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Establishment and extinction of a population of South Georgian diving petrel (*Pelecanoides georgicus*) at Mason Bay, Stewart Island, New Zealand, during the late Holocene

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Abstract A population of South Georgian diving petrels (*Pelecanoides georgicus*) (c. 130 g) became extinct at Mason Bay, on the west coast of Stewart Island, before European settlement. Pacific rat (*Rattus exulans*) bones with the diving petrel fossils provided an opportunity to determine whether the rats arrived before the petrels went extinct. Fifteen ^{14}C accelerator mass spectrometry (AMS) ages on purified diving petrel bone gelatin from various parts of Mason Bay clustered unexpectedly in the 14th and 15th centuries AD, and none was older. Bayesian statistical analysis, using a Markov Chain Monte Carlo procedure, gave a 95% probability that the diving petrel colony was founded between 1338 and 1440 AD, lasted 40–310 years, and became extinct between 1475 and 1650 AD. Possible reasons for the late colonisation of Mason Bay by South Georgian diving petrels burrow are discussed. Bayesian analysis of five ^{14}C AMS determinations on Pacific rat bone gelatin did not exclude the possibility that the Pacific rat arrived before the diving petrel colony was established. However, the enriched δ^{13}C of their bone gelatin suggests that the rats had a partially marine diet, and a terrestrial calibration procedure for their AMS ages was probably not appropriate. The Pacific rat is likely to have arrived after the diving petrel colony became established and probably caused the bird's extinction after a short period of coexistence.

Keywords New Zealand; Stewart Island; extinction; *Pelecanoides georgicus*; *Rattus exulans*; radiocarbon dating; Bayesian statistics

INTRODUCTION

The late Quaternary extinctions consumed whole faunas of large mammals on the continents (Martin 1984). New Zealand, "the smallest continent" (Diamond 1990), lost not only its megafauna but also many small (≤1000 g) vertebrates (Holdaway 1999a). This mix was unusual; small vertebrates were more likely to go extinct on small islands (Martin & Steadman 1999). The New Zealand megafauna succumbed to over-hunting and habitat destruction (Anderson 1989; Holdaway & Jacomb 2000; Worthy & Holdaway 2002), but these factors were not important for smaller species. The small vertebrates most affected included the leiopelmatid frogs (50% lost; Worthy 1987a), mainland populations of tuatara (*Sphenodon*), an undetermined but possibly substantial number of lizards (Worthy 1987b;

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Worthy & Holdaway 2002), and 25 birds (Holdaway 1999a; Holdaway et al. 2001; Worthy & Holdaway 2002) (Table 1). All of the frogs, juvenile tuatara, almost all the lizards, and most of the birds weighed less than 100 g. Such small animals would have insufficient meat for people to rely on them for food, and since most of them lived where there was little or no

Table 1 Breeding distributions and representative body masses (g) of species of small (≤ 1000 g) birds in the Holocene avifauna of New Zealand known to have become extinct as breeding species on the main (North (N), South (S), Stewart (St)) islands of New Zealand before European settlement. Taxa in bold type are globally extinct. Body masses of living taxa are from Heather & Robertson (1996); those marked * were estimated, and are as listed in Holdaway (1999a). The list is based on Holdaway et al. (2001, Appendix 2) and updates that in Holdaway (1999a, Appendix 1). *Puffinus haurakiensis* was cited as *P. assimilis* in Holdaway (1999a). *Pachyptila turtur* and *Pterodroma inexpectata* survive as tiny remnant populations (on an overhanging cliff at Dunedin (Loh 2000) and on an islet in Lake Hauroko (Taylor 2000), respectively, both in the southern South Island): they are classified as functionally extinct.

Taxon		Breeding distribution			Representative body mass (g)
Procellariiformes					
Puffinus haurakiensis		N			200
Puffinus gavia		N	S		300
Puffinus spelaeus			S		250*
Pelecanoides urinatrix		N	S		130
Pelecanoides georgicus				St	120
Pachyptila turtur		N	S	St	125
Pachyptila vittata			S	St	200
Pterodroma cookii		N	S	St	200
Pterodroma inexpectata		N	S		325
Oceanites maorianus		N	S		35*
Garrodia nereis			S		35
Pelagodroma marina		N	S	St	45
Anseriformes					
Chenonetta finschi		N	S		800*
Malacorhynchus scarletti		N	S		800*
Mergus australis		N	S	St	900*
Gruiformes					
Capellirallus karamu		N			275*
Gallinula hodgenorum		N	S		450*
Fulica prisca		N	S		1000*
Charadriiformes					
Coenocorypha barrierensis		N			105*
Coenocorypha iredalei			S	St	105*
Caprimulgiformes					
Aegotheles novaezealandiae		N	S		200*
Passeriformes					
Traversia lyalli		N	S		22*
Pachyplichas yaldwyni		N	S		50*
Dendroscansor decurvirostris			S		30*
***Corvus* sp.**		N	S	St	950*
Petrels extinct		8	8	4	
Petrels extinct per island as % of total		42.1	38.1	50	
Total extinctions		19	21	8	
Total species extinct	25				
Total petrel species extinct	12				
Petrels as % of total	48				

environmental damage during the Polynesian era, they are unlikely to have suffered from habitat loss. Thus, these small animals were probably not seriously affected by human invasion and activity. Three of the four largest (500–1000 g) birds were waterfowl (Holdaway 1999a). The merganser (*Mergus australis*), Finsch's duck (*Chenonetta finschi*), and Scarlett's duck (*Malacorhynchus scarletti*) were worth eating by people. They and the fourth species, a raven (*Corvus* sp.), are known from archaeological contexts (Worthy 1998a, 1999) and, thus, to have become extinct after Polynesian settlement.

For all the remaining species, the timing in the late Holocene and apparently synchronous extinctions of the diverse range of phylogenetic lineages suggest that an extrinsic factor was involved, but eliminates disease as a potential cause (Holdaway 1999a). The introduction to New Zealand of a small predatory mammal, the Pacific rat (*Rattus exulans*), at about the time of the extinctions, suggested that predation by *R. exulans* was a significant factor in the extinction of most, if not all, of the smallest vertebrates that were extinct by the time of European settlement (Holdaway 1999a). *R. exulans* was the only external agent (other than Polynesian settlers) known to prey on small birds and their eggs (e.g., Booth et al. 1996) before European colonisation.

Six of the 10 exclusively terrestrial (i.e., excluding petrels and ducks) extinct species of ≤ 1000 g body mass were flightless, or nearly so (Falla 1954; Vickers-Rich & Scarlett 1977; Millener 1989; Millener & Worthy 1991; Worthy & Holdaway 2002) and 11 (61.1%) of the 18 flighted species (45.8% of all extinctions in that size range) were petrels (Table 1). Of the four flighted terrestrial species, one was a rail (the coot *Fulica prisca*), two were "shorebirds" (North Island snipe, *Coenocorypha barrierensis*; South Island snipe, *C. iredalei*), and one was a songbird (a raven, *Corvus* sp.). The largest taxa (*Fulica*, *Gallinula*, three ducks, and *Corvus*) were targets for human exploitation and large enough to be worthwhile sources of food. However, most (18 of 24; 75%) of the species, and all of the petrels, had body masses of ≤ 300 g and so were within the predatory capacity of *R. exulans*. Although small petrels were important items in the diet of Polynesians on Norfolk Island (Holdaway & Anderson 2001) and the Chatham Islands (Sutton 1979), and have been found in midden deposits on Stewart Island itself (Worthy 1999), the evidence for pre-European exploitation of these species on the North and South Islands is equivocal at best because of the limited data on small taxa from archaeological excavation records (Worthy 1999).

The preponderance of extinct species with a body mass of < 300 g, or egg length ≤ 60 mm, or both, suggests that taxa with these attributes were especially vulnerable to predation by *R. exulans* (Holdaway 1999a). That a body mass of 300 g was a critical factor in the vulnerability to extinction of small petrels and flightless birds is emphasised by the fates of two petrels whose body mass is just above that threshold. The mottled petrel (*Pterodroma inexpectata*; 325 g) bred on North and South Islands until the early 20th century (Stead 1932) but vanished rapidly after the introduction of other predatory mammals. In contrast, Hutton's shearwater (*Puffinus huttoni*; 350 g) survives in montane grasslands in the Seaward Kaikoura Ranges (Harrow 1965; Sherley 1992; Taylor 2000) but may have had a much wider distribution before European settlement (Worthy & Holdaway 1995, 1996; Worthy 1997, 1998b,c,d). Its survival at high altitudes when populations of small shearwaters (*P. huttoni*, *P. gavia*, and *P. spelaeus*) went extinct at lower altitudes in the South Island suggests that the mountains provided a refugium from predation. Although the rat has been reported at altitudes up to 1300 m (Atkinson & Moller 1990), it was most common lower down; most of the remaining colonies of *P. huttoni* are at 1200–1800 m (Heather & Robertson 1996). Although both mottled petrel and Hutton's shearwater seem to be at the limits of the predatory ability of *R. exulans* anyway, and might be expected to have survived the longest in their presence, their eggs are, at 60 and 61 mm, respectively, just at the upper limit of size that *R. exulans* can open unaided (Holdaway 1999a), so a reduction in breeding success, and hence a long-term population decline, might be expected where the rat was present.

The actual year or even century of extinction for any species that vanished in prehistory will always be difficult to ascertain, as emphasised by the difficulty of determining whether and when a species becomes extinct today or in the historical past (Harrison & Stiassny 1999; MacPhee & Flemming 1999). However, when determining a potential cause of a species' extinction, the most important information is the time when the decline began. Apart from the observation that they went extinct before 1770 (Holdaway 1999a), we know little about when the species susceptible to predation by *R. exulans* started their declines towards extinction. If a series of ^{14}C accelerator mass spectrometry (AMS) radiocarbon ages is available on bones from contexts where the species could be expected to have been preserved continuously (if it were still present) before, during, and after the expected time of extinction, probability distributions can be developed for the beginning, end, and duration of the decline. These distributions can then be compared with others for the establishment of predators or other potential factors in the extinction. Such probability distributions are available at present for only two species, Finsch's duck (Holdaway et al. 2002a) and the New Zealand owlet-nightjar (Holdaway et al. 2002b). Those analyses suggest that both species may have started their declines towards extinction before the most recent estimates for initial Polynesian settlement of AD 1280–1300 (Higham et al. 1999; Lowe et al. 2000).

No such data are available yet for the small petrels, despite their dominance of the extinctions of small birds on the main islands before European contact (Table 1) and their potential importance in the prehuman ecology of New Zealand (Worthy & Holdaway 2002). Sufficient fossil material for the extensive series of age determinations is available for only two species, Scarlett's shearwater (*Puffinus spelaeus*) on the South Island (Holdaway & Worthy 1994) and the South Georgian diving petrel (*Pelecanoides georgicus*) on Stewart Island (Worthy 1998b). However, the material of Scarlett's shearwater is too valuable to sample destructively in the numbers required for the analysis. In addition, North and South Island taxa are presently of limited use in determining any relationship between arrival time of *R. exulans* and the extinction of any taxon because the time of arrival of the rat on the main islands is controversial (Anderson 1996a, 2000; Holdaway 1996, 1999b; Beavan & Sparks 1998; Beavan-Athfield et al. 1999, 2001; Holdaway & Beavan 1999; Hedges 2000; Higham & Petchey 2000; Lowe et al. 2000; Beavan-Athfield & Sparks 2001a,b; Holdaway et al. 2002c; Yaldwyn 2002).

In contrast, an arrival post-AD 1300 for *R. exulans* on Stewart Island is less problematical (Holdaway 1999b). Therefore, the population of *P. georgicus* that formerly bred at Mason Bay, Stewart Island (Worthy 1998b) was chosen to determine whether the extinction of a small petrel could be related, at least chronologically, to the arrival of the predator hypothesised to have exterminated it. The principal condition for the analysis, that the deposition conditions that would have prevailed when the species was present continued after the extinction (Holdaway et al. 2002a,b), appeared to be satisfied as the type of breeding habitat used by the species at Codfish Island, sparsely vegetated dune sands (Imber & Nilsson 1980), is still present at Mason Bay (Johnson 1992). Therefore, a series of radiocarbon ages on diving petrel bones from the Mason Bay dunes was anticipated to range into at least the mid Holocene, as the dunes were formed on top of a breccia layer dated to the beginning of the Holocene at c. 10 000 BP (Bishop & Mildenhall 1994) and are likely to have been large enough to support petrel colonies within a few thousand years after that. The termination of the date series should indicate when the colony vanished, some time before Europeans settled on Stewart Island in the 19th century; probably within a century or so after the arrival of *R. exulans*. Here we report the results of Bayesian statistical analyses of a series of AMS ^{14}C

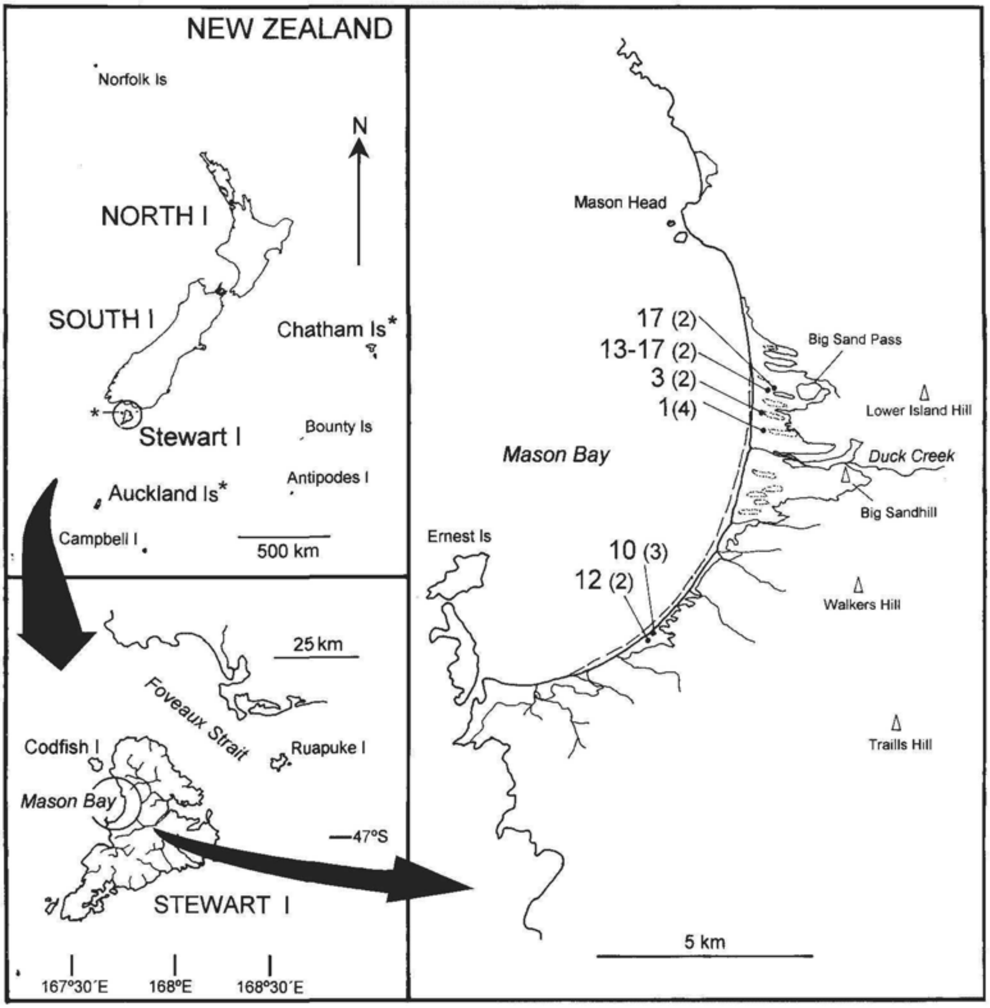

Fig. 1 Location of sample sites at Mason Bay, Stewart Island, New Zealand, and (*) of present and former colonies of South Georgian diving petrels (*Pelecanoides georgicus*) in New Zealand. Sample sites correspond to those listed in Worthy (1998b). Figures in parentheses are the number of diving petrel bones dated from each site.

ages on *P. georgicus* bones and of a previously published series of ages on *R. exulans* from Mason Bay to examine the relative chronology of arrival of the rat and the extinction of the potential prey, the South Georgian diving petrel.

MATERIALS AND METHODS

AMS ^{14}C ages: sample selection and preparation

Samples of *Pelecanoides georgicus* bone for accelerator mass spectrometry (AMS) dating were selected from collections made at different parts of Mason Bay: 10 samples were from sites north of Duck Creek and five from the southern, narrower, section of beach dunes (Fig. 1). There were sufficient *P. georgicus* fossils in collections and still eroding from dunes in several places in Mason Bay for a composite series to be selected without compromising the integrity of collections. Series of 1–4 bones were dated from each site (Fig. 1) so that the age range for occupation at each site could be established. Samples were drawn from sites at different parts of the bay to see whether the dune systems were occupied at different times. For *P. georgicus*, except for the first determination (NZA8402), left ulnae were selected to eliminate the possibility of duplicate ages on the same individual. The left humerus dated by NZA8402 was from an associated skeleton and therefore did not duplicate other samples from Site 1; it has been reported previously (Worthy 1998c, as NZA8406). For the *Rattus exulans* samples, different elements were selected, based on whether the bone was well preserved and could be spared from the sample for that site. Although different elements were dated, the dates are on different individuals because each bone came from a separate site (Table 2). Within the sampled dune system there are no known earlier fossil-bearing strata below the level yielding the diving petrel bones, and fossils are available from dunes set at varying distances from active beach sands. Thus, the analysed samples can be regarded as an unbiased random sample from throughout the duration of a colony of South Georgian diving petrels at Mason Bay.

Samples for accelerator mass spectrometry (AMS) ^{14}C ages on bone gelatin were prepared according to the protocol in Holdaway & Beavan (1999), and the ages measured, at the Rafter Laboratory, New Zealand Institute of Geological and Nuclear Sciences, Lower Hutt. AMS ^{14}C ages are reported as conventional radiocarbon ages (CRA, years BP) as defined by Stuiver & Polach (1977), using the old half-life for ^{14}C, and as calibrated ages. Historical events, such as the Polynesian settlement of New Zealand, the initiation and extinction of the petrel colony, and the introduction of *R. exulans* are discussed using calibrated (calendar) ages, for the reasons given in Taylor et al. (1996). For the radiocarbon ages of *P. georgicus* bones, the INTCAL98 (Stuiver et al. 1998) marine calibration data were used with a reservoir offset of -27 ± 15 (Higham & Hogg 1995) and correlated reservoir offset values after Jones & Nicholls (2001). For the *R. exulans* samples, terrestrial calibration data from INTCAL98 (Stuiver et al. 1998) were used, using a reservoir offset of 25 ± 5 (McCormac et al. 1998) and correlated reservoir offset values after Jones & Nicholls (2001).

%C, %N, δ^{13}C, δ^{15}N, C:N ratio

Proportions of C and N and the enrichment of ^{13}C and ^{15}N in the purified bone gelatin samples were measured at the Rafter Laboratory on splits from the dated gelatin, using the methods described in Beavan-Athfield et al. (2001). Isotope ratios are expressed conventionally as δ values (in parts per thousand, ‰), according to the standard equation:

$$\delta(^{13}\mathrm{C}, ^{15}\mathrm{N}) = [(R_{\mathrm{sample}}/R_{\mathrm{standard}})-1] \times 1000$$

where R_{sample} is the ratio ^{13}C/^{12}C or ^{15}N/^{14}N, and R_{standard} is the isotope ratio of the respective standard. Levels of enrichment of ^{13}C in the petrel and rat bones and between rat bones from Mason Bay and other published data were compared using two-tailed Student's *t*-tests.

Statistical treatment

We examined the time range over which a breeding colony of *P. georgicus* existed at Mason Bay, Stewart Island, by analysis of the 15 radiocarbon determinations. We regarded the different sample locations as being part of the same breeding colony, and the dated samples as an effectively random sample of the available material. The dated samples can therefore be modelled as being randomly derived from a single phase of activity with some unknown time of onset (ψ_1 = date at which the Mason Bay *P. georgicus* breeding colony was established), and some unknown time of termination (ψ_2 = date at which the Mason Bay *P. georgicus* breeding colony ceased to exist). Nicholls & Jones (2001) presented a Bayesian calibration scheme that treats this question and allows the recovery of the unknown temporal parameters

Table 2 Sample reference, location, bone quality parameters, and conventional radiocarbon ages for bones of the South Georgian diving petrel (PEGE; *Pelecanoides georgicus*), Pacific rat (RAEX; *Rattus exulans*), and black rat (RARA; *Rattus rattus*) from natural sites at Mason Bay, Stewart Island, New Zealand. Element, bone used for sample; R or L, right or left element; hum, humerus; uln, ulna; fem, femur; dent, dentary; Lab no., Rafter Radiocarbon Laboratory sample number; NZA, Rafter Radiocarbon Laboratory ^{14}C AMS age series number; CRA, conventional radiocarbon age (in ^{14}C years before AD 1950); δ^{13}C, depletion in ^{13}C (‰) of sample against standard; δ^{15}N, enrichment in ^{15}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. Ages on *Rattus exulans* bone from Holdaway (1999b).

Taxon	Site	Lat	Long.	Cat. no.	Element	Lab no.	NZA	CRA	δ^{13}C	δ^{15}N	%C	%N	C:N	% c	% g	% i
PEGE	1	46°55′11.7″S	167°46′12.4″E	S35966	Lhum	R24101/5	8402	1015 ± 76	–16.8	NA	NA	NA	NA	17.3	83.1	6.4
	1	46°55′11.7″S	167°46′12.4″E	S35967pt	Luln	R26810/1	14927	839 ± 75	–17.47	11.2	47.2	18.4	2.6	19.6	96.9	0.8
	1	46°55′11.7″S	167°46′12.4″E	S35967pt	Luln	R26810/2	14928	991 ± 65	–17.94	12.8	44.8	17.2	2.6	19.3	95.8	<1
	1	46°55′11.7″S	167°46′12.4″E	S35967pt	Luln	R26810/3	14929	779 ± 55	–17.84	12	42.2	15.9	2.6	21.9	85.8	<1
	3	46°54′57.1″S	167°46′14.1″E	S35984pt	Luln	R26810/4	14930	876 ± 55	–16.17	14.6	43	16.2	2.7	20.5	79.3	<1
	3	46°54′57.1″S	167°46′14.1″E	S35984pt	Luln	R26810/5	14931	1026 ± 65	–17.2	12.8	51.8	20.5	2.5	16.7	90	NA
	10	46°57′38.7″S	167°43′49.3″E	S36115pt	Luln	R26810/6	14932	823 ± 55	–16.94	12.1	61.2	25.6	2.4	17.7	90	<1
	10	46°57′38.7″S	167°43′49.3″E	S36115pt	Luln	R26810/7	14933	809 ± 60	–17.08	12.5	45.9	17.1	2.7	18.9	97.3	<1
	10	46°57′38.7″S	167°43′49.3″E	S36115pt	Luln	R26810/8	14934	831 ± 55	–16.96	12.6	50.5	19.1	2.6	17.8	90	<1
	12	46°57′33.4″S	167°43′54.0″E	S36127pt	Luln	R26810/9	14935	836 ± 60	–16.61	12.7	61.2	25.1	2.4	18.7	90	6.8
	12	46°57′33.4″S	167°43′54.0″E	S36127pt	Luln	R26810/10	14936	976 ± 60	–16.6	14.4	58.6	23.5	2.5	20.4	90	<1
	13–17	c. 46°54′40″S	167°46′20″E	S36158pt	Luln	R26810/11	14937	821 ± 60	–16.8	13.7	51.4	19.6	2.6	19.8	90	2
	13–17	c. 46°54′40″S	167°46′20″E	S36158pt	Luln	R26810/12	14938	773 ± 55	–17.01	12.9	48.9	18.1	2.7	17.6	93	1.3
	17	46°54′41.8″S	167°46′27.3″E	S36156pt	Luln	R26810/13	14939	954 ± 60	–16.73	12.5	65.8	26.7	2.5	20.8	90	1.6
	17	46°54′41.8″S	167°46′27.3″E	S36156pt	Luln	R26810/14	14940	808 ± 55	–16.54	12.6	51.8	19.4	2.7	17.7	90	3.1
RAEX		"Raised beach"		FMa530pt	Rdent	R21898/3	7987	283 ± 66	–18.9	NA	NA	NA	NA	11.8	82	<1
	1	46°55′11.7″S	167°46′12.4″E	SIRE/1/1	Lfem	R24109/1	8406	453 ± 67	–17.8	NA	NA	NA	NA	14.6	NA	NA
	9	46°57′39.4″S	167°43′48.1″E	SIRE/9/1	Rfem	R24109/3	8408	280 ± 67	–19	NA	NA	NA	NA	12.0	NA	NA
	10	46°57′38.7″S	167°43′49.3″E	SIRE/10/1	Lpel	R24109/4	8409	204 ± 68	–18.6	NA	NA	NA	NA	14.8	NA	NA
	11	46°57′37.8″S	167°43′51.9″E	SIRE/11/1	Lfem	R24109/2	8407	440 ± 69	–18.2	NA	NA	NA	NA	7.6	NA	27.5
RARA	10	46°57′38.7″S	167°43′49.3′E	SIRR/10/2	Rfem	R24109/5	8410	362 ″ 67	–16.4	NA	NA	NA	NA	11.0	NA	3.7

Table 3 Comparisons of δ^{13}C values (‰) for samples of bone gelatin from Pacific rats (*Rattus exulans*) from Mason Bay and other islands in the New Zealand area, and for the samples of bone gelatin from South Georgian diving petrels (PEGE; *Pelecanoides georgicus*) from Mason Bay, Stewart Island. Mainland, North and South Islands; Chathams, Chatham Islands; Norfolk, Norfolk Island; SD, standard deviation; SEM, standard error of the mean; *n*, sample size. Variances were not significantly different in all but one pair of samples; the Mann-Whitney *U* test was used for the pair with significantly different variances and Student's *t* for the remainder.

	δ^{13}C of bone gelatin (‰)				
	Rattus exulans				*Pelecanoides georgicus*
	Mason Bay	Mainland	Chathams	Norfolk	
Mean ± SD	–18.50 ± 0.500	–20.41 ± 0.778	–19.67 ± 0.812	–19.38 ± 0.299	–16.92 ± 0.503
SEM, *n*	0.224, 5	0.149, 28	0.331, 6	0.149, 4	0.126, 15
Mainland	$P < 0.0001$*** $t = 5.270$, d.f. = 31				
Chatham	$P = 0.0211$* $t = 2.790$, d.f. = 9	$P = 0.0418$* $t = 2.121$, d.f. = 32			
Norfolk	$P = 0.0182$* $t = 3.065$, d.f. = 7	$P = 0.0139$* $t = 2.612$, d.f. = 30	$P = 0.5173$ NS $t = 0.6773$, d.f. = 8		
PEGE	$P < 0.0001$*** $t = 6.143$, d.f. = 19	$P < 0.0001$*** $U = 0.0000$	$P < 0.0004$*** $t = 9.641$, d.f. = 20	$P < 0.0001$*** $t = 9.245$, d.f. = 18	

of such phase models. We employed the Nicholls-Jones model to recover information on the unknown temporal parameters ψ_1 and ψ_2 and the related span statistic $R_1 = \psi_1 - \psi_2$ (i.e., the duration of time over which the Mason Bay breeding colony existed). The distributions of these temporal parameters were calculated using the Markov Chain Monte Carlo (MCMC) sampler implemented in Date Lab (Jones & Nicholls 2002).

The five *R. exulans* samples were analysed independently. Again, we regard the dated samples as relating to a single-phase process. However, because *R. exulans* is still present on Stewart Island (Atkinson & Towns 2001) we modelled only the single unknown parameter that defined the date at which *R. exulans* was introduced to Mason Bay (ψ_3). The modelling approach was the same as that used for the *P. georgicus* analysis except that for the rats we assumed that the *R. exulans* samples were derived from a terrestrial rather than marine carbon reservoir.

RESULTS

All 15 ^{14}C AMS ages on determinations on gelatin from fossil bones of *P. georgicus* from Mason Bay were less than 1100 radiocarbon years, but none was less than 750 radiocarbon years BP (Table 2). The ancillary data for 14 bones indicated that the bones were well preserved (Table 2). No data were available for NZA8402 because the measurement was made before nitrogen and carbon content or δ^{15}N values were measured routinely, but the physical state of the bone matched that of the other 14 and it was probably similarly well preserved. The C:N ratios and other parameters were within the ranges for which standard treatments can yield acceptable dates. In particular, the percentage of N in the samples was

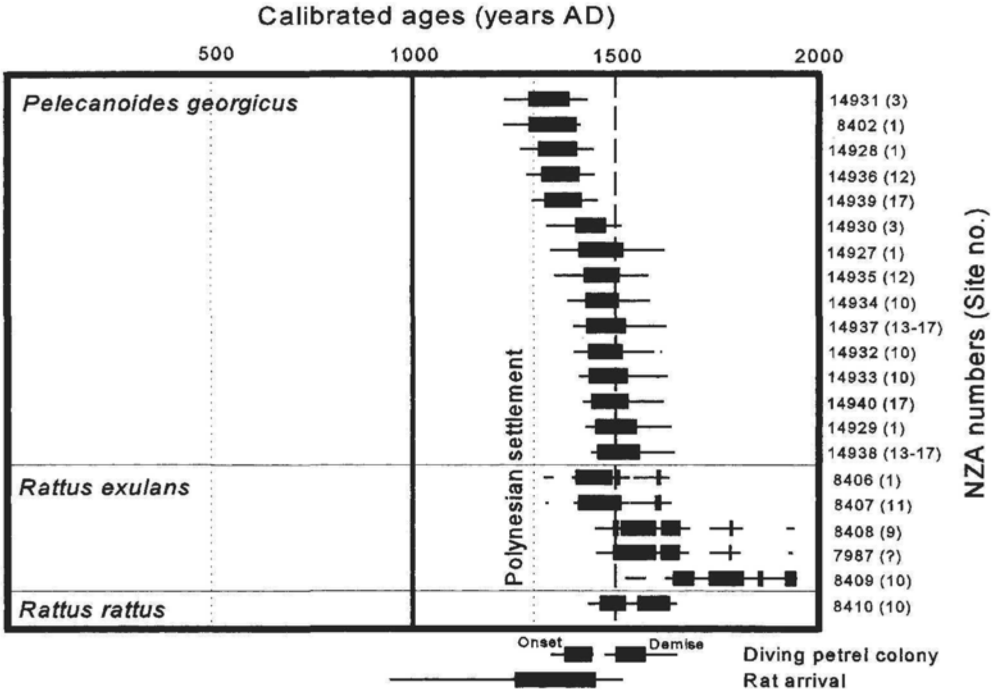

Fig. 2 Comparison of calibrated age ranges (thin line, 1σ confidence interval; thick line, 2σ confidence interval) corresponding to conventional radiocarbon ages on bones of South Georgian diving petrels (*Pelecanoides georgicus*) (marine calibration) and Pacific rats (*Rattus exulans*) (terrestrial calibration) collected from dunes of Holocene age at Mason Bay, Stewart Island, New Zealand. Likelihood distributions for the onset and demise of the diving petrel colony and the arrival of the Pacific rat at Mason Bay are indicated at bottom, with the same line conventions. NZA numbers refer to AMS date series from Rafter Laboratory, Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand. Numbers in parentheses following NZA numbers indicate the site from which the bone was collected. The dotted line at AD 1300 indicates possible time of Polynesian settlement based on Higham et al. (1999), Lowe et al. (2000), and Hogg et al. (2003). The $\delta^{13}C$ value of –16.4‰ for NZA8410 (*Rattus rattus* black rat) bone indicates that the rat had a diet based on marine carbon resources (cf. values for the *P. georgicus* bones). The terrestrial calibration standard applied here would significantly overestimate (by c. 300 years) the calendar age of the bone, which is likely to have been deposited after the mid 19th century. The black rat was probably subsisting on beach-cast carrion and beach invertebrates.

between 2.5 and 3.5%, which is well above the lower limit for satisfactory preservation. Insoluble residues were below 7% for all the petrel samples, and most were < 2% (Table 2). Not surprisingly, in view of the petrel's exclusively marine diet (Bocher et al. 2000), the $\delta^{13}C$ values for the *P. georgicus* bones were enriched (mean = –16.92‰, Table 3) relative to terrestrial values.

The calibrated ages (Table 4; Fig. 2) clustered between AD 1300 and AD 1500, rather than being spread throughout the late Holocene as expected. No spatial pattern was apparent in the age distribution, with no sampling location being demonstrably of earlier or later occupation than any other. The Bayesian analysis yielded likelihood distributions for the times of initiation, termination, and duration of the *P. georgicus* colony at Mason Bay (Fig. 3A,B,D, respectively). The results suggest that the *P. georgicus* colony at Mason Bay was short-lived

Table 4 Confidence intervals (68.3%, 95.4%) for calibrated (marine calibration: Stuiver et al. (1998) ^{14}C AMS ages on bone gelatin of the South Georgian diving petrel *Pelecanoides georgicus* and bidecadal terrestrial calibrated ages on Pacific rat (*Rattus exulans*) and black rat (*Rattus rattus*) bone gelatin samples from non-archaeological sand dune sites at Mason Bay, Stewart Island, New Zealand. Ages on *Rattus exulans* material from Holdaway (1999b).

						Confidence intervals (calendar years BP)	
Site	Lat.	Long.	Lab no.	NZA	CRA	1σ	2σ
Pelecanoides georgicus							
Site 1	46°55′11.7″S	167°46′12.4″E	R24101/5	8402	1015 ± 76	658–547	727–502
Site 1	46°55′11.7″S	167°46′12.4″E	R26810/1	14927	839 ± 75	531–442	612–333
Site 1	46°55′11.7″S	167°46′12.4″E	R26810/2	14928	991 ± 65	639–545	683–503
Site 1	46°55′11.7″S	167°46′12.4″E	R26810/3	14929	779 ± 55	499–398	515–317
Site 3	46°54′57.1″S	167°46′14.1″E	R26810/4	14930	876 ± 55	548–471	614–439
Site 3	46°54′57.1″S	167°46′14.1″E	R26810/5	14931	1026 ± 65	659–558	716–519
Site 10	46°57′38.7″S	167°43′49.3″E	R26810/6	14932	823 ± 55	516–438	552–354; 343–340
Site 10	46°57′38.7″S	167°43′49.3″E	R26810/7	14933	809 ± 60	514–421	542–325
Site 10	46°57′38.7″S	167°43′49.3″E	R26810/8	14934	831 ± 55	521–444	563–360
Site 12	46°57′33.4″S	167°43′54.0″E	R26810/9	14935	836 ± 60	528–442	597–363
Site 12	46°57′33.4″S	167°43′54.0″E	R26810/10	14936	976 ± 60	628–540	664–502
Sites 13–17	46°54′40″S	167°46′20″E	R26810/11	14937	821 ± 60	519–430	553–330
Sites 13–17	46°54′40″S	167°46′20″E	R26810/12	14938	773 ± 55	495–390	511–313
Site 17	46°54′41.8″S	167°46′27.3″E	R26810/13	14939	954 ± 60	617–527	653–492
Site 17	46°54′41.8″S	167°46′27.3″E	R26810/14	14940	808 ± 55	509–426	537–336
Rattus exulans							
“Raised beach”			R21898/3	7987	283 ± 66	456–446 (4.7%)	500–289 (81.9%)
						449–441 (60.1%)	
						336–286 (33.7%)	
						166–162 (1.4%)	
Site 1	46°55′11.7″S	167°46′12.4″E	R24109/1	8406	453 ± 67	545–456 (89.1%)	623–603 (3.3%)
						449–441 (3.9%)	558–418 (75.9%)
						350–336 (7.1%)	408–314 (20.8%)
Site 9	46°57′39.4″S	167°43′48.1″E	R24109/3	8408	280 ± 67	456–447 (4.1%)	502–266 (83.8%)
						442–350 (57.5%)	218–142 (13.4%)
						336–284 (34.2%)	24–2 (2.8%)
						167–158 (4.3%)	

Site 10	46°57′38.7″S 167°43′49.3″E	R24109/4	8409	204 ± 68	310–256 (28.8%) 224–137 (49.5%) 102–51 (6.2%) 32–1 (15.5%)	429–371 (7.0%) 324–0 (93.0%)
Site 11	46°57′37.8″S 167°43′51.9″E	R24109/2	8407	440 ± 69	538–434 (89.0%) 351–334 (11%)	618–611 (1.2%) 552–415 (71.6%) 414–313 (27.3%)
Rattus rattus						
Site 10	46°57′38.7″S 167°43′49.3″E	R24109/5	8410	362 ± 67	489–485 (1.9%) 485–424 (44.3%) 394–319 (53.8%)	514–299 (100%)

(0–260 years), and occupied the dunes during the period AD 1290–1570 (Table 5; Fig. 3D). The colony is most likely to have started during the 14th to early 15th centuries AD, and the colony is most likely to have gone extinct during the 16th century (Fig. 3; Table 5).

The AMS ^{14}C ages on five *R. exulans* bones, four of which were presented in Holdaway (1999b), are listed in Table 2, together with a single determination on a black rat (*Rattus rattus*) bone collected at Site 10. The *R. exulans* samples all yielded ages of less than 460 ^{14}C years BP. As noted in the Methods, few ancillary data were available for the rat determinations, but all were within the expected range for *R. exulans* from Stewart Island and hence are probably reliable. However, the calibration of these results is problematic.

The Mason Bay *R. exulans* samples are significantly enriched in ^{13}C (less negative $\delta^{13}C$ values) compared with those from mainland non-coastal sites and coastal sites on Chatham Island and Norfolk Island (Table 4). The levels of ^{13}C in the Mason Bay *R. exulans* bones were consistent with the individuals having consumed a partially marine diet (deNiro & Epstein 1978). The mean $\delta^{13}C$ of –18.50‰ is significantly ($t = 6.143$, $P < 0.0001$) depleted compared with the *P. georgicus* bones (purely marine diet), so the rats were apparently taking terrestrial foods as well. In contrast, the $\delta^{13}C$ value of –16.4‰ for the single *R. rattus* bone (Table 2) was indistinguishable from the mean enrichment for the diving petrel bones (Table 3), which indicated that the individual had an entirely marine diet. The marine components in the diets of both species of rat suggest that the application of a terrestrial calibration would

Table 5 Time spans for the formation, termination, and duration of the colony of South Georgian diving petrels (*Pelecanoides georgicus*) at Mason Bay, Stewart Island, New Zealand, and for the arrival of the Pacific rat (*Rattus exulans*) at Mason Bay. HPD, highest posterior density (≈ confidence interval).

	Distribution	
Parameter	68% HPD	95% HPD
Pelecanoides georgicus		
Colony formation (ψ_1)	AD 1340–1410	AD 1290–1440
Colony termination (ψ_2)	AD 1480–1530	AD 1450–1570
Colony duration (R_1)	80–190 years	30–260 years
Rattus exulans		
Initial presence (ψ_3)	AD 1260–1540	AD 830–1610

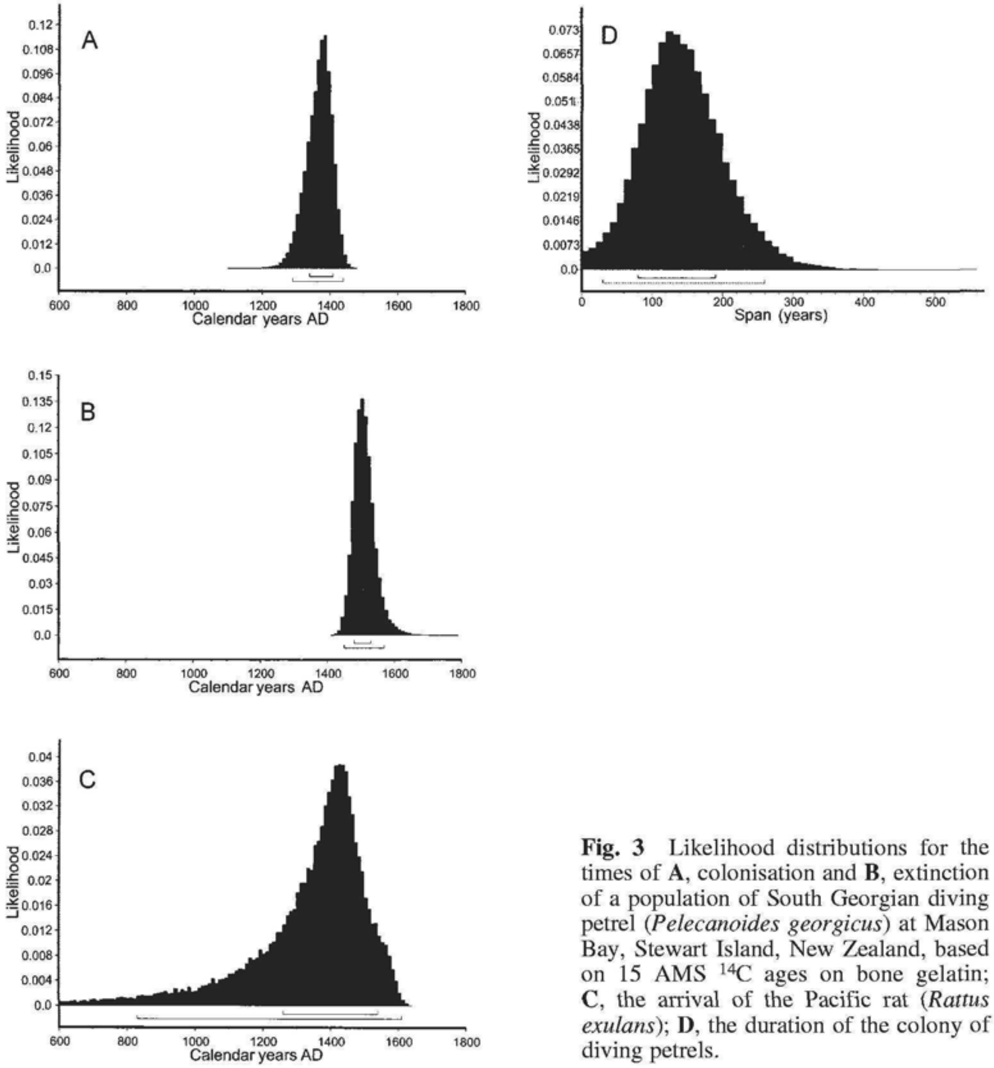

Fig. 3 Likelihood distributions for the times of **A**, colonisation and **B**, extinction of a population of South Georgian diving petrel (*Pelecanoides georgicus*) at Mason Bay, Stewart Island, New Zealand, based on 15 AMS ^{14}C ages on bone gelatin; **C**, the arrival of the Pacific rat (*Rattus exulans*); **D**, the duration of the colony of diving petrels.

overestimate the calendar age of the bones by unknown amounts, up to a possible reservoir value of 300 years for the *R. rattus* bone. In light of this, a completely terrestrial calibration function will tend to give rise to systematically early posterior distributions from the Bayesian analysis of the *R. exulans* samples. It is possible to account for this uncertainty in the analysis model. However, for the present study, this gives rise to very broad posterior distributions for the temporal parameters of the introduction of the rat to Mason Bay, to the extent that the information ceases to be useful. The results would simply allow for the introduction of *R. exulans* some time in the past 1000 years, a statement we can comfortably make in the absence of any radiocarbon determinations at all. However, we can use the *R. exulans* data calibrated using a completely terrestrial curve to assess proposed extinction scenarios. The analysis as presented here can be used as a conservative test of whether *R. exulans* can be excluded as prime agent for the observed extinction of *P. georgicus*.

The likelihood distribution of the initiation of the rat population at Mason Bay is much broader than for *P. georgicus* (Fig. 3C), as a result of the fewer ages in the series and the effects of the greater variation in the terrestrial calibration curve. This indicates that *R. exulans* was introduced into Mason Bay some time in the period AD 830–1610 (at a 95% HPD), with the caveat that the terrestrial calibration used in the calculations may have resulted in overestimation of the ages. Thus, this distribution should be regarded as providing a *Terminus post quem* for the introduction of rats into Mason Bay. The posterior distributions for the temporal parameters are given in Table 5.

In addition to recovering information on the temporal parameters presented in Table 5, it was also possible to calculate additional statistics relating to these parameters. Here we were interested in the relative timing of the temporal parameters for *P. georgicus* and *R. exulans* populations. In this instance, the comparison of relative timing of the two populations is confounded by uncertainty as to the correct carbon reservoir with which to make the calibration. This effectively makes it impossible to generate high-resolution statements on the relative timing of temporal population parameters relating to the two species. Thus, on the basis of the data and analysis presented here, the relative timing of the introduction of the two species to Mason Bay is equivocal. There is no significant support for the presence of either species before the other (i.e., the data do not discriminate between *R. exulans* arriving first and *P. georgicus* arriving first). However, the analysis does suggest that there was some period of time over which both species were present, and the results admit the possibility that both species coexisted for the entire time that *P. georgicus* was extant. At a 95% HPD (higher posterior density, approximately equivalent to a confidence interval), the *P. georgicus* and *R. exulans* populations coexisted for up to 250 years.

This analysis highlights some of the problems in applying radiocarbon dating to situations where the activity of the radiocarbon reservoir is not well understood. Here, the relative timing of *R. exulans* and *P. georgicus* introductions to Mason Bay is most appropriately argued on the basis of population biology informed by similar predator-prey interactions observed elsewhere and the observed temporal parameters of the phase of *P. georgicus* breeding at Mason Bay.

DISCUSSION

The late establishment of the *Pelecanoides georgicus* colony at Mason Bay was unexpected. The dunes probably developed in the early Holocene (Bishop & Mildenhall 1994; Worthy 1998e) and the vegetation in the area is apparently undisturbed (Wilson 1987; Johnson 1992), so it was anticipated that the *P. georgicus* colony had existed for at least several thousand years. However, the absence of diving petrels until about AD 1300 implies that there was no suitable habitat for them at Mason Bay for most of the late Holocene.

Nesting habitat

Unlike the common diving petrel (*Pelecanoides urinatrix*), which nests under dense vegetation (Payne & Prince 1979; Weimerskirch et al. 1989; Rogers 1990), including forest, *P. georgicus* is unique among burrowing petrels in selecting bare or sparsely vegetated areas of uncompacted substrate for its burrows (Warham 1996, p. 50). Descriptions of the nesting sites where the bird is abundant, and at the former and remnant colonies in New Zealand, stress the absence of substantial vegetation cover and the looseness of the substrate, which may be sand, volcanic "cinders", or fine scree (Falla et al. 1979; Payne & Prince 1979; Imber & Nilsson 1980; Weimerskirch et al. 1989). Typical breeding habitat of *P. georgicus* in the New Zealand region is illustrated in Falla et al. (1979, fig. 5).

The difference between the breeding habitats of the two species of diving petrel that breed in New Zealand is well illustrated by Payne & Prince (1979, fig. 5). At Codfish Island, *P. urinatrix* burrows were found in the same dune system as *P. georgicus* but only at the ends of the beach "high at the rear of the dunes where scrub begins" (Imber & Nilsson 1980, p. 328). Hence, the absence of *P. georgicus* from the Mason Bay dunes before about AD 1300 suggests that before then the dunes supported a substantial vegetation cover probably much the same as the remaining vegetation south of Duck Creek (Wilson 1987). Although *P. georgicus* nests within 30 m of the high-water mark at Sealers Bay, Codfish Island, it is unlikely that a colony could have been established at Mason Bay, which is exposed to the full force of westerly storms.

The apparent absence of *P. georgicus* and its habitat from Mason Bay before AD 1300 might be an artefact of the dynamics of the dune system itself. If the dune exposures presently yielding *P. georgicus* bones represent only one stage in the sequence of dune growth, evidence for earlier colonies might then be buried in older dunes farther inland. This is unlikely, because the age distributions of material from the northern and southern sections of the beach are identical despite their being from dunes set at different distances from the active beach sands. This suggests that the colonies began simultaneously regardless of the time of formation of the particular dune system.

An alternative possibility is that the extinction process has given rise to an elevated land-based mortality rate, thus biasing the sampling procedure. This effect would arise if a vast proportion of the available fossil specimens were related to the recent extinction process. The sample would therefore be biased toward selecting relatively recent fossils. In the case considered here this type of bias is highly improbable. Predatory pressure is clearly indicated as the primary extinction mechanism and samples arising from predation are easily recognised. None of the samples collected for this analysis showed any sign of predation, and the condition and nature of the fossil assemblage strongly indicates that these samples relate to "natural" attrition.

Another possible explanation for the late colonisation of the dunes is that *P. georgicus* may have colonised clear areas created when dune building was reactivated by changes in sedimentation patterns or during periods of increased windiness. McFadgen (1985) suggested that coastal dunes around New Zealand appear to have been remobilised several times during the Holocene. The Ohuan period was apparently contemporaneous with Polynesian settlement (McFadgen 1985) and the establishment of the *P. georgicus* colony. However, if this allowed *P. georgicus* to colonise it is difficult to see why the Tamatean period, which supposedly lasted from the 1850 BP Taupo eruption to 570 BP, would not also have resulted in clear areas among the dunes and allowed the colonisation by the diving petrels about 1000 years earlier than they did. Bishop & Mildenhall (1994) concluded that the westerly winds at present are not sufficiently strong and persistent to produce striated pavements or ventifacts such as those found around Big Sandhill at Mason Bay, and, by inference, during the past 1000 years.

Even if clear areas were available in the dunes before AD 1300, Hooker's sea lions (*Phocarctos hookeri*) might have prevented diving petrels breeding there. Falla et al. (1979) suggested that sea lions eliminated a population of *P. georgicus* that had been discovered on Dundas Island in the Auckland Islands in October 1943 by flattening the dune ridge nesting site and collapsing their burrows. The sea lion colony was thought to have expanded between 1943 and 1972 when Bell (1975) could not find evidence of *P. georgicus* breeding (Falla et al. 1979). The birds were not seen during a brief visit in 1978, when the damage to the ridges where birds had formerly nested was noted. Worthy (1998e) discussed the possibility raised by M. Imber (pers. comm. to Worthy) that diving petrels could still breed on Dundas Island under the cover of beds of the megaherb *Stilbocarpa polaris* (Araliaceae). However, reports from elsewhere suggest that *P. georgicus* avoids such cover (Rogers 1990).

Sea lions almost certainly bred at Mason Bay before Polynesians reached the island. They bred elsewhere on the main islands before Polynesian settlement (Crawley 1990; Worthy 1992, 1994; Gill 1998) and at Port Pegasus up to at least 1826 (Shepherd 1940). Bishop & Mildenhall (1994) suggested that rounded pebbles interbedded in earlier beach sands at Mason Bay were gastroliths from fur seals or sea lions. However, no fossils of pinnipeds were reported by Worthy (1998e) from the upper dune sands from which the diving petrel bones were eroding. Fur seals are unlikely to have occupied an extensive sandy beach, being typically associated with rocky coast lines (Crawley 1990). If sea lion colonies had existed at Mason Bay, they are unlikely to have persisted for long after Polynesians arrived. The sea lion has been extinct as a breeding species on the main islands of New Zealand since early in the Polynesian period (Smith 1978), as a result of human predation and disturbance at the colonies. Their abandonment of Mason Bay may have been one factor in the establishment of the *P. georgicus* colony at about that time.

Human settlement

Polynesians certainly reached Stewart Island soon after settlement began, as remains of meals made of moa brought from the South Island are known from the eastern side of the island (Worthy 1998d). However, although they are likely to have explored the island at that time, the evidence for human presence at Mason Bay during the moa hunter period is equivocal. Evidence for their presence at that time rests on whether a specimen of *Pachyornis elaphantopus* was associated with humans. A single ^{14}C AMS determination of 654 ± 56 radiocarbon years BP (NZA9060, Worthy 1998d; calibrated ages: 1σ, AD 1287–1328 and 1346–1394; 2σ, AD 1270–1410) is in the correct time frame, but it is not clear whether an artefact found with the moa skeleton was actually associated with it. Worthy (1998d, p. 54) suggested that the moa had a natural origin, but then (Worthy 1998d, p. 78) regarded it as possibly having been transported there whole by humans.

The vegetation of Mason Bay has been regarded as being relatively undisturbed (Wilson 1987; Johnson 1992). Elsewhere on the main islands, Polynesian settlement was accompanied by the removal of large areas of dry forest and shrubland by fire (McGlone 1989; McGlone & Wilmshurst 1999). As well as possibly hunting sea lions at Mason Bay, people could have fired the vegetation there. The pattern of remnant forest at Mason Bay, a series of "fingers" protruding into the open dunes, and the confinement of open dune vegetation to one section along the main stream with only limited areas farther south, could also reflect the outline of the paths of early fires. The forest and scrub on dune soils at Mason Bay would have been at least as prone to destruction by fire as the forests at Port Pegasus and in the Freshwater River valley (Wilson 1987). McGlone & Wilson (1996) suggested that the charcoal fragments that characterised their zone TF-1 in a pollen analytical core from Toitoi Flat, Stewart Island (c. 25 km ESE of Mason Bay) resulted from the activities accompanying Polynesian exploration of Stewart Island. However, it is difficult to assign a source to fine charcoal fragments present in a core to any particular fire event at that distance (M. McGlone pers. comm.). The founding of a *P. georgicus* colony some time after AD 1300 could be seen as evidence for the appearance of areas of open consolidated dunes after one or a series of fires.

The founding birds may have come from existing colonies of *P. georgicus* near Stewart Island (Worthy 1998e), but could have come from more distant populations. Recent examples of establishment of new breeding populations far from the "normal" breeding range include the soft-plumaged petrel (*Pterodroma mollis*) at Antipodes Island (Warham & Bell 1979; Imber 1983; Taylor 2000) and the black-browed mollymawk (*Thalassarche melanophris*) at Macquarie, Bollons, and Campbell Islands (Marchant & Higgins 1990; Tennyson et al. 1998; Taylor 2000). The nearest colonies of both taxa were in the southern Indian Ocean. Smaller species also are known to prospect far outside their normal range; two Leach's storm petrels were found, one in a burrow, on Rabbit Island, Chatham Islands, in 1980, far outside the species' normal Northern Hemisphere breeding distribution (Imber & Lovegrove 1982). Warham (1996, p. 42) acknowledged that long-distance colonisations would have gone mostly unrecorded until the recent expansion of research on remote island groups. Diving petrels normally feed in inshore waters, and long-distance dispersal is little known because the species are very difficult to identify at sea (Rogers 1990).

Regardless of the origin of the founders, our data indicate that the *P. georgicus* colony flourished only briefly at Mason Bay. There is evidence for their being there for at most 260 years and probably less than 200 years (Table 5). However, the large numbers of bones suggest the presence of a substantial population at some time in the life of the colony (Worthy 1998e), which suggests that the process of colonisation and population growth was rapid. Despite laying a single-egg clutch and having delayed sexual maturity and high adult survivorship (Warham 1990, 1996), petrels can increase their populations or recover from small population sizes on timescales of decades rather than centuries, with or without immigration. Indeed, "the potential for a rapid build up is high once some key restraint is relaxed" (Warham 1996, p. 41). For most petrels that "key restraint" is predation by introduced mammals. Some of the increases after the removal of predators have been remarkable. For example, the population of Buller's shearwater (*Puffinus bulleri*) on Aorangi Island in the Poor Knights group was reduced to about 100 pairs by the mid 1930s when feral pigs (*Sus scrofa*) were removed (Buddle 1941) and within 30 years the population had reached about 100 000 pairs (Bartle 1968), probably augmented by birds from the large population on neighbouring Tawhiti Rahi (Harper 1983). The much smaller Pycroft's petrel (*Pterodroma pycrofti*) appears to be increasing rapidly on islands in the Mercury group that have been cleared of populations of *R. exulans* (Taylor 2000). Pierce (1998) reported the incipient recovery of *P. pycrofti* and the North Island little shearwater (*Puffinus haurakiensis*) after populations of *R. exulans* were eradicated from islands in the Hen and Chickens group.

The duration of a *P. georgicus* colony at Mason Bay was brief (30–260 years), terminating some time between AD 1500 and 1650 (Fig. 3B; Table 5). Petrels are long-lived birds that exhibit strong philopatry and nest site tenacity, especially after raising a chick (Warham 1990, p. 231). So, once established, petrel colonies usually persist for long periods (perhaps up to 30 000 years) unless outside influences intervene (Warham 1990). The clear indication is that external environmental factors have caused the extinction of this colony. Once clear areas were available in the dunes, the only changes to the Stewart Island environment at that time were the presence of people and the introduction of *R. exulans*.

Polynesians harvested small petrels whenever they were available (e.g., Sutton 1979; Anderson 1996b; Holdaway & Anderson 2001). Remains of *P. urinatrix chathamensis* reported in middens on Chatham Island (Sutton 1979) may include *P. georgicus*. At the Old Neck site on the east coast of Stewart Island, people ate moa and many sooty shearwaters (*Puffinus griseus*), but Worthy (1998d) thought that the many diving petrel bones (attributed to *P. urinatrix*) in the site had eroded from skua (*Catharacta skua*) middens. *P. urinatrix* bones have been reported from 32 archaeological sites in the South Island (Worthy 1999), and it is one of only four species of petrel that is well represented in cultural contexts. Neither Anderson (1997) nor Worthy (1999) reported any archaeological sites on the western shore of Stewart Island in their lists of sites containing bird bone or evidence of exploitation of sea birds. Indeed, Anderson (1997) pointed to a lack of evidence for the harvesting of sea birds away from the Foveaux Strait islands. Therefore, at present there is no evidence that humans exploited the *P. georgicus* colony at Mason Bay and thereby caused its extinction.

Mammal predation at Mason Bay

Thus, the most likely agent of *P. georgicus* extinction at Mason Bay is *R. exulans*. Given the obvious uncertainty in the relative timing of founding of the populations of *P. georgicus* and *R. exulans*, the chronology of *P. georgicus* extinction must be informed by comparative population biology. There are good biological reasons for suggesting that *R. exulans* reached Mason Bay after *P. georgicus*. Diving petrels and other small petrels do not survive indefinitely in the presence of rats or other predators. *R. exulans* is known to take the eggs and chicks of diving petrels or species of similar size (Thoresen 1967; Booth et al. 1996; Pierce 1998; Taylor 2000). The pattern of extinctions on the North and South Islands strongly suggests that *R. exulans* was responsible for large-scale extinctions of the smaller petrels (Holdaway 1999a). Our results are entirely consistent with a scenario whereby *R. exulans* was introduced to Mason Bay some (possibly brief) time after the establishment of the *P. georgicus* colony and that rat predation on the petrels then caused the local extinction of *P. georgicus*. It is unclear, however, how rapid this extinction process may have been. As discussed above, the results of the analysis are imprecise and all we can say is that the process is likely to have taken place over a period of 250 years.

Where predator numbers are limited, however, colonies may survive. Weimerskirch et al. (1989) attributed the persistence of *P. georgicus* on the cinder plateaux of Kerguelen to introduced rabbits (*Oryctolagus cuniculus*) not being common enough in that area to sustain a significant population of cats (*Felis catus*). Taylor (2000) speculated that the population of *R. exulans* on Codfish Island may not have affected numbers of *P. georgicus* because the habitat of the open dunes may have been less commonly used by the rats, there presumably being more food in the forest.

Other terrestrial predators have been implicated in population declines of small petrels. Imber & Nilsson (1980) and West & Imber (1989) were concerned about possible predation on Codfish Island diving petrels by the introduced population of a New Zealand endemic rail, the weka (*Gallirallus australis*). Apparently the weka were seen to be the main problem because Imber & Nilsson (1980) suggested only that the effects of rats on breeding success might need to be investigated. After the weka had been removed from Codfish Island, West & Imber (1989) still could not say whether the rats had any effect on the diving petrels. Low numbers of rats in dune systems may not have been sufficient to eliminate a new colony of petrels, but it is unlikely that petrel numbers could have expanded to those suggested by the large numbers of bones in the presence of rats. After the rats were introduced, there would have been a lag phase before the population was large enough over the area of Stewart Island to be able to damage a large colony of petrels. It is unlikely that a population of South Georgian diving petrels could have been established at all at Mason Bay, if weka were indeed significant predators of small petrels in the pre-human environment.

The Bayesian analysis provided probability distributions for events that are difficult to resolve without clear stratigraphic sequences. In the previous two applications of the analysis to the extinction of a small vertebrate in New Zealand (Holdaway et al. 2002a,b), the assumption that each species had occupied the areas around the fossil deposits continuously for several thousand years was supported by the results. The history of the *P. georgicus* colony at Mason Bay proved to be more complex than expected and demonstrated that such assumptions are not always valid. Species distributions change, which affects our perceptions of what constitutes the "natural" fauna of a particular location. In this instance it is likely that the arrival of humans was responsible, first for the colonisation by *P. georgicus* and then, by the introduction of *R. exulans*, for the bird's extirpation at Mason Bay.

Conservation of *Pelecanoides georgicus* populations

The tiny population of *P. georgicus* at Codfish Island is now the only colony in the south-west Pacific, apart from a handful of pairs on the Bishop & Clerk Islets south of Macquarie Island (Garnett & Crowley 2000). The species may have bred on Macquarie Island itself, where there is apparently suitable scree habitat (Jones 1980), but the long history of introduced predators and possible misidentification of specimens make its former status there uncertain. Taking the residual population near Macquarie as indicating its former larger distribution, the species was established there, and at the Auckland Islands, Stewart Island, and the Chatham Islands, in the past millennium. Imber & Nilsson (1980) regarded the present rarity of the species in the New Zealand region as a result of the shortage of its nesting habitat, and that predatory mammals had simply exacerbated that position. The ephemeral nature of the *P. georgicus* population at Mason Bay supports both conjectures: its establishment seems to have followed the development of suitable habitat and its destruction is likely to have been caused by an introduced population of *R. exulans*.

On the basis of its relict status in the region, Worthy (1998e) argued for a higher conservation priority for the *P. georgicus* colony at Codfish Island than the Category B status presently afforded it (Molloy et al. 1994). Although there is another "colony" in the region, that is so small that the Codfish Island birds represent the last remnants of the species in the south-west Pacific. Molloy et al. (1994) highlighted the New Zealand population as being of uncertain taxonomic position, presumably because of its distance from the main breeding sites, its anomalous position well to the north of the Antarctic Convergence, and the cryptic nature of variation in the genus *Pelecanoides* which suggests that it might represent a taxon distinct from *P. georgicus*. If such a distinction were found to be justified, then the form would be critically endangered according to IUCN criteria and Category A in the New Zealand Department of Conservation ranking system.

One result of the study does offer some hope for the future of *P. georgicus* and other small petrels, at least where suitable habitat exists and introduced mammals can be excluded. The history of the species at Mason Bay shows that a species can colonise and increase substantially in numbers within a few decades. However, the Mason Bay colony also shows that the presence of even large numbers of fossil bones do not, in the absence of other information, imply long-term occupation of a site. Factors controlling the presence and extinction of the *P. georgicus* colony at Mason Bay reflect those operating elsewhere in New Zealand since first human contact. Other birds, such the Australian harrier (*Circus approximans*), that colonised New Zealand after Polynesian settlement (Holdaway et al. 2001), probably did so as new habitats appeared. *P. georgicus* was able to capitalise on the appearance of new habitat, but unlike the harrier it was small enough to be prey for the only ubiquitous predator introduced before the arrival of Europeans in the late 18th century.

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