Prehistoric bird extinctions and human hunting

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Holocene fossils document the extinction of hundreds of bird species on Pacific islands during prehistoric human occupation. Human hunting is implicated in these extinctions, but the impact of hunting is difficult to disentangle from the effects of other changes induced by humans, including habitat destruction and the introduction of other mammalian predators. Here, we use data from bones collected at a natural sand dune site and associated archaeological middens in New Zealand to show that, having controlled for differences in body mass and family membership (and hence for variation in life-history traits related to population growth rate), birds that were more intensively hunted by prehistoric humans had a higher probability of extinction. This result cannot be attributed to preservation biases and provides clear evidence that selective hunting contributed significantly to prehistoric bird extinctions at this site.

Keywords: body size; extinction; flightlessness; habitat loss; hunting; New Zealand

1. INTRODUCTION

A dramatic loss of bird diversity followed the first arrival of humans on islands throughout the Pacific (Steadman 1989, 1995; James & Olson 1991; Olson & James 1991; Worthy 1997*a*; Steadman *et al.* 1999). In New Zealand, at least 34 land-bird species became extinct on the two main islands between initial settlement by the Maori (*ca.* AD 1300) and European arrival (AD 1769), including 11 species of large flightless moa (Dinornithiformes) (Holdaway 1999). Predation by humans is implicated in these extinctions because the bones of prehistorically extinct birds are common in middens (Worthy 1997*b*), showing that people regularly killed and consumed these species, and because extinctions mainly affected those species apparently most vulnerable to human hunters, including large-bodied, flightless birds (Cassels 1984; Holdaway 1989).

However, the evidence that human predation had a role in prehistoric bird extinctions is circumstantial and can be challenged on two fronts. First, impacts associated with human arrival other than hunting, including habitat destruction and the introduction of mammalian predators, could account for bird losses on most Pacific islands (Olson & James 1982; Cassells 1984; Steadman 1995). Second, although the bones of prehistorically extinct birds are often found in middens, so too are the bones of species that survived prehistoric human occupation, showing that prehistoric humans hunted a wide variety of birds, only some of which became extinct (Worthy 1997*b*).

Prehistoric birds would have been differentially susceptible to extinction from human hunting due to differences in the rate at which their populations were harvested, and in the ability of those populations to recover from harvesting, due to differences in life-history traits related to population growth rate (e.g. clutch size, age at sexual maturity and inter-clutch interval (Holdaway & Jacomb 2000; Owens & Bennett 2000; Purvis *et al.* 2000)). One way to establish that human hunting had a role in prehistoric extinctions is to demonstrate that, having accounted for differences in life history, the extinct species were those that were most intensively hunted by humans. This requires estimating both the life-history traits of, and the hunting pressure applied to, species in a prehistoric avifauna, estimates which are difficult to obtain.

In this study, we use data on the relative abundances of species recovered from archaeological middens and from adjacent natural sand dunes in New Zealand to quantify prehistoric hunting pressure. We show that, having controlled for two variables that capture differences among species in life-history traits related to population growth rate (family membership and body mass), species more intensively hunted by prehistoric humans were more likely to have become extinct. This directly links these extinctions to human hunting.

2. METHODS

We use data from a recently described and remarkably rich fossil avifauna from Marfells Beach, northeast South Island, New Zealand (Worthy 1998). The site is a series of sand dunes that sealed off an estuary from the sea, forming a large freshwater lake, *ca.* 1800 years before present (Ota *et al.* 1995). Eight thousand, four hundred and thirty-five bones from at least 982 individuals, representing 95 avian taxa, have been described from collections here between 1944 and 1979. The bones derive from two sources: (i) dune deposits less than 1800 years old, in which the bones of birds that died on the dune surface have accumulated naturally, and (ii) archaeological middens that occur as a distinct layer in the dunes and that preserve the remains of species hunted in the area by Maori. For each taxon, we have data on the number of bones, and the minimum number of individuals (MNI) those bones represent, recovered from the dune and midden deposits (Worthy 1998).

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Table 1. *Significance tests for the fixed-effect predictors included in two GLMMs that predict prehistoric extinction at Marfells Beach, with the taxonomic variable 'family' included as a random effect.*

(In the unadjusted model, the observed values of the minimum number of individuals (MNI) in the dune and midden deposits are used in calculating the selection ratios. In the adjusted model, the MNI of non-extinct species in the dune deposits are discounted by a proportion equal to 0.61 to account for differential accumulation times (see § 3).)

	unadjusted model		adjusted model	
fixed effect	type III χ^2	p	type III χ^2	p
selection ratio	12.3	< 0.001	3.9	0.049
habitat	16.6	< 0.001	6.3	0.012
$\log_e$ (body mass)	6.8	0.009	7.9	0.005
selection ratio × $\log_e$ (body mass)	12.6	< 0.001	4.3	0.039

We excluded from our analyses taxa that were not in the pre-human breeding avifauna of New Zealand, because these may have colonized the area only after it was abandoned by the Maori (see also § 3). We also excluded birds that forage primarily at sea (petrels, gannets, penguins and shags), because these species may be over-represented in the dune deposits due to storm wrecks (Powlesland & Powlesland 1993). Out of the remaining 59 taxa (615 MNI) included in our study, 18 had become extinct in the northeast of South Island by the time Europeans arrived in New Zealand (Holdaway 1999). Four of these extinct taxa were species of moa, but moa were relatively uncommon at Marfells Beach, comprising only 16 out of 615 MNI in our analysis.

To estimate relative hunting pressure, we calculated a selection ratio (Manly *et al.* 1993), w_i, using the MNI of each taxon collected in the dune and midden deposits at Marfells Beach: $w_i = o_i/p_i$, (where o_i is the MNI of taxon i recovered from the middens divided by total MNI recovered from the middens, and p_i is the MNI of taxon i recovered from dunes divided by total MNI recovered from dunes). A value of $w_i > 1$ indicates positive selection of a taxon by Maori hunters: the taxon was disproportionately abundant in the middens relative to its abundance in the local area, as measured by its abundance in the natural dune deposits. A value of $w_i < 1$ indicates avoidance: a taxon was less abundant in the middens relative to its abundance in the natural dune deposits. Overall, larger values of w_i indicate greater hunting pressure.

For prehistorically extinct birds, we cannot estimate directly life-history traits relating to population growth rate, such as clutch size, age at sexual maturity and inter-clutch interval. However, among birds in general, such traits are correlated with body mass (Bennett 1986; Sæther 1987). These life-history traits also tend to vary relatively little among species classified in the same family, but show significant variation across families (Bennett 1986; Owens & Bennett 1995). To account for differences in life history, we therefore included body mass and a variable coding for family in our analyses. Classification to family followed Sibley & Monroe (1990) (or Turbott (1990) for the extinct species that were not classified in Sibley & Monroe (1990)). Body mass values were taken from Holdaway (1999). A further confounding factor is that the taxa recovered from Marfells Beach occurred in different habitats: 26 out of the 59 taxa occupied coastal or freshwater habitats, and the remaining 33 taxa occupied terrestrial, mostly forest, habitats. Extensive forest clearance by fire occurred in the northeast of South Island shortly after Maori arrival (McGlone 1983; McGlone & Basher 1995) and this habitat loss may have selectively reduced populations of terrestrial birds, increasing their susceptibility to

extinction. We therefore included an additional variable coding species by habitat (either coastal and freshwater, or terrestrial) in our analyses.

We tested if greater hunting pressure (larger values of the selection ratio, w_i) was associated with a higher probability of extinction, having controlled for differences among taxa in body mass, habitat use and family membership by fitting a generalized linear mixed model (GLMM), using the SAS macro GLIMMIX (Littell *et al.* 1996). GLMMs allow the modelling of variances and covariances through the specification of random effects, accommodating situations in which observations at one level are correlated because they are clustered into higher level groups and therefore may not be independent (Goldstein 1995). In this case, we included a variable coding for family as a random effect in the model. This acts to control for unmeasured life-history traits that vary among taxa at the family level, and ensures that the significance tests for the fixed-effect predictors (see below) are not biased by non-independence due to unmeasured traits shared at the family level (e.g. any avian life-history traits that vary mainly among families, as noted above). Our response variable was binary (whether taxa became prehistorically extinct or not in the Marfells Beach region), and we specified a binomial error distribution and logit link function. We included the variables selection ratio (w_i), body mass and habitat as fixed-effect predictors in the model. In addition, we tested for a significant interaction between w_i and body mass, which tested for a disproportionately higher extinction risk among larger-bodied (lower population growth rate) taxa for a given level of hunting pressure.

3. RESULTS

All three fixed effects along with the interaction between selection ratio and body mass were highly significant predictors of prehistoric extinction in a GLMM with family as a random effect (table 1). The form of these relationships is evident from table 2 and figure 1. Among freshwater and coastal species, the extinction rate was higher in taxa that were positively selected by Maori hunters (5 out of 13) compared with those that were not (0 out of 13). Furthermore, among those freshwater and coastal species that were positively selected by hunters, extinctions were concentrated in the larger-bodied taxa (figure 1). Hence, greater hunting pressure in combination with larger body mass (lower population growth rate) led to the extinction of a predictable subset of freshwater and coastal species. The same pattern holds for species from terrestrial habitats. Of the five terrestrial taxa that were positively

Table 2. *The number of fossil taxa in the prehuman avifauna (excluding seabirds) collected from Marfells Beach by habitat, selection ratio and extinction response categories.*

(A selection ratio of more than 1 indicates positive selection by Maori hunters (see § 2).)

habitat	selection ratio	extinction response	
		surviving	extinct
freshwater and coastal	< 1	13	0
	> 1	8	5
terrestrial	< 1	19	9
	> 1	1	4

selected by hunters, it was the four largest-bodied taxa that became extinct. However, nine large-bodied terrestrial taxa became extinct despite relatively low hunting pressure at Marfells Beach, elevating the extinction rate among terrestrial species (13 out of 33) compared with freshwater and coastal species (5 out of 26).

Our finding that greater hunting pressure is associated with a higher extinction rate rests on the assumption that the relative abundance of a taxon in the dune deposits provides an unbiased estimate of its relative abundance in the prehistoric avifauna. With the exception of seabirds (which we excluded from the analysis), it is unlikely that a significant bias would arise as a result of species being selectively deposited on the dunes. Unlike many natural preservation sites, which are biased towards trapping certain kinds of bird, species ought to be deposited on the dunes in direct proportion to their natural abundance in the local avifauna. We would expect, however, a significant size bias in bone preservation and collection, with the bones of larger-bodied species surviving for longer and being more readily noticed and collected (sieves are not recorded as being used at Marfells Beach). This would result in individuals of larger-bodied taxa being over-represented in the dunes relative to their abundance in the local avifauna. A similar size bias in bone recovery should also occur in the middens. The crucial point is whether the strength of this bias differs between the dune and midden deposits, thus biasing the selection ratios.

To test this, we estimated the rate of bone recovery for each taxon in the two sources (dune or midden deposit) as $\log_e$ (total number of bones collected/MNI). As expected, taxa of larger body mass had a significantly higher rate of bone recovery and, for a given body mass, the bone recovery rate was also higher in the dune relative to the midden deposits (table 3), presumably because bones of hunted individuals would have been destroyed by cooking and eating. More importantly, however, the body mass × source interaction term was non-significant when added to this model ($t = 1.30$, $p = 0.20$), showing that any difference in the size-related recovery rate for the two sources does not seriously bias the selection ratios.

The Marfells Beach site was probably abandoned by the Maori before European arrival (abandonment in the period *ca.* AD 1300–1769). There must, therefore, have been a period of at least *ca.* 200 years during which only the bones of birds that survived prehistoric Maori occupation were accumulating in the dunes. As a result, we would expect these taxa to be over-represented in the dune
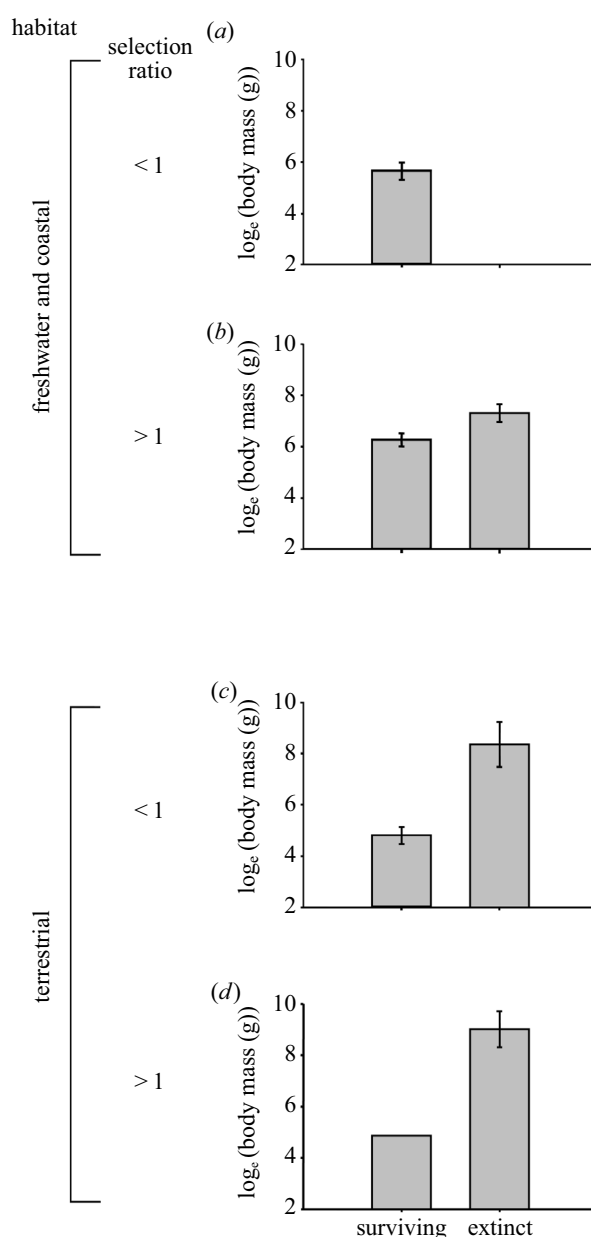

Figure 1. The mean $\log_e$ (body mass) ($\pm$ s.e.m.) of prehistorically extinct and surviving taxa collected at Marfells Beach, by habitat and selection ratio categories. A selection ratio of more than 1 indicates positive selection by Maori hunters (see § 2). Statistics show the results of *t*-tests comparing mean $\log_e$ (body mass) between surviving and extinct taxa in each category ((*a*) no statistical comparison possible; (*b*) $t_{11} = 2.5$, $p = 0.030$; (*c*) $t_{26} = 4.7$, $p < 0.001$; (*d*) $t_3 = 2.7$, $p = 0.077$).

deposits relative to their availability to prehistoric hunters, biasing the selection ratios in favour of the outcomes we observed. However, our conclusions are robust to this effect. For those species that survived prehistoric Maori occupation, we reduced the MNI in the dunes to a proportion equal to 0.61. Assuming that bones have accumulated in the dunes at a constant rate, this has the effect of 'resetting' the MNI of non-extinct species in the dune deposits to a point 700 years ago (the approximate time of Maori arrival, given that the dunes are 1800 years old; Ota *et al.* 1995). We then recalculated the selection ratios using these adjusted MNI values. This procedure

Table 3. Regression statistics for bone recovery rate.
(The response variable is bone recovery rate ($\log_e$ (total number of bones collected/MNI)) for the 32 taxa found in both the dune and midden deposits at Marfells Beach ($n = 64$).)

variable	d.f.	parameter estimate	standard error	t	p
$\log_e$ (body mass)	1	0.206	0.0584	3.54	< 0.001
source: midden	1	−0.602	0.1896	3.17	0.002
dune		0			

adjusts the ratios as if extinctions had followed an extreme 'blitzkrieg' scenario, in which the prehistorically extinct birds were eliminated from Marfells Beach almost as soon as the Maori arrived in New Zealand, and the site was then immediately abandoned. The selection ratios calculated using these adjusted MNI values still significantly predict the probability of extinction (table 1), showing that our results are robust even under a 'blitzkrieg' scenario.

In addition to identifying predictors of extinction probability, we tested if two traits that might affect a species' vulnerability to human hunters were associated with the level of hunting pressure. Whether taxa could fly or not was unrelated to a taxon's ranking by selection ratio (Kruskall–Wallis $\chi^2 = 0.34$, $p > 0.5$; 12 out of the 59 taxa were flightless). By contrast, there was a significant positive correlation between body mass and selection ratio (Spearman $r = 0.40$, $n = 59$, $p = 0.002$), showing that the Maori selectively hunted larger-bodied birds.

4. DISCUSSION

Our main finding is that birds subjected to greater prehistoric hunting pressure were more likely to have become extinct at Marfells Beach. This result is robust to potential differences in extinction risk among species caused by differences in their habitat use, body mass and covariation among taxa due to unmeasured family-level traits. This provides, to our knowledge, the first direct evidence that hunting contributed significantly to the selective extinction of prehistoric birds in an island avifauna.

For a given level of hunting pressure, larger-bodied taxa were also more prone to extinction, fitting the prediction that species with life-history traits associated with lower population-growth rates face a higher risk of extinction for a given level of harvesting. Large-bodied bird species were doubly doomed to extinction at Marfells Beach—not only would their life histories limit their ability to recover from hunting, but also Maori hunters selectively targeted larger-bodied birds. This combination of lower population growth rates and higher hunting pressure led to particularly high rates of extinction among large-bodied taxa.

Habitat use was also a significant predictor of extinction risk, and several large-bodied terrestrial taxa became extinct despite relatively low hunting pressure at Marfells Beach. One explanation for the greater susceptibility of terrestrial taxa is that this group would have suffered population decline as a result of widespread forest clearance in the eastern South Island following Maori arrival (McGlone 1983; McGlone & Basher 1995). This habitat destruction may have had a stronger impact on larger-bodied birds that required larger tracts of continuous habitat to persist in a locality. Overall, our results suggest that prehistoric agents of population decline (hunting and habitat destruction) interacting with the traits of the species involved acted to drive a predictable subset of species to extinction.

Numerous species of flightless birds have become extinct on Pacific islands following human arrival, leading to suggestions that flightless taxa were particularly prone to predation by humans and other introduced mammals (Diamond 1981; Steadman 1991; Milberg & Tyrberg 1993). Contrary to this, Maori hunters at Marfells Beach showed no tendency to target flightless birds. In an avifauna unaccustomed to mammalian predators, birds with the power of flight may have lacked a predator escape response and been as easy to catch as flightless species. Presented with such an avifauna, early human hunters may have been spoiled for choice. It appears they set about consuming, and eventually eliminating, the most profitable, large-bodied prey items.

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