i>	R	-	2	2
	L/F	Y	<i>Mohoua novaeseelandiae</i>		-	0	0
	L/F	Y	<i>Gerygone igata</i>		0	0	0
	L/F	Y	<i>Rhipidura fuliginosa</i>		1	1	2
	L/F	Y	<i>Petroica australis</i>		1	9	10
	L/F	Y	<i>Petroica macrocephala</i>		0+ ?1	2	2+?1
	L/F	Y	<i>Notiomystis cincta</i>	R	1	-	1
	L/F	Y	<i>Anthornis melanura</i>		4	11	15
	L/F	Y	<i>Prosthemadera novaeseelandiae</i>		29	40	69
	L/F	Y	<i>Callaeas cinerea</i>	R	20	16 *	36
	L/F	Y	<i>Philesturnus carunculatus</i>	R	6	12	18
	L/F	Y	<i>Heteralocha acutirostris</i>	H	5	-	5
	L/F	Y	<i>Turnagra capensis</i>	H	5	9	14
L/F	Y	<i>Corvus moriorum</i>	P	13	13	26	

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