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Potential for rat predation to cause decline of the globally threatened Henderson petrel *Pterodroma atrata*: evidence from the field, stable isotopes and population modelling

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ABSTRACT: Past studies have indicated that Pacific rats *Rattus exulans* are significant predators of the chicks of surface-breeding seabirds, namely gadfly petrels *Pterodroma* spp., on Henderson Island, central South Pacific. Further fieldwork in 2003 confirmed the heavy predation of chicks of Murphy's petrel *P. ultima* by rats. By extension, heavy predation is also likely each year on the endangered Henderson petrel *P. atrata*, for which Henderson Island is the only confirmed breeding site. To assess how important petrels are in the overall diet of rats, we conducted stable isotope analyses of rats from the shore, where petrels are most concentrated, and from about 1 km inland, where fewer nest. The carbon isotope results suggested that inland rats obtain about 30% of their food from marine sources, while the figure for shore rats was about 40%. We consider factors that may have acted to inflate these proportions. If, as suggested by these results, petrels are not the predominant component of the rats' diet, then rat populations and hence rat predation on petrels may not diminish even if petrel populations decrease further. In the light of probable low annual breeding success, we drew on vital rate information for the cahow *P. cahow* to model changes in the Henderson petrel population, and found a negative growth rate ($\lambda = 0.9918$) under present conditions. Growth rate became positive if annual adult survival rose above 0.95 or breeding success above 0.25, the latter unlikely while rats remain on Henderson. We conclude that the Henderson petrel population will probably continue to decline in the absence of conservation intervention.

KEY WORDS: Density dependence · Invasive alien species · Kiore · *Rattus exulans* · South Pacific · Carbon · Nitrogen · Collagen · Diet · Murphy's petrel

INTRODUCTION

Many gadfly petrel species (genus *Pterodroma*) are endemic to single oceanic islands or archipelagos. Populations of many of these species have been reduced to a small fraction of their former sizes owing to exploitation by man and predation by introduced mammals (Iredale 1914, Nichols & Mowbray 1916, Steadman & Olson 1985, Brooke 1990). Particular damage has been caused by the introduction of rats *Rattus* spp. over the past 3000 yr (Atkinson 1985, Jones et al. 2008, Traveset et al. 2009, but see Ruffino et al. 2009 for examples of long-term rat–seabird coexistence). Because of these factors, a substantial proportion of the extant *Pterodroma* species is currently classified as threatened (21 out of 32 species; BirdLife International 2009). Following decline, recovery in numbers has rarely been observed, partly because of the difficulty of removing alien vertebrates

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from islands and partly because the species' life history characteristics, notably slow reproductive rate and delayed maturity, militate against population recovery. However, there are examples where appropriate management of factors limiting population growth has promoted slow but steady population recovery (Carlile et al. 2003).

Henderson Island (24° 20' S, 128° 20' W), a World Heritage Site in the central South Pacific, is one of the most important breeding sites in the world for gadfly petrels. This exceptionally isolated island, administratively part of the UK Overseas Territory of the Pitcairn Islands, is the principal breeding station (>95% of the world population, ~16 000 pairs) of the Henderson petrel *Pterodroma atrata*, identified as a species distinct from the Herald petrel *P. heraldica* by Brooke & Rowe (1996) and classed as globally endangered (BirdLife International 2009). It is also a major breeding site for non-threatened Kermadec *P. neglecta* and Herald petrels (~10 000 and 11 000 pairs, respectively), in both cases holding about 20% of the world's populations (Brooke 2006). It also has a significant population of the near-threatened Murphy's petrel *P. ultima*, and Phoenix petrels *P. alba* (also globally endangered) may have been present in the past (Brooke 1995). It is probable that all these populations were substantially larger, by 1 or more orders of magnitude (Steadman & Olson 1985, Brooke 1995), before the Polynesian arrival around 1000 yr ago (Weisler 1995). Although the vegetation was apparently not profoundly altered by the period of Polynesian occupation from about 800 to 1600 AD (Waldren et al. 1995, Weisler 1995), this occupation was temporally associated with, and probably the cause of, the local extinction of at least 5 landbird and 6 terrestrial snail species (Preece 1995, Wragg 1995).

Despite its isolation, Henderson has not escaped rodent introduction: Pacific rats *Rattus exulans* have been present for about 7 centuries (Weisler 1994). Research in 1991–1992 revealed that rat predation on small chicks was causing almost complete breeding failure of Murphy's petrels and reducing productivity of Henderson petrels to 0.175 chicks per breeding pair (Brooke 1995), a value under half that of congeners at rat-free sites (e.g. Rayner et al. 2007). Most failures were due to chicks disappearing a few days after hatching. If this level of predation occurred every year and there were no sub-colonies with lower predation (cf. Cory's shearwater *Calonectris diomedea*; Igual et al. 2006), it was deemed likely to cause slow, long-term declines of the species concerned. The loss of upwards of 1 million pairs of petrels, and their importation of marine nutrients, would likely have profound impacts on the terrestrial ecosystem (Croll et al. 2005, Fukami et al. 2006, Maron et al. 2006), and predation by rats would be of particular consequence for the Henderson petrel with no known significant breeding populations beyond Henderson. However, it was impossible to tell, on the basis of a 1 yr study, whether the situation observed in 1991–1992 was typical or whether rat predation was especially intense that year.

Most of the gadfly petrel species on Henderson have a year-round breeding season and are thinly dispersed through thickly vegetated habitat. This means it is very difficult to gather data on rat predation without lengthy study. However, Murphy's petrels have a relatively synchronous breeding season and, moreover, nest in accessible coastal areas of the island. Thus the first aim of the present study was to gather rat predation data during the ca. 6 wk hatching period of Murphy's petrels in a second breeding season, 2003. Such data would be a surrogate for data on the other species, including the more threatened Henderson petrel, all of which are of similar size and nest equally accessibly on the ground surface (and not in burrows).

The second aim of the present study was to collect and analyse petrel and rat tissues using stable isotope analysis to assess the contribution of petrels to rat diet. Carbon and nitrogen stable isotope analysis is a powerful technique for the quantitative assessment of an individual's diet that is widely used in the fields of archaeology and ecology (Ben-David et al. 1997, Gannes et al. 1998, Richards & Hedges 1999, Kelly 2000, Privat et al. 2002). For example, stable isotope analysis was used to investigate the impact of predation by ship rats *Rattus rattus* on sea birds in the Shiant Islands, Scotland, and demonstrated the greater importance of marine foods, including sea birds, for rat colonies closer to seabird nesting sites than those further inland (Stapp 2002). Similarly, on Langara Island, British Columbia, Canada, Norway rats *R. norvegicus* sampled from the large breeding colony of ancient murrelets *Synthliboramphus antiquus* ate predominantly murrelet adults, chicks and eggs, while rats from elsewhere on the island ate terrestrial foods or intertidal invertebrates (Hobson et al. 1999). Dietary reconstruction using stable isotopic analysis has advantages over other techniques, such as observation and scat analysis, because it is a relatively long-term record of diet (depending on the body sample analysed) and avoids complications due to differential digestion. Disadvantages are that potential food sources must have distinct isotopic signatures if their contributions are to be distinguished.

In the present context, if isotope analysis indicated that petrels were a major constituent of rat diet, then a petrel decline might be followed by a rat decline, with the result that the remaining petrels would experience less intense predation. Alternatively, if petrels were a relatively minor, albeit preferred, component of the rats' diet, there would be less prospect of a decline in seabird

numbers being followed by a decline in rat numbers and a density-dependent reduction in rat predation.

The consequences of low productivity for Henderson petrel population trends are difficult to determine empirically since, as mentioned, the species nests year-round within almost impenetrable forest on one of the most remote islands on the planet. Population modelling can provide a tool to predict population trends from estimates of productivity in combination with other demographic rates and has previously been used to determine population trends of Henderson petrel (Brooke 1995) as well as other species of gadfly petrel (Hawaiian petrel *Pterodroma sandwichensis*, Simons 1984; Galapagos petrel *P. phaeopygia*, Tomkins 1985). However, some parameter values for these models were not available and thus had to be assumed, and no long-term data on productivity and population change were available to validate the model predictions given these assumptions.

Therefore, the third aim of the present study was to develop a population model for a gadfly petrel population that predicts population multiplication rate from annual estimates of productivity. We validated and refined the model using a data set which is unique for *Pterodroma* species: long-term data on numbers and productivity for the cahow *Pterodroma cahow*, a Bermuda endemic for which very accurate counts of breeding pairs and fledglings for a closed population over 43 yr are available, and which nests at a similar subtropical latitude to Henderson Island. We used this model to examine the population trajectory of the Henderson petrel population, assuming the observed productivity, and explored changes in the remaining demographic parameters that would be required for the population to be stable or to increase.

In summary, the present study reports: (1) whether predation of Murphy's petrel chicks was as high in 2003 as observed in 1991 and, therefore, whether high rat predation on *Pterodroma* chicks can reasonably be assumed to be normal on Henderson Island; (2) stable isotope analyses directed towards assessing the importance or otherwise of petrels in the overall diet of Henderson Island's rats; and (3) the likely population trajectories of Henderson petrels based on parameters that yielded an accurate description of the observed trajectory of cahow based on productivity estimates over the same period. The implications of these results for the Henderson petrel's conservation status and for conservation management of the island are discussed.

MATERIALS AND METHODS

Ornithological fieldwork. Fieldwork on Henderson Island lasted from 6 July to 20 August 2003. At the time of arrival, no Murphy's petrel eggs had hatched. Shortly after arrival, 77 nests were located by random searching in vegetation immediately behind North Beach and checked regularly so that the date of hatching could be ascertained. After hatching, nests were checked daily to determine the fate of the chick.

Sample collection for stable isotope analysis. To assess the rats' diet via stable isotope analysis, animals were caught in 2 groups on Henderson Island. Group 1 consisted of 5 rats (hereafter 'shore rats') and was caught between 9 and 11 August 2003 in breakback traps in North Beach beachback vegetation, dominated by *Argusia argentea*, *Thespesia populnea* and *Cordia subcordata* (Waldren et al. 1995), in the immediate vicinity of the Murphy's petrel nests that were under observation. Any marine component of these rats' diets could derive from predation or scavenging of petrels and other seabirds, and also from the consumption of other marine foods (e.g. dead fish) washed up on the beach. Group 2 consisted of 7 rats (hereafter 'inland rats') caught on 17 and 18 August 750 to 800 m inland from the beach on the island's plateau about 30 m above sea level. Since home ranges of Pacific rats are typically less than 1 ha and movements greater than 100 m are rare (Moller & Craig 1987, Harper 2006), we assumed the inland rats would never have travelled to the shore, and therefore any marine component of their diet would be due to the probably infrequent predation of petrel species other than Murphy's petrel, nesting on the plateau. All rats were treated and despatched in accordance with best practice of the Pitcairn Islands. From all the above rats, tissue samples (blood, liver, muscle and bone) were preserved in 90% ethanol (v/v) and returned to the UK for stable isotope analysis.

Stable isotope analysis potentially reveals whether the shore rats eat more marine food, such as petrels, than the inland rats, but does not quantify precisely how much marine food the 2 groups eat (Stapp 2002). A large difference between the inland rats (assumed to have minimal marine input but for occasional consumption of the chicks of Henderson and Kermadec petrels) and the shore rats would indicate that the shore rats have a substantially different diet, and if the shore rats have much higher carbon and nitrogen isotopic values, this would suggest that they are consuming more food of marine origin. To assess the endpoints of the spectrum between likely terrestrial and marine components of the rats' diet, we also collected samples of coconut *Cocos nucifera* flesh and hatchling petrel chicks, the latter the remains of rat predation. Since the range of food eaten by rats on Henderson is undoubtedly wide, but unstudied, coconut and petrel chicks may not be perfect proxies of terrestrial and marine diets, respectively. While there may be Crassu-

lacean acid metabolism (CAM) and C_4 plants on Henderson (Waldren et al. 1995, S. Waldren pers. comm.), their contribution to rat diet is slight (M. de L. Brooke pers. obs.) compared to that of C_3 plants such as coconut. The limited number of food sources collected also restricts the use that can be made of mixing models (e.g. Isosource, Phillips & Gregg 2003) to determine diet.

Since a small amount of fractionation occurs as isotopes are passed along the food chain (known as the trophic level effect; Minagawa & Wada 1984, Kelly 2000), an individual's tissue isotope composition is not identical to its dietary intake. Thus the isotopic values of body tissues reflect the isotope signature of the foods consumed plus a reasonably predictable amount of fractionation. We can calculate the expected isotopic values of the rats' dietary intake if we can correct for the diet–tissue isotopic fractionation. Using the diet–tissue offsets measured in previous feeding experiments on rodents (carbon: DeNiro & Epstein 1978, Tieszen et al. 1983, Nakagawa et al. 1985, Ambrose & Norr 1993, Tieszen & Fagre 1993; nitrogen: DeNiro & Epstein 1981, Nakagawa et al. 1985, Ambrose 2000), we calculated the mean isotopic offsets from diet to bone collagen, liver and blood, assuming that skin collagen has the same offset as bone collagen, since they are similar proteins.

Applying correction factors is not without problems. Measured diet–tissue offsets have been observed to vary substantially, especially for animals fed artificial or synthesised diets or those consuming diets that vary in macronutrient composition, and the offsets measured under laboratory conditions are often at variance from those predicted for animals observed and sampled under free-living conditions (Ambrose & Norr 1993, Tieszen & Fagre 1993, Sponheimer et al. 2003). However, the single study assessing the effect of dietary protein levels and stress on carbon and nitrogen isotopic values in rats found no effect of either on the carbon or nitrogen diet–tissue isotopic fractionation, suggesting that this is not a factor that needs to be considered in this situation (Ambrose & Norr 1993, Ambrose 2000). To avoid any bias due to selectivity, we have used the mean offsets derived from all rodent studies.

Sample preparation and analysis. Samples were prepared for isotopic analysis following standard methodologies. Collagen was extracted from bone and skin samples for analysis, whereas liver, blood, feather and coconut samples were defatted and then analysed after drying. Since all samples were defatted prior to analysis, no correction for the effects of ethanol preservation was applied (Sweeting et al. 2004).

Collagen was extracted from the bone samples of both rats and petrel chicks, following a process of defatting, demineralisation, gelatinatisation and lyophilisation (O'Connell et al. 2001). Rat bones and the hindlimb bones of petrel chicks were removed from the ethanol in which they had been stored, physically scraped of flesh and periosteum, crushed and the marrow scraped out as far as possible. Defatting was done using a solvent extraction of a mixture of methanol: chloroform (6 ml 2:1 v/v), the samples further crushed with a glass rod, placed in an ultrasonic bath for 30 min and left in the solvent overnight. Samples were then rinsed twice in 10 ml water (with 45 min in an ultrasonic bath during the second rinse), demineralised in 0·5 M aqueous hydrochloric acid for 24 h at room temperature (until all the mineral had dissolved) and gelatinised in water of pH 3 (adjusted with hydrochloric acid) at 75°C for 60 h. The supernate containing the solubilised collagen was filtered off (0.8 µm Ezee filters, Elkay), frozen at –40°C for 4 h and then lyophilised until dry.

Collagen was extracted from the skin samples, following a process of defatting, gelatinatisation and lyophilisation. Samples were removed from the ethanol in which they had been transported and stored, and defatted using a solvent extraction of a mixture of methanol:chloroform (6 ml 2:1 v/v), with the samples initially pummelled with a glass rod before being placed in an ultrasonic bath for 30 min and left in the solvent overnight. Samples were then rinsed 3 times in 10 ml water (with 15 min in an ultrasonic bath during the second rinse) and gelatinised in water of pH 3 (adjusted with hydrochloric acid) at 75°C for 60 h. The supernate containing the solubilised collagen was filtered off (0.8 µm Ezee filters, Elkay), frozen at –40°C for 4 h and then lyophilised until dry.

Liver samples were defatted and then dried. Samples were removed from the ethanol in which they had been transported and stored, and defatted using a combination of solvent and water extraction: 2 extractions in methanol:chloroform (6 ml 2:1 v/v) for 24 h each (with the samples initially pummelled with a glass rod and then placed in an ultrasonic bath for 30 min). This was followed by 2 subsequent rinses in 5 ml methanol (15 min each time in an ultrasonic bath) and 2 subsequent rinses in water (15 min each time in an ultrasonic bath). Samples were frozen at –40°C for 4 h and then lyophilised until dry.

Blood samples were defatted and then dried. Samples were centrifuged at 6000 rpm for 5 min, the supernate removed and then 1 ml of water added, the vials shaken and centrifuged again. The process was repeated 3 times. The samples were frozen at –40°C for 4 h and then lyophilised until dry.

Petrel feathers were removed from the solvent, rinsed in 8 ml methanol twice for 1 h and then twice in water for 1 h and finally dried under vacuum. Coconut

samples were removed from the solvent, rinsed in 20 ml water twice for 1 h and dried under vacuum.

Samples were analysed using an automated carbon and nitrogen analyser (Carlo Erba NA1000) coupled to a continuous-flow isotope ratio-monitoring mass spectrometer (Geo 20/20 mass spectrometer, PDZ-Europa). Samples were run at least in duplicate, and where possible, material permitting, in triplicate, with aliquots of approximately 2 mg analysed each time. Stable isotope concentrations were measured as the ratio of the heavier isotope to the lighter isotope relative to an internationally defined scale, VPDB for carbon, and AIR for nitrogen (Hoefs 1997). Isotopic results are reported as δ values ($\delta^{13}C$ and $\delta^{15}N$) in parts per 1000 (δ) values, where $\delta^{15}N_{AIR} = [(^{15/14}N_{sample}/^{15/14}N_{AIR}) - 1] \times 1000$. The analytical error (1ρ) for all samples was ±0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$.

Population modelling. Since we lacked data on population trends and vital rates for Henderson petrels, we relied on those of a congener to provide the parameters required to predict population multiplication rates from productivity. We used long-term annual data (1962 to 2005) on numbers of pairs and fledglings for the cahow. This species occupies a single colony in Bermuda that is largely free from predation and is increasing following release from density-dependent regulation by nest site availability (Carlile et al. 2003). It therefore represents an ideal population with which to validate relationships between productivity and growth rate of a gadfly petrel population below its carrying capacity, since the confounding variables of emigration and density-dependent regulation are both absent. In these respects there are important similarities between the cahow and Henderson petrel.

We used an age- and stage-structured population model to fit a predicted population trend to that observed (Fig. 1). Productivity, the probability of a breeding attempt fledging a female chick was calculated as:

$$F = \{BS + [(1 - BS) \times R \times BS]\} \times PF$$

where F is productivity, BS is breeding success per nesting attempt, R is the probability of renesting following failure of the first nesting attempt and PF is the proportion of female chicks at fledging. Breeding population size in each year of simulation can be calculated as the sum of all B*x*.

The cahow population was so small that there was potential for demographic stochasticity to slow population growth rates, and hence we used an individual-based model for all simulations to allow for this, in which each bird in the population was subjected to the probabilities of surviving, attempting to breed and successfully fledging chicks in each year of life. The only parameter in the model allowed to vary was the observed annual productivity. The actual productivity values were fed into the model in chronological order, and productivity of all age classes (F4 to F7) was assumed the same within each year. Cahows have a breeding probability of zero for 1 to 3 yr olds, 0.15 for Age 4 (PB4), 0.65 for Age 5 (PB5) and 0.8 for Age 6 (PB6; J. Madeiros unpubl. data). We assumed that the probability of older birds breeding (PB7) was 0.89 and adult survival (for birds over 1 yr old; S1 to S7) was 0.93, both based on a study of Hawaiian petrels (Simons 1984). No reliable estimates of first-year survival exist for any *Pterodroma* species, so we iteratively varied the value for first-year survival rate (from fledging to Age 1; S0) on successive model runs, and selected that which minimised the sum of the squared deviations between observed and predicted numbers of breeding birds for further modelling. R was assumed to be zero and the proportion of females at fledging 0.5.

Having acquired plausible population parameters (age-related survival, breeding probability) for a gadfly petrel population, we proceeded to estimate the trend in numbers that would result if productivity were that observed for the Henderson petrel. We also explored plausible demographic scenarios that could potentially increase population multiplication rates by elevating survival rates, breeding probabilities or productivity (by allowing for annual variability or renesting after failure of the first nesting attempt). Numbers of Henderson petrels, at 16 000 pairs (Brooke 1995), were well above levels at which demographic stochasticity occurs, and all vital rates simulated were constants. Therefore, we adopted a population-based, deterministic modelling approach. We used the model to generate estimates of breeding numbers over 100

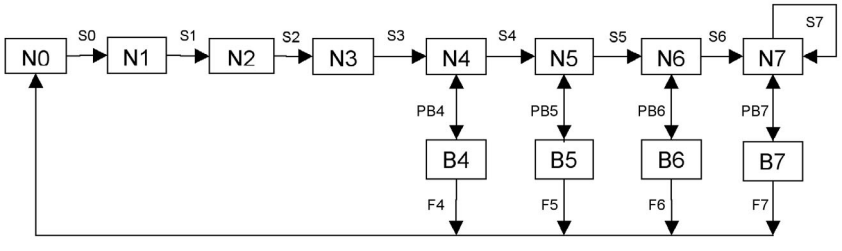

Fig. 1. Structure of the basic age- and stage-structured model. N*x*, B*x*: no. of non-breeding and breeding females in age class *x*, respectively; S*x*: survival from the age class *x* to the next; PB*x*: probability of a non-breeding female of age class *x* at the start of the breeding season transiting into a breeding state (these all return to non-breeders of the same age before being subject to S*x*); F*x*: productivity (probability of a breeding attempt fledging a female chick) for a female of age class *x*

consecutive years, and derived estimates of population multiplication rates (λ) from these. We ran all models using bespoke programmes written in Microsoft Visual Basic 6.0.

RESULTS

Fieldwork

The first Murphy's petrel egg hatched on 16 July and the fate of the 77 eggs was as follows: 9 failed at the egg stage for natural reasons (e.g. rotten egg), 2 failed at the egg stage due to human interference, 2 failed naturally, but it was not established whether at egg stage or post-hatching, 62 hatched but the chick then disappeared within 6 or fewer days, 2 eggs were still being incubated when last checked just prior to departure (19 August) and no chicks remained alive at departure.

Thus, the pattern was exactly as observed in 1991–1992 (Brooke 1995): losses during the egg stage were unremarkable for a petrel, but were then heavy and total immediately after hatching. The time course of chick disappearances in 1991 and 2003 is compared in Table 1. Fitting a logarithmic curve to these data allows daily chick mortality to be estimated at 59.7% in 1991 and 59.5% in 2003.

Not only was the temporal pattern of chick disappearance similar in 1991 and 2003, so too was the sequence of events at the nest; namely, a healthy chick one day, a nest that was empty the following day but for remains of the hatched shell and, at a minority of nests, a few traces of down or flesh 1 m or more from the nest. This indicated that the same predator was responsible; indeed, in 2003, the seizing of petrel chicks by rats was captured on film (A. Henricson pers. comm.). The rats ate the entire petrel chick and, therefore, we averaged stable isotope values from all petrel tissues to estimate the isotope signature of a petrel diet (see section 'Stable isotope analyses'). No evidence of the involvement of other possible predators (e.g. crabs) was obtained (see also Brooke 1995). From this we concluded that predation of Murphy's petrel chicks was similarly high in 1991 and 2003. In the modelling below, we therefore initially assumed that breeding success of Henderson petrel was 0.175, the value reported by Brooke (1995) for 1991–1992. However, we caution that this value is based on a small sample obtained in a single 15 mo period.

The fieldwork yielded some information on the survival of adult Murphy's petrels. The area where 77 Murphy's petrel nests were monitored in 2003 was the same as where nests were monitored in 1991. Of 60 breeding adults ringed at the 1991 nests, 16 were recaught in 2003, 12 yr later. Solving $16/60 = \text{Survival}^{12}$ gives an annual survival rate of 0.896. Alternatively, of the 30 pairs ringed in 1991, 4 were still intact in 2003. Since the pair can only remain intact if both members survive, these data allow an alternative calculation: $4/30 = (\text{Survival}^{2})^{12}$. Here annual adult survival is estimated as 0.919. These values, suggesting an annual survival among Murphy's petrels of around 0.9, are minimal because, in 2003 as in 1991, there were more nests in the study area than those monitored, creating a strong possibility that surviving ringed birds went undetected at sites not monitored.

Stable isotope analyses

The terrestrial and marine diet endpoints differed markedly in $\delta^{13}C$ values, with average values for coconut flesh of approximately –26‰ and for petrel tissues of –17‰ (Table 2, Fig. 2). Rat tissues fell between these 2 endpoints (Table 3, Fig. 2). Based on tissue-specific fractionation values estimated from the literature (Table 4), the calculated $\delta^{13}C$ of rat diets averaged –22.5‰ for shore rats and –23.4‰ for inland rats (Table 5, Fig. 3). The difference between shore and inland rats was statistically significant (Table 6), but very small (<1‰) relative to the difference between marine and terrestrial endpoints. In broad terms, these values indicate that rat diet was composed of a mixture

Table 1. *Pterodroma ultima*. Number of Murphy's petrel chicks on the North Beach study area, Henderson Island, which were still alive 1 to 6 d after hatching

Year	No. hatching	Days after hatching					
		1	2	3	4	5	6
1991	32	17	5.5[a]	2	1	0	0
2003	62	29	12	5	1	1	0

[a]Includes 1 chick that disappeared either on the 2nd or 3rd night after hatching

Table 2. Stable isotopic values (mean ± SD) of coconut and Murphy's petrel chicks from Henderson Island. Petrel chick: mean ± SD of all feather and bone collagen samples. These are the values used for the marine and terrestrial endpoints of the diet trend line of Fig. 3

Sample	N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N ratio
Coconut	3	–25.9 ± 1.3	10.7 ± 0.6	66.0
Petrel chick feather	3	–18.0 ± 0.1	15.9 ± 0.9	3.8
Petrel chick bone collagen	3	–16.7 ± 0.3	15.8 ± 0.8	3.4
Petrel chick		–17.3 ± 0.7	15.9 ± 0.8	3.6

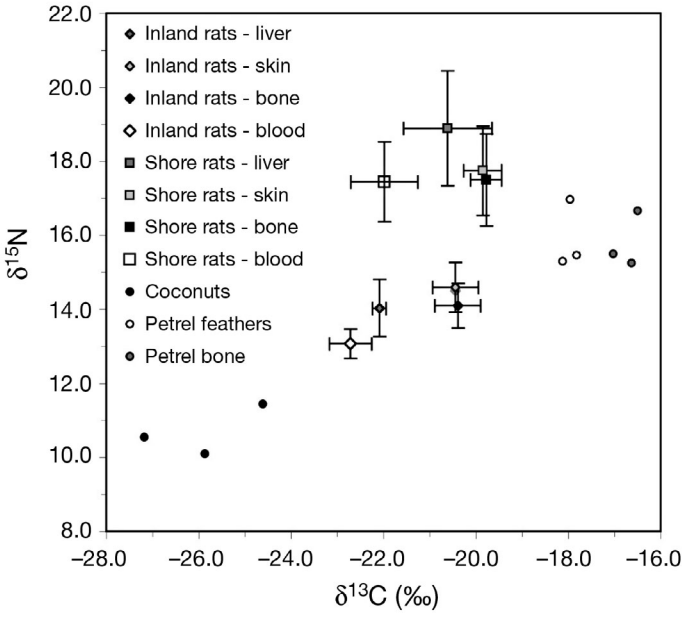

Fig. 2. Carbon and nitrogen mean isotopic values (as given in Table 3) for rat *Rattus exulans* tissue samples, coconuts and petrel *Pterodroma ultima* feathers and bone. The terms 'bone' and 'skin' refer to bone collagen and skin collagen, respectively. Vertical and horizontal error bars are 1 SD

of terrestrial and marine food sources, in a ratio of approximately 60:40 for shore rats and 70:30 for inland rats.

The calculated dietary $\delta^{13}C$ of rats differed significantly, but not greatly (Table 6), between tissues of different turnover rate, suggesting that recent diet did not differ radically from long-term diet. For both rat groups, liver and blood, with relatively rapid tissue turnover rates (half-lives in the order of weeks), had slightly lower $\delta^{13}C$ values than the bone and skin, which have tissue half-lives on the order of months (Rucklidge et al. 1992, MacAvoy et al. 2005, 2006). This implies that recent diet included slightly more marine material, although given the relative uncertainty about fractionation and how it varies between tissues (Arneson & MacAvoy 2005, MacAvoy et al. 2005, Caut et al. 2008, Moore & Semmens 2008), this is not a robust conclusion.

Table 3. Stable isotope values (mean ± SD) of Henderson Island rat tissues. Sample sizes were 5 for shore rats and 7 for inland rats, except for the liver and blood of the latter when n = 6 ind. were sampled

Sample Rat group	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N ratio
Bone collagen			
Shore	−19.8 ± 0.3	17.5 ± 1.2	3.4 ± 0.0
Inland	−20.4 ± 0.5	14.1 ± 0.6	3.4 ± 0.0
Skin collagen			
Shore	−19.9 ± 0.4	17.7 ± 1.2	3.3 ± 0.0
Inland	−20.4 ± 0.5	14.6 ± 0.7	3.2 ± 0.1
Liver			
Shore	−20.6 ± 1.0	18.9 ± 1.6	3.8 ± 0.0
Inland	−22.1 ± 0.1	14.0 ± 0.8	3.7 ± 0.0
Blood			
Shore	−22.0 ± 0.7	17.4 ± 1.1	3.6 ± 0.0
Inland	−22.7 ± 0.5	13.1 ± 0.4	3.6 ± 0.1

The $\delta^{15}N$ of shore rats was ~4‰ higher than of inland rats (Table 3), but this difference provides only limited information about rat diets on Henderson Island. While this difference could have been due to greater consumption of marine top predators (i.e. petrels) by shore rats, it could also have been substantially due to higher marine nutrient subsidy to the terrestrial ecosystem in which they foraged. At least in the coastal areas where shore rats were sampled, coconut — the terrestrial plant endpoint — had rather high $\delta^{15}N$ values of 10.7‰ (Table 2). Such values imply a considerable degree of marine nutrient subsidy to the terrestrial ecosystem, arising from the long-term presence of seabird colonies which deposit guano, dead seabirds and spilt food containing marine-derived nitrogen (e.g. Croll et al. 2005, Fukami et al. 2006, Maron et al. 2006). The import of nitrogen from tideline debris by terrestrial consumers would also contribute. Petrel tissues did have substantially higher $\delta^{15}N$ values than coconuts, averaging 15.9‰ (Table 2), as would be expected for a high trophic level predator (see also 'Discussion'), but a terrestrial food chain involving herbivorous invertebrates and their predators (which were not sampled) would include potential rat prey items with $\delta^{15}N$ in the region of 14 to 18‰, not dissimilar to petrel tissues. The extent to which the marine nitrogen signal in the terrestrial food web diminishes with distance from the coast was not directly measured.

The generalised linear mixed model (GLMM) on which Table 6 is based included individual identity as a random factor and provided no evidence that these differences between the 2 groups of rats at the 2 sites in either $\delta^{15}N$ (Wald $Z = 1.00$, $p = 0.318$) or $\delta^{13}C$ (Wald $Z = 1.53$, $p = 0.126$) values were due to statistically significant inter-individual differences.

Model validation

A first-year survival rate of 0.79 minimised the sum of the squared deviations (SSQ = 240.6, N = 37) between observed and predicted annual numbers of cahow breeding pairs (Fig. 4). The observed values all fell within the standard error of those predicted in each year, indicating that the model is a good fit and that any deviations from it can be explained by chance.

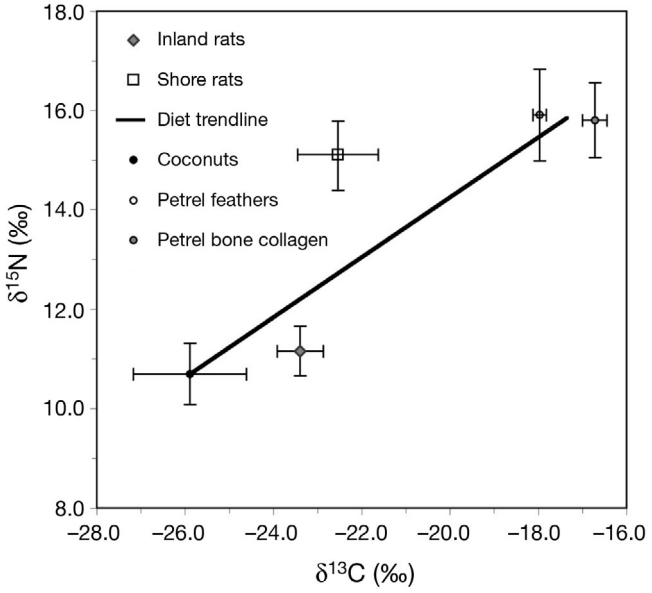

Fig. 3. *Rattus exulans*. Calculated carbon and nitrogen isotopic values of dietary intake for each group of rats. The carbon and nitrogen isotopic values used for the marine endpoint of the diet trend line are the overall mean of all petrel chick feather and bone collagen samples (see Table 2). Vertical and horizontal error bars are 1 SD

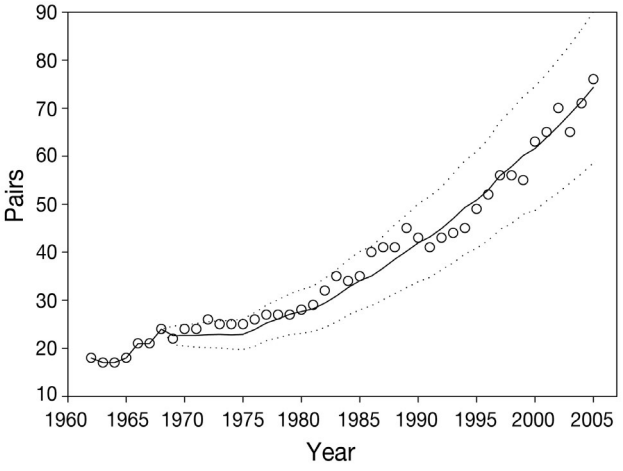

Fig. 4. *Pterodroma cahow*. Observed population trend (number of breeding pairs) for cahow between 1962 and 2005 (○), the predicted trend from the best-fit model (solid line) and the standard errors of the predictions (dotted lines). Note that the first 7 points in the series are used to seed the subsequent model predictions and so observed and predicted values are identical

Table 4. Calculated diet–tissue offsets for rodents. Carbon isotopic data are from DeNiro & Epstein (1978), Tieszen et al. (1983), Nakagawa et al. (1985), Ambrose & Norr (1993) and Tieszen & Fagre (1993). Nitrogen isotopic data are from Nakagawa et al. (1985), DeNiro & Epstein (1981) and Ambrose (2000)

Tissue–diet difference	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Bone collagen–diet	3.4	3.1
Liver–diet	0.7	3.5
Blood–diet	0.4	1.5

Table 5. Calculated dietary intake isotopic values, obtained by correcting rat tissue values by offsets derived from rodent studies. Mean calculated diet values are presented ±SD

Rat group	Tissue	Calculated diet $\delta^{13}C$ (‰)	Calculated diet $\delta^{15}N$ (‰)
Shore	Bone	−23.2	14.4
	Blood	−22.4	15.9
	Liver	−21.3	15.4
	Skin	−23.3	14.7
	Mean calculated diet	−22.5 ± 0.9	15.1 ± 0.7
Inland	Bone	−23.8	11.0
	Blood	−23.1	11.6
	Liver	−22.8	10.5
	Skin	−23.9	11.5
	Mean calculated diet	−23.4 ± 0.5	11.2 ± 0.5

Modelled population trajectories

Base model

We began by applying the base model to observed Henderson petrel breeding success. Thus breeding probability was zero for 1 to 3 yr olds, 0.15 for Age 4, 0.65 for Age 5, 0.8 for Age 6 and 0.89 for older birds (J. Madeiros unpubl. data). First year survival was 0.79 (see above) and that of older birds was 0.93 (Simons 1984). Breeding success was 0.175, as observed (Brooke 1995). Adults can breed annually but do not re-nest. With these parameters, the population declines (growth rate $\lambda = 0.9918$).

Demographic scenarios required to prevent predicted declines

This section explores how the population trajectory changes as various population parameters are altered from the base model described above. Model values are as detailed in the base model, except for the variations specified. Where appropriate, λ derived from the base model is underlined. The scenarios (1 to 5) are generated by considering variation in only one parameter at a time:

(1) Breeding probability varies (Table 7). Although the base model as-

Table 6. Generalised linear mixed model tests of the fixed effects of rat *Rattus exulans* origin and tissue type on carbon and nitrogen isotope values. Because multiple tissue samples were obtained from each individual rat, we used rat identity as a random effect, with rat origin and tissue type as fixed effects.

Source	Numerator df	Denominator df	*F*	p
Carbon				
Intercept	1	10.1	30312	<0.001
Rat origin (inland or shore)	1	10.1	12.9	0.005
Tissue	3	31.6	65.9	<0.001
Nitrogen				
Intercept	1	9.87	7439	<0.001
Rat origin (inland or shore)	1	9.87	114.4	<0.001
Tissue	3	31.6	3.670	0.022

sumes 15% of 4 yr olds breed, with the proportion actually breeding then increasing with year class up to 89% at age 7 (and older), increasing the proportion of birds breeding in the year classes 4 to 6 does not stabilise the population. It continues to decline.

(2) Re-nesting allowed. Although re-nesting is generally rare in petrels, its occurrence is not well understood (Brooke 2004). We adjusted the base model to allow 10% of birds to re-nest in the same season following a breeding failure. Then λ increases from 0.9918 to 0.9934. The population's rate of decline falls, but decline continues.

(3) Adult survival increases (Table 8). If the base model is adjusted by increasing adult survival by 0.5% increments, then the population grows when adult survival reaches 95%.

(4) Immature survival increases. If the base model is adjusted by increasing immature survival from 0.79 to 0.93 (i.e. equal to adult survival), λ alters from 0.9918 to 0.9951. The population's rate of decline falls, but decline continues. Thus, while a marked increase in immature survival has only a limited effect on population growth rate, a small increase in adult survival can have a striking effect (Scenario 3), a result long familiar to petrel biologists (Moloney et al. 1994).

Table 7. *Pterodroma atrata.* Scenario 1, breeding probability. λ: growth rate; underlined value: λ derived from the base model

Age	Breeding probability		
4	0.80	0.15	0.15
5	0.89	0.80	0.65
6	0.89	0.89	0.80
7	0.89	0.89	0.89
λ	0.9922	0.9921	0.9918

Table 8. *Pterodroma atrata.* Scenario 3, increasing adult survival by 0.5% increments. λ: growth rate; underlined value: λ derived from the base model

Adult survival	0.930	0.935	0.940	0.945	0.950
λ	0.9918	0.9940	0.9963	0.9985	1.006

(5) Breeding success increases (Table 9) . Finally, we considered what improvement in breeding success would be necessary to achieve population stability, even if all other survival and breeding parameters remain as in the base model.

With breeding success enhanced to 25%, the population is close to stable: further improvements in breeding success are followed by population growth.

Although changes in age of first breeding, juvenile survival and frequency of re-nesting can affect population growth rate, plausible changes in these parameters alone are unlikely to halt the decline of the Henderson petrel. Decline is most likely to be halted if adult survival is as high as 0.95 or if breeding success rises above 0.25, or some combination of the two. The interaction between the effects of breeding success and survival on λ is shown in Fig. 5.

DISCUSSION

Fieldwork on the Murphy's petrels of Henderson Island indicated that they suffered equally heavy predation of their chicks in 1991 and 2003, and the likelihood is that similar predation occurs every breeding season, leading to breeding success below 10%, well below the level required for population stability in our *Pterodroma* demographic model. Since fieldwork in 1991 and 2003 yielded no indication that this predation is leading to a Murphy's petrel population decline, and since adult survivorship appears typical for a medium-sized petrel, the Henderson population is presumably sustained by immigration (Bonnaud et al. 2009). Ducie, an atoll 300 km to the east of Henderson, holds a pop-

Table 9. *Pterodroma atrata.* Scenario 5, breeding success required to achieve population stability. λ: growth rate; underlined value: λ derived from the base model

Breeding success (annual)	0.175	0.25	0.30
λ	0.9918	0.9996	1.0043

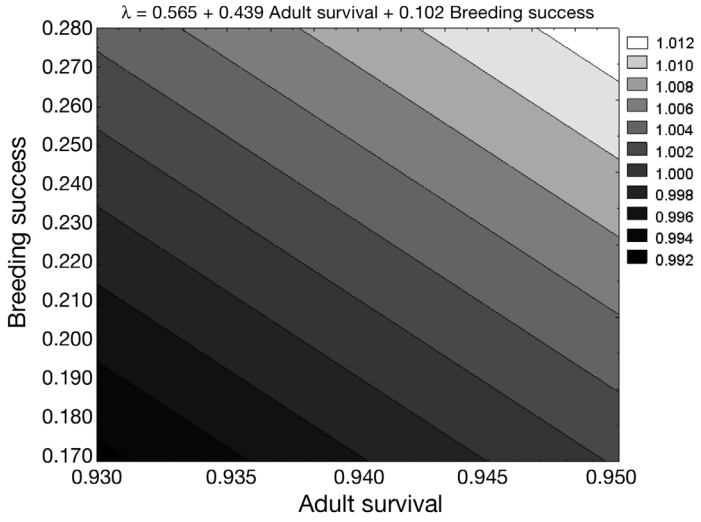

Fig. 5. *Pterodroma atrata*. Predicted population growth rate (λ) of the Henderson petrel in relation to adult survival and breeding success. To generate the plot, all other population parameters were fixed at the values in the base model (see 'Results: Base model'). The value of λ at any point on the 2-dimensional plot is given by the equation above, and the λ values beside the shading tones indicate the value of λ along a midline running top left to bottom right along the centre of each diagonal band

ulation that is around 100 times larger, and is the only realistic source of sufficient immigrants (Brooke 1995). While this suggestion could in theory be tested by ringing, it would require ringing on a scale that is probably impractical. Alternatively, microsatellite data could be informative.

The model developed for cahow showed that variations in annual productivity could give a reasonable prediction of future population growth, and returned a best-fit first year survival rate of 0.79. This value is higher than that used in previous models of *Pterodroma* population dynamics (Simons 1984, Brooke 1995). While we are duly cautious about the applicability of cahow values to other species in other oceans, albeit congenerics living at a similar latitude, these earlier models may have been excessively pessimistic in their predictions. Our model suggested *Pterodroma* populations can remain stable if productivity is about 0.25 chicks per pair, a value that might be considered too low to maintain populations of most seabird species, and one to be borne in mind when judging the likely impact of rodents on populations of other medium-sized petrels. However, the measured breeding success of the Henderson petrel was below this 0.25 threshold in 1991–1992 and, judging by the 2003 Murphy's petrel data, likely also below the threshold in 2003. Therefore a decline in Henderson petrel numbers would be expected.

Indeed, the model indicated a population with a productivity of 0.175 would decline at the modest rate of –0.82% yr^{-1}. This value is close to the decline rate of –0.77% yr^{-1} suggested by Brooke (1995) using a model that made basic and unsubstantiated assumptions about immature survival and was not validated against *Pterodroma* population dynamics observed elsewhere.

The modelled decline remains based on very sparse breeding success data, and the population trajectory improves to approximate stability if annual breeding success improves to about 0.25 (Scenario 5). It is certainly probable that the latter condition would be met if rats were to be eradicated from Henderson, a possibility now under active consideration.

If breeding success remains at 0.175, a 10% incidence of re-nesting is not sufficient to alter the prediction of population decline, nor is a substantial reduction in the age of first breeding, even to the extent that the majority of birds are breeding by Age 4, the youngest that is likely (Brooke 2004).

The prediction of decline is altered by an increase in adult survival from 0.93 to 0.95 or a slighter increase in adult survival coupled with enhancements in other parameters (e.g. Fig. 5). Thus the outcome is extremely sensitive to the precise value of adult survival. There is no information whatsoever on the survival of Henderson petrels, and there are no obvious means by which conservationists can improve adult survival of this pelagic seabird. However, while we acknowledge that our Murphy's petrel survival data are slight and no better than a surrogate for Henderson petrel data, they do not suggest that Henderson petrel survival in excess of 0.93 is impossible. Whatever the annual survival of Henderson petrels, there is little doubt that an improvement in breeding success following rat eradication would shift the Henderson petrel population from probably declining to probably increasing. This conclusion would stand even if the eradication were to have little or no impact on adult survival (Sæther & Bakke 2000, Jenouvrier et al. 2009).

If, as the model suggests, Henderson petrels have been declining since the arrival of rats around 700 yr ago (Weisler 1994), what would the species' initial population have been? Assuming λ = 0.9918, the base case, the current population would be approximately 0.3% of that when rats arrived (ignoring density-dependence). Since the current population is estimated at 16 000 pairs, that indicates a population around 5 million pairs when rats arrived. That population would have had a density about one-third that prevailing currently among Murphy's petrels on Ducie (Brooke 1995), and so could plausibly have been accommodated in Henderson's area (37 km^2) and provided the abundant food resources known to have been used by the early Polynesian settlers (Steadman & Olson 1985).

The above discussion has assumed that rat predation on petrels does not vary between habitats (Igual et al.

2006) and is not density dependent. We now consider whether the isotope analyses accord with this latter assumption, noting that the carbon and nitrogen isotopic values of the petrel samples analysed were as expected for such seabirds foraging mainly on squid (Imber et al. 1995, Takai et al. 2000).

Isotopic analyses confirmed that inland rats and shore rats have a different diet, with shore rats consuming foods with significantly higher $\delta^{15}N$ and $\delta^{13}C$ values, such as petrel chicks. However, when compared to the petrel chicks analysed, the carbon isotopic values of the shore rats are not high enough to indicate that they are highly dependent on the petrels as a food resource. Marine-type carbon isotope signatures in Henderson rats might derive from seabird consumption, but it is important to note that consumption of other foods of marine origin would also elevate $\delta^{13}C$ similarly, and is highly likely to account for part of the marine carbon signal in shore rat tissues. This is primarily likely to involve consumption of dead marine animals on the tideline, and of secondary consumers of tideline debris. However, such marine food sources are less likely to penetrate 700 m from the coast to where the inland rats were sampled, and Pacific rat home ranges, especially in a relatively dense population such as that on Henderson, would probably preclude our sampled inland rats foraging at the coast (Moller & Craig 1987).

However important the rats are as petrel predators, petrels are not the major dietary component of the rats. Similarly, a study of Pacific rats on Kapiti Island, New Zealand, showed that rats caught in the area of a sooty shearwater *Puffinus griseus* nesting colony on the island had radiocarbon ages and carbon and nitrogen isotopic values indicating a diet with a low proportion of marine foods (Beavan & Sparks 1998). These findings therefore contrast with others (Hobson et al. 1999, Stapp 2002) where isotopic analysis suggested that a large part of the diet of those rats living in seabird colonies was seabirds. However, in both these quoted cases, the seabirds occurred at substantially higher densities than the petrels on Henderson (see also Drever et al. 2000).

Simple calculations also suggest that petrels are unlikely to be a major dietary component of rats. If the rats exist at a density of at least 20 ha^{-1} (Moller & Craig 1987, M. Brooke pers. obs.), and weigh from 60 to 120 g (M. Brooke unpubl. data), then the rat biomass on 3700 ha Henderson is around 6000 kg. If a maximum of 30 000 petrel chicks of all species hatch each year (Brooke 1995) and are then eaten by rats when they weigh 100 g, 3000 kg of chick are eaten per year. If rats are eating 10 to 15% of their body weight per day (Harkness & Wagner 1989), then 3000 kg of petrel chicks can only support 6000 kg of island rats for a few days and be only a relatively minor element in the rats' diet, when viewed across the whole year.

Our conclusion is that any decrease in the petrels of Henderson Island due to rat predation will not necessarily lead to a decline in the numbers of rats, since they can subsist on alternative foods. This is a disturbing conclusion for the conservation of petrels which, as rats decline, are unlikely to enjoy a density-dependent recovery in productivity resulting in part from a reduction in rat numbers. But decline would, in all probability, be averted if rats could be eradicated from Henderson Island.

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LITERATURE CITED

Ambrose SH (2000) Controlled diet and climate experiments on nitrogen isotope ratios of rats. In: Ambrose SH, Katzenberg MA (eds) Biogeochemical approaches to paleodietary analysis. Kluwer Academic/Plenum Press, New York, p 243–259

Ambrose SH, Norr L (1993) Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In: Lambert JB, Grupe G (eds) Prehistoric human bone: archaeology at the molecular level. Springer-Verlag, Berlin, p 1–37

Arneson LS, MacAvoy SE (2005) Carbon, nitrogen, and sulfur diet–tissue discrimination in mouse tissues. Can J Zool 83:989–995

Atkinson IAE (1985) The spread of commensal species of *Rattus* to islands and their effects on island avifaunas. In: Moors PJ (ed) Conservation of island birds. International Council for Bird Preservation, Cambridge, p 35–81

Beavan NR, Sparks RJ (1998) Factors influencing ^{14}C ages of the Pacific rat *Rattus exulans*. Radiocarbon 40:601–613

Ben-David M, Flynn RW, Schell DM (1997) Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. Oecologia 111:280–291

BirdLife International (2009) Data zone. Available at www.birdlife.org/datazone

Bonnaud E, Bourgeois K, Vidal E, Kayser Y, Tranchant Y, Legrand J (2009) How can the Yelkouan shearwater survive feral cat predation? A meta-population structure as a solution? Popul Ecol 51:261–270

Brooke M (1990) The petrel crisis. BBC Wildl 8:252–259

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

Brooke MdeL (2004) Albatrosses and petrels across the world. Oxford University Press, Oxford

Brooke MdeL (2006) Pitcairn Islands. In: Sanders SM (ed) Important bird areas in the UK Overseas Territories. Royal

Society for the Protection of Birds, Sandy, p 185–199
Brooke MdeL, Rowe G (1996) Behavioural and molecular evidence for specific status of dark and light morphs of the Herald petrel *Pterodroma heraldica*. Ibis 138:420–432
Carlile N, Priddel D, Zino F, Natividad C, Wingate DB (2003) A review of four successful recovery programmes for threatened sub-tropical petrels. Mar Ornithol 31:185–192
Caut S, Angulo E, Courchamp F (2008) Discrimination factors ($\delta^{15}N$ and $\delta^{15}N$) in an omnivorous consumer: effect of diet isotopic ratio. Funct Ecol 22:255–263
Croll DA, Maron JL, Estes JA, Danner EM, Byrd GV (2005) Introduced predators transform subarctic islands from grassland to tundra. Science 307:1959–1961
DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochim Cosmochim Acta 42:495–506
DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochim Cosmochim Acta 45:341–351
Drever MC, Blight LK, Hobson KA, Bertram DF (2000) Predation on seabird eggs by Keen's mice (*Peromyscus keeni*): using stable isotopes to decipher the diet of a terrestrial omnivore on a remote offshore island. Can J Zool 78: 2010–2018
Fukami T, Wardle DA, Bellingham PJ, Mulder CPH and others (2006) Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. Ecol Lett 9:1299–1307
Gannes LZ, del Rio CM, Koch P (1998) Natural abundance variations in stable isotopes and their potential uses in animal physiological ecology. Comp Biochem Physiol A 119:725–737
Harkness JE, Wagner JE (1989) The biology and medicine of rabbits and rodents, 3rd edn. Lea & Febiger, Philadelphia, PA
Harper GA (2006) Habitat use by three rat species (*Rattus* spp.) on an island without other mammalian predators. NZ J Ecol 30:321–333
Hobson KA, Drever MC, Kaiser GW (1999) Norway rats as predators of burrow-nesting seabirds: insights from stable isotope analyses. J Wildl Manag 63:14–25
Hoefs J (1997) Stable isotope geochemistry. Springer, Berlin
Igual JM, Forero MG, Gomez T, Orueta JF, Oro D (2006) Rat control and breeding performance in Cory's shearwater (*Calonectris diomedea*): effects of poisoning effort and habitat features. Anim Conserv 9:59–65
Imber MJ, Jolly JN, Brooke MdeL (1995) Food of three sympatric gadfly petrels (*Pterodroma* spp.) breeding on the Pitcairn Islands. Biol J Linn Soc 56:233–240
Iredale T (1914) The surface breeding petrels of the Kermadec Group. Ibis 2:423–436
Jenouvrier S, Barbraud C, Weimerskirch H, Caswell H (2009) Limitation of population recovery: a stochastic approach to the case of the emperor penguin. Oikos 118:1292–1298
Jones HP, Tershy BR, Zavaleta ES, Croll DA, Keitt BS, Finkelstein ME, Howald GR (2008) Severity of the effects of invasive rats on seabirds: a global review. Conserv Biol 22:16–26
Kelly JF (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. Can J Zool 78:1–27
MacAvoy SE, Macko SA, Arneson LS (2005) Growth versus metabolic tissue replacement in mouse tissues determined by stable carbon and nitrogen isotope analysis. Can J Zool 83:631–641
MacAvoy SE, Arneson LS, Bassett E (2006) Correlation of metabolism with tissue carbon and nitrogen turnover rate in small mammals. Oecologia 150:190–201
Maron JL, Estes JA, Croll DA, Danner EM, Elmendorf SC, Buckelew SL (2006) An introduced predator alters Aleutian Island plant communities by thwarting nutrient subsidies. Ecol Monogr 76:3–24
Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}N$ and animal age. Geochim Cosmochim Acta 48:1135–1140
Moller H, Craig JL (1987) The population ecology of *Rattus exulans* on Tiritiri Matangi Island, and a model of comparative population dynamics in New Zealand. NZ J Zool 14:305–328
Moloney CL, Cooper J, Ryan PG, Siegfried WR (1994) Use of a population model to assess the impact of longline fishing on wandering albatross *Diomedea exulans* populations. Biol Conserv 70:195–203
Moore JW, Semmens BX (2008) Incorporating uncertainty and prior information into stable isotope mixing models. Ecol Lett 11:470–480
Nakagawa A, Kitagawa A, Asami M, Nakamura K and others (1985) Evaluation of isotope ratio (IR) mass spectrometry for the study of drug metabolism. Biomed Mass Spectrom 12:502–506
Nichols JT, Mowbray LL (1916) Two new forms of petrels from the Bermudas. Auk 33:194–195
O'Connell TC, Healey MA, Hedges REM, Simpson AHW (2001) Isotopic comparison of hair, bone and nail: modern analyses. J Archaeol Sci 28:1247–1255
Phillips DL, Gregg JW (2003) Source partitioning using stable isotopes: coping with too many sources. Oecologia 136: 261–269
Preece RC (1995) Systematic review of the land snails of the Pitcairn Islands. Biol J Linn Soc 56:273–307
Privat KL, O'Connell TC, Richards MP (2002) Stable isotope analysis of human and faunal remains from the Anglo-Saxon cemetery at Berinsfield, Oxfordshire: dietary and social implications. J Archaeol Sci 29:779–790
Rayner MJ, Hauber ME, Imber MJ, Stamp RK, Clout MN (2007) Spatial heterogeneity of mesopredator release within an oceanic island system. Proc Natl Acad Sci USA 104:20862–20865
Richards MP, Hedges REM (1999) A Neolithic revolution? New evidence of diet in the British Neolithic. Antiquity 73: 891–897
Rucklidge GJ, Milne G, McGaw BA, Milne E, Robins SP (1992) Turnover rates of different collagen types measured by isotope ratio mass spectrometry. Biochim Biophys Acta 1156:57–61
Ruffino L, Bourgeois K, Vidal E, Duhem C and others (2009) Invasive rats and seabirds after 2,000 years of unwanted coexistence on Mediterranean islands. Biol Invasions 11: 1631–1651
Sæther BE, Bakke Ø (2000) Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81:642–653
Simons TR (1984) A population model of the endangered Hawaiian dark-rumped petrel. J Wildl Manag 48: 1065–1076
Sponheimer M, Robinson T, Ayliffe L, Roeder B and others (2003) Nitrogen isotopes in mammalian herbivores: hair $\delta^{15}N$ values from a controlled feeding study. Int J Osteoarchaeol 13:80–87
Stapp P (2002) Stable isotopes reveal evidence of predation by ship rats on seabirds of the Shiant Islands, Scotland. J Appl Ecol 39:831–840
Steadman DW, Olson SL (1985) Bird remains from an archae-

ological site on Henderson Island, South Pacific: man-caused extinctions on an 'uninhabited' island. Proc Natl Acad Sci USA 82:6191–6195

Sweeting CJ, Polunin NVC, Jennings S (2004) Tissue and fixative dependent shifts of $\delta^{13}C$ and $\delta^{15}N$ in preserved ecological material. Rapid Commun Mass Spectrom 18: 2587–2592

Takai N, Onaka S, Ikeda Y, Yatsu A, Kidokoro H, Sakamoto W (2000) Geographical variations in carbon and nitrogen stable isotope ratios in squid. J Mar Biol Assoc UK 80: 675–684

Tieszen LL, Fagre T (1993) Effect of diet quality and composition on the isotopic composition of respiratory CO_2, bone collagen, bioapatite, and soft tissues. In: Lambert J, Grupe G (eds) Prehistoric human bone: archaeology at the molecular level. Springer-Verlag, Berlin, p 121–155

Tieszen LL, Boutton TW, Tesdahl KG, Slade NA (1983) Fractionation and turnover of stable isotopes in animal tissues: implications for $\delta^{13}C$ analysis of diet. Oecologia 57:32–37

Tomkins RJ (1985) Breeding success and mortality of dark-rumped petrels in the Galapagos, and control of their predators. In: Moors PJ (ed) Conservation of island birds. International Council for Bird Preservation, Tech Publ 3, Cambridge, p 159–175

Traveset A, Nogales M, Alcover JA, Delgado JD and others (2009) A review of the effects of alien rodents in the Balearic (western Mediterranean Sea) and Canary Islands (eastern Atlantic Ocean). Biol Invasions 11:1653–1670

Waldren S, Florence J, Chepstow-Lusty AJ (1995) A comparison of the vegetation communities from the islands of the Pitcairn Group. Biol J Linn Soc 56:121–144

Weisler MI (1994) The settlement of marginal Polynesia: new evidence from Henderson Island. J Field Archaeol 21: 83–102

Weisler MI (1995) Henderson Island prehistory: colonization and extinction on a remote Polynesian island. Biol J Linn Soc 56:377–404

Wragg GM (1995) The fossil birds of Henderson Island, Pitcairn Group: natural turnover and human impact, a synopsis. Biol J Linn Soc 56:405–414

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