Extinction and endemism in the New Zealand avifauna

Richard P. Duncan1,2,* and Tim M. Blackburn3

ABSTRACT

Aim Species belonging to higher taxa endemic to islands are more likely to go extinct following human arrival. This selectivity may occur because more highly endemic island species possess features that make them uniquely vulnerable to impacts associated with human arrival, specifically: (1) restricted distribution (2) reduced predator escape response, including loss of flight, and (3) life history traits, such as large body mass, associated with greater susceptibility to hunting or habitat loss. This study aims to identify which of these features can explain the selective extinction of more highly endemic bird species in New Zealand.

Location North and South Island, New Zealand.

Methods Bird species breeding in New Zealand prior to human arrival were classified according to whether they became extinct or not during two periods of human settlement, prehistoric (post-Maori but pre-European arrival) and historic (post-European arrival). We modelled the relationships between extinction probability, level of endemism and life history traits in both periods.

Results The prehistoric extinction–endemism relationship can be explained entirely by the selective extinction of large-bodied species, whereas the historic extinction–endemism relationship appears due to increased susceptibility to introduced predators resulting from the loss of predator escape responses, including loss of flight.

Conclusions These features may explain extinction–endemism relationships more generally, given that human hunting and predator introductions are major impacts associated with human arrival on islands.

Keywords Avifauna, birds, endemic species, extinction, human impacts, islands, predation, New Zealand.

INTRODUCTION

The extinction of species results in a loss of evolutionary history, but how much is lost depends on how extinctions are distributed across a phylogeny. Greater loss of evolutionary history occurs when extinctions are clumped and result in the loss of whole clades (Nee & May, 1997; Purvis et al., 2000). For birds, the extinction of island species has been a major factor driving recent losses of evolutionary history, for two reasons. First, isolation on islands is a major factor in the evolutionary diversification of birds so that islands frequently harbour endemic clades (Carlquist, 1974) and second, island species are disproportionately prone to extinction (King, 1985; Johnson & Stattersfield, 1990). Significantly, these two features are linked: more highly endemic island species tend to be more susceptible to extinction (McDowall, 1969; Steadman, 1991; Adler, 1992). For example, the probability of extinction since human arrival increases steadily with the taxonomic level at which bird species are endemic to New Zealand (McDowall, 1969; Table 1), a pattern that markedly accelerates the loss of evolutionary history. In New Zealand, the loss of 10 species of moa (Bunce et al., 2003) meant the global extinction of an entire order of birds (Dinornithiformes).

Recent extinctions of birds on islands have been associated with human arrival and impacts such as habitat destruction and predation (Olson & James, 1982; Steadman, 1995; Holdaway, 1999; Holdaway & Jacomb, 2000; Grayson, 2001; Duncan et al.,...
2002). The susceptibility to extinction of more highly endemic island birds suggests that these species may share traits that make them especially vulnerable to human arrival. Three features have been associated with more highly endemic island birds that might explain this vulnerability to extinction: (1) Wilson (1961) proposed that species colonizing island groups undergo a series of evolutionary changes leading to a decline in population size as their distribution becomes increasingly restricted within an archipelago, increasing their susceptibility to extinction (the taxon cycle, see Greenslade, 1968; Ricklefs & Cox, 1972; Jones et al., 2001); (2) islands frequently lack native predatory mammals, so that birds isolated on islands often lose predator escape responses, including the ability to fly (Diamond, 1981; McNab, 1994a, 1994b; Roff, 1994), making them easy prey when mammalian predators arrive (Milberg & Tyrberg, 1993; Grant, 1998); (3) life-history traits associated with high levels of endemism in island birds, particularly large body mass and low reproductive output, may increase their susceptibility to hunting and habitat loss (Cassels, 1984; Diamond, 1989; Holdaway, 1989; Holdaway & Jacomb, 2000; Cassey, 2001; Duncan et al., 2002).

While these features have been associated with extinction susceptibility in island endemics, few quantitative studies have addressed traits that predispose more highly endemic species to extinction. Our aim in this study is to use the avifauna of New Zealand as a case study to test the different explanations for why more highly endemic island birds suffer higher rates of extinction. New Zealand provides a unique opportunity to do this because it is an isolated archipelago only recently colonized by humans (c. 700 years ago) that contains abundant, well-preserved remains of the Holocene bird assemblage. Consequently, it is the only place in the world where the prehuman avifauna has been comprehensively reconstructed (Atkinson & Millener, 1991; Worthy & Holdaway, 1993, 2002; Worthy, 1997, 1998a, 1998b; Holdaway et al., 2001). Humans colonized New Zealand in two waves, with Maori settlement beginning c. 1300 AD, and European settlement following their arrival in 1769 AD. Bird extinctions following human arrival can reliably be assigned to one of these two settlement periods (Worthy & Holdaway, 2002). Furthermore, the impacts associated with human arrival differ between these periods due, in particular, to the different species of mammalian predators introduced (Holdaway, 1999). The major introduced predators in prehistoric (Maori) times were humans and kiore (Pacific rat, *Rattus exulans*). Europeans introduced the brushtail possum (*Trichosurus vulpecula*), brown rat (*Rattus norvegicus*), black rat (*R. rattus*), house mouse (*Mus domesticus*), domestic cat (*Felis catus*), hedgehog (*Erinaceus europaeus*) and three mustelids (*Mustela erminea*, *M. furo* and *M. nivalis*). Several of these introduced predators have extensively invaded native habitats (King, 1990). Because predators will have had different impacts (Holdaway, 1999), we examine relationships between level of endemism, species traits and extinction vulnerability separately for the two episodes of human arrival.

### METHODS

#### Data sources

We used the recently updated list of 131 species in the prehuman breeding avifauna of the two main islands of New Zealand (North and South Islands) listed in Appendix 2 of Holdaway et al. (2001), but with the classification of *Dinornis* species following Bunce et al. (2003).

Species were assigned to one of four endemism classes (non-endemic, species, genus, higher) reflecting the taxonomic level of their association with New Zealand (defined for this purpose as North, South and Stewart Islands and their associated inshore islets, and New Zealand’s outlying island groups: Auckland, Campbell, Chatham, Antipodes, Bounty, Kermadec and Snares Islands). Level of endemism was determined from taxonomic relationships in Sibley & Monroe (1990) and Holdaway et al. (2001).

Extinct species in the prehuman avifauna were classified as either prehistorically extinct — species that have become extinct on the two main islands since human arrival but prior to European

#### Table 1

Breeding birds in the prehuman New Zealand avifauna classified by level of endemism, extinction outcome, geographical range, life history and flying ability. The numbers in columns are the percentage of species exhibiting a trait for all species in the avifauna and for species at each level of endemism. *n* = number of species in the avifauna at each endemism level with *n* = 131 for all species, except where *n* is given in the column title. *χ²* = the chi-square value for a test of association between level of endemism and the trait in that column. **P < 0.01, ***P < 0.001

<table>
<thead>
<tr>
<th>Endemism level</th>
<th>Extinction outcome (% extinct historic)</th>
<th>Geographic range (% confined to one island)</th>
<th>Life history (% terrestrial</th>
<th>% ground or burrow nesting</th>
<th>% egg size ≤ 60 mm</th>
<th>Flying ability (% flightless)</th>
<th>% lost flight in NZ</th>
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<tr>
<td>All species</td>
<td>31</td>
<td>24</td>
<td>39</td>
<td>53</td>
<td>69</td>
<td>69</td>
<td>25</td>
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<td>13</td>
<td>16</td>
<td>71</td>
<td>74</td>
<td>3</td>
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<td>Species</td>
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<td>26</td>
<td>42</td>
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<td>75</td>
<td>39</td>
<td>71</td>
</tr>
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<td><em>χ²</em></td>
<td>13.9**</td>
<td>14.4**</td>
<td>31.7***</td>
<td>47.8***</td>
<td>7.4</td>
<td>14.7**</td>
<td>45.3***</td>
</tr>
</tbody>
</table>
arrival in New Zealand (pre 1769 AD), or historically extinct — species that have become extinct on the two main islands since European arrival (1769 AD — present day). We classified as historically extinct several species that no longer have natural populations on the two main islands, but that still exist on offshore islands or as small, intensively managed populations (e.g. stitchbird Notiomystis cinerea, kakapo Strigops habroptila, South Island takahē Porphyrio hochstetteri and black stilt Himantopus novaezelandiae).

We collated data on the following life history traits considered likely to influence species susceptibility to extinction (see Holdaway, 1999).

1. Adult body mass (g), log_{10} transformed. We conducted our analyses two ways: including body mass as a continuous variable; and including body mass as a categorical variable divided into four classes \([1 = \leq 1.5 \text{ log}_{10}(g) \leq 32 \text{ g}, 2 = > 1.5–2.5 \text{ log}_{10}(g) \leq 32–320 \text{ g}, 3 = > 2.5–3.5 \text{ log}_{10}(g) \leq 320–3200 \text{ g}, 4 = > 3.5 \text{ log}_{10}(g) \geq 3200 \text{ g})\). The results were qualitatively the same, and for ease of presentation we include only results with body mass treated as a categorical variable.

2. Egg length (mm). Following Holdaway (1999) we divided species into two vulnerability groups based on their susceptibility to predation by introduced kiore Rattus exulans (Atkinson, 1978, 1985): those with eggs \(\leq 60 \text{ mm}\) (more susceptible) and those with eggs \(> 60 \text{ mm}\) (less susceptible).

3. Nest site. Species were classed as ground/burrow nesters, elevated nesters using open nest sites, and elevated nesters using holes.

4. Habitat. Species were allocated to one of four classes (oceanic seabird, coastal, freshwater, terrestrial) depending on the foraging habitat they were principally associated with. Body mass and egg length data were taken from Holdaway (1999).

As an estimate of prehuman geographical range size, we classified each species as having a prehuman population on either one or two of the main islands from the distributions in Appendix 2 of Holdaway et al. (2001) and from Bunce et al. (2003). A more precise estimate of prehuman range size is not available for most species.

We classified species according to their ability to fly. Loss of flight may evolve in response to a lack of mammalian predators (Diamond, 1981; McNab, 1994a; Roff, 1994), increasing susceptibility to mammalian predators when they are encountered. Thirty-four species in the prehuman breeding avifauna of North and South Island are flightless. Eighteen of these species, however, have closest relatives elsewhere that are also flightless (10 species of moa, Dinornithiformes; five species of kiwi, Apterygiformes; and three species of penguin, Sphenisciformes).

We classified these species in one group: as being flightless, but most likely having lost the ability to fly prior to colonizing New Zealand, and not in response to a lack of mammalian predators in New Zealand. The remaining 15 flightless species have close relatives elsewhere that can fly. We classified these species in a second group: because they have volant relatives elsewhere, they most likely lost the ability to fly after colonizing New Zealand (Worthy, 1988; Trewick, 1997), probably in response to the lack of mammalian predators. The third group comprised species able to fly.

Data analysis

First, we tested whether the previously observed relationship between level of endemism and extinction probability for terrestrial New Zealand birds (McDowall, 1969) holds for both prehistoric and historic extinctions using our updated list of breeding species in the prehuman avifauna. A significant relationship between level of endemism and extinction probability would imply a greater loss of evolutionary history than expected if extinctions occurred at random, because more highly endemic clades would be more likely to go extinct. To quantify this, we calculated the actual amount of evolutionary history lost at four taxonomic levels (order, family, genus and species). The amount of history lost was defined simply as the number of endemic New Zealand clades at each level that became extinct following human arrival (for example, extinction of the moa clade resulted in the loss of one endemic order, two endemic families, six endemic genera and 10 endemic species). We then tested if the actual loss of evolutionary history at each level was greater than that expected from random extinction. We did this by simulating extinction of the same number of species as actually went extinct assuming that each species had an equal probability of extinction, calculated the resulting loss of evolutionary history, and repeated the simulation 5000 times to generate a distribution of expected losses under random extinction. We then compared the actual loss of evolutionary history at each taxonomic level with the distribution of losses expected from random extinction.

Second, we identified traits associated with high levels of endemism in New Zealand birds by testing whether geographical range size, life history traits and loss of flying ability vary predictably with taxonomic level of endemism.

Third, we identified traits that were significantly associated with the probability of both prehistoric and historic extinction. Our response variable was whether species became extinct or not (either prehistorically or historically) and we included geographical range size, life history traits and flying ability as explanatory variables. These traits allow us to distinguish among the three hypotheses proposed to explain the relationship between extinction and endemism outlined in the introduction. Our analysis of prehistoric extinctions included all 131 species in the original avifauna, while our analysis of historic extinctions included only the 91 species that survived the prehistoric period.

An issue with comparative studies is that species may not represent independent data points in across-species comparisons (Harvey & Pagel, 1991). To allow for the fact that more closely related species tend to share traits in common that could confound the relationships we are testing, we analysed the data using Generalized Estimating Equations (GEE). GEE are extensions of Generalized Linear Models (GLM) that allow for correlated, non-normal response data (Diggle et al., 1994; Paradis & Claude, 2002). Here, our response variable is binary (extinct or not) and we specified a logit link function and binomial error structure. We modelled likely non-independence in our data by assuming a common correlation among extinction outcomes in the same family, the level at which much important variation in avian life
history resides (Bennett & Owens, 2002). To do this, we specified an exchangeable working correlation structure with family as the clustering variable in all our analyses. GEE were fitted using the ‘repeated’ statement in PROC GENMOD in SAS v. 6.12 (SAS Institute, 1990).

We fitted univariate GEE including each explanatory variable alone to determine its association with extinction probability. We then constructed a minimal adequate model (MAM) starting with a model containing all explanatory variables, except level of endemism, and then dropping the variable that resulted in the greatest improvement to model fit (i.e. a backward selection process). This was continued until the MAM was obtained in which the removal of any variable resulted in a poorer fitting model. We assessed model fit using $\text{QIC}_u$. This is a modified version of Akaike's Information Criterion that can be used with GEE, where the likelihood has been replaced by the quasi-likelihood (see Pan, 2001). Smaller values of $\text{QIC}_u$ indicate a better fitting model.

Having identified a MAM we then tested if that model could be improved by the addition of level of endemism as an explanatory variable. This step allows us to test the central question of our paper: can the extinction–endemism relationship be accounted for by other variables included in this study? If level of endemism is significantly associated with extinction probability in a univariate model, but adding level of endemism to the MAM does not improve the model fit, then the extinction–endemism relationship can be accounted for by one or more of the explanatory variables in the MAM. Alternatively, if adding level of endemism to the MAM improves the model fit, then something other than the explanatory variables in the MAM must explain at least part of the extinction–endemism relationship.

**RESULTS**

Species endemic to New Zealand at progressively higher taxonomic levels have suffered higher rates of extinction both prehistorically and historically (Table 1). This has caused a significantly greater loss of evolutionary history than expected from random extinction. Sixty-two of the 131 species in the prehuman breeding avifauna of North and South Islands have gone extinct since human arrival. This equates to the following loss of evolutionary history due to the loss of endemic New Zealand clades from these islands: one endemic order, three endemic families, 21 endemic genera and 44 endemic species (the probabilities that these levels of extinction would occur by chance alone given random extinction, as calculated by comparing the actual losses with the distribution of losses obtained from simulating random extinction, are: order $P = 0.023$; family $P < 0.001$; genus $P < 0.001$; species $P < 0.001$).

In New Zealand, more highly endemic species tended to possess the following traits (Table 1, Fig. 1): (1) they had more restricted distributions, being more likely to occur on only one of the two main islands; (2) species endemic at the genus level or higher were more likely to occur towards the extremes of the body mass distribution for this assemblage, with species endemic at the family level or higher tending to be relatively larger-bodied and less likely to have eggs in the size range susceptible to kiore predation ($\leq 60$ mm in length); (3) more highly endemic species were more likely to be terrestrial (predominantly forest) birds rather than freshwater, coastal or oceanic seabirds; and (4) they were more likely to be flightless and, excluding those species with flightless relatives elsewhere, were more likely to have lost the ability to fly since arriving in New Zealand.

Figure 1  Body mass frequency distributions for bird species in the prehuman New Zealand avifauna classified according to the level at which they are endemic to New Zealand: (a) non-endemic, (b) endemic species, (c) endemic genus, (d) endemic at the family level or higher. Numbers in brackets are the number of species at each level of endemism. The body mass classes are: $1 = \leq 32$ g, $2 = > 32–320$ g, $3 = > 320–3200$ g, $4 = > 3200$ g.
The MAM for prehistoric extinctions included body mass, habitat, nesting site and egg size (Table 2). This model shows that larger-bodied species were more likely to go extinct, that extinction probability varied with habitat and increased from coastal to freshwater to terrestrial to seabirds, that ground or burrow nesting species had a higher probability of extinction than species with elevated nest sites, and that species with eggs \( \leq 60 \text{ mm} \) in length had a higher probability of extinction relative to species with larger eggs. Adding level of endemism to the MAM resulted in a poorer-fitting model (\( QIC_u \) for the MAM = 116.0, \( QIC_u \) for the MAM plus level of endemism = 117.3).

These results imply that the significant relationship between level of endemism and prehistoric extinction probability (Table 1) results from an association of level of endemism with one or more of body mass, habitat, nesting site, or egg size. Of these, the greater susceptibility of more highly endemic birds can be entirely accounted for by the association of body mass with level of endemism. A GEE model that includes body mass alone as a variable explaining prehistoric extinction provides a better fit (\( QIC_u \) = 139.4) than a model including both body mass and level of endemism (\( QIC_u \) = 142.1), implying that variation in body mass can adequately account for the extinction–endemism relationship. In contrast, level of endemism improves the fit when added to models containing each of habitat, nesting site and egg size, implying that these variables alone cannot adequately account for the relationship.

Three variables were retained in the MAM for historic extinctions: body mass, flying ability and habitat. Adding level of endemism to this MAM significantly improved model fit (\( QIC_u \) for the MAM = 94.3, \( QIC_u \) for the MAM plus level of endemism = 86.6). Furthermore, having included level of endemism, removal of any other variables led to a poorer fitting model, so that the final model explaining historic extinctions included level of endemism, body mass, flight and habitat (Table 3). For historic extinctions, more highly endemic species were more prone to extinction, species of intermediate body mass (in the range 32–320 g) suffered a higher rate of extinction than other species, species classed as having lost the ability to fly since arriving in New Zealand were more prone to extinction than either volant species or those flightless species with flightless relatives elsewhere, and seabirds were more prone to extinction than species reliant on other habitats.
DISCUSSION

Following human arrival, extinctions in the New Zealand avifauna have resulted in a greater loss of evolutionary history than expected by chance. This has occurred because species in more highly endemic clades suffered higher rates of extinction. The limited data available suggest that this pattern holds for other islands where more highly endemic bird species are also especially vulnerable to extinction (Ricklefs & Cox, 1972; Steadman, 1991; Adler, 1992). Understanding why loss of evolutionary history is accelerated through the biased extinction of more highly endemic species requires that we identify features associated with higher levels of endemism that might explain extinction vulnerability following human arrival on islands.

We identified three features previously associated with more highly endemic island birds that might explain their extinction vulnerability (see Introduction): restricted distribution, flightlessness, and traits associated with large body mass. All three features tend to characterize more highly endemic birds in New Zealand (Table 1). Nevertheless, restricted distribution, as measured by the number of islands occupied, was not included in any of the models explaining extinction patterns (Tables 2 and 3). Hence, while restricted distribution may be a feature of more highly endemic island taxa (Wilson, 1961; Ricklefs & Cox, 1972), other traits associated with higher levels of endemism account for extinction patterns in New Zealand birds (see also Webb et al., 2001).

A greater proportion of more highly endemic species were both flightless and appeared to have lost the ability to fly since colonizing New Zealand (see also Worthy, 1988; Trewick, 1997). The repeated evolution of flightlessness in island birds has been attributed to the reduced need for predator escape on islands that lack native predatory mammals (Diamond, 1981; Roff, 1994), coupled with the benefits to energy conservation associated with reducing the muscle mass required for flight (McNab, 1994a, 1994b). Numerous species of flightless bird have gone extinct on islands following human arrival, leading to the suggestion that loss of flight renders species particularly prone to predation by humans and other introduced mammals (Cassels, 1984; Daugherty et al., 1993; Milberg & Tyrberg, 1993; Holdaway, 1999; Cassey, 2001).

For prehistoric extinctions in New Zealand, however, flightlessness was not included as a factor predisposing species to

<table>
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<tr>
<th>Trait Category</th>
<th>Univariate Parameter Z</th>
<th>Final model Parameter</th>
<th>Empirical SE</th>
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Table 3 Parameter estimates for traits used to predict the probability of historic extinction for birds in the prehuman New Zealand avifauna (n = 91), obtained by fitting generalized estimating equations (GEE) with family included as a clustering variable. For each trait, species in categories with more negative parameter estimates had a higher probability of extinction relative to species in the category with a parameter estimate of 0. For univariate models, each trait was included alone and the Z scores test whether the parameter estimate for a category differs significantly from the category with a parameter estimate of 0. For the final model (see text) the parameter estimates and empirical standard errors (SE) obtained from the GEE are shown.

*P < 0.05, **P < 0.01, ***P < 0.001
extinction in the MAM. This result is supported by independent data on Maori hunting preferences at Marfell's Beach, South Island. There, a comparison of archaeological and natural bone deposits showed that Maori did not selectively hunt flightless species, although they targeted larger-bodied species, several of which were flightless (Duncan et al., 2002). The other important prehistoric mammalian predator, kiore, most likely had greatest impact as a ground nest predator, targeting the nests of ground-nesting birds regardless of whether they could fly or not (Holdaway, 1999). Our results support this: birds with eggs in the size range susceptible to kiore predation (< 60 mm in length), and ground- or burrow-nesting birds were more likely to suffer prehistoric extinction (Table 2). These include many species of volant, burrow-nesting seabirds that bred on New Zealand's main islands prior to human arrival (see also Roff & Roff, 2003).

In contrast, species that have lost the ability to fly since colonizing New Zealand were more prone to extinction following European arrival, compared with either volant species or species with flightless relatives elsewhere. This suggests that loss of flight, in response to an absence of native mammalian predators, may have predisposed New Zealand's more highly endemic species to extinction following the arrival of European-introduced predators. Unlike kiore, which may have been primarily a nest predator, many of the European-introduced predators hunt adult birds (King, 1990). In these circumstances, loss of flight, in species that previously used flight to escape mammalian predators, may have been a significant disadvantage. Nevertheless, loss of flight cannot account for the higher extinction rate among more highly endemic species: adding level of endemism significantly improves model fit having accounted for variation in historic extinction probability due to flying ability.

Larger-bodied species were more prone to prehistoric extinction, a pattern that can entirely explain the relationship between prehistoric extinction risk and level of endemism in New Zealand birds. Large body mass may have predisposed species to prehistoric extinction because Maori selectively hunted larger-bodied birds (Duncan et al., 2002), which would have been the most profitable prey items, and because larger-bodied birds tend to have lower rates of population growth (Sæther, 1987), so their populations are less able to recover from hunting or habitat loss. The combination of greater hunting pressure and lower population growth rate led to particularly high levels of prehistoric extinction among larger-bodied New Zealand birds (Holdaway & Jacomb, 2000; Duncan et al., 2002).

In contrast, species of intermediate body mass (32–320 g) were most susceptible to historic extinction. This most likely reflects the arrival of a suite of European-introduced predators (including the larger-bodied black and brown rats, possum, cats and mustelids), most of which were capable of hunting intermediate-sized species that were too large to be effectively preyed on by kiore (Holdaway, 1999). Unlike for prehistoric extinctions, this selective extinction of intermediate-sized species cannot account for the relationship between level of endemism and extinction probability, because more highly endemic species tend to occur toward the extremes of the body-mass distribution (Fig. 1).

Only foraging habitat showed a consistent pattern for both prehistoric and historic extinctions: during both periods oceanic seabirds were particularly prone to extinction. This relationship held having controlled for two traits, small egg size and ground- or burrow-nesting behaviour, which further predisposed most seabirds to prehistoric extinction. The particularly slow population growth rate of most seabird species (they lay clutches of one egg and have long incubation and fledging stages) might explain the increased extinction vulnerability of this group over that of other ground-nesting species laying similar-sized eggs.

Level of endemism accounted for significant variation in historic extinction probability independent of other traits included in this study, implying that some unmeasured feature(s) associated with higher levels of endemism was important in predisposing New Zealand birds to historic extinction. One possibility is that this reflects unmeasured aspects of reduced predator escape response, particularly the loss of a behavioural response to predators (predator naivety, see Milberg & Tyrberg, 1993). Island endemic birds are often observed to be particularly tame when they encounter unfamiliar species (Grant, 1998). Given that one aspect of reduced predator escape response, loss of flight, predisposed more highly endemic species to historic extinction, it is plausible that an associated loss of behavioural response was also important, although we are unable to test this directly.

In conclusion, different traits predisposed species to extinction during the two periods of human colonization of New Zealand. The importance of traits such as body mass, egg size, nesting site and loss of flight suggest that introduced predators were a key factor driving species extinctions in this avifauna (Holdaway, 1999). More highly endemic species were more prone to extinction during both the prehistoric and historic periods. However, because different traits predisposed species to extinction during these two periods, different factors explain the extinction–endemism relationship in each case. Traits that partly account for the historic extinction–endemism relationship appear to be those related to increased susceptibility to introduced non-human predators resulting from loss of predator escape responses, including loss of flight, which have been suggested as a major driver of extinction in island birds (Milberg & Tyrberg, 1993; Paulay, 1994). In contrast, the prehistoric extinction–endemism relationship can be explained entirely by the loss of larger-bodied species, primarily as a result of human hunting (Holdaway & Jacomb, 2000; Duncan et al., 2002). If large body size and reduced predator escape responses characterize more highly endemic island birds elsewhere, then these features may underlie similar extinction–endemism relationships in other island avifaunas, given that human hunting and the introduction of mammalian predators have had major impacts on most islands (see review in Blackburn & Gaston, 2005). While this may provide a general explanation for extinction–endemism relationships elsewhere, our results emphasize the idiosyncratic response of the New Zealand avifauna to the specific impacts associated with different episodes of human arrival. As for the case of prehistoric and historic extinctions in New Zealand, several traits may predispose more highly endemic species to extinction, with different traits being important under different circumstances.
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REFERENCES


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