

Impact of introduced house mice (*Mus musculus*) on burrowing seabirds on Steeple Jason and Grand Jason Islands, Falklands, South Atlantic

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Abstract Whilst there is good evidence for negative impacts of introduced rat species on island ecosystems, the effects of house mice (*Mus musculus*) are generally less well documented. In some situations, introduced house mice can exert severe impacts, particularly where this is the only introduced mammal. Here, we examine the distribution, relative abundance and breeding success of small burrowing seabirds on Steeple Jason Island, Falklands, in relation to habitat types and the distribution of house mice which is the sole introduced mammal species, and we make comparisons with seabird distribution and densities on the neighbouring island of Grand Jason where mice are absent. Grey-backed storm-petrel (*Garrodia nereis*) and Wilson's storm-petrel (*Oceanites oceanicus*), which due to their extremely small size are likely to be the most vulnerable to mouse predation, were considerably more abundant on mouse-free Grand Jason than on Steeple Jason. Grey-backed storm-petrel,

which are typically associated with tussac grass, avoided this habitat on Steeple Jason where it is associated with high levels of house mouse activity (assessed from the proportion of wax baits gnawed overnight), whereas on mouse-free Grand Jason, there was no such avoidance. Wilson's storm-petrel nesting on Steeple Jason suffered high rates of egg and chick loss. Whilst we found evidence for detrimental impacts of house mice on the two small storm-petrel species, there was no relationship between relative mouse activity levels and the distribution or abundance of the larger thin-billed Prion (*Pachyptila belcheri*).

Keywords Non-native mammalian predator · Rodent · Storm-petrel · Eradication

Introduction

Commensal species of rodents have invaded around 90 % of the world's island archipelagos, resulting in often far reaching and negative impacts on natural ecosystems (Blackburn et al. 2004; Towns et al. 2006; Jones et al. 2008). The most commonly introduced rodents are the brown rat (*Rattus norvegicus*), black rat (*Rattus rattus*), Pacific rat (*Rattus exulans*) and the house mouse (*Mus musculus*). The Pacific rat was spread primarily through the historical expansion of Polynesians (Roberts 1991) and the other species through European exploration from the early sixteenth century onwards (Hilton and Cuthbert 2010). There is a growing body of evidence documenting the devastating impacts introduced rodents may have on the flora, invertebrates and seabirds native to the islands invaded, which frequently include endemic species with highly restricted breeding distributions and small populations. Globally, invasive rodents have caused the extinction

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of at least 50 native species (Blackburn et al. 2004; Towns et al. 2006; Jones et al. 2008; Butchart 2008; Hilton and Cuthbert 2010). To reduce such negative impacts, by 2007, rodents had been successfully eradicated from 284 hundred islands worldwide (Howald et al. 2007). As the number of eradication attempts has grown, and lessons have been learned from failed attempts, the success rate has improved and the size of islands successfully cleared of rodents has increased to over 110 km² (McClelland and Tyree 2002). However, large eradications are usually very costly and logistically complex, so priority should be given to islands where conservation impacts have been clearly demonstrated and the benefits of eradication are therefore likely to be greatest (see Ratcliffe et al. 2009 for such a prioritization exercise). Compared with the larger *Rattus* species, there is less evidence for severe impacts of introduced house mice on native island species, especially seabirds (see Angel et al. 2009 for a review). Both Wanless et al. (2007) and Angel et al. (2009) hypothesized that the negative impacts of invasive house mice are most severe on islands where mice are the sole species of introduced mammal and the absence of the effects of dominance, competition and predation by the larger rodent species allows house mice to reach higher population densities. Whilst several studies have shown that invertebrates and plant material predominate in the diet (Le Roux et al. 2002; Smith et al. 2002), in some instances where house mice are the sole introduced rodent, the effects on seabirds have been devastating, most notably on Gough Island where their predatory behaviour has contributed to two species, the Tristan albatross (*Diomedea dabbenena*) and endemic Gough bunting (*Rowettia goughensis*), being listed as critically endangered (Ryan and Cuthbert 2008; Wanless et al. 2009) and where there are concerns that the island's other formerly abundant seabird populations are in large-scale decline (Cuthbert et al. 2013). Elsewhere, introduced mice have been associated with negative impacts on the smaller burrowing petrels, namely the blue petrel *Halobaena caerulea* (Fugler et al. 1987), ashy storm-petrel *Oceanodroma homochroa* (Ainley et al. 1990), the grey-backed storm-petrel *Garrodia nereis* (Burger and Gochfeld 1994), the white-faced storm-petrel *Pelagodroma marina* (Campos and Granadeiro 1999) and Leach's storm-petrel *Oceanodroma leucorhoa* (Bicknell et al. 2009).

The Falklands Islands (51°S, 59°W) host internationally significant seabird populations, including taxa shown to have been adversely affected by introduced rodents elsewhere (e.g. albatrosses Diomedidae), petrels (Procellariidae) and storm-petrel (Hydrobatidae). Brown rats, black rats and house mice have been unintentionally introduced to the islands since they were settled by man in the eighteenth century, but specific impacts on seabird populations in the Falklands are generally not well documented, with

the exception of a study on New Island that found a relatively small impact of introduced brown rats, house mice and cats on the island's very large population of thin-billed Prions (*Pachyptila belcheri*) (Catry et al. 2007; Quillfeldt et al. 2008) and impacts of cats on white-chinned petrel (Matias and Catry 2008). Here, we examine the distribution and relative abundance of three small burrowing seabird species on Steeple Jason Island in relation to habitat types and the distribution of house mice which is the sole introduced mammal species on the island. Further, we measure the breeding success of Wilson's storm-petrel in relation to mouse presence on Steeple Jason and make comparisons with seabird distribution and densities on the neighbouring island of Grand Jason where mice are absent.

Methods

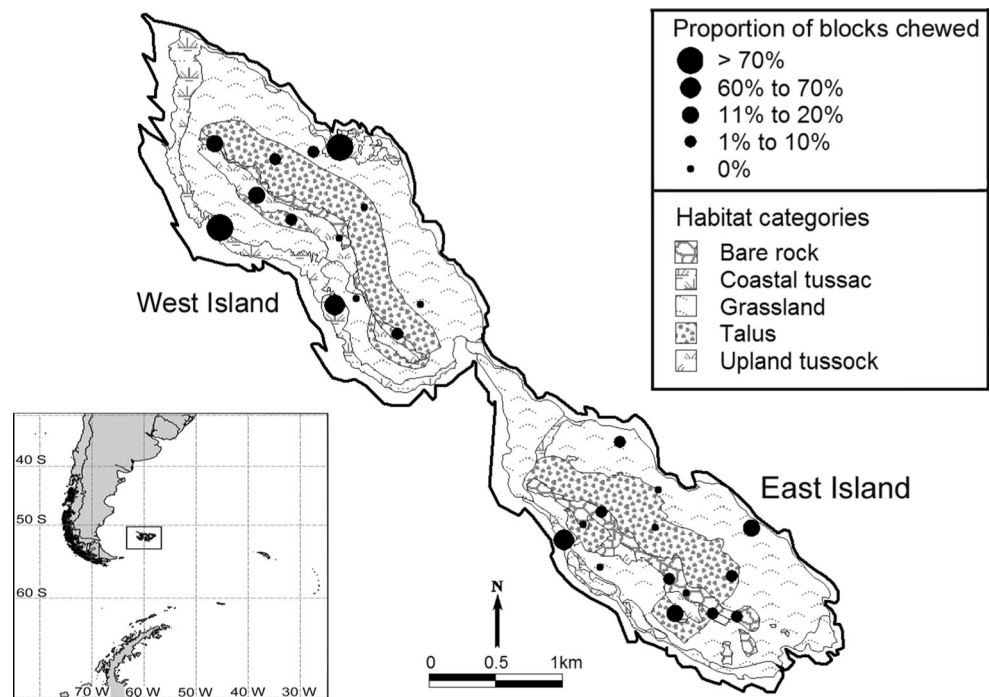
Study sites

The islands of Steeple Jason (51.04°S, 61.21°W, 790 ha) and Grand Jason (51.06°S and 61.09°W, 1,380 ha) lie 3 km apart in the extreme north-west of the Falklands archipelago. Topography and habitats of the two islands are similar, both rising to a rocky ridge orientated on a north-west to south-east axis. The maximum height of Steeple Jason is 290 m, compared with 358 m for Grand Jason. Steeple Jason is further divided into two islands ("West Island" and "East Island" see Fig. 1) connected by a narrow isthmus. The habitats on both islands are generally aligned with altitude. We identified five broad habitat categories for petrel and mice surveys:

1. Coastal tussac, comprising the endemic tussac grass *Poa flabellata* (see Woods 1970).
2. Grassland, generally located below 30 m a.s.l. and comprising a variety of native and introduced species such as cinnamon grass *Hierochloa redolens*; white grass *Cortaderia pilosa*; small fern *Blechnum penna-marina*; sheep's sorrel *Rumex acetosella*; Yorkshire fog *Holcus lanatus*, common bent *Agrostis capillaris* and spiked oat grass *Trisetum phleoides*. This habitat also includes areas of eroded peat.
3. Talus slopes, extending from 30 to 150 m altitude, comprising loose rock and boulders.
4. Rocky ridge, generally above 120 m, comprising fixed rock.
5. Upland tussac, comprising areas of tussac grass above 140 m, growing on talus slopes or the rocky ridge.

Both islands were sheep-grazed until 1968 (Anon 2009), though neither has held a permanent human population. House mice are thought to have been accidentally introduced to Steeple Jason by early whalers or sealers, or by

Fig. 1 Distribution of habitat classes and mouse activity on Steeple Jason. Location of the Falkland Islands indicated by the box on map inset



sheep farmers before the mid-twentieth century (Anon 2009). House mice have never been recorded on Grand Jason, and no rat species occurs on either island. Both islands support large populations of breeding seabirds and land birds, including the world's largest colony of black-browed albatross (*Thalassarche melanophrys*) comprising 171,000 pairs on Steeple Jason and 49,000 pairs on Grand Jason (Huin and Reid 2007), as well as tens of thousands of nesting gentoo (*Pygoscelis papua*) and southern rockhopper (*Eudyptes chrysocome*) and Magellanic (*Spheniscus magellanicus*) penguins.

Fieldwork methodology

Mice surveys

Mouse activity was assessed using chocolate-flavoured wax blocks, in which tooth marks left by mice tasting the bait could easily be distinguished from those left by other animals such as birds, due to the characteristic paired impressions left by the incisors of the upper and lower jaws. A stratified random procedure was used to select 28 survey locations to assess the activity distribution of house mice on Steeple Jason, ensuring all habitats, and both sides of the central ridge of both the West Island and East Island of Steeple Jason were adequately sampled. Distribution of broad habitat types and location of survey locations are shown in Fig. 1. At each of the 28 locations, 25 wax baits were deployed on a 5 × 5 grid, with 10-m spacing between adjacent baits. The survey was conducted between 25

October and 4 November 2009. Data were expressed as the proportion of baits showing signs of having been chewed by mice overnight. Whilst there has never been evidence of the presence of house mice on Grand Jason, we deployed baits following identical procedures to those used on Steeple Jason, to verify the absence of house mice. Two bait grids, each comprising 25 baits at 10-m intervals, were laid in the habitat type found to support the highest densities of house mice on Steeple Jason.

Chocolate wax baits were, on occasion, damaged or removed by striated caracaras (*Phalacrocorax australis*) which occur on both islands. In all but one case, a small number (≤ 4) of baits were affected, and the level of mice activity was assessed from the remaining unspoiled baits. However, at one of the 28 bait locations on Steeple Jason, 16 of 25 baits were either removed or so badly damaged that the incidence of mice activity could not be reliably assessed. The data from this location were not included in subsequent analyses.

Distribution and relative abundance of burrowing petrels

The three species of seabird selected for this study were those which, due to their small size and burrow-nesting habitats, were most likely to be negatively impacted by house mice (Angel et al. 2009; Cuthbert et al. 2013). Wilson's storm-petrel (*Oceanites oceanicus*) and grey-backed storm-petrel have a body mass of 28–43 g, and thin-billed Prions weigh 118–180 g. Nesting habitat preferences differ among the species: Wilson's storm-petrel,

nest in rock crevices, grey-backed storm-petrel dig shallow nesting cavities in the fibrous pedestals of tussac grass clumps (Woods 1970) and thin-billed Prions dig nest burrows in soft soil on steep slopes (Catry et al. 2003). Although suitable habitat exists on both islands, there is no population estimate for any of these three species, and the timing of breeding is not well documented, for either island. The study was initiated to coincide with the presumed pre-laying period of the species' breeding seasons, based on information from colonies elsewhere (see Brooke 2004), with fieldwork undertaken from 29 October 2009 to 24 January 2010 (see details below). Although common diving petrels (*Pelecanoides urinatrix*) breed on Steeple Jason, this species was not included in the study, since there were few observations of this species during the period of fieldwork.

The distribution and abundance of the three study species were assessed through nocturnal surveys, since pilot work commencing on 22 October 2009 indicated that egg-laying had not begun and consequently, birds were not consistently attending nest sites during daylight. Habitat-stratified point transects were employed, giving greater survey effort to those areas likely to hold breeding petrels (Bibby et al. 1992). Survey points were located 400 m apart along the transect with totals of 92 and 21 survey points on Steeple Jason and Grand Jason, respectively. Petrel surveys were carried out at all 28 mice survey points on Steeple Jason to allow direct assessment of petrel numbers in relation to levels of mice activity. Although the five habitat types were broadly aligned with altitude, there was appreciable inter-gradation of neighbouring habitat types at the scale of the survey areas, resulting in more than one habitat type occurring within individual petrel survey areas. All habitat types occurring within the survey radius (50 m) were recorded. On Steeple Jason, 92 survey points were surveyed on ten nights between 29 Oct and 9 Nov 2009 with 62 of these resurveyed on six further nights between 15 and 20 Jan 2010. On Grand Jason, 21 points were surveyed on two nights from 10 to 11 Nov 2009, with 20 of these resurveyed, and a further 14 points surveyed on four nights between 21 and 24 Jan 2010. Bias in the number of birds recorded in each habitat could arise from large variation in the number of birds attending the colony from night to night. We therefore organized fieldwork to ensure that multiple habitats were surveyed on the same night and that the survey of each habitat occurred over multiple nights. We took further steps to statistically control for any residual bias resulting from nightly variation in colony attendance, as described in the analysis below.

Seabird surveys commenced 2 h after sunset and continued for 3.5 h, when flight activity diminished. Each observer was equipped with an 85 lumen LED head torch and recorded the number of birds of each species flying

through the beam during a 10-min period. The beam was orientated horizontally with an arc of approximately 45°. The three study species differ substantially in size, colouration and flight action, so reliable identification was possible, although detection ranges varied according to species: Wilson's storm-petrel could be detected and identified up to 30 m range, grey-back storm-petrel up to 40 m and thin-billed Prion up to 50 m. The area under observation was therefore small which resulted in typically low numbers of birds detected during a 10-min period (means of 1.0, 2.3 and 4.1 occurrences for grey-backed storm-petrel, Wilson's storm-petrel and thin-billed Prion, respectively) which reduced the likelihood of the same individual being recorded repeatedly circling around the observer. However, we cannot discount this possibility, and these survey methods do not permit estimation of the number of individuals or breeding pairs of each species, nor do they allow reliable comparisons of relative abundance across species, due to inter-specific differences in detectability, but the data do allow assessment of relative levels of flight activity in different habitats and different areas of each island, which is assumed to reflect local breeding density.

Breeding success of Wilson's storm-petrel

A sample of Wilson's storm-petrel nests was marked on Steeple Jason between 11 and 19 January 2011 in order to determine egg and chick survival rates. Nests were located by listening for birds calling from burrows at night, the nocturnal use of playback of burrow calls to elicit responses from nesting birds and by searching suitable habitat during daylight. All habitat types on the North Island were searched, but nests were only found above 50 m a.s.l among crevices in the talus slopes, high tussac and rocky outcrops. Some storm-petrel nests have a complex series of cavities where chicks can hide from view, so only those where the nest contents could be unambiguously determined were included in the analysis. The contents (incubating/brooding adult and egg or chick) were noted when each nest was first located and each nest was inspected almost daily thereafter, until 24 January, and nests were again inspected on 11 February 2011. Despite intensive searches, we found no nests of grey-backed storm-petrel on Steeple Jason. To relate storm-petrel nest survival rates to levels of mouse activity around each nest, we placed a single chocolate-flavoured wax block within 20 cm of each nest entrance. Each block was inspected for up to 12 days for mouse tooth marks on each subsequent nest inspection, and blocks were removed if mouse presence was detected at a nest. Mouse activity was expressed as the reciprocal of the number of days required for mouse presence to be detected, or zero if mice were not detected, and therefore reflects the daily rate of mouse occurrence.

Statistical analysis

Data on mouse distribution were analysed in relation to habitat type and altitude using a generalized linear model employing binomial errors with a logit link. The response variable, calculated for each of the 28 survey locations, was the number of wax blocks within each array of 25 that showed signs of mouse activity (“successes”, taking a value from zero to 25), and the binomial denominator (trials) was the number of blocks deployed, minus the number which was spoiled (removed by Caracaras, or pecked by birds to the extent that rodent tooth marks would be obscured), taking values from 21 to 25. Hence, we modelled, for each survey location, the probability of mouse activity. Petrel distribution and habitat associations were assessed using a mixed model with Poisson errors and a log link and Satterthwaite’s correction to degrees of freedom. We examined potential bias in the number of petrels counted due to the effects of time of night, observer, date (linear covariate), survey episode (Oct/Nov 2009 vs. Jan 2010) or slope aspect, by firstly examining the univariate effects of each of these variables. Any that were found to be significant at $P < 0.1$ were entered as candidate variables into subsequent models of habitat association. To examine petrel density in each habitat and any differences in habitat associations between islands which might be related to levels of mouse activity, we then constructed a series of models in relation to the occurrence of each habitat type at each survey point. Since the survey areas on occasion incorporated more than one of the five habitat types, each habitat type was coded as a binomial variable (presence/absence). With the exception of high tussac, which occurred in only one sample point on Grand Jason, we also examined the interaction of each habitat type with island (Steeple or Grand Jason) to determine whether habitat preferences differed between the two islands. Survey point identity was included as a random term to control for pseudo-replication since most points were surveyed twice, and calendar date was also included as a random term in all models to account for multiple surveys per night and the possibility that levels of colony attendance may be higher on some nights than others. The full model therefore included those variables identified as potential sources of bias in the univariate models described above, and the occurrence in all habitat types and their interaction with island. Non-significant interactions were removed in a stepwise procedure until only significant terms (or non-significant, first-order terms which featured in significant interactions) remained. Where model tests indicated a significant interaction of fixed effects, post hoc pairwise tests were conducted, using Bonferroni corrections to account for Type 1 errors. Daily nest survival rates for Wilson’s storm-petrel were calculated using the Mayfield approach (Mayfield 1975), for the egg and chick stage separately. We estimated the proportion of

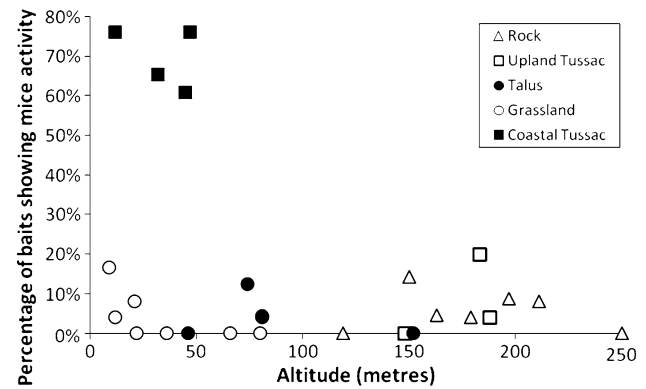


Fig. 2 Level of mice activity with habitat and altitude on Steeple Jason

nests surviving to fledging assuming incubation and fledging periods of 44 and 63 days, respectively (Copestake and Croxall 1985; del Hoyo et al. 1992). Data on petrel nest failure rates were examined in relation to the activity level of mice at each nest using a binomial errors general linear model which incorporated nest failure as the response variable, with the number of exposure days as the binomial denominator, breeding stage (egg or chick) as a two-level fixed factor and a logit link (Aebischer 1999). All analyses were implemented in SAS® v 9.2, and means are presented ± 1 standard error (SE) throughout.

Results

Mice distribution on Steeple Jason

Mice were recorded up to 210 m a.s.l. in both upland tussac and on the rocky central ridge of Steeple Jason (Fig. 1). While there was a decline in mouse activity with altitude (Fig. 2, $\chi^2_1 = 41.1$, $P < 0.0001$), this was primarily driven by substantially higher activity in coastal tussac compared with all other habitat types ($\chi^2_4 = 205.1$, $P < 0.0001$) and altitudinal differences were not significant once habitat type was accounted for ($\chi^2_1 = 0.08$, $P = 0.77$). There were no differences in the habitat-specific levels of mice activity between West Island and East Island ($\chi^2_1 = 0.46$, $P = 0.50$), or between the exposed south-west side of the ridge and the sheltered north-east ($\chi^2_1 = 0.58$, $P = 0.45$), indicating similar habitat use across the whole of Steeple Jason. No evidence of mice was detected on Grand Jason.

Petrel distribution (Steeple Jason and Grand Jason)

Grey-backed storm-petrel

We found no effect of date, survey episode or time of night on the numbers of grey-backed storm-petrel counted

Table 1 Minimum adequate models of petrel habitat associations on Steeple Jason and Grand Jason

Species	Effect	Factor level	Parameter estimate (birds/10 min, mean \pm SE)	<i>df</i>	<i>F</i>	<i>P</i>
Grey-backed storm-petrel	Slope aspect	North-east	0.17 \pm 0.09	1, 135.3	11.4	0.001
		South-west	0.53 \pm 0.24	3, 31.7	4.56	0.009
	Observer	AB	0.36 \pm 0.22			
		AS	0.14 \pm 0.09			
		JB	0.35 \pm 0.20			
		MB	0.46 \pm 0.26			
	Island	Grand Jason	0.40 \pm 0.25	1, 35.42	0.65	0.42
		Steeple Jason	0.23 \pm 0.15			
	Rock	Absent	0.27 \pm 0.11	1, 102.8	0.30	0.58
		Present	0.33 \pm 0.19			
	Grassland	Absent	0.46 \pm 0.19	197.55	5.15	0.025
		Present	0.20 \pm 0.11			
	Coastal_tussac	Absent	0.58 \pm 0.19	1, 183.6	5.30	0.023
		Present	0.16 \pm 0.12			
	Island*rock	Grand Jason rock absent	0.66 \pm 0.44	1, 96.47	12.56	0.0006
		Grand Jason rock present	0.24 \pm 0.20			
		Steeple Jason rock absent	0.11 \pm 0.07			
		Steeple Jason rock present	0.47 \pm 0.39			
	Island*coastal_tussac	Grand Jason coastal tussac absent	0.45 \pm 0.29	1, 197	3.98	0.047
		Grand Jason coastal tussac present	0.35 \pm 0.34			
		Steeple Jason coastal tussac absent	0.74 \pm 0.28			
		Steeple Jason coastal tussac present	0.07 \pm 0.10			
Wilson's storm-petrel	Slope aspect	North-east	0.23 \pm 0.11	1, 125.7	17.11	0.0001
		South-west	0.94 \pm 0.35			
	Island	Grand Jason	1.39 \pm 0.77	1, 18.69	18.83	0.0004
		Steeple Jason	0.15 \pm 0.07			
	Heath	absent	0.70 \pm 0.26	1, 95.68	6.02	0.016
		present	0.31 \pm 0.15			
	Coastal tussac	Absent	1.36 \pm 0.41	1, 111.1	16.44	0.0001
		Present	0.16 \pm 0.11			
Thin-billed Prion	Slope aspect	North-east	0.12 \pm 0.07	1, 94.83	35.75	<0.0001
		South-west	0.97 \pm 0.49			
	Observer	AB	0.49 \pm 0.30	3, 31.36	3.76	0.21
		AS	0.22 \pm 0.15			
		JB	0.31 \pm 0.20			
		MB	0.45 \pm 0.30			
	Island	Grand Jason	0.11 \pm 0.09	1, 21.45	11.18	0.003
		Steeple Jason	1.16 \pm 0.57			
	Rock	Absent	0.24 \pm 0.12	1, 139.8	2.8	0.10
		Present	0.51 \pm 0.33			
	Grassland	Absent	0.54 \pm 0.26	1, 86.76	5.62	0.02
		Present	0.23 \pm 0.14			
	Coastal tussac	Absent	0.83 \pm 0.36	1, 122.9	9.40	<0.0027
		Present	0.15 \pm 0.12			
	Island*rock	Grand Jason Rock absent	0.12 \pm 1.90	1, 163.2	4.69	0.032
		Grand Jason Rock present	0.10 \pm 5.90			
		Steeple Jason Rock absent	0.50 \pm 0.96			
		Steeple Jason Rock present	2.68 \pm 1.94			

Petrel abundance (birds observed/10 min) was fitted as a Poisson errors model with a log link, with the survey location and calendar date fitted as random terms. Parameter estimates of the significant terms retained in the final model are shown

* Interaction between two terms

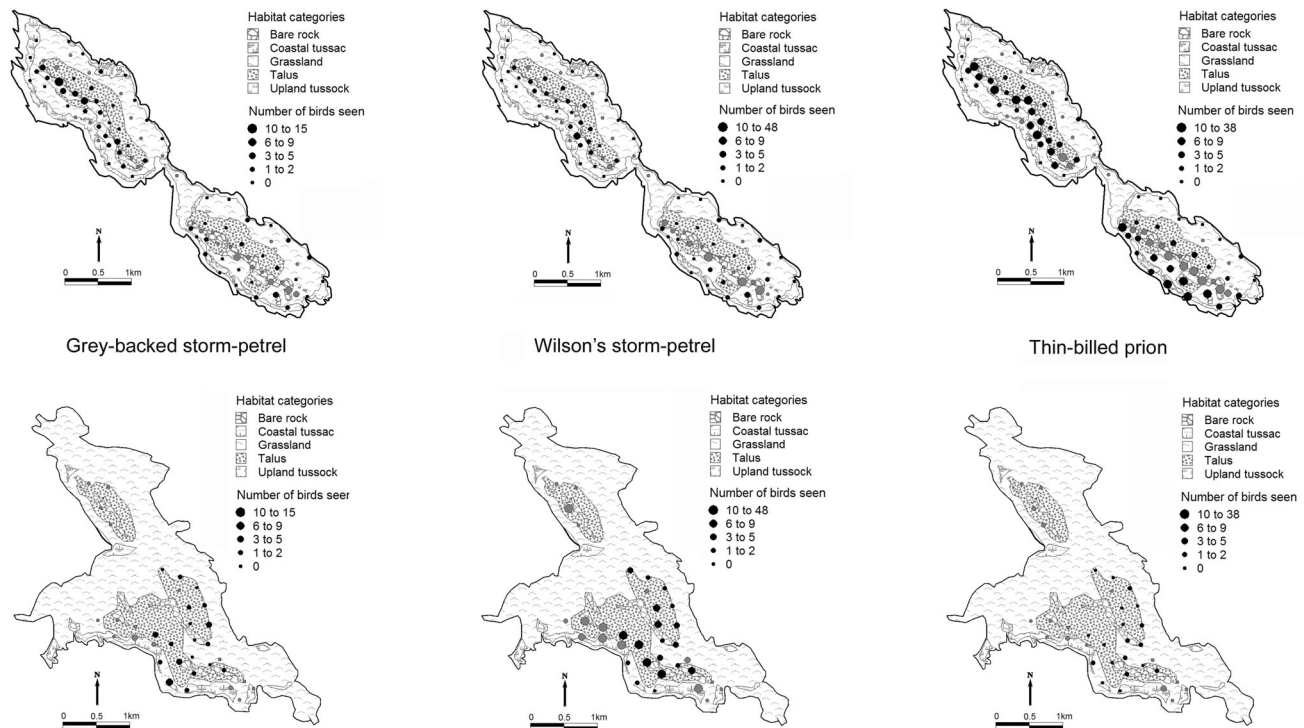


Fig. 3 Distributions of grey-backed (*left*) and Wilson's storm-petrel (*centre*) and thin-billed Prions (*right*) on Steeple Jason (*upper*) where mice are present, and Grand Jason (*lower*) where mice are absent.

Black symbols show mean values at locations where two surveys were conducted, grey symbols show values at locations where one survey was conducted

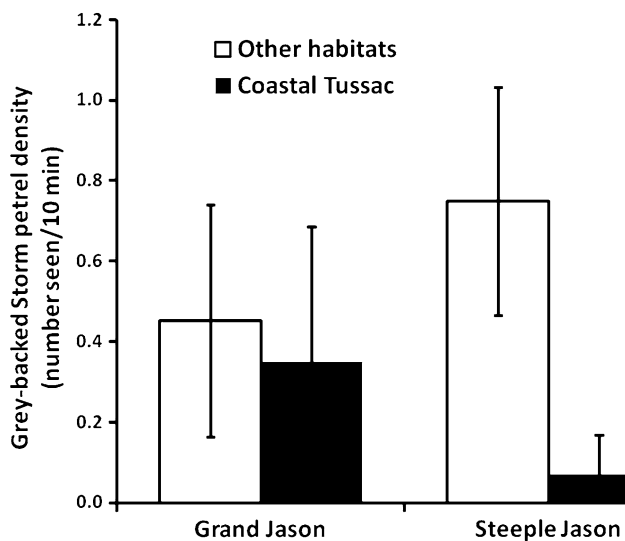


Fig. 4 Grey-backed storm-petrel density on the islands of Grand Jason (mice absent) and Steeple Jason (mice present) in relation to the occurrence of coastal tussock habitat, which is associated with high mouse densities (model least-squares means, accounting for differences in numbers seen due to slope aspect, observer and date)

($P > 0.1$ in all cases). However, there were significant differences in relation to slope aspect ($F_{1,143.7} = 6.25$, $P = 0.014$) and observer ($F_{3,34.43} = 4.77$, $P = 0.007$)

which were accounted for in the final models. The minimum adequate model (MAM) indicated that grey-backed storm-petrel were almost twice as abundant on Grand Jason than Steeple Jason and showed a preference for grassland on both islands (Table 1; Fig. 3). In contrast, the association with coastal tussock habitat differed between the two islands. On Steeple Jason, where mice occur at high densities in coastal tussock, densities of grey-backed storm-petrel were significantly lower in this habitat than elsewhere (Fig. 2, $t_{197} = 2.66$, $P_{\text{adj}} = 0.05$), whereas on Grand Jason, where mice are absent, grey-backed storm-petrel were equally numerous in coastal tussock as elsewhere (Figs. 3, 4).

Wilson's storm-petrel

There were significant univariate effects of time of night ($F_{1,25.29} = 24.09$, $P < 0.0001$) and slope aspect ($F_{1,147.9} = 7.34$, $P < 0.007$), but not date, observer or survey episode on the numbers of Wilson's storm-petrel counted, and the significant effects were included as candidate variables in subsequent habitat association models. The MAM (Table 1) indicated ninefold higher number of Wilson's storm-petrel on mouse-free Grand Jason in comparison with Steeple Jason (mean densities 1.39 ± 0.77 and 0.15 ± 0.07 birds/10 min, respectively) (Fig. 3), and on

both islands, birds occurred in lower densities in coastal tussac (mean 0.16 ± 0.11 birds/10 min) than elsewhere (mean 1.36 ± 0.41 birds/10 min).

Thin-billed Prion

There were significant univariate effects of slope aspect ($F_{1,89.93} = 24.66$, $P < 0.0001$) and observer ($F_{3,34.57} = 5.95$, $P = 0.002$) on the numbers of thin-billed Prions counted, and these were included in subsequent habitat association models. There were substantially higher numbers (ten-fold) of thin-billed Prions on Steeple Jason than Grand Jason (Table 1; Fig. 3). Significantly, lower densities were associated with coastal tussac and grassland, and higher densities were found in rock habitats.

Breeding success of Wilson's storm-petrel

Twenty-nine active nests that were suitable for monitoring were located, of which 16 contained adults incubating eggs or brooding recently hatched chicks when first located and 13 contained an unattended chick, including six which were already well developed with emerged primaries. Since nests were then monitored for further four weeks, we were able to assess survival across all chick development stages. Eight nests failed during the study period, with 5 and 3 nests failing during the incubation and chick stages, respectively. Mayfield estimates of daily egg and chick survival were 0.975 ± 0.011 and 0.993 ± 0.004 , respectively, which equate to hatching and fledging rates of 33 and 66 % assuming the durations of incubation and chick-rearing periods of 44 and 63 days. Overall breeding success was therefore estimated as 22 %. The wax blocks placed in the vicinity of petrel nests indicated high levels of mice activity. Signs of mice were found at 24 of 28 nests (the wax block was removed at one nest). Whilst all nest failures occurred at nests where mice were detected, we found no significant relationship between nest survival rates and either the presence of mouse activity ($\chi^2_1 = 0.85$, $P = 0.36$) or the intensity of mouse activity (daily rate of mouse occurrence, $\chi^2_1 = 0.10$, $P = 0.76$) among the sample of studied nests, although with a limited sample of nests the statistical power to detect such an effect was low.

Discussion

The results of our study indicate that densities of both Wilson's storm-petrel and grey-backed storm-petrel were substantially lower on Steeple Jason than on neighbouring mouse-free Grand Jason, suggesting negative impacts of house mice on both these species. In contrast, the larger thin-billed Prion occurred at higher densities on Steeple

Jason than Grand Jason. These differing patterns of abundance and impact may be due to the relative vulnerability of the different species to predation by house mice. Several studies have reported that egg and chicks of storm-petrel are vulnerable to predation by small rodents (Ainley et al. 1990; Campos and Granadeiro 1999; Bicknell et al. 2009) and that invasive rats have a greater impact on smaller seabird species (Baker et al. 2002; Jones et al. 2008). Such a pattern is also found on Gough Island, where house mice prey upon one of world's largest seabird species (the Tristan Albatross; Cuthbert and Hilton 2004; Wanless et al. 2007), yet exert even larger impacts on the smaller-sized (and winter-breeding) burrowing petrels (Cuthbert et al. 2013). Given the evidence for the vulnerability of smaller-sized species, we consider the lower abundance of both Wilson's storm-petrel and grey-backed storm-petrel on Steeple Jason to be a consequence of mice impacts. Further evidence to support this conclusion comes from the clear pattern of habitat choice of grey-backed storm-petrel on Steeple Jason: as found in another study (Rexer-Huber et al. 2013), mice occurred at very high densities in coastal tussac habitat on Steeple Jason, and whilst this habitat supported high densities of grey-backed storm-petrel on mouse-free Grand Jason, on Steeple Jason it was strongly avoided. The thin-billed Prion is larger than the storm-petrel and is expected to be less affected by house mice. Evidence for limited impact of predators on this species has been found on New Island, in the Falkland Islands, where it coexists with a range of introduced predators including black rats, house mice and Feral Cats (*Felis catus*) (Quillfeldt et al. 2008). The limited impact of these predators on New Island may be a consequence of the extremely large Prion population (two million pairs; Catry et al. 2007) and that population level impacts are limited by predator swamping as observed in other burrowing petrels (Cuthbert 2002; Jones 2003) and hypothesized for New Island (Catry et al. 2007).

No nests of grey-backed storm-petrel could be located on Steeple Jason, and nests of Wilson's storm-petrel were restricted to the talus slopes and rocky summit, where mouse densities were low earlier in the breeding season. Although levels of mice activity were not systematically assessed throughout Steeple Jason later in the breeding season of Wilson's storm-petrel, monitoring in the vicinity of study nests revealed high levels of mice activity on the boulder-strewn slopes, especially those that contained dense swathes of grasses and wood rushes with large seed heads that would provide a food source for mice. Daily egg and chick survival rates were low, leading to estimated breeding success of 22 %. Other studies of more southerly colonies of Wilson's storm-petrel also report low egg and chick survival rates: hatching success 35–50 %, fledging success 28–52 %, breeding success 10–30 % (Marchant

and Higgins 1990; Brooke 2004). However, low breeding success in those studies is believed to occur due to unfavourable environmental conditions and when sea ice cover is low the previous winter (Quillfeldt 2001). Reported nest survival rates are also considered to be biased low by nest desertion caused by observer disturbance (Copestake and Croxall 1985). Such disturbance was low in our study, as adult birds were not handled and birds were never observed to move off the egg when nests were inspected. If the level of breeding success of Wilson's storm-petrel on Steeple Jason estimated in this study is accurate and consistently low, then given the age of maturity (3 years) and adult survival rates (90.8 %) reported elsewhere for this species (Beck and Brown 1972), it would be unlikely that the species could sustain a stable population in the long term. However, precise demographic information is lacking.

Direct evidence of the impact of mice of seabirds may take the form of video surveillance of predation events or examination of remains of depredated eggs or chicks (Cuthbert and Hilton 2004). However, for species that occur at low density and nest in burrows, such direct evidence may be hard to obtain. Time series data showing species decline following predator invasion may also provide compelling evidence of impacts, but in the case of predators introduced many decades, or even centuries previously, such seabird population monitoring data are unlikely to exist. In the absence of such sources of information for burrowing petrels on Steeple Jason, our study presents the first, albeit indirect, evidence for a detrimental impact of house mice on seabird populations. This is restricted to two of the island's smallest seabird species which are predicted to be most vulnerable. Other evidence pointing to the detrimental impact of house mice on Steeple Jason includes the absence of Cobb's wren (*Troglodytes cobbi*) and camel crickets (*Parudenus falklandicus*) from the island (Woods and Woods 1997, RSPB unpubl. data). Both Cobb's wren and camel crickets are acutely vulnerable to predation by rats in the Falklands (St Clair 2011; St Clair et al. 2011), and their absence on Steeple Jason suggests that they may have been extirpated by house mice. The range of evidence available indicates that the house mouse is having a detrimental impact on the ecology of Steeple Jason and that predator management is required if the island is to be restored to a natural state. Steeple Jason falls within the size range of islands where house mice have previously been eradicated. A feasibility study and baiting trials indicate no major obstacle to their removal other than key consideration and mitigation to limit the impact of such an operation on the island's large population of striated caracara (Rexer-Huber et al. 2013; Brown and Cuthbert 2013).

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