

## Late Holocene extinction of the New Zealand owlet-nightjar *Aegotheles novaezealandiae*

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**Abstract** The New Zealand owlet-nightjar (*Aegotheles novaezealandiae*) was a small (c. 150 g), almost flightless endemic bird that was widely distributed before human settlement. It was extinct before European settlement and has not so far been found definitely in a Polynesian cultural context. A series of accelerator mass spectrometry <sup>14</sup>C ages on gelatin from owlet-nightjar bones from non-cultural deposits was analysed using Bayesian statistics. The results indicate that the owlet-nightjar may have begun to decline before Polynesian settlement. Such a decline would be consistent with the effects of predation by a new predator—most probably the Pacific rat *Rattus exulans*.

**Keywords** New Zealand owlet-nightjar; *Aegotheles novaezealandiae*; extinction; *Rattus exulans*; predation; human impact

### INTRODUCTION

Three size classes within the late Quaternary avifauna of New Zealand experienced different levels of extinction at different times (Holdaway 1999). The different extinction rates indicate that taxa of different sizes were affected differently by the new factors in the environment, including predation by humans and Pacific rats (*Rattus exulans*), and habitat destruction. Hunting and habitat removal drove almost all birds >5 kg in body mass to extinction shortly after human settlement (Holdaway 1999; Holdaway & Jacomb 2000). Only one species, the yellow-eyed penguin (*Megadyptes antipodes*), survived, but it may have been reduced to a remnant population at the southern end of its mainland range before expanding north again (Worthy 1997).

Species of less than “megafaunal” size varied in their response to the new predation pressures and habitat loss in ways determined by their body size, flying ability, breeding habits, and habitat (Holdaway 1999). Most coastal, freshwater, and arboreal species were relatively little affected until large, arboreal, and water-tolerating predators such as stoats (*Mustela erminea*) and Norway (*Rattus norvegicus*) and black (*R. rattus*) rats were introduced by Europeans after AD 1760.

On the other hand, terrestrial species, and especially flightless taxa, were less successful. The second of the three size groups, mid-sized species of 1–5 kg, were least affected by the

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first wave of extinctions (Holdaway 1999). The lower limit of this size range is difficult to define. Some birds of 1–5 kg laid small eggs for their body size or were particularly helpless on land and therefore subject to predation by Pacific rats (Holdaway 1999). Several, however, survived into European times, including the kakapo (*Strigops habroptilus*) and South Island takahe (*Porphyrio hochstetteri*) which are among the most endangered species and subject to intensive management. Both species started to decline well before European arrival (Williams 1956; Holdaway 1999; Holdaway et al. 2001), but the adults are too large to be threatened by Pacific rats. Apparently, attrition of eggs and young was slow enough in high altitude habitats (where Pacific rats were rare) to allow remnant populations to survive. Survival at the periphery rather than the centre of the former range is common with many endangered taxa (Lomolino & Channell 1995).

Extinction in the late Quaternary of New Zealand vertebrates <500 g in body mass requires a separate explanation to that of the extinction of the large flightless birds, seals, and sea lions. Many smaller species became extinct almost simultaneously, soon after first human contact and after surviving the sudden and dramatic climatic changes of the previous 30 000 years. They could not have been major parts of the diet of human settlers. They were too small, and offered too little return for effort in capturing them. While most of these small species were probably eaten when available, none was likely to have been subjected to the steady attrition visited upon the 11 species of moa (Dinornithiformes), geese (Anatidae), and other large birds (Cassels 1984; Holdaway 1989; Holdaway & Jacomb 2000; Worthy & Holdaway 2002).

Elsewhere (Holdaway et al. 2002), we have discussed the timing and causes of extinction of a small, terrestrial species, Finsch's duck (*Chenonetta finschi*), that was likely to have been both palatable to humans and large enough to be considered as worthwhile prey. Adult Finsch's ducks were probably not particularly vulnerable to direct predation by Pacific rats. However, the egg was within the size range accessible to the rat (60 mm long) (Holdaway 1999) and its extinction was probably initiated by rat predation on eggs and young and completed in the earliest stage of human settlement by human and rat predation (Holdaway et al. 2002).

Although the data suggest that the numbers of Finsch's duck began to decline before widespread human settlement, it is possible that such a species, being palatable to humans and relatively easy to catch because it was primarily terrestrial and almost flightless (Worthy 1988), could have succumbed very quickly to human hunting. If so, its apparent rarity in the archaeological record may be an artefact of the rapidity of the human assault. To further test the hypothesis that Pacific rats initiated extinctions of small vertebrates before widespread human settlement, it is necessary to examine the fate of even smaller species that are unlikely to have featured prominently in the diet of settlers, and yet whose fossil distribution is known well enough for us to be certain that it was both widespread and abundant in the immediately pre-human environment. Such a species has to have been both accessible to Pacific rats and vulnerable to predation by them on its adults as well as eggs and young (Holdaway 1999). According to the hypothesis of an early arrival of the Pacific rat with transient human visitors, these species are likely to have suffered extinction earlier than others because no life history stage was safe from predation. They had no "demographic refuge", such as high adult survival, that helped species such as small petrels to withstand the effects of mammalian predators for decades if not centuries in the presence of high populations of rats.

One species that fulfils all the above criteria, including being common in the Holocene fossil record, is the New Zealand owlet-nightjar *Aegotheles novaezealandiae* (Scarlett, 1968). Scarlett (1968) described the species from material he had accumulated over several years from sites in both the North and South Islands. He made it the type species of a new

genus, *Megaegotheles*, which was based on the New Zealand species' large size and the reduction in its wing and pectoral girdle. Rich & Scarlett (1977) reviewed the species when new material was available and discussed its wing and leg proportions in relation to whether the species was flightless, accepting that it probably flew poorly, if at all, and spent much of its time on or near the ground. Olson et al. (1987) reviewed the Aegothelidae and referred the New Zealand species to *Aegotheles*. They considered that the differences between it and other taxa in *Aegotheles* are related to a weakening of flight and increased leg development, characteristics that are not sufficient for separation at generic level. Holdaway et al. (2001) accepted this decision and recommended that the species be listed under *Aegotheles*. The species was one of the largest in the genus, and weighed about 150–200 g, based on estimates from allometric relationships between limb bone measurements and body mass (Worthy & Holdaway 2002). It was similar in size to *A. savesi* from New Caledonia, which is known from a single skin and a few fossils (Olson et al. 1987), and much larger than the common *A. cristatus* of Australia.

Despite being nocturnal, owls were eaten by early Polynesians in New Zealand (Worthy 1999). Therefore, although owl-nightjars are nocturnal and cryptic and would not have been encountered regularly by people, they are likely to have been eaten when available. Certainly they were larger than other species such as the robins (*Petroica* spp.) and pipits (*Anthus novaeseelandiae*) which were eaten regularly (Worthy 1999). If so, owl-nightjar remains should be present in archaeological sites, especially those dating from the settlement period in late 13th and early 14th centuries (Anderson 1991; Higham et al. 1999; Lowe et al. 2000). The two published reports of the species in apparent cultural contexts (McCulloch 1994; Worthy 1999) are dealt with below.

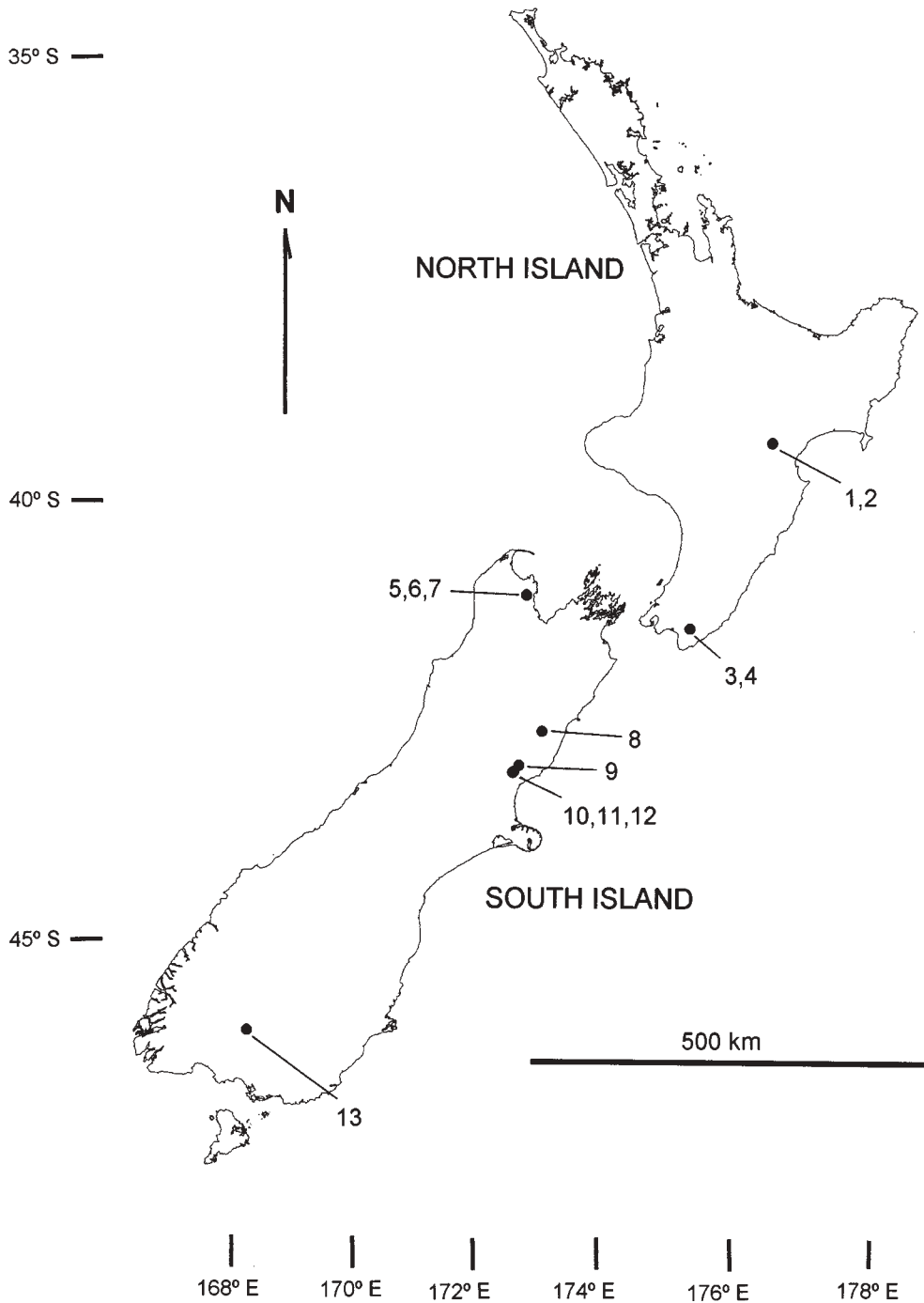
In this paper, we outline the distribution of the owl-nightjar during the Holocene, as determined from the presence of its remains in non-cultural fossil deposits. Based on a series of radiocarbon ages from situations where there was evidence that the deposition of fossils began before human settlement and continued into the European period (Holdaway et al. 2002), we provide probability distributions for critical events in the extinction of the species. These include the dates of the start of its decline to extinction at various sites, and of its final extinction defined by its last appearance in the fossil record. The implications of the time of its extinction in relation to other factors in the New Zealand environment are then explored.

## METHODS

### Late Holocene distribution

The natural (non-cultural) and archaeological records for *A. novaeseelandiae* were compiled and plotted to examine the natural distribution of the species during the Holocene and test for evidence for a range reduction before Polynesian settlement. Non-cultural fossil distributions were plotted from an unpublished database developed from continuing work in both major islands (see Worthy & Holdaway 2002 for a list of references to 2000). The archaeological distribution of the species and the distribution of sites of archaic age containing faunal material were compiled from Anderson (1989) and Worthy (1999).

Sites for radiocarbon analysis of the time of incorporation of *A. novaeseelandiae* bones into deposits were chosen using criteria that included presence of large samples and evidence that the main sampling mechanism (primarily predation by the laughing owl *Sceloglaux albifacies*) continued to the European period (Worthy & Holdaway 1994a,b; Holdaway & Worthy 1996). In all, <sup>14</sup>C AMS determinations were obtained on samples from 13 sites (Fig. 1). If a site contained the remains of taxa introduced by Europeans and the remains of extinct taxa, it was assumed that the record in that site was continuous through the period of interest.



**Fig. 1** Location of sites from which New Zealand owl-nightjar (*Aegotheles novaeseelandiae*) bones were dated for this study. 1, Hukanui Pool; 2, Hukanui 7a; 3, Martinborough #2; 4, Glowworm Fissure; 5, Predator Cave; 6, Hawke's Cave; 7, Kairuru Cave; 8, Holocene Hole; 9, Ardenest; 10, Euan Murchison #1; 11, Gowan Hill "old"; 12, Gowan Hill "young"; 13, Castle Rocks.

**AMS <sup>14</sup>C dates, sample preparation**

Samples were selected from the material collected by RNH and by T. H. Worthy, from collections of the Museum of New Zealand Te Papa Tongarewa, and from collections made by RNH (Hukanui Pool, Hukanui #7a), THW (Glowworm fissure), and THW and RNH (Predator Cave, Kairuru Cave, Hawke’s Cave, Holocene Hole, Ardenest, Gowan Hill). The locations of sample sites are given in Fig. 1. All sample treatment was done by NRBA, and AMS measurements were made after 1995 at the Rafter Radiocarbon Laboratory of the New Zealand Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand, according to the protocols described in Holdaway et al. (2002).

AMS <sup>14</sup>C dates are reported as conventional radiocarbon ages (CRA, years BP) as defined by Stuiver & Polach (1977), and as calibrated dates. Calibrated dates were obtained using a bi-decadal calibration based on Stuiver et al. (1998), and the program Winscal 4.0 (Institute of Geological and Nuclear Sciences). Calibrated dates were used for the reasons given by Taylor et al. (1996).

**%C, %N, δ<sup>13</sup>C, δ<sup>15</sup>N, C:N ratio**

Proportions of C and N and the enrichment of <sup>13</sup>C and <sup>15</sup>N in bone gelatin samples were measured at the Rafter Laboratory using the method described in Holdaway et al. (2002).

**Statistical treatment**

Using 12 of the 20 determinations on *A. novaezealandiae* bone, we sought to establish the time range over which the extinction of this species occurred using the Bayesian model presented by Holdaway et al. (2002) to examine the extinction of Finsch’s duck (*Chenonetta finschi*). Briefly, assuming that the dated capture events (an owl-nightjar caught by a laughing owl) can be described as a constant rate Poisson process (this describes discrete random temporal events of relatively low temporal frequency), we can compute posterior distributions for parameters of interest via sample-based Bayesian inference.

Let  $y_{m,n}$  denote the value of the  $n$ th radiocarbon age measured in the  $m$ th phase (e.g., for the Ardenest site  $m = 1$  as opposed to the Gowan Hills site where  $m = 2$ ), reported with associated standard error  $\sigma_{m,n}$  and  $\theta_{m,n}$  denote the calibrated date for the specimen ( $m,n$ ). Let  $\psi_{si}$  and  $\psi_{ei}$ , respectively, denote the (unknown and undated) calendar dates of the beginning and end of pre-extinction phase  $i$ , and  $\psi_1$  and  $\psi_2$  denote the (unknown and undated) calendar dates of the beginning and end of the global extinction process. Then the state space ( $\Omega$ ) for the  $i = 1..k$  phases can be given as

$$\Omega \equiv (\psi, \theta);$$

$$\begin{matrix} TPQ & \psi_{si} & \theta_i & \psi_{ei} \\ TPQ & \psi_1 & \psi_{e1, \dots, e_k} & \psi_2 & TAQ \end{matrix} \quad (1)$$

where the *TAQ* (Terminus Ante Quem) and *TPQ* (Terminus Post Quem) are 100 BP and 13 000 BP, respectively, with four phases (i.e.,  $k = 4$ ) corresponding to the Ardenest, Gowan Hills, Predator Cave, and Kairuru Cave sites.

Following the standard Bayesian inferential framework the posterior distribution of  $\psi$  and  $\theta$  conditional upon the observed dates  $y(h(\psi, \theta | y))$  is defined in terms of an unnormalised prior density  $f(\psi, \theta)$ , and likelihood  $L(y | \theta)$  as,

$$h(\theta, \psi | y) = L(y | \theta) \times f(\psi, \theta). \quad (2)$$

Here the prior density  $f(\psi, \theta)$  follows that given in Nicholls & Jones (1998, 2001). This prior specifies that the span of activity for any process is *a priori* uniform between two parent bounds. This prior is considered non-informative in that it does not bias the span as may occur under other priors that have been proposed (Nicholls & Jones 2001).

The likelihood  $L(y|\theta)$  used here follows the standard definition of the radiocarbon likelihood (Buck et al. 1996) and derives from the CRAs associated with each  $\theta$ . Let  $\theta_{m,n}$  be a calibrated date for specimen  $(m,n)$ , measured in units of calendar years AD, and assumed to equal the context date associated with the  $(m,n)$ th specimen. The observation model for  $y_{m,n}$  is

$$y_{m,n} \sim \text{Normal}(\mu(\theta_{m,n}), \sigma(\theta_{m,n})^2) \quad (3)$$

where

$$\sigma(\theta_{m,n})^2 \equiv \hat{\sigma}(\theta_{m,n})^2 + \tilde{\sigma}_{m,n}^2 \quad (4)$$

and  $\mu(\theta_{m,n})$  and  $\hat{\sigma}(\theta_{m,n})$  are standard, empirically determined radiocarbon calibration functions (e.g., Stuiver et al. 1998). In this instance, the 1998 INTERCAL terrestrial data are used (Stuiver et al. 1998). Let  $\lambda(\gamma_{m,n}|\theta_{m,n})$  denote the likelihood of parameter  $\theta_{m,n}$ ,

$$\lambda(\gamma_{m,n}|\theta_{m,n}) = \frac{1}{\sigma(\theta_{m,n})\sqrt{2\pi}} \exp\left(-(\gamma_{m,n} - \mu(\theta_{m,n}))^2 / 2\sigma(\theta_{m,n})^2\right) \quad (5)$$

Thus  $\lambda(\gamma_{m,n}|\theta_{m,n})$  is a density distribution normalised over  $\gamma_{m,n}$  values, and unnormalised over  $\theta_{m,n}$  values. Observations are assumed independent, so the joint likelihood,  $L(y|\theta)$ , is

$$L(y|\theta) = \prod_{m=1}^M \prod_{n=1}^{N_m} \lambda(\gamma_{m,n}|\theta_{m,n}) \quad (6)$$

The posterior distribution of any individual parameter (i.e.,  $\psi_i$  or  $\theta_i$ ) or statistic such as phase span (i.e.,  $\psi_1 - \psi_0$ ) is simply a marginal integrated from the joint distribution  $h(y, \theta|\gamma)$ . A terrestrial reservoir offset of  $-27 \pm 5$  years (McCormac et al. 1998) has been applied in this analysis following the correlated model given by Jones & Nicholls (2001).

In the present analysis, we are most interested in the following parameter statistics:

Onset of the overall owlet-nightjar extinction process	= $\psi_1$
Termination of the overall owlet-nightjar extinction process	= $\psi_2$
Span of the the overall owlet-nightjar extinction process	= $\psi_1 - \psi_2$

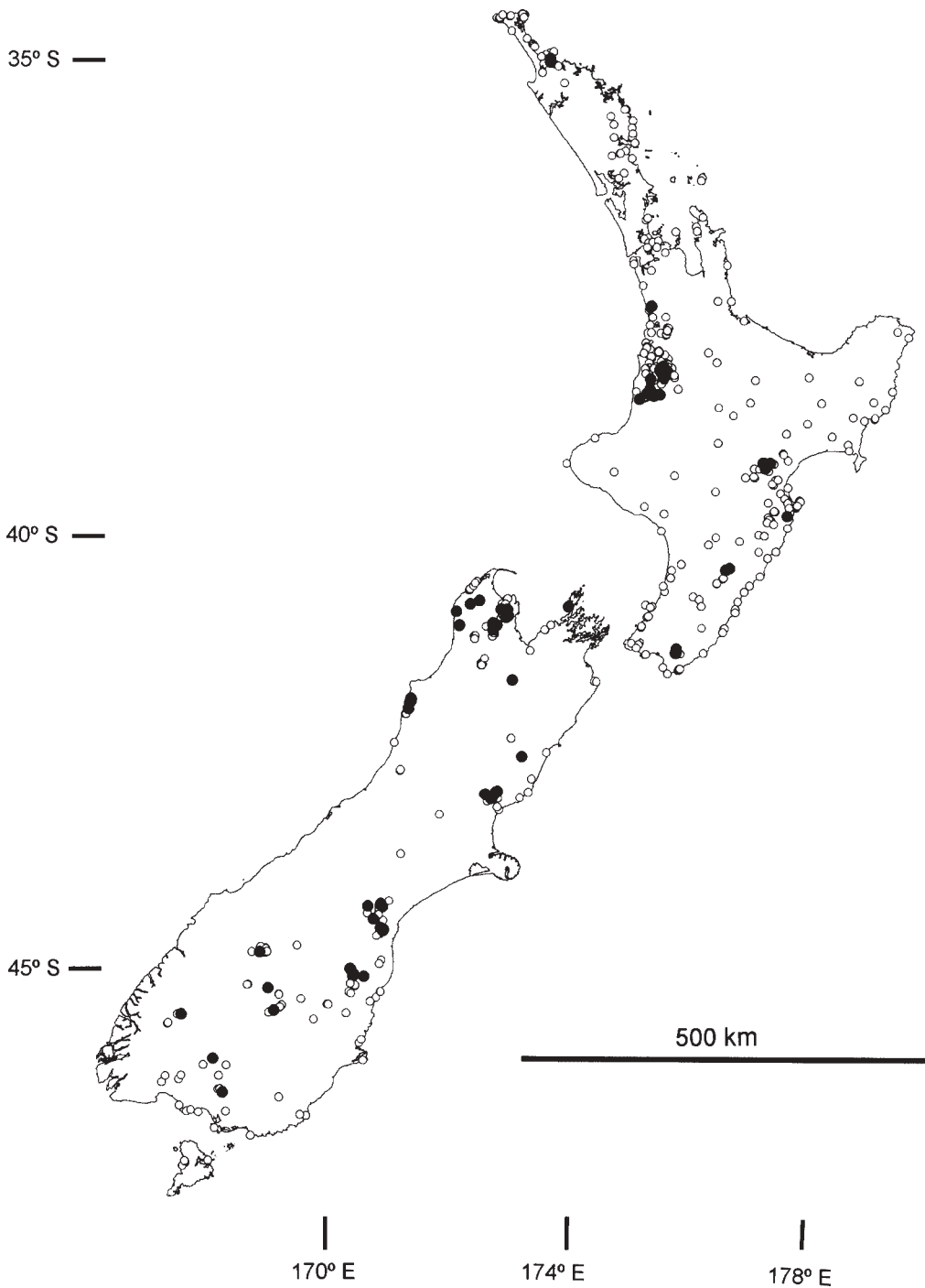
These statistics were calculated using a Markov Chain Monte Carlo (MCMC) based Bayesian analysis following the Metropolis-Hastings sampler described by Nicholls & Jones (1998, 2001). The corresponding statistics for parameters governing the local termination events at Ardenest, Gowan Hills, Predator Cave, and Kairuru Cave were also obtained. The confidence intervals (highest posterior densities, HPD) of these statistics were determined and plotted.

## RESULTS

### Holocene distribution

In the late Holocene, immediately before first human contact with the archipelago, *A. novaezealandiae* was found almost throughout the two main islands, and on D'Urville Island (Holdaway et al. 2001) (Fig. 2). Scarlett (1968) summarised the distribution as then known, and other sites were known by the time Rich & Scarlett (1977) redescribed the species. Since 1977, remains of the species have been identified from a further 91 sites of (mainly) Holocene age, and four sites of definitely Pleistocene age (RNH and T. H. Worthy unpubl. data; Fig. 1). Many of these additional sites are listed in Worthy (1997, 1998a,b) and in Worthy & Holdaway (1993, 1994a, 1995, 1996a, 2000).

None of the sites listed by Scarlett (1968) or Rich & Scarlett (1977), or in the New Zealand database (Fig. 2) has a cultural context. McCulloch (1994) suggested that the material from two sites (Frenchmans Gully, South Canterbury, and a rockshelter at Weka Pass, North Canterbury) were associated with the early Polynesian sites at those places. The rockshelter near Weka Pass was identified by Worthy & Holdaway (1996a) as Euan Murchison's



**Fig. 2** Distribution of non-archaeological sites containing New Zealand owl-nightjar (*Aegotheles novaezealandiae*) bones of mainly Holocene age (filled circles), compared with distribution of non-archaeological sites of Holocene age from which fossil bones have been recovered. Because of the scale, many of the sites lacking *A. novaezealandiae* are obscured, e.g., there are 43 sites in the Punakaiki karst (West Coast) and a further 43 on Takaka Hill and in Takaka Valley (north-west Nelson).

Rockshelter #1 as listed by Scarlett (1969) and catalogued as such in the collections at Canterbury Museum. Material at that site was interpreted by Worthy & Holdaway (1996a) as being of mixed origins, with only a few bones being associated with the thin cultural layer and most being from a pre-existing predator (probably laughing owl *Sceloglaux albifacies*) deposit in the sediments on which the cultural deposit was laid. The material from an archaeological site at Opito on the Coromandel Peninsula (Jolly & Murdoch 1973) has not been re-examined and as with material of other species from similar sites in the area, such as that of Eyles's harrier (*Circus eylesi*) from Hot Water Beach (Canterbury Museum Av16209), it is likely to be from a natural deposit in the dunes on which people settled later.

The owllet-nightjar is not likely to have been pitfall-trapped. It had strong legs (Rich & Scarlett 1977; Worthy & Holdaway 2002) and could have climbed relatively steep walls even if it could not have flown out. It did, however, frequent the entrances of caves, penetrated passages farther than most species, and probably nested in such places as the entrance to Kairuru Cave on Takaka Hill, where remains of adults and juveniles were found together below a possible nest niche (RNH and T. H. Worthy unpubl. data). Remains of the species are therefore common in suitable cave deposits in both islands (Worthy & Holdaway 1993, 1994a, 2000). By far the most important new information on the distribution of the species, especially in the eastern South Island, has come from deposits accumulated by laughing owls (Worthy & Holdaway 1994b, 1996b). The owl survived into the early 20th century (Worthy 1997). As the owllet-nightjar was a normal part of the owl's prey (Holdaway & Worthy 1996), owllet-nightjar bones would be incorporated in the sites so long as they were available to the owl. Therefore, the youngest bones from a series of owl should provide information on the time of the owllet-nightjar's extinction.

On the evidence of these non-cultural sites, interpreted as being the remains of birds, mammals (bats), frogs, and reptiles collected by the owls from within 1–2 km of the site (Holdaway & Worthy 1996), the owllet-nightjar was abundant in many parts of both islands. Importantly for analysis of the reasons for its extinction, the species was found widely in both the wet forests of the West Coast and in the drier eastern mosaic forest-shrublands of the South Island. These vegetation types fared very differently during the extensive fire-induced deforestation immediately after Polynesian settlement (McGlone et al. 1993).

The other reputed association of *A. novaezealandiae* with humans mentioned by McCulloch (1994) was a single bone from a deposit at Frenchmans Gully. Worthy (1997) pointed out that the location of the site is recorded in the Canterbury Museum catalogue as being on "the farm at the head of Frenchmans Gully" which does not tally with either of the recorded archaeological sites (J39/17 and J39/26) in that area, neither of which has any recorded excavations. Site B, which contained one bone of *A. novaezealandiae* (Av19890), was identified by Worthy (1997) as a rockshelter with a fallen roof slab on Tuarangi Station at the head of the gully. There are early Polynesian rock drawings in this shelter but no evidence that the fossil material was associated with cultural remains. The only other record in the archaeological literature is for Opito, on the Coromandel Peninsula. However, other material from there is not associated with cultural remains and it is likely that the owllet-nightjar material was from a natural deposit in the dunes.

### **Radiocarbon**

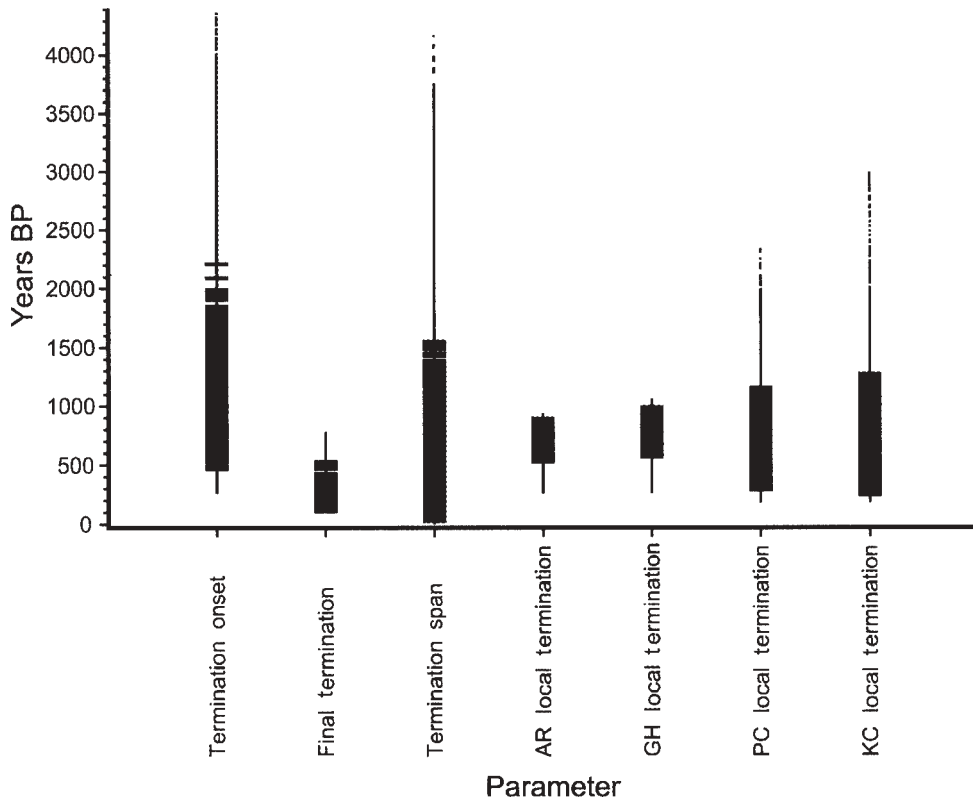
The conventional radiocarbon ages of 4 bones of the owllet-nightjar from 4 sites in 2 areas of the North Island and 16 bones from 9 sites in 4 areas of the South Island are given in Table 1. The corresponding calibrated calendar ages (based on terrestrial reservoir data) are shown in Table 2. None of the bones gave a conventional radiocarbon age of <950 years BP (Table 1), despite younger ages on other taxa and from the same sites, and the presence at those sites

**Table 1** Sample, bone quality parameters, and conventional radiocarbon ages for bones of the New Zealand owl-nightjar (*Aegotheles novaezealandiae*) from natural sites in North and South Islands. Map ref. is to NZMS 260 Sheet/Grid ref.; Element, bone used for sample; R or L, right or left element; imm, immature; -d, lacking distal end; hum, humerus; uln, ulna; fem, femur; tbt, tibiotarsus; tmt, tarsometatarsus; Lab no., Rafter Radiocarbon Laboratory sample number; NZA, Rafter Radiocarbon Laboratory <sup>14</sup>C AMS age series number; CRA, conventional radiocarbon age (in <sup>14</sup>C years before AD 1950); δ<sup>13</sup>C, depletion in <sup>13</sup>C (‰) of sample against standard; δ<sup>15</sup>N, enrichment in <sup>15</sup>N of sample with respect to atmospheric N; %C, percentage of carbon in purified gelatin; %N, percentage of nitrogen in purified gelatin; C:N, carbon:nitrogen ratio in purified gelatin; %c, percentage of collagen yield from demineralised bone; %g, percentage of gelatin extracted from gelatinised collagen; %i, percentage of insoluble residue filtered from gelatinised collagen; k, phase in Bayesian analysis (see Methods); i, number of radiocarbon ages in each phase (see Methods).

Site	Map ref.	Cat. no.	Element	Lab no.	NZA	CRA	δ <sup>13</sup> C	δ <sup>15</sup> N	%C	%N	C:N	%c	%g	%i	k	i
<b>North Island</b>																
Hukanui Pool	V20/149115	MINZ unreg.	Tbt	R21701/5	7635	2069 ± 70	-20.7	NA	NA	NA	NA	7.0	NA	NA	7.5	
Hukanui #7a	V20/149111	S37290	Rtmt	R26525/4	13433	1689 ± 55	-20.3	10.2	34.1	11.8	2.9	17.0	89.6	7.3		
Glowworm Fissure	c.S28/096779	S25804	Rtbtmm	R26525/2	13431	2115 ± 55	-19.8	9.1	35.7	12.7	2.8	15.5	89.7	3.7		
Martinborough #2	c.S28/096779	S24595	Ltbt	R26525/5	13434	4181 ± 65	-19.4	10.0	19.8	6.5	3.1	17.2	89.9	6.6		
<b>South Island</b>																
Predator Cave	N26/017211	S32362	Rtbtmm	R24707/17	10343	11 805 ± 70	-19.4	6.7	24.6	8.3	2.9	11.9	92.7	1.7	3	1
			Lhumimm	R24874/19	10882	6645 ± 60	-19.9	6.1	20.4	7.6	2.7	10.2	c. 90	3.0	3	2
			Lhumimm	R24874/21	10883	2454 ± 60	-20.1	5.8	45.3	16.3	2.8	14.5	c. 90	3.4	3	3
Hawke's Cave	N26/017217	S30215	Rfem-d	R24707/16	10345	2586 ± 60	-19.7	5.3	24.1	8.3	2.9	16.8	c. 90	6.0		
Kairuru Cave	N26/020215	S unreg.	Ltbtsh	R26051/3	11226	3154 ± 55	-18.8	NA	NA	NA	NA	14.2	84.8	3.3	4	1
			Ltbtsh	R26051/4	11227	2901 ± 55	-19.1	NA	NA	NA	NA	15.7	96.0	2.4	4	2
Euan Murchison #1	M33/853001	Av17784	Ruln	R24707/13	10340	10 951 ± 70	-20.8	11.1	33.0	11.4	2.9	12.7	c. 90	7.8		
Ardenest	M33/916073	S33678pt	Rfem-d	R24707/11	10338	2486 ± 70	-20.0	12.8	36.3	12.7	2.9	12.4	c. 90	0	1	1
			Tbtid	R24707/12	10339	1301 ± 70	-20.5	13.2	34.3	13.2	2.9	17.6	95.0	2.2	1	2
			Lhumimm	R24874/18	10881	954 ± 60	-21.5	13.9	54.2	19.7	2.7	14.4	c. 90	1.2	1	3
Gowan Hills "younger"	M34/836988	S33449pt	Rtmt	R24707/15	10342	3296 ± 60	-21.5	14.1	29.2	10.1	2.9	18.4	90.0	4.0	2	1
Gowan Hills "older"	M34/836988	S33810pt	Rfem	R24707/14	10341	1076 ± 60	-20.8	13.3	35.9	12.2	2.9	16.5	85.5	9.8	2	2
			Rhum	R24874/16	10879	3066 ± 60	-20.9	14.1	32.6	12.1	2.7	16.8	c. 90	6.2	2	3
			Rhum	R24874/17	10880	3052 ± 60	-21.4	13.7	16.6	5.9	2.8	11.9	92.7	1.7	2	4
Holocene Hole	M32/214496	S33351	Lhum	R26525/3	13432	4622 ± 55	-20.1	11.7	26.3	8.9	3.0	17.6	89.8	11.8		
Castle Rocks	E44/445718	S23305	Rhum	R26525/1	13430	1014 ± 60	-21.3	11.9	44.4	16.3	2.7	20.0	90.2	4.9		

**Table 2** Confidence intervals for calibrated AMS <sup>14</sup>C ages on bone gelatin of the New Zealand owllet-nightjar *Argotheles novaeseelandiae* from natural sites in North and South Islands, New Zealand.

Site	Lab no.	NZA	GRA	Confidence intervals for calibrated dates (calendar years BP)		
				1σ	2σ	2σ
<b>North Island</b>						
Hukanui Pool	R21701/5	7635	2069 ± 70	2121–1936	2296–2263; 2153–1869	
Hukanui #7a	R26525/4	13433	1689 ± 55	1689–165; 1626–1530	1718–1489; 1441–1424	
Glowwor -Fi&cure	R26525/2	13431	2115 ± 55	2148–2000	2305–2231; 2204–1945	
Martinborough #2	R26525/5	13434	4181 ± 65	4834–4578	4856–4522	
<b>South Island</b>						
Predator Cave	R24707/17	10343	11 805 ± 70	13976–13608	15192–14772; 14069–13469	
	R24874/19	10882	6645 ± 60	7577–7465	7614–7426	
	R24874/21	10883	2454 ± 60	2715–2358	2740–2343	
Hawke's Cave	R24707/16	10345	2586 ± 60	2759–2717	2781–2697; 2663–2486	
Kairuru Cave	R26051/3	11226	3154 ± 55	3442–3425; 3407–3340; 3277–3272	3470–3254	
	R26051/4	11227	2901 ± 55	3157–3149; 3139–3126; 3110–2949	3236–2868	
Euan Murchison #1	R24707/13	10340	10 951 ± 70	13085–12887	13149–12822; 12728–12655	
Ardenest	R24707/11	10338	2486 ± 70	2734–2364	2753–2345	
	R24707/12	10339	1301 ± 70	1289–1172	1327–1061	
	R24874/18	10881	954 ± 60	933–767	967–734	
Gowan Hills "younger"	R24707/15	10342	3296 ± 60	3625–3607; 3583–3459	3684–3379	
Gowan Hills "older"	R24707/14	10341	1076 ± 60	1055–933	1130–1107; 1088–915	
	R24874/16	10879	3066 ± 60	3357–3210	2781–2697; 2663–2486	
Holocene Hole	R24874/17	10880	3052 ± 60	3350–3205; 3184–3167	15192–14772; 14069–13469	
	R26525/3	13432	4622 ± 55	5451–5383; 5329–5304	5566–5552; 5471–5277; 5163–5132; 5104–5074	
Castle Rocks	R26525/1	13430	1014 ± 60	966–915	1055–787	



**Fig. 3** Confidence intervals for date of termination of the New Zealand owl-nightjar (*Aegotheles novaezealandiae*) in the North and South Islands. Years BP, calendar years before present (AD 1950); boxes, 68% HPD (highest posterior density confidence interval); lines, 95% HPD; Termination onset, start of the final phase of the modelled extinction process; Final termination, end of the modelled extinction process; AR, Ardenest; GH, Gowan Hill; PC, Predator Cave; KC, Kairuru Cave.

of taxa introduced after the mid 19th century (Worthy 1998a,b; Worthy & Holdaway 1994a, 1995, 1996a). The youngest calibrated age was NZA10881 with a lower ( $1\sigma$ ) confidence limit of 767 years BP, equivalent to 1183 AD. This sample was from Ardenest, a site that was occupied by laughing owls until at least the second half of the 19th century (Worthy & Holdaway 1996a).

The carbon and nitrogen contents, C:N ratio, and enrichment in  $^{13}\text{C}$  and  $^{15}\text{N}$  of the gelatin samples are also given in Table 1, as indicators of bone quality. All samples had a C:N ratio in the range 2.7–3.1, and total bone %N of 0.65–2.94 and hence were Class II (very well to well preserved) according to the bone quality classification of Stafford et al. (1988). The ages determined for the bones are therefore assumed to reflect the time of deposition. The older sample (R26525/5) from Martinborough had low amounts of C (19.8%) and N (6.5%) despite high yields of collagen (15.5%) and gelatin (89.7% of total collagen). This suggests that the bone was more altered than the other from that area (from a different site) which had values of 35.7 and 12.7% for C and N, respectively, and 15.5% for total collagen of which 89.7% was recovered as purified gelatin.

The oldest age on an owlet-nightjar bone was from Predator Cave ( $11\,805 \pm 70$   $^{14}\text{C}$  years BP; NZA10343). The age was consistent with NZA3065 ( $10\,879 \pm 83$   $^{14}\text{C}$  years BP) on a robin (*Petroica australis*) bone from the same deposit of laughing owl prey (Worthy & Holdaway 1996b). Nearly as old was a bone from the rockshelter on Euan Murchison's farm at Waikari, North Canterbury, which yielded a conventional radiocarbon age of  $10\,951 \pm 71$   $^{14}\text{C}$  years BP (NZA10340). This is much greater than would be expected if the bone came from the thin cultural layer in the site, as reported by McCulloch (1994). However, the age of the owlet-nightjar bone agreed broadly with that on a bone of Finsch's duck from the same site ( $9157 \pm 60$   $^{14}\text{C}$  years BP; NZA10193) (Holdaway et al. 2002). The consistently much greater ages on these bones support the interpretation that the cultural site was superimposed on a pre-existing site of predator origin (Worthy & Holdaway 1996a). The calibrated dates for the two bones are c. 3000 years apart, but several predator sites are known where deposition proceeded for more than 3000 years, including Predator Cave on Takaka Hill (Worthy & Holdaway 1994a) and Gowan Hill (Table 1; Holdaway 1999).

### Statistical analysis

The 68 and 95% highest posterior distributions for the parameters of interest in the extinction of the New Zealand owlet-nightjar in the South Island in general, and at four specific sites in the South Island, are shown in Fig. 3. Deposition apparently began at all the sites about or after the mid Holocene, and, most importantly, owlet-nightjars became unavailable for incorporation into the local traps within the past 1000 years.

The start and end of these local termination events indicate that, nationwide, local terminations began some time in the interval 460–2000 BP, which was the 68% HPD (confidence interval) for the likelihood of the start of the termination phase. The local terminations began before 600 BP (95% HPD) and final extinction would have occurred some time in the period 540–100 BP (68% HPD). Further, it is apparent that the nationwide extinction process may have taken a considerable period of time (68% HPD for duration of the local extinctions was 20–1400 years). It is likely that the species had declined in numbers before widespread human settlement to the extent that it was available to early settlers in only a few places within its former range. The extinction probably occupied several centuries, and small residual populations may have persisted into the period of European settlement.

## DISCUSSION

### Lack of an archaeological record

The non-association between the archaeological and non-cultural deposits at Rockshelter #1 points to the problem of interpretation of thin cultural deposits in places where natural processes can accumulate fossils. Deposits at other, similar, sites in the Waikari area should be re-analysed in light of the situation now known to have prevailed at Rockshelter #1. In particular, the large collection of jaws of the Pacific rat in Canterbury Museum from the Timpendean Rockshelter, whose accumulation has been attributed to human exploitation, should be re-examined to see whether they were part of a pre-existing predator deposit.

The results indicate that the owlet-nightjar populations in the South Island collapsed, and the species was massively reduced in range, by the time of widespread Polynesian settlement in New Zealand in the late 13th century (Anderson 1991; Higham et al. 1999; Lowe et al. 2000). With the rejection of two reported cultural contexts for the species in the South Island, there is presently no direct evidence for the species' survival there at the time of Polynesian settlement. The cultural context is equivocal, however, because the species was unlikely to

have been eaten regularly; it is possible that the apparent absence from cultural sites is a sampling artefact.

Although the four available ages suggest that the owl-nightjar also began to decline in the North Island before widespread Polynesian settlement, the available data are inadequate to constrain the probability distributions. The report from a cultural context at Opito is also insufficient evidence for its survival after Polynesian settlement. Remains of other birds from these sites, including bones of *Circus eylesi* from Hot Water Beach (Canterbury Museum Av16209), show that archaeological and natural remains have been mixed in the collections, and there is no independent evidence for association with the cultural site.

The lack of evidence for owl-nightjar remains in cultural contexts, in conjunction with a high probability for extinction beginning before 600 BP, indicates a reduction to near extinction by the time of widespread human settlement. Thus, the direct effects of human settlement (hunting and habitat destruction) are unlikely to have been major factors in the extinction of owl-nightjar. Indeed, substantial areas of habitat remained well into the European period on the West Coast of the South Island and in the interior of the North Island.

In the absence of significant environmental change during the period of decline and extinction (Burrows & Greenland 1979; Burrows 1982; Hellstrom et al. 1998), or evidence of disease (Holdaway 1999), and the apparent ubiquity if not abundance of the owl-nightjar during the Holocene, its extinction must be primarily attributed to predation by Pacific rats (Holdaway 1999). No other factor could conceivably have removed the species from throughout the main islands of the archipelago. Without refuges on other rat-free islands, which saved species such as Lyall's wren (*Traversia lyalli*) on Stephens Island in Cook Strait, and the South Island saddleback (*Philesturnus carunculatus*), bush wren (*Xenicus longipes*), and snipe (*Coenocorypha iredalei*) on the South Cape Islands south-west of Stewart Island at least until the European period, the owl-nightjar succumbed to predation pressure that probably lasted 1000 years before extensive Polynesian settlement (Holdaway 1996, 1999).

The loss of this small, vulnerable, and economically unimportant species with broad habitat requirements before widespread human settlement provides, along with the extinction of many other species with similar characteristics (Holdaway 1989, 1999), prima facie evidence for the presence of the Pacific rat in New Zealand before widespread permanent human settlement. Further work will be necessary to define the extinction time of other species and, particularly, to ascertain when population declines began before a complete picture of the pattern and causes of small vertebrate extinctions in New Zealand can be developed.

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