Detecting predation of a burrow-nesting seabird by two introduced predators, using stable isotopes, dietary analysis and experimental removals

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Abstract. Burrowing seabirds are vulnerable to extirpation by introduced predators such as rats, but much evidence of predation is circumstantial. On Taukihepa, an island off southern New Zealand, two possible predators exist with sooty shearwaters (*Puffinus griseus*): the weka (*Gallirallus australis*), a large rail, and the ship rat (*Rattus rattus*), both introduced to the island. It was expected that chick predation would be principally by weka, the much larger of the two predators. To measure losses of sooty shearwater chicks to weka or rats, nests were monitored with burrow-scopes at six sites in the summers of 2003–04 and 2004–05. In three of the sites rats were removed on 4-ha grids by trapping. In the other three sites rats were not trapped. In addition, weka were removed from all six sites in 2005. Concurrent diet analysis of weka and rat stomachs was undertaken as well as stable isotopic analysis (δ^{13}C, δ^{15}N) of samples from rats and weka. These were compared with possible prey items including sooty shearwaters. Additional stable isotope samples were taken from Pacific rats (*Rattus exulans*), a small rat species present with weka and sooty shearwaters on nearby Moginui Island. Weka diet comprised ~40% of bird remains by volume and calculations using Isosource, an isotopic source portioning model, estimated sooty shearwaters contributed 59% (range: 15–71%) of weka diet during the sooty shearwater chick-raising period. Ship rats, in contrast, had very depleted δ^{13}C isotope signatures compared with sooty shearwaters and bird remains contributed <9% of diet by volume, with Isosource calculations suggesting that ship rats consumed more passerine birds (mean: 30%; range 5–51%) than sooty shearwaters (mean 24%; range: 0–44%). In both summers, more chicks were lost on sites from which rats had been removed than on control sites. When weka were removed in 2005, fewer chicks were lost than in 2004 and significantly fewer weka-killed chicks were found on weka-removal sites than on non-removal sites. Weka were the principal predator of sooty shearwater chicks, depredating an estimated 9.9% of nests. Combining several techniques quantified the loss and identified the principal predator of a seabird in decline.

Introduction

Burrowing seabird populations are particularly vulnerable to introduced predators (Moors and Atkinson 1984), and this is especially true on islands. When mammalian predators, such as rats (*Rattus* spp.) or domestic cats (*Felis catus*), are introduced to islands, resident populations of seabirds invariably decline or go extinct (Atkinson 1985; Burger and Gochfeld 1994). Non-native avian predators introduced to islands can also kill seabirds. An example is on subantarctic Macquarie Island, where the weka (*Gallirallus australis*, ~750 g), an omnivorous rail endemic to New Zealand, was introduced in 1872, and the ship rat (*Rattus rattus*) in early 1900s (Taylor 1979). Weka, ship rats and cats, introduced *c*. 1810, have been recorded preying on the numerous seabird species present, resulting in populations of smaller seabirds disappearing from the island (Brothers 1984).

In some instances, seabird populations persist on islands where exotic predators have been introduced. On some of the Titi Islands in southern New Zealand, burrowing sooty shearwaters, or titi, breed in large numbers despite the presence of ship rats, which were introduced in 1963 (Bell 1978), and weka, introduced early in the 20th century (Miskelly 1987) and also

implicated as predators of sooty shearwaters (Imber 1975; Brothers 1984). The abundance of sooty shearwaters is declining worldwide, which has been variously attributed to climate change, drift-netting, and predation by introduced mammals (Lyver *et al*. 1999, 2000; Scofield and Christie 2002; Uhlmann *et al*. 2005). Predation by ship rats on eggs and small chicks is inferred in sooty shearwater populations elsewhere and in other similar-sized burrowing petrels (Lane 1962; Harris 1970; Grant *et al*. 1981; Thibault 1995). Imber (1975) suggested, however, that nesting petrels are only likely to be extirpated if the maximum weight of a rat predator is about the same as, or exceeds, the average adult weight of the petrel species. Similarly, Major *et al*. (2006) concluded that Norway rats (*Rattus norvegicus*, 170 g) caused deaths in least auklet (*Aethis pusilla*) chicks (adult weight 84 g), rather than adults or eggs, but principally through disturbance of the adults and subsequent exposure of chicks rather than predation. Sooty shearwaters weigh ~800 g and male ship rats ~200 g (Heather and Robertson 1996; Innes 2005), so the inferences for predation of this species are equivocal. However, like other petrels (Imber *et al*. 2003), sooty shearwater chicks are most vulnerable just after the brief

guard stage, when chicks weigh 90–150 g (Richdale 1945), because foraging adults are increasingly absent (Richdale 1945). So it was possible that rats would depredate sooty shearwater chicks in the first week or two after hatching. The magnitude of loss of sooty shearwater chicks from introduced predators on offshore islands is unknown, however, because egg or chick depredation has not been measured.

As direct observations of predation are rare, effects of rats on seabirds are often inferred from observations of chick remains or emptied nests (Brothers 1984; Brooke 1995; Seto and Conant 1996; Major and Jones 2005) and, increasingly, from ratios of the stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) (Hobson *et al*. 1999; Drever *et al*. 2000; Major *et al*. 2007). Hobson *et al*. (1999) suggested combining stomach content analysis and stable isotopes to clarify the nature of introduced predators' effects on seabirds. Subsequently, Stapp (2002) used both techniques to investigate the impact of ship rats on seabirds, but was unable to establish whether rats killed or simply scavenged seabirds. Scavenging yields very similar stomach contents and stable isotope values as predation (Stapp. 2002). Differential nesting success between sites where rats were present or removed can be used to measure the effect of rats on seabirds (Seto and Conant 1996; Thibault 1995; Bried and Jouventin 1999). Invariably, nesting success was higher where rats were extirpated or reduced to low densities. In light of these findings, a predator-removal and non-removal experiment was established on Taukihepa, in concert with gut samples and stable isotope analysis. Comparing breeding success of sooty shearwaters on sites where predators were present or removed would provide the level of loss attributable to predators. Stable isotope samples from Pacific rats (*Rattus exulans*) on an island with sooty shearwaters were also sought, to provide comparative data from a small predator less likely to kill a large shearwater.

The objectives of the study were to quantify the loss of sooty shearwater chicks and eggs, and to identify the principal predator responsible for any losses. As both rat species were smaller than sooty shearwaters it was expected that the weka was likely to be the principal predator.

Methods

Study sites

Taukihepa, or Big South Cape Island (797 ha, 47°14′S, 169°25′E), lies ~2 km south-west of Stewart Island/Rakiura, New Zealand (Fig. 1). It is the largest island in the southern Titi Islands, so named because of dense populations of titi or sooty shearwaters that breed there over the austral summer and autumn. Soils are derived from peat and are highly modified in the upper horizons by massive mixing and addition of marine-derived nutrients from the burrowing of titi (Hawke and Newman 2005). The climate is wet (1400 mm), with over 250 rain days (>0.1 mm) spread throughout the year. The mean annual temperature is 10.3°C (Sansom 1984). Strong winds are normal. A detailed description of the habitat on the islands is given by Johnston (1982).

Pacific rats were trapped on nearby Moginui or Big Moggy Island (68 ha) (Fig. 1). Moginui has very similar rocks, soils, climate, and forest to Taukihepa. Moginui slopes upward from

the east to high cliffs in the west, and Pacific rats, weka and sooty shearwaters were present.

Assessing nesting success

Burrows in six sites on Taukihepa were randomly selected in December 2003 (Fig. 1). The sites were a minimum of 400 m apart to maintain the independence of individual predators. Within each site we used an infrared burrowscope (Lyver *et al.* 1998) to select between 36 and 51 burrows occupied by sooty shearwaters incubating eggs. Nests were initially checked once or twice in early December. To record hatching success and chick survival, burrows were then examined before eggs hatched in mid-January, and observations then repeated every three days until mid-February. By this time the chicks were assumed to be large enough (~400 g) to defend themselves from rats. Nest failures were recorded when eggs did not hatch but were still present. The burrows were examined again in March to record any further losses. The process was repeated between December 2004 and March 2005.

Statistical analysis of each measure of nest failure, egg loss and chick loss was carried out using an ANOVA, where the reproductive measure equalled the year plus treatment results. Replicates were the site and year combination ($n = 12$) and year
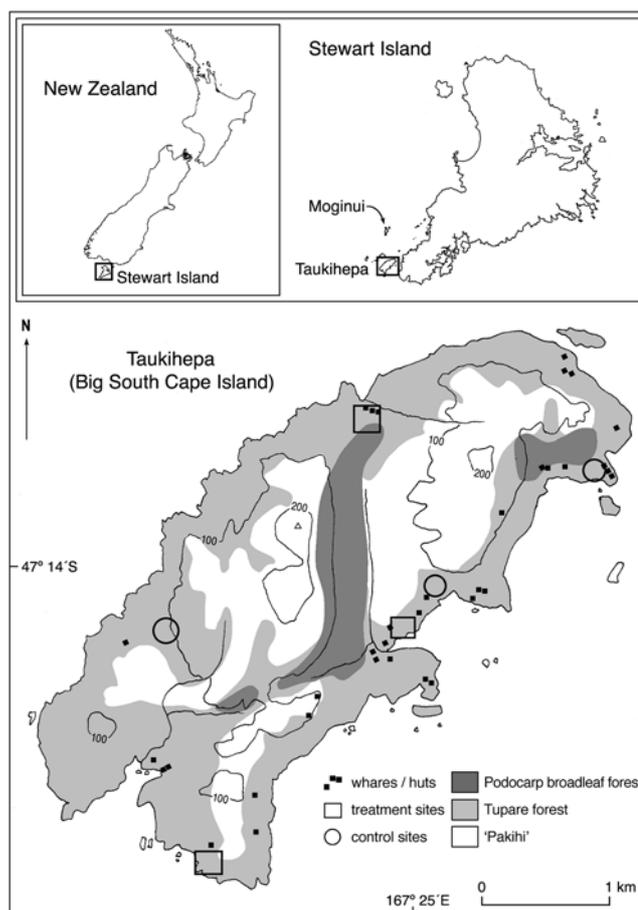

Fig. 1. The location of treatment (rat-trapped) and control (non-trapped) sites on Taukihepa and location of Moginui and the southern Titi Islands, south-west New Zealand.

and treatment were explanatory variables. Percentage losses were square-root transformed before analysis.

Predator removals

Rats were trapped and removed from three treatment sites out of the six monitoring areas situated across the island (Fig. 1). A compass and fabric measuring tape were used to establish the traps on grids. The location of the corners of the 200 m by 200 m (4 ha) grids were recorded by Global Positioning System (GPS) using a Garmin Etrex. Trapping grids consisted of 85 'Victor'™ snap-traps, in a grid of seven traps at 33-m intervals on 13 alternate offset rows 16 m apart. The traps were baited with a mixture of rolled oats and peanut butter and secured with wire stakes under 12-mm galvanised mesh covers. Traps were set when they were put out and operated continuously for the following 4–5 weeks.

To obtain stable isotope samples from Pacific rats on Moginui, a trapping grid of 49 traps under mesh covers was established on the northern end on 16 March 2005 and run for five days. The 100 m by 100 m (1 ha) grid consisted of seven rows 15 m apart, each of seven traps at 15-m intervals. The numbers of traps used was limited by transport restrictions.

Traps were checked every morning, and all rats removed and processed on the day of capture, following Cunningham and Moors (1996). Muscle samples for stable isotopic analysis were taken from the left hind leg.

Within- and between-season measures of chick losses due to weka were made during the study period. Sooty shearwater chicks found with the distinctive injuries caused by weka (Harper 2006) were collected on the six monitoring sites and on tracks between monitoring sites (Fig. 1) in January and February 2004 and 2005. Search effort for dead chicks was approximately equal on the monitoring sites and tracks each year. In January and February 2005, in addition to rat removals on three sites, any weka found on all six monitoring sites were removed. Weka were killed immediately by pithing. Each weka was measured, sexed and weighed and the crop and a pectoral muscle sample were removed for dietary and stable isotopic analysis, respectively.

Diet analysis

Stomachs from rats and crops from weka removed from experimental sites were later analysed. Each stomach or crop was stored in a vial in 75% ethanol. A subsample of rat stomach samples from January 2005 was used to compare rat and weka diets for the same period. Birds were identified mainly by feather and shell remains, and some bones. Insects were identified from exoskeleton remains. Plant material, including leaves, seed or fruit, were recorded. For rats, bait ingested from traps was also recorded. Results were recorded in two ways: (1) frequency of occurrence (percentage of guts containing a prey item), and (2) estimated volume of food items. Two methods were used, because the former does not take into account prey weight and its relative contribution to daily food intake. The frequency-of-occurrence method has been used in many studies of rat or weka diet (Carroll 1963; Gales 1982; Brothers and Skira 1984; Moors 1985) and is therefore useful for comparisons.

Muscle tissue samples from ship rat, Pacific rat, and weka were stored frozen in a propane freezer and transferred later to a laboratory freezer. Additional possible diet items, including pectoral muscle from freshly dead sooty shearwater adults and chicks, invertebrates, and plant material were obtained opportunistically. Although this sampling was not random, major diet items of rats and weka were chosen.

Stable isotope analysis

Samples were analysed for stable isotope ratios by Iso-Trace New Zealand Ltd, Dunedin. Samples were freeze-dried and ground into a powder, then lipids were extracted using a chloroform–methanol rinse. Isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) were measured using isotope ratio mass spectrometry (IRMS; Hydra® 20/20 mass spectrometer). Stable isotopes are expressed in δ notation (in parts per thousand; per mil; ‰) as follows:

$$\delta X(‰) = 1000 \times (R_{sample} - R_{standard}) / R_{standard}$$

where X is the ratio of ^{15}N to ^{14}N or ^{13}C to ^{12}C and R is the ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$ as measured for the samples and relevant standards (atmospheric N_2, VPDB, respectively). The notations ($\delta^{13}C$ and $\delta^{15}N$) refer to the enrichment (positive values) or depletion (negative values) relative to these standards. Measurement errors are shown in Table 2. Turnover time for muscle tissue is ~4 weeks (Tieszen *et al*. 1983), so the ratios reflect the diet during the period before death.

The possible percentage contribution of several potential prey items to rat or weka diet was estimated using the mean isotopic values of prey in the computer program Isosource (Phillips *et al*. 2005). The calculation involved pairs of carbon and nitrogen isotopic signatures being compared with all other isotopic pairs of possible prey, in an iterative model, as possible solutions to the observed predator's isotopic signature. Appropriate diet-tissue fractionation values between prey and consumer were selected for the model. For weka, values of +1.9‰ and +3.1‰ for $\delta^{13}C$ and $\delta^{15}N$ respectively were applied to possible prey items to estimate fractionation to consumer tissue. These values were derived from pectoral muscle of dunlin (*Calidris alpina pacifica*) (Ogden *et al*. 2004). Potential prey items for rats had fractionation values of +0.5‰ for $\delta^{13}C$ and +3.0‰ for $\delta^{15}N$ applied using values from gerbil (*Meriones unguiculatus*) muscle tissue (Tieszen *et al*. 1983). The stable isotope values for muscle of weka and ship rats are listed in Table 2. Uncertainty in the source contribution estimates due to measurement error and sample variability can be included in the Isosource model by choosing tolerance values. The tolerance value and source increment value were set at 0.1‰ and 1‰ respectively. Results were graphed as a mean value with maximum and minimum range values. Comparisons of the results were made with the percentage contribution of prey to predator diet as assessed from stomach or crop samples.

Results

Sooty shearwater nesting success

Of 347 marked burrows, 280 (81%) were occupied by nesting birds in 2003–04 and 253 of 349 burrows (72%) in 2004–05. In both 2004 and 2005 eggs began hatching on ~12 January. The last eggs hatched on ~1 February.

In 2004, seven nests failed on control sites and 15 failed on treatment sites (Fig. 2*a*). In 2005, 11 nests failed on control sites and nine on treatment sites. There was no significant treatment

effect over both years ($F = 3.67$, $P = 0.09$). There was also no significant difference between years ($F = 0.02$, $P = 0.9$) or treatment sites ($F = 0.25$, $P = 0.63$). Most eggs from failed nests were retrieved and checked for cause of death and all appeared to have been fertile but died during development.

In 2004, 15 eggs disappeared on the treatment sites and 10 disappeared on the control sites (Fig. 2*b*). In 2005, 14 eggs disappeared on the treatment sites and eight disappeared on the control sites. There was no significant treatment effect over both years ($F = 1.14$, $P = 0.32$). Similarly, there was no significant difference in egg loss between years ($F = 0.81$, $P = 0.39$) or treatment sites ($F = 3.24$, $P = 0.11$).

Predator removals

In total, 2132 ship rats were trapped over the five trapping sessions on all the trapping grids. Rat captures were initially high, but captures declined rapidly to average about one rat or less trapped per hectare from about the fifth day of trapping. From about then most trapped rats were likely invading the trapping area from outside the grids. Fifteen weka were removed from the six burrow-scoped sites (mean number of weka removed: 2.5, s.e. 0.62). The mean density of radio-tracked weka on Taukihepa was estimated at 0.76 ha^{-1} (s.e. 0.07) in tupare forest (Cunninghame 2006), which yielded an approximate density of 3.04 weka on the 4-ha grid sites.

The percentage loss of chicks was not significantly affected by treatment over both years ($F = 0.01$, $P = 0.97$) or significantly different between treatment sites ($F = 1.21$, $P = 0.3$). However, there was a difference between years that approached significance ($F = 4.83$, $P = 0.06$). There was a substantially smaller percentage of chicks lost in 2005, on the control and treatment sites combined, than in 2004 (Fig. 2*c*.). In 2004 more chicks were lost on treatment sites (19) than the nine lost on the control sites. In contrast, when weka were removed from both treatment and control sites in 2005, only five chicks were lost on the treatment sites and two on the control sites. In addition, ~60% fewer weka-killed chicks ($n = 13$) were found on weka-controlled sites in 2005 than in 2004 ($n = 29$). However, on tracks with no weka control in 2005, more weka-killed chicks were found ($n = 9$) than in 2004 ($n = 4$). This was a significant departure from homogeneity ($\chi^2 = 4.57$, d.f. =1, $P = 0.033$).

Diet analysis

Crop samples from 15 weka were analysed. Although insects occurred more often in weka diet than did bird remains, insects and bird remains contributed approximately the same (38.8% and 39.6% respectively) to diet by volume (Fig. 3*a*). Fruit or seeds were the next most common diet items. Two crops, from separate sites, were full of sooty shearwater chick remains, including skin, feathers and a foot in each.

Rat diets in January 2005 consisted mainly of insect and plant remains by either volume or occurrence (Fig. 3*b*). Bait was recorded in the results but normally would not be present. Bird remains, including meat and down feathers, constituted only 8.7% of rat diet by volume and occurred 11 times in 60 rat stomachs. This included three cases where eggshell was recorded. Insects occurred more often than the other diet items, but contributed a similar amount, by volume, to rat diet as plant material. There was no significant departure from homogeneity for the
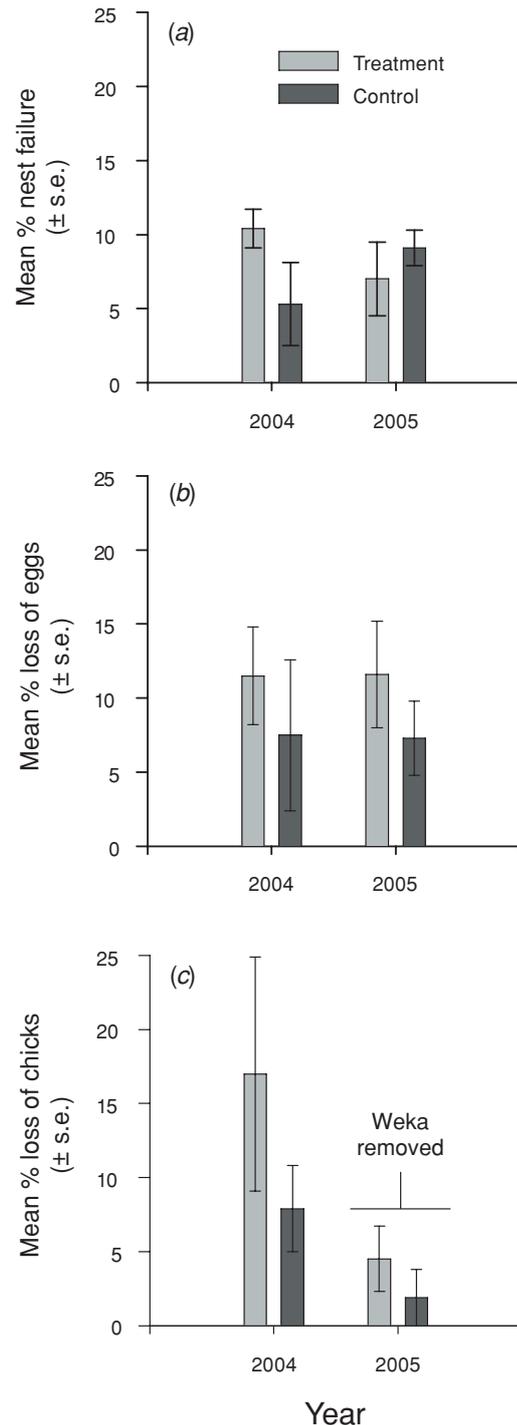

Fig. 2. (*a*). Estimated failure rate (%) of sooty shearwater nests on six sites on Taukihepa, summer 2004 ($n = 280$ occupied burrows) and 2005 ($n = 253$ occupied burrows). (*b*). Estimated loss of sooty shearwater eggs (%) from burrows on six sites with ship rats and weka were present on Taukihepa, summer 2004 ($n = 258$ burrows with incubated eggs) and 2005 ($n = 233$ burrows with incubated eggs). (*c*). Estimated loss of sooty shearwater chicks (%) from burrows at three treatment sites (ship rats removed) and three control sites (ship rats present) on Taukihepa, summer 2004 ($n = 233$ burrows with eggs remaining) and 2005 ($n = 213$ burrows with eggs remaining). Weka were present in 2004 but removed in 2005.

Table 1.   Results of statistical analysis, using Mann–Whitney U-tests, to determine comparative differences in the stable-nitrogen and -carbon signatures of muscle tissue collected from ship rats, Pacific rats, weka and sooty shearwater chicks and adults on Taukihepa and Moginui, 2005

Statistically significant values are indicated: *, $P \leq 0.05$; **, $P \leq 0.01$

		Sooty shearwater (Taukihepa) ($n = 5$)		Ship rat (Taukihepa)		Pacific rat (Moginui)		Weka (Taukihepa)	
		$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$
Ship rat (Taukihepa) ($n = 11$)	U	1.0	44.0						
	P	>0.01**	0.06						
Pacific rat (Moginui) ($n = 4$)	U	0.0	12.0	40.5	61.0				
	P	0.01*	0.62	0.45	>0.01**				
Weka (Taukihepa) ($n = 7$)	U	2.5	18.5	66.5	68.5				
	P	0.01*	0.87	0.01*	>0.01**				
Weka (Moginui) ($n = 2$)	U	–	–	–	–	8.0	8.0	4.0	13.0
Weka (Moginui) ($n = 2$)	P	–	–	–	–	0.06	0.06	0.38	0.08

seasonal occurrence of plant or insect items in rat diet in January and May of 2004 and 2005 (plants: $\chi^2 = 0.62$, d.f. =1, $P = 0.43$; insects: $\chi^2 = 0.02$, d.f. =1, $P = 0.89$). However, there was a significant departure from homogeneity for bird remains ($\chi^2 = 4.35$, d.f. =1, $P = 0.04$). Fewer bird remains were found in rat stomachs in January 2005 than in January 2004, and much more in May 2005 than the corresponding month in 2004.

Stable isotope analysis

The mean isotopic values of weka, ship rats, Pacific rats and possible diet items are shown in Fig. 4, (details in Table 2), with statistical comparisons between the possible predators and sooty shearwaters in Table 1. $\delta^{13}C$ and $\delta^{15}N$ values were obtained from 11 ship rat and four Pacific rat muscle samples for Taukihepa and Moginui respectively. Seven weka muscle samples from Taukihepa were analysed for stable isotope ratios and two from Moginui. Three muscle samples were obtained from adult sooty shearwaters and two from chicks. The isotopic values for sooty shearwater adults and chicks were combined for the analyses. Replicate measurements of internal laboratory standards (EDTA-OAS) indicated measurement values of –0.9 (±0.3) for $\delta^{15}N$ and –38.3 (±0.03) for $\delta^{13}C$.

Table 2.   Stable–nitrogen ($\delta^{15}N$) and –carbon isotope ($\delta^{13}C$) values of muscle tissue of rats and weka, and sooty shearwater muscle tissue and possible terrestrial prey values from Taukihepa and Moginui Islands

Sample	n	$\delta^{15}N$ (±0.3%) Mean	s.e.	$\delta^{13}C$ (±0.03%) Mean	s.e.
Ship rat (Taukihepa)	11	14.66	0.58	–22.76	0.23
Pacific rat (Moginui)	4	14.85	0.53	–22.05	0.17
Weka (Taukihepa)	7	12	0.53	–21.8	0.28
Weka (Moginui)	2	12.6	0.20	–20.35	0.25
Sooty shearwater chick	2	10.35	0.95	–21.1	1.10
Sooty shearwater adult	3	9.53	0.43	–21.5	0.82
Spider	1	14.3	–	–24.4	–
Grass (*Poa tennantiana*)	1	13.7	–	–27.8	–
Amphipod	3	10.27	0.30	–24.87	0.37
Weta (Orthoptera)	1	8.6	–	–25.7	–
Tupare (*Brachyglottis colensoi*)	5	8.5	1.06	–27.28	0.88
Beetle	2	8.5	1.80	–23.65	0.65
Fern (*Histiopteris incisca*)	3	3.87	0.73	–28.77	1.14
Rata (*Metrosideros umbellata*)	1	–3.9	–	–25.1	–

All the possible predators were significantly more enriched in $\delta^{15}N$ than sooty shearwaters. Sooty shearwaters were not significantly more enriched in $\delta^{13}C$ than Taukihepa weka or Pacific rats, but were close to being significantly more enriched than ship rats.

When compared with ship rats, weka sampled on Taukihepa in January were significantly depleted in $\delta^{15}N$, but were significantly more enriched in $\delta^{13}C$. Similarly, weka on Moginui in mid-March were depleted in $\delta^{15}N$ in comparison with Pacific rats, but the difference was not statistically significant, possibly due to the small sample sizes involved. Weka on Moginui were also approaching significance in enrichment of $\delta^{13}C$ when compared with Pacific rats. Ship rats sampled on Taukihepa in January did not have significantly different $\delta^{15}N$ values than Pacific rats but Pacific rats were significantly more enriched in $\delta^{13}C$. There was no significant difference in the $\delta^{15}N$ values between weka from Taukihepa and Moginui, but differences between $\delta^{13}C$ values approached statistical significance.

There was no significant difference between seasonal values of both $\delta^{15}N$ and $\delta^{13}C$ from ship rats trapped in December, February and May ($\delta^{15}N$: Kruskal–Wallis test statistic = 4.35, d.f. = 2, $P = 0.11$; $\delta^{13}C$: Kruskal–Wallis test statistic = 0.39, d.f. = 2, $P = 0.82$).

Of the other possible diet items the spider sample was enriched in $\delta^{15}N$, comparable with both rat species, but was slightly depleted in $\delta^{13}C$. The other invertebrates sampled had similar $\delta^{15}N$ values to sooty shearwaters but were relatively depleted in $\delta^{13}C$. Of the plant samples the single grass stalk base (*Poa tennantiana*) had similar $\delta^{15}N$ enrichment as the rat species but was less enriched in $\delta^{13}C$. The tupare petioles, which were known to be eaten by rats (pers. obs.), were depleted in both $\delta^{15}N$ and $\delta^{13}C$ relative to rats. The sole sample of rata, of a seed pod, was taken from shrubland on the edge of pakihi, some 10 m from the nearest sooty shearwater burrows. This sample was very depleted in $\delta^{15}N$ compared with all other samples, but was more enriched in $\delta^{13}C$ than other plants.

The isotopic ratios of feathers from two passerines, tomtit (*Petroica macrocephala*) and thrush (*Turdus philomelos*), were included in Fig. 4 (J. Newman, unpubl. data). These small birds exist on seabird islands, the Snares, some 90 km south of Taukihepa, with a similarly dense colony of sooty shearwaters. The Snares are a similar size to Moginui Island and are covered in the same *Olearia* forest. These passerines feed on a mix of

invertebrates and fruit, and provided useful comparative values for rats and weka, with similarly omnivorous diets. In both cases the birds were more enriched in $\delta^{15}N$ than either rats or weka, and thrush were more enriched in $\delta^{13}C$ than the rats.

The results of the Isosource model are presented in Fig. 5. Sooty shearwaters were estimated to contribute a mean of 59% (range: 15–71%) to weka diet in summer, with invertebrates comprising a large portion of the remainder of their diet. Ship rats relied more on small passerines (range: 5–51%; mean:
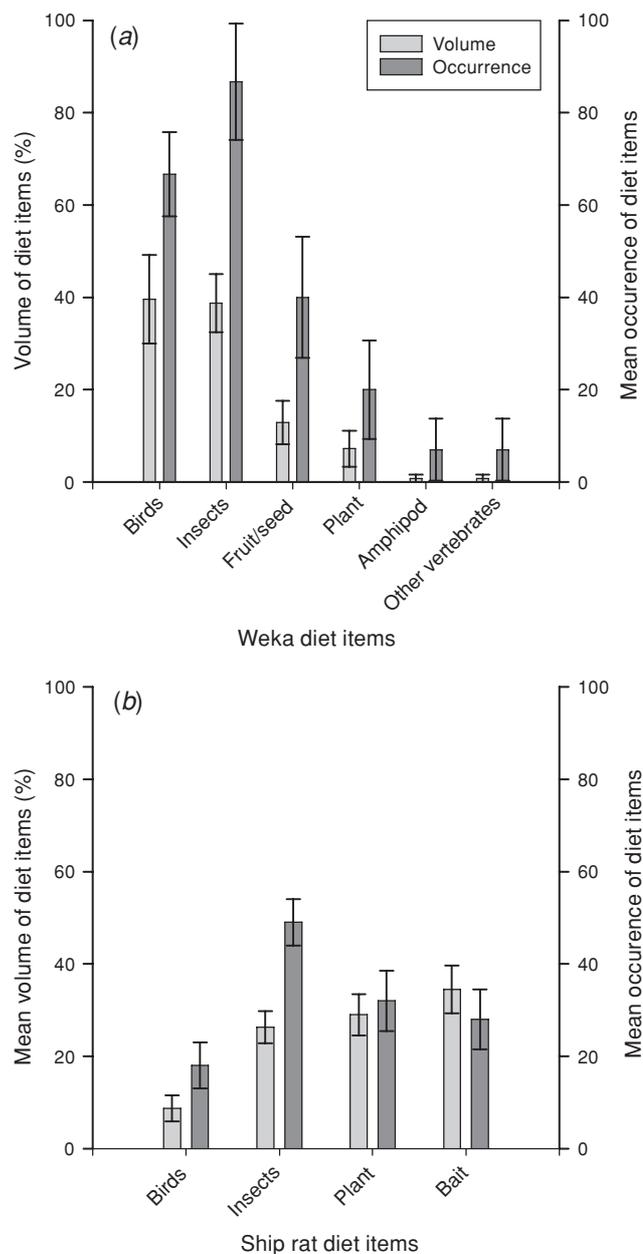
30%) than sooty shearwaters (0–44%; 24%), with a mix of invertebrates and plant material forming the remainder of summer diet.

Discussion

Nest predators of sooty shearwaters

The hypothesis that weka were principal predators of sooty shearwater chicks was strongly supported by the results of this study. Weka probably also depredated eggs, whereas ship rats scavenged the sooty shearwater remains left by weka. Combining three different, but complimentary, techniques provided more conclusive results than was possible using one or even two methods. Although weka had been observed killing titi chicks (Harper 2006), these observations, in themselves, did not prove that weka were the principal predators. Inferred predation of large burrowing seabirds by ship rats on islands elsewhere, along with the stomach analysis presented here, could have led to a conclusion that ship rats also depredated sooty shearwater chicks and eggs. Similarly, relying on stable isotope analysis alone would not have revealed weka predation, as results are sometimes counterintuitive. For example, animals feeding on plants on seabird islands often have more enriched $\delta^{15}N$ signatures than the same species feeding at higher trophic levels (Stapp *et al*. 1999; Drever *et al*. 2000).

Experimental removal of predators

The removal of weka provided the strongest evidence for their effect on nesting success of sooty shearwaters, even though the result was probably confounded by unrelated yearly variation in reproductive success of sooty shearwaters. Despite this likely variation, a substantial reduction in weka density on treatment and control sites in 2005 reduced sooty shearwater chick losses by 75% compared with 2004. There was also a decline in the number of dead chicks found on treatment and control sites whereas the number of dead chicks increased where weka control was absent. This large reduction in chick losses was unlikely to be entirely due to a difference in reproductive success, especially as nest failure and egg loss changed little between years. However, several natural deaths are likely in these figures (Warham 1996), which means the recorded chick losses are not entirely attributable to weka. Indeed, the mean chick loss on the treatment site in 2005 could be assumed to be natural, as predators were almost entirely absent. In this instance, the difference in chick losses on treatment sites between 2004 (17.0% ± s.e. 7.9) and 2005 (4.5% ± s.e. 2.2) which could be attributable to weka would therefore be ~12%. Additionally, if rats are assumed to be largely benign, then control sites could be added to the same equation, which would yield a mean percentage loss of chicks to weka predation of 9.9% (±s.e. 3.5).

The removal of rats on treatment sites in each summer yielded no discernible change in chick losses. More chicks were lost at sites where rats had been removed compared with control sites in both years, which was skewed by large losses on a single site. These asymmetric loss rates may result from different predation pressure between sites by only a few 'rogue' weka apparently 'keyed into' killing titi chicks. Brothers and Skira (1984) suggested that only few individual weka killed burrowing

Fig. 3. (*a*). Diet items recorded in stomachs of 60 ship rats on Taukihepa, summer 2005. Items recorded by estimated volume and occurrence in stomachs (±s.e.). (*b*) Diet items recorded in crops of 15 weka on Taukihepa, summer 2005. Items recorded by estimated volume and occurrence in crops (±s.e.).

petrels on Macquarie Island and Cunninghame (2006) recorded one radio-tagged male weka on Taukihepa killing titi chicks more often than other radio-tagged individuals. More dead titi chicks were also found in the territory of this weka than in other weka home ranges (Cunninghame 2006). Body parts of titi chicks in some weka crops show that titi chicks formed a large portion of the diet for at least some weka in late summer and early autumn.

Stable isotope analysis

The stable isotope signature of weka was also much closer to that of sooty shearwaters than were the two signatures of either rat species. The $\delta^{13}C$ values of weka and sooty shearwaters were very close, which would be expected if weka were feeding on sooty shearwaters, as there is only ~1% enrichment of $\delta^{13}C$ between predator and prey (Stapp *et al*. 1999; Kelly 2000). However, Taukihepa weka were enriched only 2.5‰ and 1.7‰ in $\delta^{15}N$ over sooty shearwater adults and chicks respectively, less than the possible 3.3‰ enrichment expected if weka were feeding exclusively on sooty shearwaters (Robbins *et al*. 2005). The omnivorous foraging of weka would be expected to reduce their $\delta^{15}N$ signature relative to a diet based solely on seabirds. Stable isotopic analysis showed that Titi Island weka were ingesting significantly more marine-derived diet items than were rats, and were also more enriched in $\delta^{13}C$ than a single weka sample from mainland New Zealand. Moginui weka were more enriched in $\delta^{13}C$ than Taukihepa weka, by 3.1‰ and 2.3‰ compared with sooty shearwater adults and chicks respectively. This may be due to sampling occurring some 4–6 weeks later on Moginui. Longer exposure to titi chicks as prey was likely to lead to enrichment of $\delta^{13}C$ in weka.

The Isosource calculations supported the diet analysis results. The use of stable isotopes in these calculations also provided a longer period for evidence of the prey source, as turnover time for muscle tissue is ~4 weeks (Dalerum and Angerbjörn 2005). For example, although diet analysis revealed that both weka and rats consumed birds, the Isosource program

suggested that sooty shearwaters contributed much more to weka diet than to rat diet, and the reverse was apparent for small passerines (Fig. 5). Similarly, the relatively low consumption of plant material relative to invertebrates in weka diet was repeated in the Isosource results. The inclusion of fruit (*Coprosma* spp. in particular) may have improved the model for weka, as these fruits contributed to weka diet on Taukihepa. Indeed, the higher consumption rates of sooty shearwater recorded by Isosource for both weka and ship rats when compared with the gut analyses was probably due to two factors. One factor is likely to have been that fewer prey items were sampled than the predators actually consumed. Another factor is that multiple source mixing models tend to overestimate proportions of rarely consumed food items and underestimate abundant food items (Rosing *et al*. 1998). As such, the Isosource model provided indices of prey items consumed rather than actual values.

Interactions between weka and ship rats

Weka did not appear to be a significant predator of rats on Taukihepa. Very few possible mammal remains were found in weka crops and $\delta^{15}N$ values of weka were significantly depleted compared with ship rats, whereas the $\delta^{15}N$ values of weka eating rats should have been relatively enriched. In contrast, ship rats comprised a significant portion of weka diet on Macquarie Island (Brothers and Skira 1984).

Predation by ship rats and pacific rats

Ship rats were not the principal cause of chick loss in sooty shearwaters. Even when ship rats were reduced to very low densities on treatment sites losses of chicks continued at an overall higher rate of loss than control sites The lack of seasonal variation in the isotopic values of samples supported this conclusion. If sooty shearwater adults or chicks were being killed by rats, enrichment of $\delta^{13}C$ in rat tissue in February and May was likely, but not recorded. Stable isotope analysis did reveal that ship rats and Pacific rats were ingesting a similar mix of food at a significantly higher trophic level than weka, which was
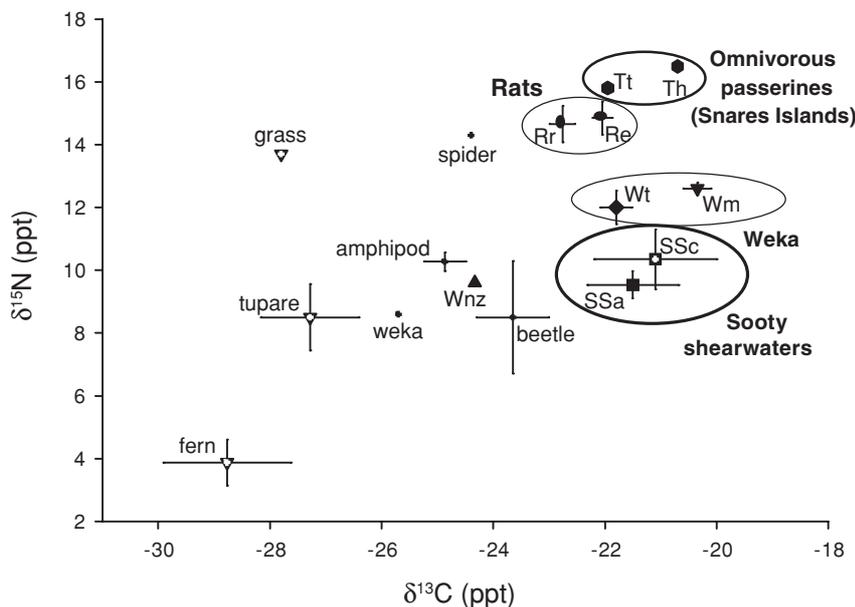
Fig. 4. Stable-nitrogen and -carbon isotope values of muscle tissue of rats and weka with possible terrestrial prey and sooty shearwater muscle tissue values from Taukihepa in summer 2005 and Moginui Islands in early autumn 2005. Values are means ± 95% confidence intervals and are corrected for fractionation. Included are single stable isotope values of feathers from passerines from Snares Islands. SSa = Sooty shearwater adult, SSc = Sooty shearwater chick, Wt = Weka from Taukihepa, Wm = Weka from Moginui, Wnz = Weka from New Zealand mainland, Rr = Ship rat (Taukihepa), Re = Pacific rat (Moginui), Tt = Snares Island tomtit, Th = thrush (Snares Islands).
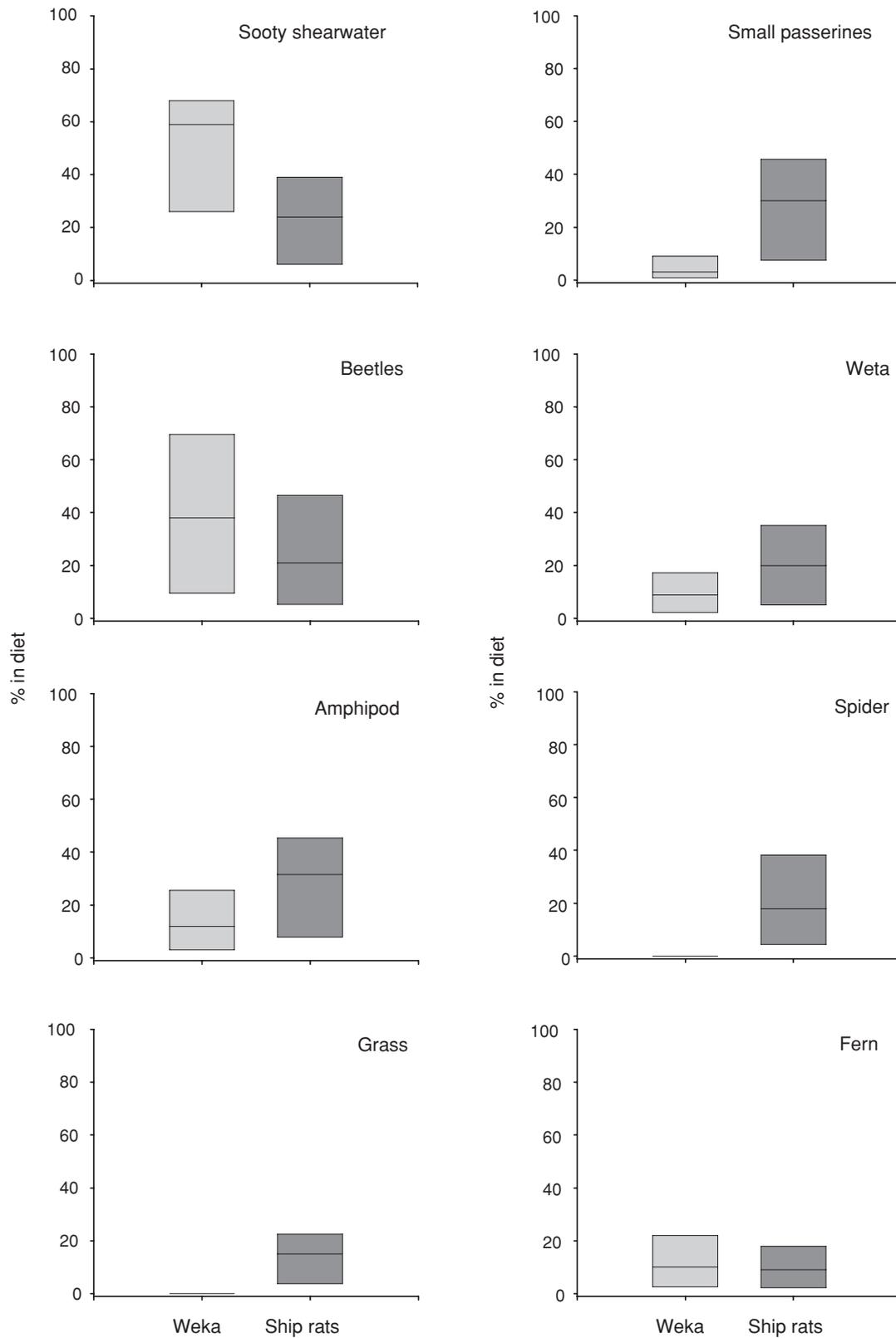
Fig. 5. Possible percentage contribution of prey to weka and ship rat diet as calculated using stable-nitrogen and -carbon isotope values of potential prey items in the Isosource program. Possible percentage contributions are presented as means and ranges. The stable isotope values of potential prey items are in Table 2.

initially surprising as diet analysis showed that weka were eating proportionally more birds as prey than rats. However, the Isosource calculations suggested that rats were consuming more passerines, which had higher $\delta^{15}N$ values than sooty shearwaters (Fig. 4), and which further confirms ship rats as predators of small passerines (Innes 2005). Although Pacific rats had very similar $\delta^{15}N$ enrichment to ship rats, they were even less likely to kill titi chicks because Pacific rats are small (Imber 1975). In addition, if rats were eating more plant-based prey items from grasses, seeds for example, then this would enrich rats' observed $\delta^{15}N$ values, but would not result in enrichment of $\delta^{13}C$ (Stapp *et al.* 1999). Similarly, mice (*Peromyscus keeni*) and voles (*Microtus townsendii*) on a seabird island in British Columbia, which fed on terrestrial plants and insects, had higher $\delta^{15}N$ values than mice feeding largely on seabird eggs (Drever *et al.* 2000). The similarly enriched $\delta^{15}N$ values for both rat species, a spider and the Snares Islands passerines imply at least two, possibly complementary, nutrient pathways for marine N to accumulate in omnivores on seabird islands. One would be via plants fertilised by guano and seabird remains and another through invertebrates, which have fed on guano, guano-fertilised plants, or seabird remains (Hawke and Newman 2005), which suggests that the pathways are complex. Pacific rats were significantly more enriched in $\delta^{13}C$ than ship rats, possibly for the same reasons that Moginui weka were enriched compared with Taukihepa weka. The lack of seasonal variation in the $\delta^{13}C$ values for ship rats tends to argue against this conclusion, however, and suggests that the small size of Moginui may increase exposure of plants there to marine spray, or that weka and Pacific rats had a slightly more marine-derived diet. Sampling of probable diet items at Moginui would have possibly assisted the analysis.

Nest failure and hatching success in sooty shearwaters

Nesting failure was highly variable, with no obvious pattern between treatment or control sites, or between years. This suggests that weka or rats did not affect nesting success, especially as these predators were controlled only during the last 1–2 weeks of incubation. Brothers (1984) also noted abandoned sooty shearwater eggs on Macquarie Island untouched by ship rats for up to a month. Egg failures in Procellariidae most likely result from egg chilling or nest abandonment, if one of the adults did not return to relieve the nesting bird, for example (Warham 1996). Comparisons with later egg and chick-loss patterns suggest that nest failures occur because of environmental factors affecting the breeding success of sooty shearwaters rather than through predation. In fact, the mean percentage nest failure rate over the control and treatment sites over two years was 7.9% (±1.16 s.e.), which was generally lower than that of many other procellariids (Warham 1996). It is unlikely that research activity unduly affected nesting success, because nests were checked once only early in the nesting stage, and then adult attendance only was checked again immediately before hatching.

In contrast to the variable nesting success, a repeated pattern of higher losses of eggs occurred on treatment sites which closely matched the pattern of chick losses. Egg loss may have been due to nesting failure and subsequent abandonment by the adult, but this is unlikely as some abandoned eggs should have been found later when burrowscoping. This loss pattern adds to the suggestion that weka will steal eggs from occupied nests (St Clair and St Clair 1992; Harper 2006).

Nesting success during the egg and early chick stage appeared to be comparatively high despite predation over the two breeding seasons. The little data available from breeding colonies where predators were absent or controlled suggested that ~59–68% of sooty shearwater chicks survived the egg and small chick stage (Jones *et al.* 2003). This result is actually slightly lower than the 65–80% of chicks that survived on Taukihepa, where predation occurred. At colonies where predators such as mustelids (*Mustela* spp.), feral cats and Norway rats were present, fewer than 44% of chicks survived to the end of the small chick stage (Jones *et al.* 2003). These data, although limited, suggest that productivity on Taukihepa is high, with a comparatively small impact by weka. The mean hatching success of sooty shearwaters on Taukihepa of 83.2% (±1.67 s.e.), which was higher than on predator-free Snares (58%: Warham *et al.* 1982), or short-tailed shearwaters in Tasmania (70%: Norman 1985), supports this conclusion. The reduced nesting success on predator-free islands may be a density-dependence effect, possibly through increased interference (Warham 1996), as burrow density is significantly higher on Snares (1.38 burrows m^{-2} (s.e. 0.06): D. Scott, pers. comm.) than Taukihepa (0.43 burrows m^{-2} (s.e. 0.04): J. Newman, pers. comm.), assuming that burrow occupancy is similar.

Despite the lack of evidence for an effect of ship rats on the breeding success of sooty shearwaters, there is anecdotal information that rat irruptions can reduce breeding success of sooty shearwaters immediately after rats invade an island. Extremely poor titi harvesting seasons on three islands apparently coincided with irruptions of ship rats (Drummond 1910; Anonymous 1934; Newman 2006), with one (Newman 2006) noting that the concurrent harvest had been 'typical' on an adjacent island 150 m away without rats. Harvest of sooty shearwaters returned to normal despite the continuing, but lower, rat density. This suggests that the extremely high rat densities and concomitant food shortages during the peak and initial decline phases of an irruption result in increasingly desperate foraging for rodents as recorded in irruptions elsewhere (Ylönen *et al.* 2002; Harper 2005). This risky feeding behaviour could conceivably result in rats killing chicks much heavier than themselves. Rat irruptions on the Titi Islands appear to have occurred only once during the invasion stage as no reccurrence of a rat irruption coupled with extremely poor chick survival has been reported on these islands. This may be due to an apparent lack of other multiannual high-energy food pulses, such as seed-masting tree species (Harper 2005).

Combining methods to detect principal predators

When two or more predators are present with prey, these results suggest caution in attributing most of the predation to one or other species. Even in this case a lack of predation by ship rats was not unequivocally shown, and possibly occurred at low levels but remained undetected. However, the use of complementary techniques did clarify the magnitude of predation that occurred, highlighted the principal predator responsible and showed the degree to which weka and ship rats relied on sooty shearwater chicks as prey or as scavenged food. Similar multiple-source approaches can be used to elucidate other more

complex predator–prey relationships. When resources are limited this approach could be particularly useful for revealing which specific predator to concentrate on for control or eradication when they threaten the survival of native species.

Acknowledgements

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