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Of rats and Maoris: a novel method for the analysis of patterns of extinction in the New Zealand avifauna before European contact

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ABSTRACT

The avifauna of New Zealand underwent a large-scale extinction event before its discovery by Europeans. This extinction coincides with the colonization of New Zealand by the Maoris and it is currently thought that the decimation of the avifauna was a direct and indirect effect of this colonization. Some species were eliminated through direct hunting, while others probably fell prey to the pacific rat, *Rattus exulans*, which was introduced by the Maoris. The destruction of habitat by both the Maoris and the pacific rat may have also played a role. To date, there has been no systematic statistical analysis of the factors that characterize the species that went extinct and those that persisted. In this paper, we introduce a novel statistical approach, the regression tree, for the analysis of such data. The purpose of the analysis is to generate a hierarchical predictive tree. The method establishes predictive characteristics from which causal mechansims can be hypothesized. Using regression tree analysis, we identify four main patterns in the avifaunal extinctions: (1) very large (>3.75 kg) bird species all went extinct (whether volant or flightless); (2) the probability of flightless species less than 3.75 kg going extinct decreased with body size; (3) volant species nesting in cavities in the ground (petrels) showed a qualitatively similar pattern (i.e. probability of extinction decreased with body size); (4) in contrast, the probability of volant species nesting in other sites going extinct increased with body size. We discuss possible mechanisms that could generate these patterns.

Keywords: extinction, logistic regression, Maoris, pacific rat, regression trees.

INTRODUCTION

The large-scale extinction of the avifauna of New Zealand in the centuries following the colonization of the islands by the Maoris is probably the best documented case of extinction caused by the direct or indirect actions of a stone-age people (Cumberland, 1962; Fleming, 1962; Williams, 1962; Scarlett, 1974; Cassels, 1984; Anderson, 1989a,b; Worthy and Holdaway, 2002). The most frequently cited example is the extinction of the moas, but many other taxa, including geese, ducks, rails, petrels and passerines, also became extinct in the period between Maori colonization and European contact (Holdaway *et al.*, 2001; Worthy and Holdaway, 2002). Similar mass extinctions of the avifauna prior to European

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expansion into the Pacific have been recorded throughout the Polynesian islands (Olson and James, 1982, 1984; James *et al.*, 1987; Steadman, 1989, 1995, 1997; Milberg and Tyrberg, 1993; Pimm *et al.*, 1994; Pimm, 1996; Steadman and Rolett, 1996; Burney *et al.*, 2001; Curnutt and Pimm, 2001).

Frequently cited reasons for the extinction of the New Zealand avifauna include direct hunting by the Maoris, destruction of the habitat by the Maoris and the impact of the pacific rat, *Rattus exulans*, through predation and/or habitat alteration (Simmons, 1962; Caughley, 1989; Anderson, 1997; Holdaway, 1999a; Worthy, 1999a; Worthy and Holdaway, 2002). Although it is accepted that the pacific rat was introduced into New Zealand by the Maoris (Matisoo-Smith *et al.*, 1998), the exact date of introduction remains controversial. Evidence that the pacific rat was introduced 1000 years before the colonization of New Zealand by the Maoris (Holdaway, 1999b; Holdaway and Beavan, 1999; Beavan-Athfield and Sparks, 2001) has been questioned (Anderson, 1996, 2000; Smith and Anderson, 1998; Hedges, 2000; Higham and Petchey, 2000) and the question remains unresolved. In any event, the effects of the pacific rat, whenever they immigrated, were a consequence of Maori contact and hence represent an anthropogenic effect. Climate has been discounted as unimportant except in so much as it caused local reorganization of communities (Worthy, 1999b; Worthy and Swabey, 2002).

Much of the early literature discussed the possible causes of the extinction but did not attempt a statistical analysis of such causes or the factors associated with extinction. More recently, statistical analyses and mathematical modelling have placed the discussions on a more rigorous footing. For example, Duncan *et al.* (2002) compared selection ratios of taxa from middens with those from the surrounding dunes and showed a significant association between the intensity of hunting and the probability of extinction. Anderson (1989a) and Holdaway and Jacomb (2000) used mathematical modelling to demonstrate that the estimated rate of Maori hunting on moas would have led to their extinction.

Although there has been general discussion of the factors characterizing those taxa that went extinct (e.g. Cassels, 1984; Holdaway, 1989), there has been only one systematic attempt at quantitative analysis. Holdaway (1999a) divided species into six vulnerability groups – (1) flightless species, (2) petrels, (3) coastal and freshwater species, (4) arboreal volant species, (5) ground dwelling volant species, (6) predators – and then examined patterns of extinction within each group. Two potential weaknesses with this insightful analysis are: (1) the vulnerability categories were based on a multitude of disparate characters and it is not clear whether such categories were those that would necessarily have been erected in the absence of knowledge of which birds actually went extinct; and (2) the patterns of extinction were not tested statistically.

A fundamental problem in the analysis of patterns is that of erecting and testing hypotheses after inspection of the data. For example, visual inspection of the list of extinct and extant taxa suggests that flightless forms have a higher probability of extinction than volant forms. However, after such an inspection, it is not statistically valid to then test this hypothesis using the same data, although of course it is typically the only data we have. What is required is a method of objectively finding patterns given a suite of potential candidate characteristics. The problem is that the factors underlying extinction probability may differ between taxa in highly non-linear ways. For example, birds laying small eggs may be more vulnerable to pacific rat predation (one, but not the only, possible impact of the pacific rat) than those laying large eggs, whereas large birds may be invulnerable to rat predation but be a focus of human hunting.

A technique specifically designed to deal with this type of complex interaction is the method of regression trees. The use of this method has recently increased in both clinical and ecological research. Most ecological studies using regression tree analysis have involved community structure. In this paper, we illustrate the use of this technique in the analysis of the importance of life-history variables in the extinction risk of species. Specifically, we use the technique to discern the factors that correlate best with the probability of extinction in the New Zealand avifauna before European contact.

METHODS

Regression trees: a brief description

For detailed discussions of regression trees, see Breiman *et al.* (1984), Venables and Ripley (1997, pp. 413–430), LeBlanc and Crowley (1992) or Marshall (2001). De'ath and Fabricius (2000) provide an excellent example of the method applied to community data.

The general approach of regression tree analysis is to produce a binary tree in which each node of the tree represents a binary division of the data present at that node, determined by some statistical criterion such as least squares. Each node is considered separately and analyses all the available predictor variables; thus, for example, at the first split the data may be best divided according to some predictor variable X_1, while at a subsequent node the best split of the data passing through that node may be accomplished using some other predictor variable, say X_2. Regression trees should be viewed as hypothesis-generating routines rather than hypothesis-testing routines. They have a number of important attributes: they are easy to interpret when the predictors consist of both categorical and continuous variables; they are invariant to monotone transformations of the predictor variables; they can capture non-additive behaviour; and they allow very general interactions between predictor variables.

In the present case, the dependent variable is the probability of extinction. A hypothetical tree is shown in Fig. 1, in which the response variable is the proportion of extinct species, shown at each terminal node. As in logistic regression, the dependent variable is binary, with 1 equalling extinction and 0 equalling presence for each species. The nodes of the regression tree give the probability of extinction, estimated as the number of extinct species divided by

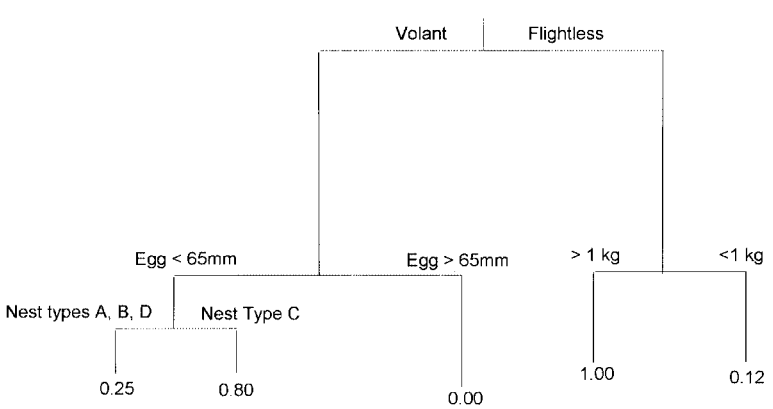


Fig. 1. A hypothetical regression tree illustrating the main features. Terminal nodes show the probability of extinction.

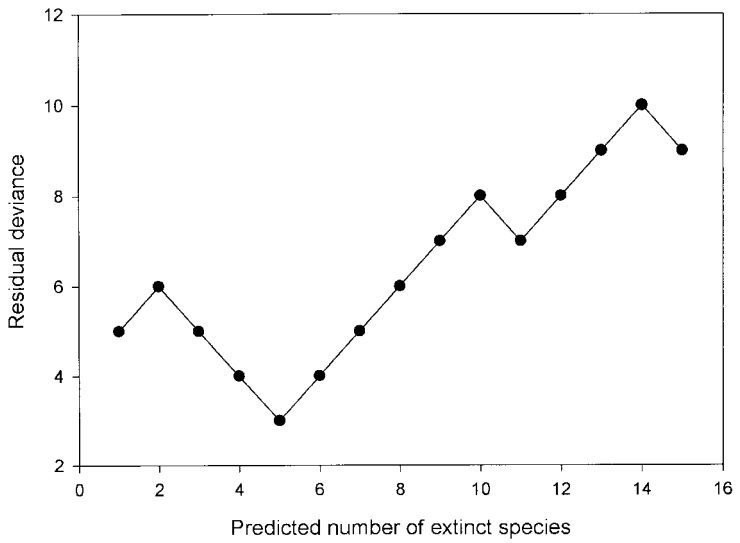
the total number of species in that node (because of the binary definition, it is also the arithmetic mean value of the node). In the hypothetical example, the data are divided initially into two groups, volant (capable of flight) or flightless. The flightless group is then split into two terminal groups depending upon body mass. All flightless species greater than 1 kg became extinct, whereas only 12% of flightless species less than 1 kg became extinct. Among the volant species, the fitting algorithm first splits the group according to egg length and then in the group with egg lengths less than 65 mm according to nest type. No volant species with egg lengths greater than 65 mm went extinct. Volant species with egg lengths less than 65 mm that produced a nest of type C had an 80% probability of going extinct, whereas those producing nest types A, B or D had a 25% probability of going extinct.

Note that, as shown in the above example, predictor (independent) variables can be categorical or continuous. For example, birds could be classified according to three categorical variables, such as habitat type, nest type or food type, and two continuous variables, such as body mass and egg length. The regression tree algorithm seeks a tree comprising binary nodes that minimizes some measure of lack of fit. The tree is constructed recursively with the binary partitioning algorithm applied at each node until either the node is homogeneous or the node contains a preset minimum number of observations (5 in the present analysis). Partitioning is done on a one-step lookahead, which ensures an optimal split at each node but not necessarily the optimal performance over the whole tree. Each partitioning uses only a single predictor variable, although combinations of predictor variables can be included as separate variables. The final tree need not contain all the predictor variables (e.g. habitat type and food type might not be incorporated by the algorithm).

Several partitioning criteria are available: the one used in the present analysis is that implemented by SPLUS, which consists of minimizing the squared difference at each node between the predicted and observed value, called the residual deviance. An example of how this is computed is presented in Fig 2. The data consist of 16 species of birds (actually those comprising nodes 2 and 3 in the North Island regression tree shown in Fig. 4). First, the species are ranked according to body mass. There are 16 possible split points, from only one species predicted to be extinct (*Malacorhynchus scarletti*) to 15 species predicted to be extinct (all except *Leucocarbo chalconotus*). For each possible split, the residual deviance is calculated; Fig. 2 shows the calculation for the split at body mass = 975 (between *Corvus morium* and *Botaurus poiciloptilus*), which has a residual deviance of 3. The residual deviance varies according to the split point and is a minimum at the fifth split point, which is that shown in the sample calculation. The residual mean deviance is defined as the summed residual deviance divided by the degrees of freedom (= number of observations – number of terminal nodes). There is no clear-cut rule for deleting nodes, but inspection of the reduction in deviance as a function of the number of nodes can indicate where the addition of further nodes has little effect on the deviance.

The data set

Holdaway (1999a) gives a list of (1) bird species present on the North and South Islands of New Zealand at the time of Maori colonization, (2) those species extinct by the time of European settlement, (3) bird masses and (4) egg lengths. Two species lacked data for egg lengths and were not used in the construction of the trees. Using various sources, we used the following categorical variables in the analysis (see online database for sources and data):



Species	Observed Extinction	Body mass	"Predicted" Extinction	Residual deviance
Malacorhynchus scarletti	1	800	1	0
Larus dominicanus	0	850	1	1
Mergus australis	1	900	1	0
Egretta alba	1	900	1	0
Corvus moriorum	1	950	1	0
Botaurus poiciloptilus	0	1000	0	0
Anas superciliosa	0	1000	0	0
Podiceps cristatus	0	1100	0	0
Stictocarbo punctatus	0	1200	0	0
Catharacta skua	0	1950	0	0
Biziura delautouri	1	2000	0	1
Phalacrocorax varius	0	2000	0	0
Phalacrocorax carbo	0	2200	0	0
Morus serrator	0	2300	0	0
Leucocarbo carunculatus	1	2500	0	1
Leucocarbo chalconotus	0	2500	0	0
			Deviance =	3

Fig. 2. An example of how the best split is calculated. The data consist of 16 species ranked according to body mass. 'Observed Extinction' is a binary variable taking the value 0 if the species is extinct and 1 if it is extant. 'Predicted Extinction' is similarly a binary variable. The graph shows the residual deviance calculated for each successive inclusion of a species in the 'predicted extinct' category.

1. *Flight capability*: *volant or flightless*. Several species, such as the Stephens Island Wren, may not have been entirely flightless but, because their powers of flight are reported to be highly reduced, we included them in the 'flightless' category. Flightless species are probably more vulnerable than volant species.
2. *Habitat type*: (a) aquatic, e.g. grebes, petrels, penguins, waterfowl; (b) terrestrial and spending most time on the ground, e.g. all flightless species, some rails; (c) terrestrial and aerial, e.g. most passerines, raptors. Of these categories, species in category (b) are probably most vulnerable.

3. *Nesting site*: (a) in a cavity within the ground or, for example, in a fallen log, e.g. petrels, kiwis; (b) on the ground but not in a cavity, e.g. terns, most ducks; (c) arboreal, e.g. most passerines, egrets and herons; (d) in a cavity not on the ground, e.g. some parrots. Birds such as petrels that nest in ground cavities are vulnerable to a wide range of predators, including humans and smaller predators such as the pacific rat.
4. *Nest density*: (a) high, nesting in colonies or nesting territories closely packed, e.g. petrels, egrets, some terns; (b) low, e.g. most passerines, kiwis. Because of their visibility, birds nesting at high densities are likely to be more vulnerable.
5. *Food*: (a) fish, e.g. terns, cormorants; (b) vertebrates other than fish, e.g. raptors; (c) vegetable matter, e.g. geese, parrots, moas; (d) invertebrates, e.g. many passerines, kiwis, some rails. Humans typically eat animals that feed primarily on vegetable matter and hence species in category (c) would be at most risk from humans. However, seabirds may have formed a significant food source of some Polynesians (Moniz, 1997) and both penguin and petrel bones occur in New Zealand archaeological sites (Worthy, 1999a)

Some species became extinct on one island but not the other (e.g. the penguin *Eudyptes pachyrhynchus* became extinct on the North Island but not the South Island) or were present on only one island (e.g. the petrel *Puffinus huttoni*, the eagle *Harpagomis moorei*). For this reason, we treated the two islands separately. The separate treatment also provides a type of cross-validation: the islands are not so different as to expect radically different results for them. As a further test, we did the analysis using both islands together, with 'Island' as a predictor variable.

RESULTS

On the North Island, there were 109 species prior to the Maori colonization, of which 34 (31%) were extinct by 1770 (the time of European colonization). Of the 118 species on the South Island, 37 (31%) were extinct by 1770. A wide variety of birds were exterminated: all eleven moas, most petrel species, some penguins, waterfowl, birds of prey, rails and several passerines (see online database). This very disparate set of species lost suggests a variety of causes were responsible.

The fully fitted regression trees both had 11 terminal nodes. A plot of the deviance versus the number of terminal nodes shows that in both cases there was a marked decrease in deviance up to eight terminal nodes but further splitting produced little change in the model fit (Fig. 3). We therefore limited the trees to eight terminal nodes (Fig. 4). Terminal nodes are arbitrarily labelled 1–8. For the North Island, the predictor variables included were body mass (BM), flight condition and type of nesting site. All of these variables were selected for the South Island model, but nest density was also included (Fig. 4). The regression tree obtained using both islands together gave the same tree as for the North Island, except that the first split was at a body mass of 4500 g rather than 3750 g. This difference is consistent with the difference between the islands in extinction of a single bird species (see below): because the division point is computed as the midpoint between the two adjacent species that occur in different categories (for example, see Fig. 2), the split point varies as data sets are combined.

In both trees, the first split was based on body mass: in the North Island all species greater than 3750 g became extinct, whereas on the South Island the lower limit was 7625 g. The difference in the threshold is due to two species of penguins becoming extinct on the North

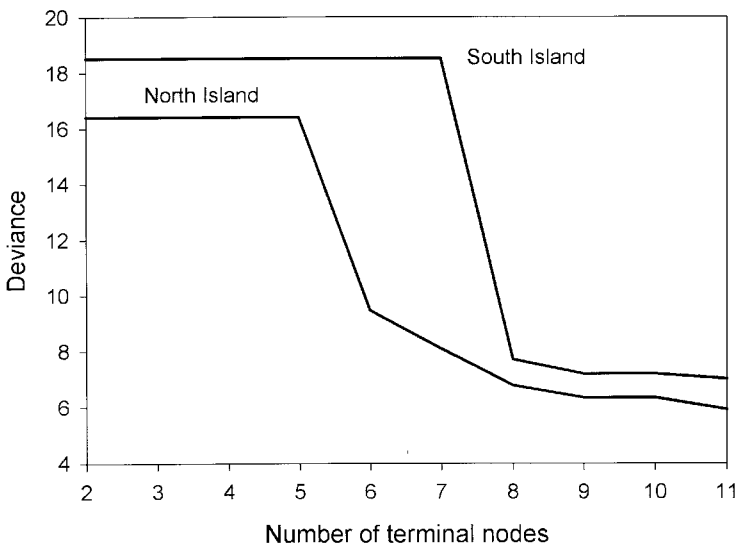


Fig. 3. Deviance versus the number of terminal nodes of the separately fitted regression trees for the North and South Islands of New Zealand.

Island but not the South Island. All of the species exceeding the size threshold of 7625 g and included in the analysis were flightless. However, one of the species excluded from the analysis because it lacked egg length data is the extinct eagle *Harpagomis moorei*, which weighed 12,000 g and hence would have been included within terminal node 8 (extinction probability = 1). The second species omitted from the analysis for lack of egg length data was the harrier *Circus eytesi*, which went extinct on both islands but would have been placed in the left-hand split because its estimated adult weight was 2500 g.

Both trees produced the same divisions for the next two levels: first the data were split according to flight capability and then either by nesting site or body mass. For flightless species, the probability of extinction was a function of body mass, with extinction probability being greater for smaller species. Flightless species in terminal node 7 (low probability of extinction) included the kiwis, penguins, a parrot and a rail, while the species in terminal node 6 (higher probability of extinction) consisted of rails, a waterfowl and three passerines.

Volant species nesting in cavities within the ground (category a) were separated from species nesting in the other three nest site categories (b, c, d). The former group are all petrel species. Within this group, the probability of extinction decreases with size (cf. terminal nodes 4 and 5). The group of species not nesting in ground cavities were split according to the same threshold body mass for both islands, with species less than 775 g being assigned to terminal node 1. This node, which includes species from almost all taxa (e.g. grebes, cormorants, herons, waterfowl, falcons, gamebirds, rails, shorebirds, gulls, pigeons, parrots, songbirds), has a very low probability of extinction (0.04 for North Island, 0.06 for South Island). Terminal nodes 2 and 3 are defined differently in the two analyses: for the North Island, the birds are split according to body mass, with smaller species having the highest probability of extinction (0.80 for body mass <975 g and 0.18 for larger species). On the other hand, the South Island analysis split species according to nest density, with species

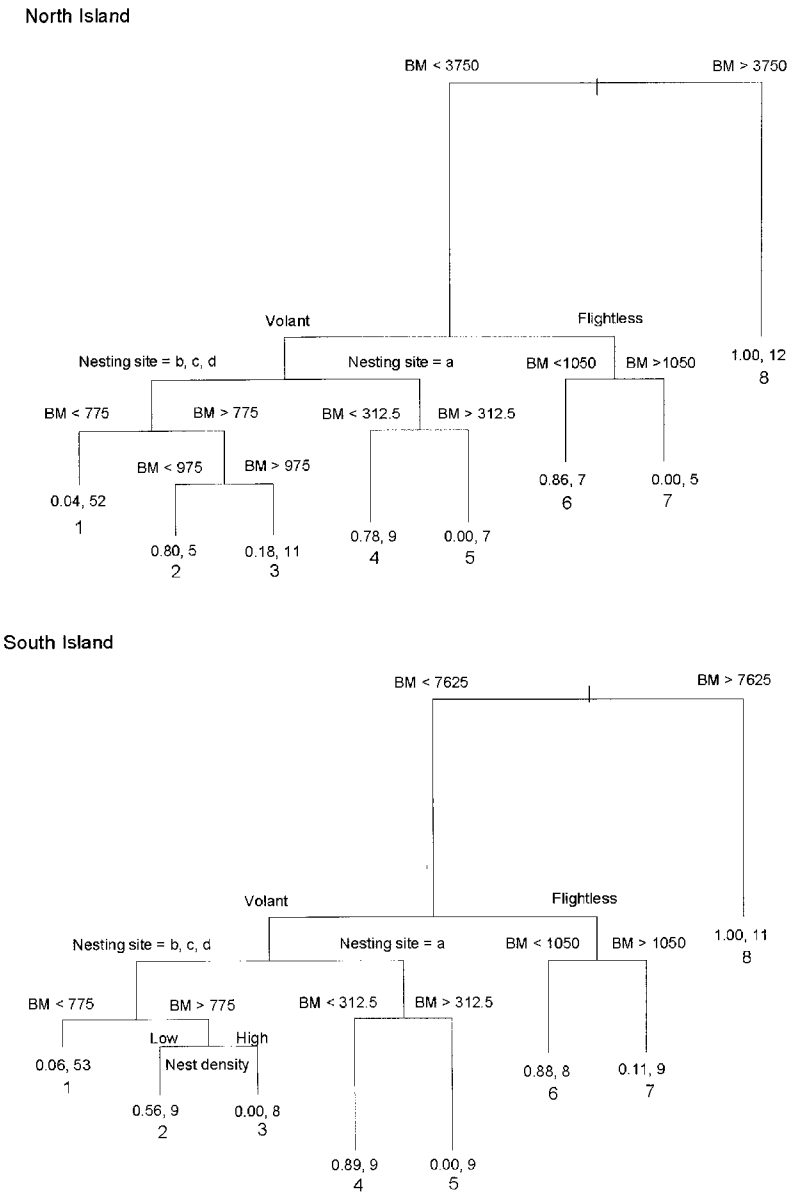


Fig. 4. The pruned regression trees for the North and South Islands of New Zealand. BM = body mass in grams. At each terminal node is shown the probability of extinction and the sample size. For discussion, the terminal nodes are arbitarily labelled 1–8.

nesting at high density having the highest probability of extinction (0.56 for low density versus 0.00 for high density). Taking the North Island terminal node with 0.80 probability to correspond to the South Island terminal node with 0.56 probability, we have nine species that are classed in the same group on both islands and seven that are grouped differently. Comparing the similarities and differences between the two trees suggests that there are

four broad terminal groups: (a) nodes 1, 2 and 3; (b) nodes 4 and 5; (c) nodes 6 and 7; and (d) node 8. This classification is supported by the combined analysis of both islands. With the exception of terminal node 8, in which there is no variation in extinction probability, within each grouping of nodes the probability of extinction appears to be associated with body size, although the functional relationship differs among the groups. On the basis of the North Island classification, the probability of extinction for species within the 1, 2, 3 grouping of nodes first increases with body size and then decreases. The latter possibility (decreasing probability of extinction with body size) is not supported by the South Island classification. Both analyses indicate that for the grouping of nodes 4 and 5 and the grouping of nodes 6 and 7, the probability of extinction decreases with body size.

The regression tree analysis necessarily partitions the data into binary groups. However, the probability of extinction is unlikely to fall neatly into two groups based on a continuous measure such as body size. More realistically, the probability of extinction is likely to follow some relationship such as the logistic.

The regression tree analysis does not provide significance tests for the splits, but we tested *post-hoc* the pattern associated with body size using logistic regression. As before, we tested both islands separately. Because both analyses gave qualitatively the same results, we present only those for the North Island. In the case of the grouping of nodes 1, 2 and 3, we added a quadratic term to test for the presence of a decreasing probability at the largest body masses. Model fit was tested using log-likelihood (Tabachnick and Fidell, 2001). The quadratic term was not significant ($\chi^2_1 = 1.06$, $P = 0.30$) and was dropped from the model. The model involving body mass was highly significant for all three groupings (nodes 1, 2, 3: $\chi^2_1 = 7.32$, $P = 0.007$; nodes 4 and 5: $\chi^2_1 = 10.67$, $P = 0.001$; nodes 6 and 7: $\chi^2_1 = 9.68$, $P = 0.002$). In agreement with the regression tree analysis, the probability of extinction declines with body mass for two groupings and increases with body mass for the third (Fig. 5). The final regression tree with the terminal node logistic regressions is shown pictorially in Fig. 6.

DISCUSSION

The regression tree analysis of the two New Zealand islands produced four basic groupings, discussed below. Although the statistical analysis itself does not indicate the factor or factors responsible for extinction rates within each of these groupings, we can use these groupings to formulate hypotheses. Two causes of extinction that have received attention are predation and habitat alteration. Both Maoris and the pacific rat have been implicated as predators of the Polynesian avifauna and agents of habitat destruction (see Introduction). Several authors have postulated that extinction of the avifauna of other Polynesian islands was also a result of human activities (Olson and James, 1982; Milberg and Tyrberg, 1993; Steadman, 1995, 1997; Burney *et al.*, 2001). The importance of predation or habitat alteration by the pacific rat on extinction throughout Polynesia is less certain (see below).

Group 1: large birds greater than 3.75 kg

With one exception, all of these species were flightless. Humans targeted these species (moas, waterfowl and penguins) and the extinction of the large eagle is explicable as a consequence of the loss of its possible principal prey, the moas. Holdaway (1989) suggested that humans may also have hunted the eagle.

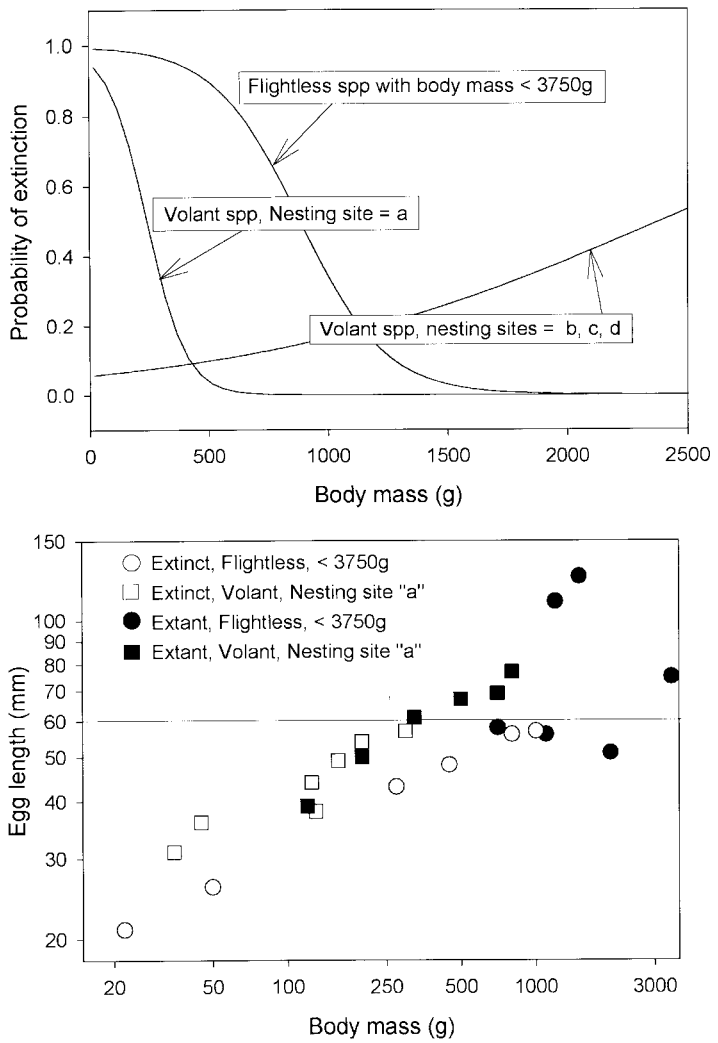


Fig. 5. (Top) The fitted logistic regression functions for the probability of extinction on the North Island as a function of body size in the three groupings of terminal nodes in which there is variation in extinction probability. Nesting site categories: (a) in a cavity within the ground or in a fallen log, etc. (because of prior partitions, the group 'volant spp., nesting site = a' consists solely of petrels); (b) on the ground but not in a cavity; (c) arboreal; (d) in a cavity not on the ground. (Bottom) Egg length as a function of body mass for the two species groups in which the probability of extinction on the North Island decreased with body mass. The horizontal line is drawn at 60 mm, which is the approximate length at which eggs are too large to be preyed upon by the pacific rat.

Group 2: flightless birds smaller than 3.75 kg

In this group, the probability of extinction decreased with body mass. The largest birds in this group are certainly within the range where human hunting would have been profitable and there is no obvious single factor that would have by itself protected the birds. The general trend for vulnerability to decrease with size suggests that this group was at risk from

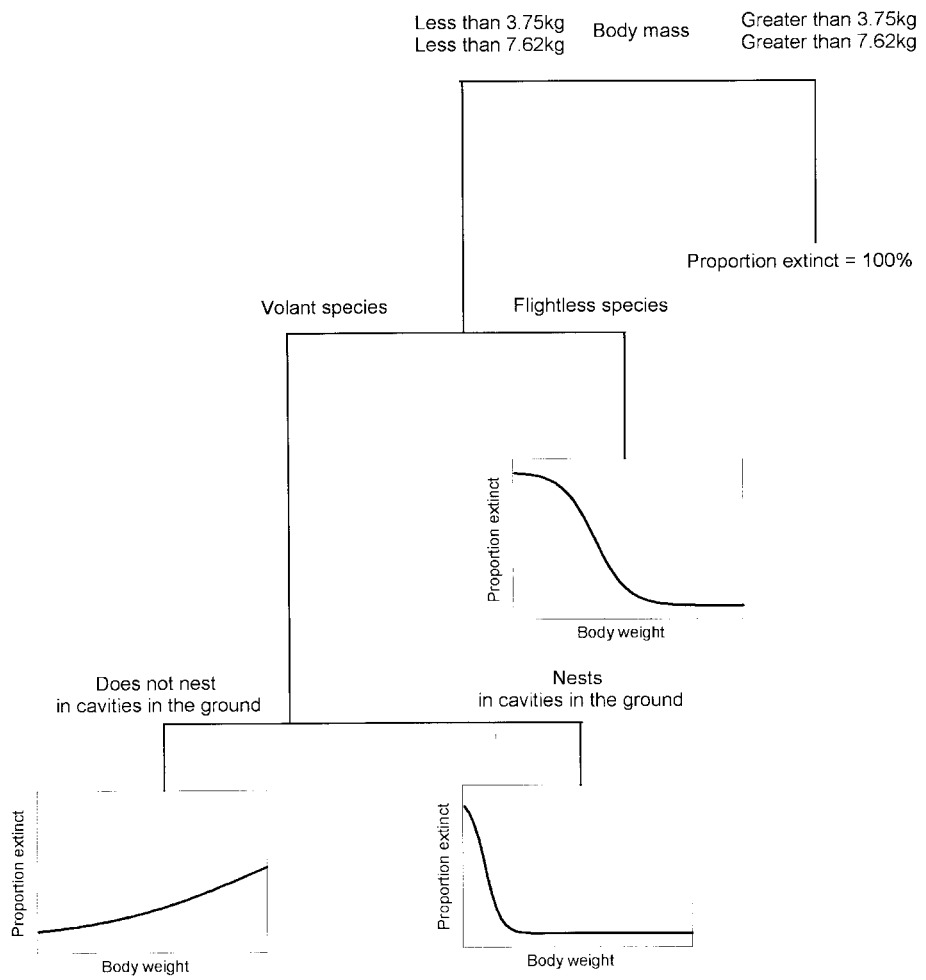


Fig. 6. A pictorial summary of the regression tree analysis.

a size-limited predator. A plausible candidate is the pacific rat (*Rattus exulans*), which has a body mass generally in the range 60–80 g but can grow as large as 180 g. Although primarily a herbivore (Mosby *et al.*, 1973; Temme, 1982; Bunn and Craig, 1989), like other rats, the pacific rat is quite catholic in its diet (Newman and McFadden, 1990; Lovegrove, 1996) and has been implicated as a predator of small vertebrates such as amphibians, reptiles and birds (Anderson, 1997; Worthy and Holdaway, 2002). For example, the New Zealand tuatara, *Sphenodon punctatus*, is reduced or absent on islands where the pacific rat is present (Cassels, 1984; Towns, 2002). On Korapuki Island (northeastern New Zealand), populations of the shore skink, *Oligosoma smithi*, increased following the removal of the pacific rat. Based on estimated changes in survival rate, Towns (1996) attributed this increase in the skink population to the lack of rat predation. Similar studies on the Mercury Islands of New Zealand have also implicated the pacific rat in causing a depauperate lizard assemblage (Towns, 1991). Pacific rats also prey upon a variety of bird species (Kepler, 1967; Fleet,

1972; Brooke, 1995; Lovegrove, 1996). Petrels in particular appear to be highly vulnerable to rats in general and the pacific rat in particular (Marchant and Higgins, 1990; Newman and McFadden, 1990; Brooke, 1995; Booth *et al.*, 1996). The pacific rat has also been implicated in habitat alteration (Athens, 1997; Campbell and Atkinson, 1999, 2002; Athens *et al.*, 2002). While the impact of humans on the extinction of the avifauna of Polynesia is generally accepted (see above), the importance of the pacific rat has been questioned (Steadman and Olson, 1985; Weisler and Gargett, 1993).

Potential prey of the pacific rat include ground-nesters with eggs less than 57 mm in length and small ground-nesting birds of less than 100 g (Holdaway, 1999a). Although some of the species that went extinct within this group were too large as adults to be taken by the pacific rat, all of the extinct species had egg lengths less than 60 mm (Fig. 5). Three species that did not go extinct also had egg lengths less than 60 mm, but all are large species and their egg lengths (58, 56 and 51 mm, respectively) are close to the size limit (57 mm) suggested for the pacific rat.

Group 3: volant species that nest in a cavity within the ground or in a fallen log

All of the species in this group are petrels. As noted above, there is evidence of pacific rat predation on the eggs and young of petrels and hence it is a reasonable hypothesis that this rodent was the primary culprit in the extinction (Holdaway and Worthy, 1994; Holdaway, 1999a; Worthy and Holdaway, 2002). It is also significant in this regard that all the species eliminated laid eggs less than 60 mm in length (Fig. 5). Two species that lay eggs less than 60 mm did not go extinct on North Island. However, one of these, *Pelacanoides georgicus*, did go extinct on South Island.

The foregoing discussion for this group and the preceding group might lead one to suspect that egg size is likely to be a more important determinant of species survival than adult body size. This is not what the regression tree analysis concludes, as this possibility would have been considered at the ultimate partitions. To investigate further the possible effect of body size versus egg size, we did the logistic regression analysis for the four possible combinations (two groups and two islands). In all cases, the addition of egg length did not significantly improve the fit (Type 1 sums of squares). Entering egg length as the first variable left residual variance that was accounted for by body size. Thus the logistic regression analysis agrees with the regression tree analysis in concluding that body size is the better predictor of persistence. This suggests that persistence is not due simply to a relatively large egg. It is possible that the larger adult body size permits the parent bird to fend off the rat. More behavioural information on the mode of predation by rodents is needed.

Group 4: volant species that nest on or above the ground

The probability of extinction was small in this group but showed a significant increase with body size (Fig. 4). Species becoming extinct were a cormorant (2500 g) and a heron (900 g) on North but not South Island, a merganser (900 g), a falcon (2500 g), a shorebird (105 g), an owlet-nightjar (200 g) and a crow (950 g). The species that went extinct were as a group neither those likely to be hunted by the Maoris nor, because of their size, significantly preyed upon by the pacific rat. These species may have become extinct as the result of other causes.

The power of the regression tree approach is that it focuses attention on the characteristics of not only the extinct species but also the extant species. It provides an objective means of integrating a large amount of information and indicates where profitable avenues of study lie. Furthermore, it provides a means of assessing the potential for extant species to become threatened.

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REFERENCES

Anderson, A. 1989. Mechanics of overkill in the extinction of New Zealand moas. *J. Arch. Sci.*, **16**: 137–152.

Anderson, A. 1989. *Prodigious Birds*. Cambridge: Cambridge University Press.

Anderson, A. 1996. Was *Rattus exulans* in New Zealand 2000 years ago? AMS radiocarbon ages from Shag River Mouth. *Arch. Oceania*, **31**: 178–184.

Anderson, A. 1997. Prehistoric Polynesian impact on the New Zealand environment: Te Whenua Hou. In *Historical Ecology in the Pacific Islands* (P.V. Kirch and T.L. Hunt, eds), pp. 271–283. New Haven, CT: Yale University Press.

Anderson, A. 2000. Differential reliability of 14C AMS ages of *Rattus exulans* bone gelatin in south Pacific prehistory. *J. R. Soc. NZ*, **30**: 243–261.

Athens, J.S. 1997. Hawaiian native lowland vegetation in prehistory. In *Historical Ecology in the Pacific Islands* (P.V. Kirch and T.L. Hunt, eds), pp. 248–270. New Haven, CT: Yale University Press.

Athens, J.S., Tuggle, H.D., Ward, J.V. and Welch, D.J. 2002. Avifaunal extinctions, vegetation change, Polynesian impacts in prehistoric Hawai'i. *Arch. Oceania*, **37**: 57–78.

Beavan-Athfield, N. and Sparks, R.J. 2001. Dating of *Rattus exulans* and bird bone from Pleasant River (Otago, New Zealand): radiocarbon anomalies from diet. *J. R. Soc. NZ*, **31**: 801–809.

Booth, A.M., Minot, E.O., Fordham, R.A. and Innes, J.G. 1996. Kiore (*Rattus exulans*) predation on the eggs of the Little Shearwater (*Puffinus assimilis baurakiensis*). *Notornis*, **43**: 147–153.

Breiman, L., Friedman, J.H., Olshen, R.A. and Stone, C.G. 1984. *Classification and Regression Trees*. Belmont, CA: Wadsworth International Group.

Brooke, M.D.L. 1995. The breeding biology of the gadfly petrels *Pterodroma* spp. of the Pitcairn Islands: characteristics, population sizes and controls. *Biol. J. Linn. Soc.*, **56**: 213–231.

Bunn, T.J. and Craig, J.L. 1989. Population cycles of *Rattus exulans*: population changes, diet, and food availability. *NZ J. Zool.*, **16**: 409–418.

Burney, D.A., James, H.F., Burney, L.P. *et al.* 2001. Fossil evidence for a diverse biota from Kaua'i and its transformation since human arrival. *Ecol. Monogr.*, **71**: 615–641.

Campbell, D.J. and Atkinson, I.A.E. 1999. Effects of kiore (*Rattus exulans* Peale) on recruitment of indigenous coastal trees on northern offshore islands of New Zealand. *J. R. Soc. NZ*, **29**: 265–290.

Campbell, D.J. and Atkinson, I.A.E. 2002. Depression of tree recruitment by the Pacific rat (*Rattus exulans* Peale) on New Zealand's northern offshore islands. *Biol. Conserv.*, **107**: 19–35.

Cassels, R. 1984. The role of prehistoric man in the faunal extinctions of New Zealand and other Pacific Islands. In *Quaternary Extinctions* (P.S. Martin and R.G. Klein, eds), pp. 741–767. Tucson, AZ: University of Arizona Press.

Caughley, G. 1989. New Zealand and plant–herbivore systems: past and present. *NZ J. Ecol.*, **12**: 3–10.

Cumberland, K.B. 1962. Moas and men: New Zealand about AD 1250. *Geogr. Rev.*, **LII**: 151–173.
Curnutt, J. and Pimm, S.L. 2001. How many bird species in Hawai'i and the central Pacific before first contact? *Stud. Avian Biol.*, **22**: 15–30.
De'ath, G. and Fabricius, K.E. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology*, **81**: 3178–3192.
Duncan, R.P., Blackburn, T.M. and Worthy, T.H. 2002. Prehistoric bird extinctions and human hunting. *Proc. R. Soc. Lond., Biol. Sci. Ser. B*, **269**: 517–521.
Fleet, R.R. 1972. Nesting success of the red-tailed tropic bird on Kure atoll. *Auk*, **89**: 651–659.
Fleming, C.A. 1962. The extinction of moas and other animals during the Holocene period. *Notornis*, **10**: 113–117.
Fuller, E. 2001. *Extinct Birds*. Ithaca, NY: Comstock Publishing.
Hedges, R.E.M. 2000. Appraisal of radiocarbon dating of kiore bones (Pacific rat *Rattus exulans*) in New Zealand. *J. R. Soc. NZ*, **30**: 385–398.
Higham, T.F.G. and Petchey, F.J. 2000. On the reliability of archaeological rat bone for radiocarbon dating in New Zealand. *J. R. Soc. NZ*, **30**: 399–409.
Holdaway, R.N. 1989. New Zealand's pre-human avifauna and its vulnerability. *NZ J. Ecol.*, **12**: 11–25.
Holdaway, R.N. 1999a. Introduced predators and avifaunal extinction in New Zealand. In *Extinctions in Near Time* (R.D.E. MacPhee, ed.), pp. 189–238. New York: Kluwer Academic/ Plenum Press.
Holdaway, R.N. 1999b. A spatio-temporal model for the invasion of the New Zealand archipelago by the Pacific rat *Rattus exulans*. *J. R. Soc. NZ*, **29**: 91–105.
Holdaway, R.N. and Beavan, N.R. 1999. Reliable 14C AMS dates on bird and Pacific rat *Rattus exulans* bone gelatin, from a $CaCO_3$-rich deposit. *J. R. Soc. NZ*, **29**: 185–211.
Holdaway, R.N. and Jacomb, C. 2000. Rapid extinction of the moas (Aves: Dinornithiformes): model, test, and implications. *Science*, **287**: 2250–2254.
Holdaway, R.N. and Worthy, T.H. 1994. A new fossil species of shearwater *Puffinus* from the late Quaternary of the South Island, New Zealand, and notes on the biogeography and evolution of the *Puffinus gavia* superspecies. *Emu*, **94**: 201–215.
Holdaway, R.N., Worthy, T.H. and Tennyson, A.J.D. 2001. A working list of breeding bird species of the New Zealand region at first human contact. *NZ J. Zool.*, **28**: 119–187.
James, H.T.W., Stanford, J., Steadman, D.W., Olson, S.L., Martin, P.S., Jull, A.J.T. and McCoy, P.C. 1987. Radiocarbon dates on bones of extinct birds from Hawaii. *Proc. Natl. Acad. Sci. USA*, **84**: 2350–2354.
Kepler, C.B. 1967. Polynesian rat predation on nesting Laysan albatrosses and other Pacific birds. *Auk*, **84**: 651–659.
LeBlanc, M. and Crowley, J. 1992. Relative risk trees for censored survival data. *Biometrics*, **48**: 411–425.
Lovegrove, T.G. 1996. A comparison of the effects of predation by Norway (*Rattus norvegicus*) and Polynesian rats (*R. exulans*) on the saddleback (*Philesturnus carunculatus*). *Notornis*, **43**: 91–112.
Marchant, S. and Higgins, P.J.C. 1990. *Handbook of Australian, New Zealand & Antarctic Birds*. Melbourne: Oxford University Press.
Marshall, R.J. 2001. The use of classification and regression trees in clinical epidemiology. *J. Clin. Epidemiol.*, **54**: 603–609.
Matisoo-Smith, E., Roberts, R.M., Irwin, G.J., Allen, J.S., Penny, D. and Lambert, D.M. 1998. Patterns of prehistoric human mobility in Polynesia indicated by mtDNA from the Pacific rat. *Proc. Natl. Acad. Sci. USA*, **95**: 15145–15150.
Milberg, P. and Tyrberg, T. 1993. Naive birds and noble savages – a review of man-caused prehistoric extinctions of island birds. *Ecography*, **16**: 229–250.
Moniz, J.J. 1997. The role of seabirds in Hawaiian subsistence: implications for interpreting avian extinction and exterpation in Polynesia. *Asian Persp.*, **36**: 27–50.

Mosby, J.M., Wodzicki, K. and Thompson, H.R. 1973. Food of the Kimoa *Rattus exulans* in the Tokelau Islands and other habitats in the Pacific. *NZ J. Sci.*, **16**: 799–810.

Newman, D.G. and McFadden, I. 1990. Seasonal fluctuations of numbers, breeding, and food of kiore (*Rattus exulans*) on Lady Alice Island (Hen and Chickens group), with a consideration of kiore–Tuatara (*Sphenodon punctatus*) relationships in New Zealand. *NZ J. Zool.*, **17**: 55–64.

Olson, S.L. and James, H.F. 1982. Fossil birds from the Hawaiian Islands: evidence for wholesale extinction by Man before western contact. *Science*, **217**: 633–635.

Olson, S.L. and James, H.F. 1984. The role of Polynesians in the extinction of the avifauna of the Hawaiian islands. In *Quaternary Extinctions* (P.S. Martin and R.G. Klein, eds), pp. 768–780. Tucson, AZ: University of Arizona Press.

Pimm, S.L. 1996. Lessons from a kill. *Biodivers. Conserv.*, **5**: 1059–1067.

Pimm, S.L., Moulton, M.P. and Justice, L.J. 1994. Bird extinctions in the central Pacific. *Phil. Trans. R. Soc. Lond. B, Biol. Sci.*, **344**: 27–33.

Scarlett, R.J. 1974. Moa and Man in New Zealand. *Notornis*, **21**: 1–12.

Simmons, D.R. 1962. Man, moa and the forest. *Trans. R. Soc. NZ*, **2**: 115–127.

Smith, I. and Anderson, A. 1998. Radiocarbon dates from archaeological rat bones: the Pleasant River case. *Arch. Oceania*, **33**: 88–91.

Steadman, D.W. 1989. Extinction of birds in Eastern Polynesia: a review of the record, and comparisons with other Pacific Island groups. *J. Arch. Sci.*, **16**: 177–205.

Steadman, D.W. 1995. Prehistoric extinctions of Pacific Island birds: biodiversity meets zooarchaeology. *Science*, **267**: 1123–1131.

Steadman, D.W. 1997. Human-caused extinction of birds. In *Biodiversity II* (M.L. Reaka-Kudla, D.E. Wilson and E.O. Wilson, eds), pp. 139–161. Washington, DC: Joseph Henry Press.

Steadman, D.W. and Olson, S.L. 1985. Bird remains from an archaeological site on Henderson Island, South Pacific: Man-caused extinctions on an 'unihabited' island. *Proc. Natl. Acad. Sci. USA*, **82**: 6191–6195.

Steadman, D.W. and Rolett, B. 1996. A chronostratigraphic analysis of landbird extinction on Tahuata, Marquesas Islands. *J. Arch. Sci.*, **23**: 81–94.

Tabachnick, B.G. and Fidell, L.S. 2001. *Using Multivariate Statistics*. Boston, MA: Allyn & Bacon.

Temme, M. 1982. Feeding pattern of the Polynesian rat *Rattus exulans* in the Northern Marshall Islands, Pacific Ocean. *Zeits. Ange. Zool.*, **69**: 463–480.

Towns, D.R. 1991. Response of lizard assemblages in the Mercury Islands, New Zealand to removal of an introduced rodent, the kiore *Rattus exulans*. *J. R. Soc. NZ*, **21**: 119–136.

Towns, D.R. 1996. Changes in habitat use by lizards on a New Zealand island following removal of the introduced Pacific rat, *Rattus exulans*. *Pacific Conserv. Biol.*, **2**: 286–292.

Towns, D.R. 2002. Korapuki Island as a case study for restoration of insular ecosystems in New Zealand. *J. Biogeogr.*, **29**: 593–607.

Venables, W.N. and Ripley, B.D. 1997. *Modern Applied Statistics with S-PLUS*. New York: Springer-Verlag.

Weisler, M.I. and Gargett, R.H. 1993. Pacific island avian extinctions: the taphonomy of human predation. *Arch. Oceania*, **28**: 85–93.

Williams, G.R. 1962. Extinction and the land- and freshwater-inhabiting birds of New Zealand. *Notornis*, **10**: 15–32.

Worthy, T.H. 1999a. What was on the menu? Avian extinction in New Zealand. *NZ J. Arch.*, **19**: 125–160.

Worthy, T.H. 1999b. The role of climate change versus human impacts – avian extinction on South Island, New Zealand. *Smiths. Contrib. Paleobiol.*, **89**: 111–123.

Worthy, T.H. and Holdaway, R.N. 2002. *The Lost World of the Moa*. Bloomington, IN: Indiana University Press.

Worthy, T.H. and Swabey, S.E.J. 2002. Avifaunal changes revealed in quaternary deposits near Waitomo Caves, North Island, New Zealand. *J. R. Soc. NZ*, **32**: 293–325.

APPENDIX

List of extant bird species and their characteristics on the North and South (including the Stewart) Islands of New Zealand at the time of Maori contact. *Data sources*: Holdaway (1989, 1999a), Marchant and Higgins (1990), Fuller (2001). In those cases where species are extinct, we have used data from related species

Species	North Island	South Island	NI node	SI node	Habitat type	Nest site	Nest density	Diet	Volant ?	Body mass (g)	Egg length (mm)
Grebes											
Podiceps cristatus	0	0	3	2	A	G	L	F	Y	1100	57
Poliocephalus rufopectus	0	0	1	1	A	G	L	F	Y	250	43
Percent extinct =	**0.00**	**0.00**									
Petrels											
Puffinus gavia	1	1	4	4	A	GC	H	F	Y	300	57
Puffinus huttoni	a	0		5	A	GC	H	F	Y	350	60
Puffinus spelaeus	a	1		4	A	GC	H	F	Y	250	55
Puffinus assimilis	1	1	4	4	A	GC	H	F	Y	200	54
Pelecanoides urinatrix	1	1	4	4	A	GC	H	F	Y	130	38
Pelecanoides georgicus	0	1	4	4	A	GC	H	F	Y	120	39
Pachyptila turtur	1	1	4	4	A	GC	H	F	Y	125	44
Pterodroma pycrofti	1	a	4		A	GC	H	F	Y	160	49
Pterodroma cookii	0	0	4	4	A	GC	H	F	Y	200	50
Garrodia nereis	1	1	4	4	A	GC	H	F	Y	35	31
Pelagodroma marina	1	1	4	4	A	GC	H	F	Y	45	36
Pterodroma inexpectata	0	0	5	5	A	GC	H	F	Y	325	61
Pterodroma macroptera	0	0	5	5	A	GC	H	F	Y	500	67
Puffinus griseus	0	0	5	5	A	GC	H	F	Y	800	77
Procellaria parkinsoni	0	0	5	5	A	GC	H	F	Y	700	69
Procellaria westlandica	a	0		5	A	GC	H	F	Y	1100	81
Percent extinct =	**53.85**	**50.00**									
Penguins											
Eudyptula minor	0	0	7	7	A	GC	H	F	N	1100	56
Eudyptes pachyrhynchus	1	0	8	7	A	G	H	F	N	4000	67
Megadyptes antipodes	1	0	8	7	A	G	L	F	N	5250	77
Percent extinct =	**66.67**	**0.00**									

Cormorants and shags											
Phalacrocorax melanoleucos	0	0	1	1	A	A	H	F	Y	700	48
Stictocarbo punctatus	0	0	3	3	A	A	H	F	Y	1200	58
Phalacrocorax carbo	0	0	3	3	A	A	H	F	Y	2200	61
Phalacrocorax varius	0	0	3	3	A	A	H	F	Y	2000	59
Leucocarbo carunculatus	1	0	3	3	A	G	H	F	Y	2500	65
Leucocarbo chalconotus	0	0	3	3	A	G	H	F	Y	2500	66
Percent extinct =	**16.67**	**0.00**									
Herons and bitterns											
Egretta alba	1	0	2	3	A	A	H	F	Y	900	52
Egretta sacra	0	a	1		A	G	L	F	Y	400	46
Botaurus poiciloptilus	0	0	3	2	A	G	L	F	Y	1000	51
Ixobrychus novaezelandiae	0	0	1	1	A	G	L	F	Y	150	46
Percent extinct =	**25.00**	**0.00**									
Waterfowl											
Anas superciliosa	0	0	3	2	A	G	L	H	Y	1000	58
Anas gracilis	0	0	5	5	A	GC	L	H	Y	425	50
Anas chlorotis	0	0	1	1	A	G	L	H	Y	500	60
Mergus australis	1	1	2	2	A	G	L	F	Y	900	57
Euryanas finschi	1	1	6	6	A	G	L	H	N	800	56
Malacorhynchus scarletti	1	1	2	2	A	G	L	H	Y	800	56
Hymenolaimus malacorhynchos	0	0	1	1	A	G	L	I	Y	750	65
Aythya novaeseelandiae	0	0	1	1	A	G	L	F	Y	650	64
Cnemiornis gracilis	1	a	8		TG	G	L	H	N	8000	105
Cnemiornis calcitrans	a	1		8	TG	G	L	H	N	10000	110
Cygnus atratus	1	1	8	2	A	G	L	H	Y	5000	104
Tadorna variegata	0	0	5	5	A	GC	L	H	Y	1400	67
Biziura delautouri	1	1	3	2	A	G	L	H	Y	2000	76
Percent extinct =	**50.00**	**50.00**									
Falcons, hawks and eagles											
Falco novaeseelandiae	0	0	1	1	TA	A	L	V	Y	500	49
Circus eytesi	1	1	NP	NP	TA	A	L	V	Y	2500	U
Harpagornis moorei	a	1	NP	NP	TA	A	L	V	Y	12000	U
Percent extinct =	**50.00**	**66.67**									

Appendix – *cont.*

Species	North Island	South Island	NI node	SI node	Habitat type	Nest site	Nest density	Diet	Volant ?	Body mass (g)	Egg length (mm)
Gamebirds											
Coturnix novaezealandiae	0	0	1	1	TG	G	L	H	Y	100	30
Percent extinct =	**0.00**	**0.00**									
Rails											
Gallirallus philippensis	0	0	1	1	A	G	L	I	Y	170	40
Gallirallus australis	0	0	6	6	TG	G	L	I	N	700	58
Porzana tabuensis	0	0	1	1	A	G	L	I	Y	45	30
Porzana pusilla	0	0	1	1	A	G	L	I	Y	40	28
Fulica prisca	1	1	6	6	A	G	L	H	N	1000	57
Capellirallus karamu	1	1	6	6	A	G	L	I	N	275	43
Gallinula hodgenorum	1	1	6	6	A	G	L	I	N	450	48
Porphyrio hochstetteri	a	0		7	TG	G	L	H	N	3000	74
Porphyrio mantelli	0	a	7		TG	G	L	H	N	3500	75
Percent extinct =	**37.50**	**37.50**									
Shorebirds											
Haematopus ostralegus	0	0	1	1	A	G	H	I	Y	550	56
Haematopus unicolor	0	0	1	1	A	G	H	I	Y	725	59
Himantopus novaezelandiae	0	0	1	1	A	G	L	I	Y	220	45
Charadrius obscurus	0	0	1	1	A	G	L	I	Y	145	46
Charadrius novaeseelandiae	0	0	1	1	A	G	H	I	Y	60	37
Charadrius bicinctus	0	0	1	1	A	G	L	I	Y	60	34
Charadrius frontalis	a	0		1	A	G	L	I	Y	55	35
Coenocorypha barrierensis	1	a	1		TG	G	L	I	Y	105	42
Coenocorypha South Island	a	1		1	TG	G	L	I	Y	105	42
Coenocorypha iredalei	a	1		1	TG	G	L	I	Y	105	42
Percent extinct =	**14.29**	**22.22**									
Gulls, terns and gannets											
Larus novaehollandiae	0	0	1	1	A	G	H	F	Y	260	52
Larus bulleri	0	0	1	1	A	G	H	F	Y	250	55
Sterna albostriata	0	0	1	1	A	G	H	F	Y	80	40

Sterna striata	0	0	1	1	A	G	H	F	Y	160	46
Sterna nereis	0	0	1	1	A	G	H	F	Y	70	35
Larus dominicanus	0	0	2	3	A	G	H	F	Y	850	69
Sterna caspia	0	0	1	1	A	G	H	F	Y	700	68
Catharacta skua	0	0	3	2	A	G	L	F	Y	1950	74
Morus serrator	0	0	3	3	A	G	H	F	Y	2300	77
Percent extinct =	**0.00**	**0.00**									
Pigeons											
Hemiphaga novaeseelandiae	0	0	1	1	TA	A	L	H	Y	650	49
Percent extinct =	**0.00**	**0.00**									
Parrots											
Strigops habroptilus	0	0	7	7	TG	GC	L	H	N	2000	51
Nestor meridionalis	0	0	1	1	TA	C	L	H	Y	425	42
Nestor notabilis	0	0	5	5	TA	GC	L	H	Y	800	44
Cyanoramphus novaezelandiae	0	0	1	1	TA	C	L	H	Y	70	25
Cyanoramphus auriceps	0	0	1	1	TA	C	L	H	Y	40	24
Cyanoramphus malherbi	0	0	1	1	TA	A	L	H	Y	35	23
Percent extinct =	**0.00**	**0.00**									
Cuckoos											
Chrysococcyx lucidus	0	0	1	1	TA	A	L	I	Y	25	18.5
Eudynamys taitensis	0	0	1	1	TA	A	L	I	Y	125	23
Percent extinct =	**0.00**	**0.00**									
Kingfishers											
Halcyon sancta	0	0	1	1	TA	C	L	F	Y	65	29
Percent extinct =	**0.00**	**0.00**									
Owls											
Ninox novaeseelandiae	0	0	1	1	TA	C	L	I	Y	175	38
Sceloglaux albifacies	0	0	1	1	TA	G	L	V	Y	600	48
Percent extinct =	**0.00**	**0.00**									

Appendix – *cont.*

Species	North Island	South Island	NI node	SI node	Habitat type	Nest site	Nest density	Diet	Volant ?	Body mass (g)	Egg length (mm)
Owlet-nightjars											
Aegotheles novaezealandiae	1	1	1	1	TA	A	L	I	Y	200	35
Percent extinct =	**100**	**100**									
Songbirds											
Acanthisitta chloris	0	0	1	1	TA	A	L	I	Y	7	16
Xenicus longipes	0	0	1	1	TA	G	L	I	Y	16	20
Xenicus gilviventris		0		1	TG	A	L	I	Y	20	20
Pachyplichas yaldwyni	1	1	6	6	TG	G	L	I	N	50	26
Traversia lyalli	1	1	6	6	TG	G	L	I	N	22	21
Dendroscansor decurvirostris	a	1		6	TG	G	L	I	N	30	23
Anthus novaeseelandiae	0	0	1	1	TG	G	L	I	Y	40	23
Bowdleria punctata	0	0	1	1	TG	G	L	I	Y	35	19.5
Mohoua albicilla	0	a	1		TA	A	L	I	Y	15	20
Mohoua achrocephala	a	0		1	TA	C	L	I	Y	25	23.5
Mohoua novaeseelandiae		0		1	TA	A	L	I	Y	11	18.5
Gerygone igata	0	0	1	1	TA	A	L	I	Y	7	17
Rhipidura fuliginosa	0	0	1	1	TA	A	L	I	Y	8	16
Petroica macrocephala	0	0	1	1	TA	A	L	I	Y	11	18
Petroica australis	0	0	1	1	TA	A	L	I	Y	35	25
Notiomystis cincta	0	a	1		TA	C	L	H	Y	30	19
Anthornis melanura	0	0	1	1	TA	A	L	I	Y	26	23
Prosthemadera novaeseelandiae	0	0	1	1	TA	A	L	H	Y	90	29
Callaeas cinerea	a	0	1	1	TA	A	L	H	Y	230	40
Callaeas wilsoni	0	a			TA	A	L	H	Y	230	35
Philesturmus carunculatus	a	0		1	TA	C	L	I	Y	70	29
Philesturnus rufusater	0	a	1		TA	C	L	I	Y	70	29
Heteralocha acutirostris	0	a	1		TA	A	L	I	Y	300	45
Tumagra capensis	a	0		1	TA	A	L	I	Y	130	35
Tumagra tanagra	0	a	1		TA	A	L	I	Y	130	35
Corvus moriorum	1	1	2	2	TA	A	L	I	Y	950	56
Percent extinct =	**15.79**	**20.00**									

Kiwis											
Apteryx Eastern South Island	a	1		7	TG	GC	L	I	N	1400	120
Apteryx australis	0	0	7	7	TG	GC	L	I	N	1500	125
Apteryx owenii	0	0	7	7	TG	GC	L	I	N	1200	110
Apteryx haastii		0		7	TG	GC	L	I	N	2200	124
Percent extinct =	**0.00**	**0.00**									
Moas											
Anomalopteryx didifonnis	1	1	8	8	TG	G	L	H	N	50000	160
Meealapteryx didinus		1		8	TG	G	L	H	N	20000	125
Pachyomis elephantopus		1		8	TG	G	L	H	N	145000	216
Pachyomis australis		1		8	TG	G	L	H	N	120000	205
Pachyomis mappini	1	a	8		TG	G	L	H	N	20000	125
Emeus crassus		1		8	TG	G	L	H	N	50000	160
Euryapteryx geranoides	1	1	8	8	TG	G	L	H	N	95000	192
Euryapteryx curtus	1	a	8		TG	G	L	H	N	20000	125
Dinomis struthoides	1	1	8	8	TG	G	L	H	N	100000	195
Dinomis novaezealandiae	1	1	8	8	TG	G	L	H	N	150000	218
Dinomis giganteus	1	1	8	8	TG	G	L	H	N	200000	236
Percent extinct =	**100**	**100**									
Gruiforms											
Aptomis defossor	a	1		8	TG	G	L	H	N	10000	94
Aptomis otidiformis	1	a	8		TG	G	L	H	N	8000	90

Notes:
0 = still present at time of European contact, 1 = extinct, a = absent from the Island.
NI node, SI node = terminal node number from Fig. 3 for the North (NI) and South (SI) Islands, respectively.
Habitat type: (a) A = aquatic; (b) TG = terrestrial and spending most time on the ground; (c) TA = terrestrial and aerial.
Nesting site: (a) GC = in a cavity within the ground or in a fallen log, etc.; (b) G = on the ground but not in a cavity; (c) A = arboreal; (d) C = in a cavity not on the ground.
Nest density: (a) H = high, nesting in colonies or nesting territories closely packed; (b) L = low.
Food: (a) F = fish; (b) V = vertebrates other than fish; (c) H = vegetable matter; (d) I = invertebrates.
Volant: Y(es) or N(o).