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ORIGINAL PAPER

Introduced mammals coexist with seabirds at New Island, Falkland Islands: abundance, habitat preferences, and stable isotope analysis of diet

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Abstract The largest known colony of Thin-billed prions *Pachyptila belcheri* has been coexisting with introduced mammals for more than 100 years. Three of the introduced mammals are potential predators of adults, eggs and chicks, namely ship rats *Rattus rattus*, house mice *Mus musculus* and feral cats *Felis catus*. We here determine habitat preferences over three seasons and dietary patterns of the unique set of introduced predators at New Island, Falkland Islands, with emphasis on the ship rats. Our study highlights spatial and temporal differences in the levels of interaction between predators and native seabirds. Rats and mice had a preference for areas providing cover in the form of the native tussac grass *Parodiochloa flabellata* or introduced gorse *Ulex europaeus*. Their diet differed markedly between areas, over the season and between age groups in rats. During the incubation period of the prions in November–December, ship rats had mixed diets, composed mainly of plants and mammals, while only 3% of rats had ingested birds. The proportion of ingested birds, including scavenged, increased in the prion chick-rearing period, when 60% of the rats consumed prions. We used δ^{13}C and δ^{15}N to compare the importance of marine-derived food between mammal species and individuals, and found that rats in all but one area took diet of partly marine origin, prions being the most frequently encountered marine food. Most house mice at New Island mainly had terrestrial diet. The stable isotope analysis of tissues with different turnover times indicated that individual rats and mice were consistent in their diet over weeks, but opportunistic in the short term. Some individuals (12% of rats and 7% of mice) were highly specialized in marine-derived food. According to the isotope ratios in a small sample of cat faeces, rodents and rabbits were the chief prey of cats at New Island. Although some individuals of all three predators supplement their terrestrial diet with marine-derived food, the current impact of predation by mammals on the large population of Thin-billed prions at New Island appears small due to a number of factors, including the small size of rodent populations and restriction mainly to small areas providing cover.

Keywords Ship rat · House mouse · Invasive species · Stable isotopes

Introduction

Small ground-nesting birds on islands rarely survive introductions of mammalian predators such as rats (e.g. Atkinson 1985), because their dispersal opportunities are limited and because often such insular populations evolved in the

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Ingrid Schenk: deceased

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absence of natural enemies. Thus, many population declines and extinctions of nesting colonies on islands have been observed after accidental or deliberate introduction of exotic predators, notably feral cats and rats, but also foxes and wekas (e.g. Moors and Atkinson 1984; Brothers 1984), and studies of the effects of introduced species have become a key issue for conservation biology.

However, New Island is an example where a population of around two million pairs of Thin-billed prions breeds successfully at a site with more than 100 years' history of introduced ship rats, house mice and feral cats. Understanding the mechanisms of such coexistence is important, as it is important to establish a baseline for future monitoring. New Island is an Important Bird Area (IBA), hosting the largest seabird colony in the Falkland Islands, and significant populations of several globally threatened species. Seabirds breeding here include black-browed albatross *Thalassarche melanophrys*, white-chinned petrel *Procellaria aequinoctialis*, rockhopper penguin *Eudyptes chrysocome*, gentoo penguin *Pygoscelis papua*, Magellanic penguin *Spheniscus magellanicus*, Falkland skua *Stercorarius antarctica*, dolphin gull *Larus scoresbii*, kelp gull *Larus dominicanus*, imperial (blue-eyed) shag *Phalacrocorax (atriceps) albiventer* and rock shag *Phalacrocorax magellanicus*.

New Island also has a unique set of introduced mammals, not found elsewhere in the Falkland Islands. New Island is the only island in the Falkland archipelago where the black or ship rat *Rattus rattus* has been found. New Island has no evidence of the larger Norway rat *Rattus norvegicus*, which is common elsewhere in the Islands. With New Island's long history of occupation by man, commencing around 1774 by American whalers, and the start of permanent settlement with sheep farming in 1860, the absence of Norway rats is fortuitous. There is little evidence of when the ship or black rat may have been introduced, although possibly around 1906 when New Island became a site for a new whaling operation employing a factory ship the *Admiralen.* However, introductions were more probable in 1908 when a land-based whaling factory was established in South Harbour. This latter operation was a relatively large facility employing some 80 men, had a jetty to receive fairly large vessels and a slipway for the repair of ships used in whaling. (Strange 1995). Such a facility with its considerable ship traffic presented very favourable conditions for the introduction of rats and mice. A resident at the time of the 1908 whaling station, wrote of the station's closure in 1916, that "Rats of all shapes, sizes and colours—without food from the station—started to roam the island, so our cats had to soon earn their keep" (D. McRae)—a strong inference that rats were not present before the establishment of the station.

Cats were also present in the whaling station, and in the 1920s about 30 cats were brought to New Island in order to control rats. Cottontail rabbits *Sylvilagus* sp. were deliberately introduced by whalers as a source of food. The identification of the rabbit species, including the possibility of the presence of European rabbits *Oryctolagus cuniculus*, is currently underway (I.J. Strange).

Thus, the alien fauna of New Island today comprises four species including three predators or omnivorous species, and represents a potential threat to the seabirds, especially to the small burrowing thin-billed prions. Since 1972, efforts have been directed at reducing rats and mice by general island husbandry. This has involved a strict control on the disposal of household waste, burning rubbish, installation of better sewage disposal, plus disposal of animal remains such as old sheep and cattle carcasses. Sheep and cattle were completely removed from New Island South in 1975. For the last 18 years, a programme of rodent control using bait and traps has been in operation.

After preliminary studies in the season 2000–2001, a programme of systematic trapping was set up by the late Ingrid Schenk and Ian Strange and carried out by them and subsequent field assistants in three seasons (2001–02, 2002–03 and 2003–04). The present paper reviews and synthesizes the work carried out so far. We report the results of the trapping study (previously unpublished), including an analysis of diet of ship rats during the incubation period (previously unpublished) and additional new diet data as well as data published in reports only locally available (MacKay et al. 2001) on diet during the chick-rearing period of the thin-billed prions. The latter aspect is given the most attention, and is complemented with a stable isotope analysis.

A stable isotope approach has been used by previous successful studies of diets of introduced predators (Hobson et al. 1999; Stapp 2002; Major et al. 2007), using carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) isotope ratios. Differences in nitrogen isotope ratios are frequently used to determine trophic level and diet composition (e.g. Dahl et al. 2003; Morrison and Hobson 2004; Quillfeldt et al. 2005). In contrast to nitrogen, carbon isotope ratios differ more between terrestrial versus marine, inshore versus offshore, and pelagic versus benthic food webs than by trophic level. Carbon can therefore be used to assess foraging location (reviewed in Hobson 1999; Rubenstein and Hobson 2004). Carbon and nitrogen isotope analysis gives an integrated picture of what is assimilated into tissue from diet unlike conventional dietary methods, which may provide a partial or biased snapshot of diet. Study of stomach contents or faeces, for example, may under-represent food items which leave little or no visual trace in samples and prone to overestimation of less digestible materials which are highly visible. Stable isotope data of tissues of different turnover rates also allow detection of diet switches (e.g. Tieszen et al. 1983) and patterns of individual diet specialization (e.g. Bearhop et al. 2006).

In this paper we consider carbon and nitrogen stable isotope data from the introduced mammals of New Island, and discuss them in the context of mammal abundances and in comparison with dietary data obtained by visual analysis of stomach contents, to assess the impact of introduced mammals on the native bird populations, in particular the thin-billed prion. Specifically, we will:

1. Describe patterns of abundance and habitat preference of *Rattus rattus* and *Mus musculus*.
2. Summarize dietary data obtained by visual analysis of stomach contents of *Rattus rattus*
3. Compare C and N stable isotope ratios of mammal tissues and faeces with potential marine prey (seabirds, marine invertebrates, marine algae) and terrestrial prey (rabbits, rodents, terrestrial plants), in order to analyse diets of *Rattus rattus, Felis catus* and *Mus musculus*.
4. Investigate intra-specific dietary differences in rodents from different areas (open areas with low abundance of rodents and high prion numbers vs. sheltered areas with high abundance of rodents)
5. Investigate inter-individual variability in patterns of diet of the two rodent species.

Materials and methods

Study site

New Island, West Falkland (51°43′S, 61°17′W), is 13 km long and on average 0.75 km wide, with a total of 2,362 ha. Until recently, it was divided in two properties, and all data presented were collected in New Island South (1,181 ha). The management of New Island South as a wildlife reserve started in 1972 with all sheep being removed in 1975.

In section, the island is wedge shaped, with cliffs forming the western and northern coasts, while the eastern coasts are lower lying and gently sloped, comprising rocky shores and sandy bays. Upland areas are rocky or covered with short heath, Diddle dee *Empetrum rubrum*, Mountain Berry *Pernettya pumila* and cushion plants (feldmark), while the slopes are mainly covered with short (oceanic heath) vegetation, in many places dominated by Small Fern *Blechnum penna-marina* and the introduced grass Yorkshire fog *Holcus lanatus*. Some areas, in particular two shallow valleys (South End Tussac area and the southern slopes of Rookery Hill), are covered with dense or loose formations of tussac grass *Parodiochloa flabellata* and Blue Couch grass *Agropyron magellanicum* interspersed with Wild Celery *Apium australe*. Some areas, in particular two shallow valleys, are covered with tussac grass (South End tussac area and Settlement Rookery tussac area; see map and photos in Electronic appendix 1).

New Island is an Important Bird Area (IBA, BirdLife), and by far the most numerous seabird species breeding here is the thin-billed prion. The prions arrive at the breeding grounds in September to October, lay their single egg in November and after incubation for 46–48 days the chicks hatch in the first half of January (Strange 1980; Quillfeldt et al. 2003). Chicks are brooded for few days, and during the remainder of the chick-feeding period of 48 to 56 days they are usually only attended by the parents for short periods at night (e.g. Quillfeldt et al. 2007a).

Sample collection 2000–2005: trapping programmes

Trapping was carried out in five seasons in total (austral summers 2000–01 to 2004–05). In the season 2000–2001, rodents were caught to establish whether Norway rats were present, as they would represent a significant threat to the thin-billed prions on the island. In October and November 2000, a total of 43 bait and trap stations were set out in two areas of tussac grass. In addition, rats were trapped around three study areas of thin-billed prions to reduce rat numbers and the potential level of predation (MacKay et al. 2001). The rodents caught in the preliminary studies were identified as the ship rat and the house mouse (Derek Brown, New Zealand Department of Conservation, Prof Tom Berry and Dr Scobie Pye, on site identification).

Following this, systematic trapping across the southern half of New Island was conducted in the three seasons 2001–02 to 2003–04. In the other years, less extense trapping focused on the impact of rats on seabirds, conducted in or adjacent to prion nesting areas and close to the Settlement Rookery, a mixed colony of rockhopper penguins imperial (blue-eyed) shags and black-browed albatross.

Snap traps (Victor E-Z Set, model M206, Woodstream Corporation, PA, USA) were set in the field, baited with a teaspoon of peanut butter, and attached by thin plastic covered wire to a pin fashioned from No 8 or No 10 fence wire (4.0–3.5 mm). The pin is then secured firmly into the ground to prevent possible removal by scavengers (striated caracara *Phalcoboenus australis* or cats). A cost-efficient cover was developed to protect the traps from incidental by-catch (like birds and small rabbits), but still allow easy visual inspection of traps (see Electronic appendix 2).

Traps were placed in lines consisting of 10 to 25 traps placed in line with a distance of about 10–25 m and checked daily during daylight. Lines were opened for periods of several days, and some were reopened one or two more times during the season, with an interval of about 10 days to allow rodents to move into any vacant territories.

Captured dead rodents were determined, and measurements were taken for all intact rats. A stopped rule was used to measure body length (from the tip of the nose to the end of the fur at the base of the tail), tail length (end of fur to end of tail), foot length (from heel of right hind foot to tip of toe, excluding the claw) and ear length (from the lowest point of the basal notch to the furthest extremity, excluding any hairs), to nearest millimetre. A Pesola spring balance was used to determine body weight, in grams, if animals were intact (i.e. not partly eaten by scavenging rodents). Sex was determined by examination of external genitalia.

Rats of three seasons (2000–01 to 2002–03) were classed in three colour morphs according to Corbet and Southern (1977): all black (*rattus* type), grey with grey belly (*alexandrinus* type) and grey with cream belly (*frugivorous* type). A small number of specimens were not determined because observers did not agree on their classification. The stomach contents of a sub-sample of captured rats of the periods 19 to 27 February 2001 ($N = 15$) and 14 November 2002–17 January 2003 ($N = 187$) were checked visually, as a stereomicroscope was not available during that time. Of the latter sample, the contents of 17 rats were undistinguishable, such that 161 stomach contents were used for the analysis.

Sample collection 2005–2006: stable isotope samples

The stable isotope study includes samples collected from 19 to 27 February 2005 and 10 February to 7 March 2006, when prion chicks were in the second half of their nestling stage, close to fledging. The data from both years are combined in the present analysis.

When captured, rats were dissected to obtain stomach contents, faecal matter from the terminal part of the gut, as well as liver and muscle tissue. The samples were stored in 80% ethanol. Prior to preservation in ethanol, the stomach contents of all intact captured rats of the period 19 to 27 February 2005 and 14 February to 7 March 2006 ($n = 28$) were checked using a stereomicroscope at 20× magnification. Captured mice ($n = 12$) were dissected to obtain gut contents, as well as liver and muscle tissue, and samples were stored in 80% ethanol. For cats, we only obtained faecal pellets (scats). However, such scats contained a high proportion of undigested material such as small bones, fur and feathers and thus were the best samples available to represent cat diets, as isotopic depletion should be minimal in such little digested samples. Faecal pellets of cats ($n = 15$) were collected across the island to avoid replication of individuals, and were stored at −20°C.

Rabbit fur was collected opportunistically around the settlement, and most likely originates from rabbits predated by cats or birds of prey.

Feathers and blood cell samples from seabird chicks were collected opportunistically from dead chicks or as part of ongoing projects. Feathers of Falkland thrushes *Turdus falcklandii* and upland geese *Chloephaga picta* were collected opportunistically in the field (moulted feathers). Plants and algae were collected and dried, and terrestrial invertebrates (undetermined beetle larvae and spiders) were collected and stored in 80% ethanol.

Sample preparation for stable isotope analysis

Before isotopic analysis, the lipids of all rodent tissues, stomach contents and faeces were extracted in a Soxhlet apparatus for 6 h using chloroform and methanol mixture at 2:1. Following extraction, the samples were dried under a fume hood for at least 12 h and ground to a homogeneous fine powder.

Feathers were cut into small fragments, and red blood cells were freeze-dried and ground. Plant samples, rabbit fur and cat faeces were ground to a homogeneous fine powder at liquid nitrogen temperature in a ball mill. Carbon and nitrogen isotope assays were carried out on aliquots of homogenized powder and weighed into tin cups.

Carbon and Nitrogen isotope ratios were measured by continuous-flow isotope ratio mass spectrometry (CF-IRMS) using a Costech Elemental Analyser (EA) linked to a Thermo Finnigan Delta Plus XP Mass Spectrometer. Approximately 0.7 mg of each sample of animal tissue and 1–2 mg of plant tissues were combusted in a tin cup for the simultaneous determination of carbon and nitrogen isotope ratios. Two laboratory standards were analysed for every 10 unknown samples, allowing any instrument drift over a typical 16 h run to be corrected. Stable isotope ratios were expressed in δ notation as parts per thousand (‰) deviation from the international standards V-Pee dee belemnite (carbon) and AIR (nitrogen), according to the following equation $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1{,}000$ where X is ^{15}N or ^{13}C and R is the corresponding ratio $^{15}N/^{14}N$ or $^{13}C/^{12}C$. Measurement precision of both $\delta^{15}N$ and $\delta^{13}C$ was estimated to be less than 0.3‰.

Data analysis

Trapping effort was calculated as total number of trap nights. Trapping efficiency was calculated for each line, as the number of rats or mice per 100 trap nights following the method described by Cunningham and Moors (1996). To analyse differences in distribution and abundance, trap lines covering one of four distinct habitat areas (open areas, gorse *Ulex europaeus* close to the settlement, tussac grassland around the Settlement Rookery and tussac grassland at the South End Tussac area) were distinguished, and mean values for all lines of a particular habitat area are given. Some lines did not enter in any these categories, and were therefore not included in this analysis.

Due to different metabolic routing, different tissues have different isotopic signatures. To compare and interpret isotopic differences between tissues, we took these differences into account as follows. In order to correct for the biochemical components of food change when incorporated into the tissues of a consumer, we applied a discrimination factor of 1–2‰ for carbon and 3% for nitrogen to the d13C and d15N values (Tieszen et al. 1983; Minagawa and Wada 1984; Major et al. 2007). To account for the biochemical differences between the sampled liver and muscle tissue and feathers in the samples of birds, we used discrimination factors found by Mizutani and Wada (1991).

In the statistical comparisons of groups, we compared δ^{15}N and δ^{13}C values of similar tissues among rodents of different species, area, and year using one-way ANOVA.

For tests of dietary consistency we correlated the different sample types of each individual using General Linear Models that controlled for the effect of the trapping area by including area as a categorical independent variable (‘factor’). In these tests we assumed that discrimination factors vary between tissues, but much less between individuals. Significance was assumed at $P < 0.05$.

Results

Abundance and habitat preference

Ship rats and house mice were caught in all seasons. The distribution of rats and mice differed between habitats (χ^2 tests for each season and species, all $P < 0.001$). The data indicated that open areas, which are the most extensive habitat on the island, have a very low density of rats and mice (Fig. 1). In contrast, areas providing cover in the form of the native tussac grass or introduced gorse may contain considerable numbers of both species of rodents (Fig. 1). The density was consistently higher in one of the two tussac areas, close to the Settlement Rookery (paired *t*-test of data of four seasons; $t = -3.264$, $df = 3$, $P = 0.047$, Fig. 1).

Inter-annual variability in abundance

Two index lines were used identically in 2001–02 and 2003–04 (Table 1), and one survey line has been used over the whole 6-year period. The data from the index lines suggest that the abundance of mice differed between years in the two lines (Diddle dee line: $\chi^2 = 42.2$, $df = 1$, $P < 0.001$; South End tussac area line: $\chi^2 = 105.6$, $df = 1$, $P < 0.001$), but that of rats was similar (Diddle dee line: no rats, South End tussac area line: $\chi^2 = 0.129$, $df = 1$, $P = 0.720$). The data from the survey line (Settlement gorse, Table 2) indicated seasonal changes both in rats ($\chi^2 = 25.7$, $df = 4$, $P < 0.001$), and, more strongly, in mice ($\chi^2 = 103.2$, $df = 4$, $P < 0.001$).

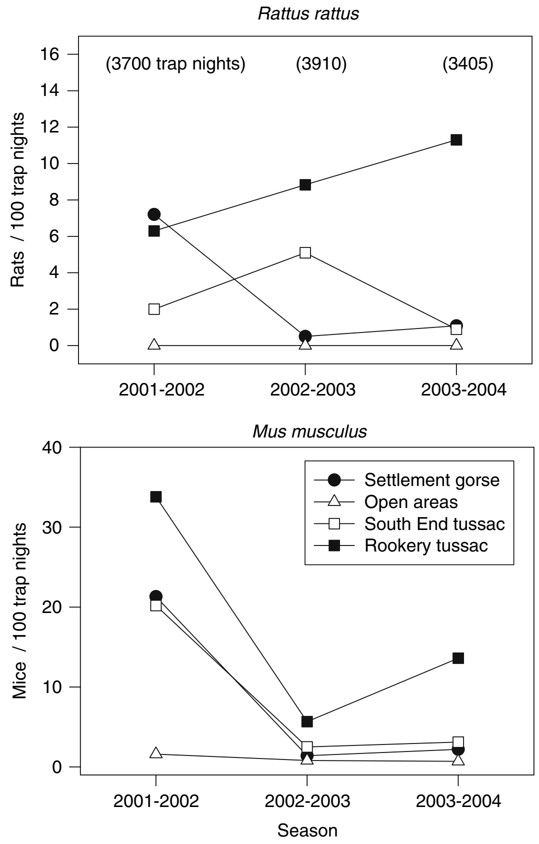

Fig. 1 Rodent abundance during three seasons of systematic trapping at New Island, Falkland Islands

Colour morphs, sexes and measurements of ship rats

Of the trapped rats, *frugivorous* was the most common type with 67–75% over the years (Table 3), followed by *alexandrinus* with 25–33%. *Rattus* was uncommon, as only three specimens were recorded in total, two of which were caught at the settlement. The difference in the occurrence of each type was highly significant in all years (Table 3).

The sex ratio of trapped animals was even in the first two seasons 2000–01 (31 females: 41 males, Binomial test, $P = 0.289$) and 2001–02 (34 females: 25 males, Binomial test, $P = 0.298$). In the last two seasons, however, it became strongly male-skewed with a ratio of about 1:10 in both 2002–03 (17 females: 167 males, Binomial test, $P < 0.001$) and 2003–04 (5 females: 65 males, Binomial test, $P < 0.001$).

The mean size and weight of trapped male and female rats did not differ (Table 4), except for the slightly larger foot length of females (difference of less than 1 mm). The size distribution of trapped ship rats, however, differed between years (Fig. 2). Initially, the distribution was unimodal,

Table 1 Numbers of ship rats trapped in lines used repeatedly in two seasons

	Trap nights	Number of rats	Trap efficiency	Number mice	Trap efficiency
Open area (50 traps in open diddle dee heath)					
Season 2001–02	450	0	0	27	6.0
Season 2003–04	900	0	0	2	0.2
South End tussac area line (50 traps, mainly in dense tussac, with some grass patches)					
Season 2001–02	550	11	2.0	111	20.2
Season 2003–04	600	15	2.7	1	0.2

Table 2 Numbers of ship rats trapped in Settlement Gorse Survey lines in six seasons

	Trap nights	Number of rats	Trap efficiency	Number mice	Trap efficiency
Season 2000–01	1378	56	4.1	71	5.2
Season 2001–02	320	23	7.2	63	19.8
Season 2002–03	220	1	0.5	3	1.4
Season 2003–04	460	5	1.1	10	2.2
Season 2004–05	84	4	4.8	3	3.6

Table 3 Distribution of colour morphs of ship rats at New Island

	Season 2000–01 ($N = 56$)	Season 2001–02 ($N = 61$)	Season 2002–03 ($N = 180$)	Season 2003–04 ($N = 21$)
Alexandrinus	26.8%	24.6%	29.4%	33.3%
Frugivorous	69.6%	75.4%	70.0%	66.7%
Rattus	3.6%	0%	0.6%	0%
Test ($df = 2$)	$\chi^2 = 28.0, P < 0.001$	$\chi^2 = 39.9, P < 0.001$	$\chi^2 = 101.0, P < 0.001$	$\chi^2 = 11.2, P = 0.004$

The percentage of occurrence in the sample of trapped animals is given, and chi-square tests were carried out on raw data

Table 4 Mean size and weight of trapped male and female ship rats *Rattus rattus* at New Island 2000–01 to 2003–04 (Mean ± SE, all seasons and ages combined)

Parameter	Males ($N = 231$)	Females ($N = 75$)	Mann–Whitney *U* test
Weight (g)	122.8 ± 4.1	130.6 ± 7.6	$U = 8070.5$, $P = 0.374$
Body length (mm)	154.4 ± 1.9	159.0 ± 3.4	$U = 7845.0$, $P = 0.219$
Tail length (mm)	175.4 ± 2.0	178.9 ± 3.8	$U = 8027.5$, $P = 0.340$
Foot length (mm)	31.3 ± 0.2	32.0 ± 0.4	$U = 7302.0$, $P = 0.040$
Ear length (mm)	21.6 ± 0.2	21.8 ± 0.3	$U = 7907.0$, $P = 0.252$

with the strongest class of 150–170 mm body length found in the middle of the distribution and comprising 40% of the cases in 2000–01. This changed progressively to a bimodal distribution with the strongest classes found to comprise more than 32% of the trapped rats each, at 110–130 and 170 to 190 mm in 2003–04. The initially strong size class of 150–170 mm body length had completely disappeared in the sample of 2003–04 (Fig. 2), and this change in distribution was found in both males and females.

Visual determination of ship rat diet

Rats sampled during the incubation period of the prions had a mixed diet (Table 5), with plants occurring in 128 of 161 stomach contents (80%) and animal items in 82 of 161 stomach contents (51%). The stomach contents were classed as 20% pure animal matter, 49% pure plant matter, and 31% of mixed origin. Of vegetation, tussac grass fibres were the most important food source by occurrence, present in 74 of 128 stomach contents of vegetal content (58%). Vegetal content also included the flowers of gorse. Items were identified in 58 samples (i.e. stomach contents of one individual) of animal origin. Of these, 43 (74%) contained mammals, as determined by the presence of hairs, of which at least 5 were scavenged as indicated by the presence of maggots in the stomach contents. 10 samples (17%) contained insects and insect larvae, and 5 samples (8% of animal items or 3% of total samples) contained traces of ingested birds, three feathers and two yolks. The time and place of the samples collected with yolk suggest that they originated from displaced rockhopper penguin eggs (F. Zuñiga, personal communication). The overall distribution of animal versus vegetal diet did not differ between rats trapped in three areas (Table 5: vegetal diet: $\chi^2 = 0.04$, $df = 2$, $P = 0.97$, Animal diet: $\chi^2 = 0.20$, $df = 2$, $P = 0.91$). However, there was a

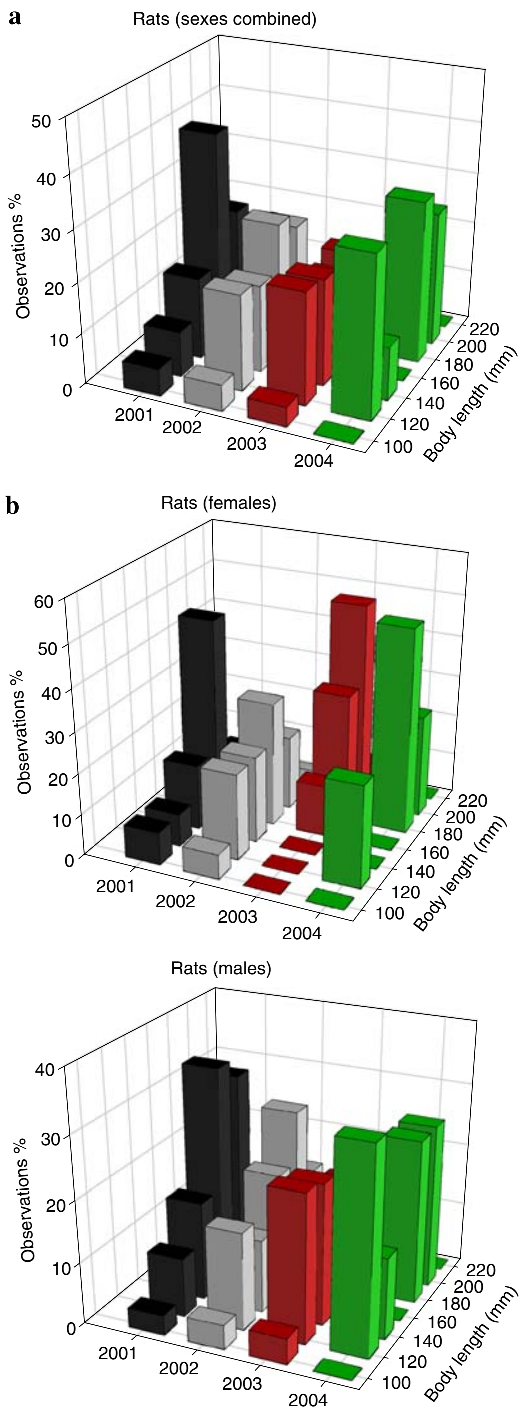

Fig. 2 Distribution of body sizes of ship rats trapped at New Island in four seasons. **a** Both sexes combined and **b** separate for each sex

difference in the diet between young and adult rats. Young rats fed largely on vegetation, as only 18 of 64 stomachs from young rats (28%) contained any animal material. In comparison, adult rats had a significantly higher proportion of ingested animals (52 of 82 stomachs, or 63%, Chi-square test of young vs. adults $\chi^2 = 5.1$, $df = 1$, $P = 0.016$). The most pronounced difference in diet between adults and young rats was found in the South End Tussac area (Fig. 3) where more than 80% of the samples of adults were of animal origin. Sampled adults were mainly males, but there was no sex difference in the proportion of animal diet (63% in 68 samples of males, 64% in 14 samples of females, $\chi^2 = 0.001$, $df = 1$, $P = 0.971$).

A small data set was collected in February 2001, and is consistent with data from 2005–06 (Table 5). During the nestling period of Thin-billed prions, ship rats took a mixed diet of rats, with prions being an important component. Prion feathers occurred in the stomach contents of some rats from all habitats, although in low incidence in the Settlement Rookery tussac where prions are uncommon. Of other components of the diet, plants were particularly important in the Settlement Rookery tussac, mammals were consumed in all areas and some marine food (fish and crustaceans) was also consumed. The presence of maggots indicates that a part of the animal diet was obtained by scavenging.

Isotopic background data and comparison of mammal species and prions

We found that the carbon isotope ratios varied between terrestrial and marine organisms (Fig. 4). However, the three habitat types overlapped considerably in δ^{15}N, where the main difference was found in highly elevated values for tussac grass sampled around seabird colonies (Fig. 4).

The δ^{13}C measured in the fur of rabbits and the diet of rats, mice and cats is shown in Fig. 5. Rabbits, although not a potential predator, are included as reference for a terrestrial herbivore. Among the other mammals, δ^{13}C values of the diet of rats, mice and cats differed ($H = 12.7$, $df = 2$, $P = 0.002$). Dunn's post hoc tests indicated a significant difference between the diets of rats and the cats only ($P < 0.05$), the δ^{13}C in cat faeces being lower (i.e. indicating more terrestrial diet) than that of rats. The δ^{13}C measured in the diet of all three potential predators of prions (rats, mice and cats) differed from the δ^{13}C of prion chick red blood cells ($H = 44.7$, $df = 3$, $P < 0.001$, Dunn's post hoc tests for prions vs. each mammal $P < 0.05$). Thus, all three mammals had a δ^{13}C indicative of a mixture of prey derived from marine and terrestrial sources.

Stable isotope analysis of rat diet

Rats captured in the four areas are analysed separately in order to gain a deeper insight into the variability of foraging strategies. Consistent with the observed mixed diets in rat stomach contents, the carbon isotope ratios of stomach contents of rats showed a wide range (Fig. 5), but also considerable overlap with the δ^{13}C found in prion chick red blood cells.

Table 5 Summary of ship rat diet data obtained by visual stomach content analysis during the incubation period of Thin-billed prions (three areas in the period 14 November 2002 to 17 January 2003), compared to the chick-rearing periods 2001 (19 to 26 February 2001, MacKay et al. 2001) and 2005–2006 (19 to 27 February 2005 and 14 February to 7 March 2006)

Diet type	Incubation 2003				Chick-rearing 2001 + 2006				
	Rookery Tussac ($N = 96$)	South End Tussac ($N = 32$)	Gorse areas ($N = 13$)	February 2001 ($N = 15$)	Rookery Tussac ($N = 7$)	South End Tussac area ($N = 8$)	Gorse areas ($N = 11$)	Open areas ($N = 2$)	All 2005–6 ($N = 28$)
Vegetal	*78%*	*81%*	*85%*	*60%*	*86%*	*25%*	*18%*	*100%*	*43%*
Tussac grass	56%	77%	18%	-	86%	13%	0%	0%	25%
Animal	*51%*	*56%*	*62%*	*93%*	*71%*	*100%*	*100%*	*100%*	*93%*
Mammals (hairs)	71%	79%	86%	7%	14%	25%	27%	50%	25%
Birds (feathers)	0%	7%	0%	60%	14%	88%	64%	100%	61%
Birds (eggs)	6%	0%	0%	0%	0%	0%	0%	0%	0%
Fish	–	–	–	–	28%	0%	0%	0%	7%
Invertebrates	23%	14%	14%	0%	–	–	–	–	–
Crustaceans	–	–	–	–	14%	0%	9%	0%	7%
Maggots	–	–	–	13%	0%	25%	9%	0%	11%

Figures denote % occurrence; a line indicates a parameter not recorded in the dataset

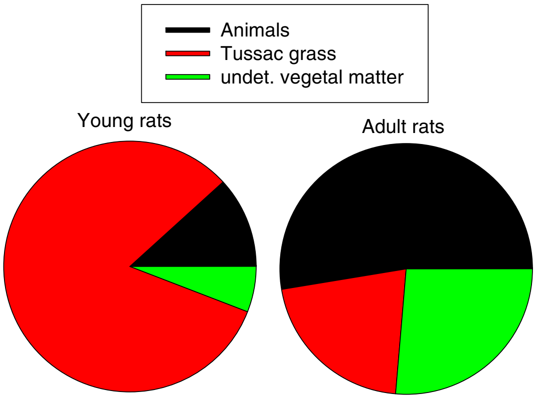

Fig. 3 Difference in the diet composition of adult and young rats trapped in the South End tussac area at New Island

The isotope ratios of all sample types (stomach contents, faeces, liver and muscle tissue) differed between the areas (Table 6). When carbon and nitrogen were analysed separately, nitrogen differed between areas for all sample types (ANOVAs, all tissues $P < 0.001$). There was no difference in δ^{13}C of samples of stomach contents, faeces and liver (ANOVAs, all $P > 0.05$). However, the rats from different areas had distinct δ^{13}C values in muscle tissue (ANOVA, $F_{3,30} = 10.4$, $P < 0.001$). Post hoc tests revealed that the rats of the Settlement Rookery tussac were distinguished from all other areas by low δ^{13}C (all $P < 0.01$), whereas rats from the South End tussac, the gorse areas and the open areas did not differ in δ^{13}C.

The liver and muscle were between 1 and 4‰ enriched in δ^{13}C compared with stomach contents and faeces (Table 6), and between 3 and 5‰ enriched in δ^{15}N. Mean values found in liver and muscle were similar within areas (Table 6). Within-individual correlation of isotope ratios of the four sample types of ship rats indicated some degree of individual consistency of diet, especially a strong correlation between liver and muscle samples. The evidence for a consistency of tissues with the last few meals (stomach contents and faeces) was more mixed (Table 7), indicating some day-to day variability in the diet.

Of all rats, those caught in the Settlement Rookery tussac showed the most terrestrial diet according to their muscle tissue and stomach contents (Fig. 6; Table 6), and elevated δ^{15}N values in all sample types indicated that tussac grass was an important part of the diet for rats in this area both in the long and short term. The data of the stomach contents are also consistent with predation or scavenging on mice and rats, as these are not distinguished well from the tussock-forming grasses. A single stomach that contained fish had an isotope signature well separated from the other values, and grouping with the marine isotopic data (Fig. 6).

In contrast to the rats from the Settlement Rookery tussac, the isotope ratios of rats from the South End tussac area indicated a mixed diet with terrestrial and marine components (Fig. 7). The muscle and liver isotope ratios of rats from the South End tussac area fell between the terrestrial and the marine background data, except for one rat, which grouped with the marine data, indicating consistent preference for marine-derived food over a period of several weeks. The stomach of that latter rat contained feathers of thin-billed prions as well as green plant material.

Rats caught in traps adjacent to gorse lines bordering prion areas also showed a mixed diet (Table 5), and their isotope ratios spanned a wide range within and between the marine and the terrestrial data (Fig. 8). As in the South End

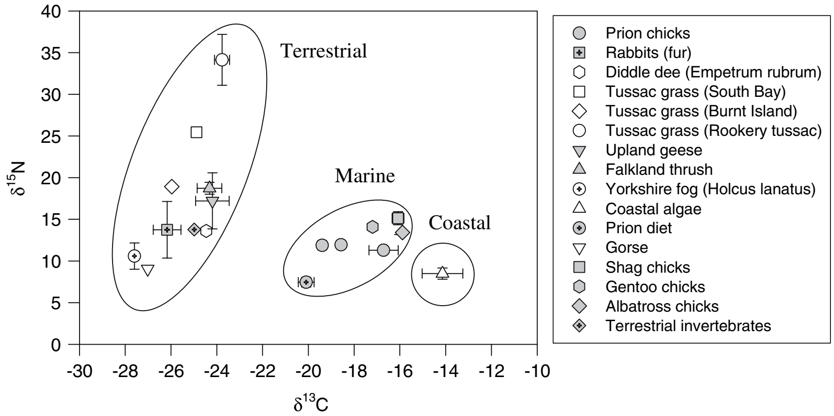

Fig. 4 Carbon and nitrogen stable isotope ratios for animals and plants from different areas and habitat types at New Island, Falkland Islands. *White symbols* mark plants, *white grey symbols* mark animals. For thin-billed prions, three means were included, which had similar δ^{15}N, but differed in their and δ^{13}C (from *left* to *right*: chick feathers, chick down, egg membranes). Prion diet consisted of a mixture of crustaceans (mainly euphausids, amphipods and copepods, Quillfeldt unpublished data)

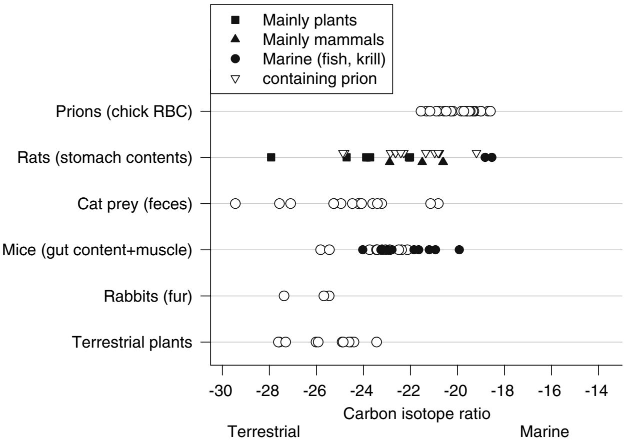

Fig. 5 Carbon stable isotope ratio of diet and tissue samples of four introduced mammals at New Island. Terrestrial plants and red blood cells (RBC) of prion chicks are included for reference. For house mice, *open symbols* are used for gut contents, *filled symbols* for muscle samples. Rat stomach contents are subdivided in categories according to the visual identification of contents

tussac area, one individual had high muscle and liver δ^{13}C, indicating consistent preference for marine-derived food over a period of several weeks. The stomach of that latter rat contained a mash of crustaceans, including legs of krill *Euphausia* sp., but no traces of prion feathers or tissues.

Finally, two rats were caught in open areas with short vegetation, close to prion burrows. The low sample size here is explained by the scarcity of rats in this habitat, see above. The stable isotope ratios of stomach contents and faeces of the two individuals (Fig. 9) again suggested a mixed marine and terrestrial diet, consistent with their stomach contents (containing prion feathers in both cases, one mixed with plants, one with hairs). The liver and muscle isotope ratios suggested that prions were a regular component of the diet of both rats caught in open areas.

Thus, we found individuals that specialized on marine-derived food during the time of our analyses in two of three areas (in total 4 of 34 rats or 12%).

Stable isotope analysis of mouse diet

Feral house mice at New Island mainly had a terrestrial diet (Fig. 10). None of their gut contents overlapped with prion red blood cells (Fig. 5), but one mouse from an open area grouped with the marine data for muscle isotope ratios (Fig. 10), indicating a specialisation of this latter mouse in marine-derived food. In muscle tissue, several mice had isotope ratios in a position intermediate between terrestrial and marine values, indicative of a mixed diet, while most individuals grouped best with a terrestrial diet (Fig. 10). Mice of the different areas differed in their isotope ratios (Table 8), mainly due to elevated nitrogen isotope ratios in the vegetation of the tussac areas, particularly in the Settlement Rookery Tussac area.

Within-individual correlation of isotope ratios of the three sample types of mice indicated a high degree of individual consistency of diet, with a strong correlation between gut contents, liver and muscle samples (Table 9).

Stable isotope analysis of cat diet

We consider four main prey species observed: rabbits, rats, mice and prions (Figs. 5, 11). Of 15 cat scats analysed, 2 (13%) were separated in δ^{13}C values and matched with prion chick red blood cells (Fig. 5), but also overlapped with the higher values within rat and mice muscle tissues; thus providing only a maximum estimate for prion predation by cats. For the remaining samples, potential prey consists of rabbits, mice and rats. The lowest δ^{13}C values observed in mice muscle tissue and rat muscle tissue were

Table 6 Stable isotope signatures (‰) of ship rats at New Island (mean and standard error), and results from Multivariate ANOVA tests for differences between areas

	Rookery Tussac ($n = 7$)	South End Tussac area ($n = 8$)	Gorse areas ($n = 11$)	Open areas ($n = 2$)	All ($n = 28$)
Stomach content					
δ^{13}C	−22.4 ± 0.7	−23.1 ± 0.9	−23.1 ± 0.9	−20.8 ± 0.2	Wilk's $\lambda = 0.229$, $P < 0.001$
δ^{15}N	26.8 ± 2.4	17.3 ± 1.3	12.2 ± 0.4	14.3 ± 1.3	
Feces					
δ^{13}C	−23.6 ± 0.3	−23.9 ± 0.3	−23.2 ± 0.9	−22.6	Wilk's $\lambda = 0.107$, $P < 0.001$
δ^{15}N	27.3 ± 0.4	17.9 ± 1.7	12.6 ± 0.5	14.8	
Liver					
δ^{13}C	−21.2 ± 0.4	−19.9 ± 0.4	−20.0 ± 0.4	−18.6 ± 0.2	Wilk's $\lambda = 0.086$, $P < 0.001$
δ^{15}N	32.2 ± 1.2	22.1 ± 1.0	16.9 ± 0.2	17.1 ± 1.3	
Muscle					
δ^{13}C	−21.8 ± 0.2	−19.5 ± 0.3	−20.2 ± 0.4	−18.0 ± 0.2	Wilk's $\lambda = 0.061$, $P < 0.001$
δ^{15}N	32.6 ± 0.9	21.0 ± 1.0	16.8 ± 0.2	17.9 ± 0.5	

Table 7 Within-individual correlation of isotope ratios of four sample types of ship rats (*Rattus rattus*) at New Island

Sample type	Faeces	Liver	Muscle
Carbon			
Stomach contents	0.153	0.249**	0.142*
Faeces	–	0.568**	0.603**
Liver	–	–	0.726***
Nitrogen			
Stomach contents	0.341*	0.123	0.102
Faeces	–	0.009	0.004
Liver	–	–	0.699***

GLM were used to control for the effect of area, but for readability we give only the effect size (eta squared value) of pair-wise correlations between sample types

* denotes significance values of $P < 0.05$, while ** denotes significance values of $P < 0.01$ and *** $P < 0.001$

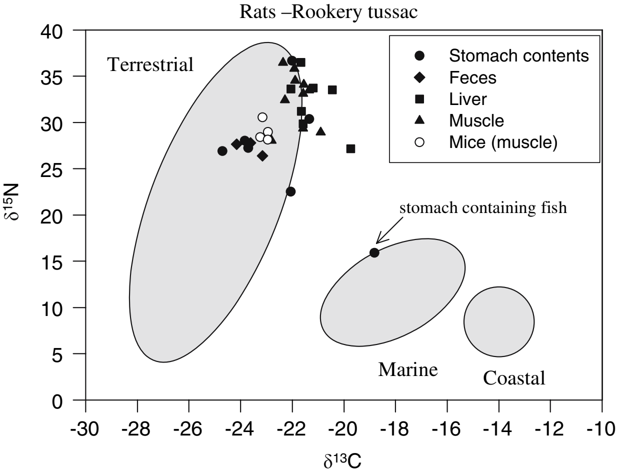

Fig. 6 Carbon and nitrogen stable isotope ratios for ship rats from the Rookery tussac area, New Island. The background data, indicated in *grey shades*, correspond to the data given in Fig. 4

−24.03 and −22.81‰, respectively, whereas the highest value observed for rabbit fur was −25.5%; and fur is likely to be slightly elevated compared with rabbit muscle. Thus, scats consisting mainly of rabbits may be separated using a cut-off point of −26‰ (e.g. Fig. 4), mixed samples of rodent and rabbit origin are expected in the range of −26 to −24‰, and rodent prey would be expected above −24‰. According to this, a total of 3 samples (20%) contained mainly rabbit tissue, while 3 samples (20%) contained mainly rodents, and the remaining 7 samples were most likely of mixed origin (rabbits and rodents). In summary, our estimate for the occurrence of prey is: prions in 13% of scats (maximum estimate), rodents in 67% of scats and rabbits in 67% of scats.

Discussion

In the present study, the trophic relationships between introduced mammals and seabirds in a remote subantarctic island are investigated. The present study highlights spatial and temporal differences in the levels of interaction between predators and native seabirds.

Presence and abundance of rodents in different habitats

The abundance of both rats and mice differed strongly between habitats. Open areas, which are by far the most extensive habitat on New Island, had very low densities of

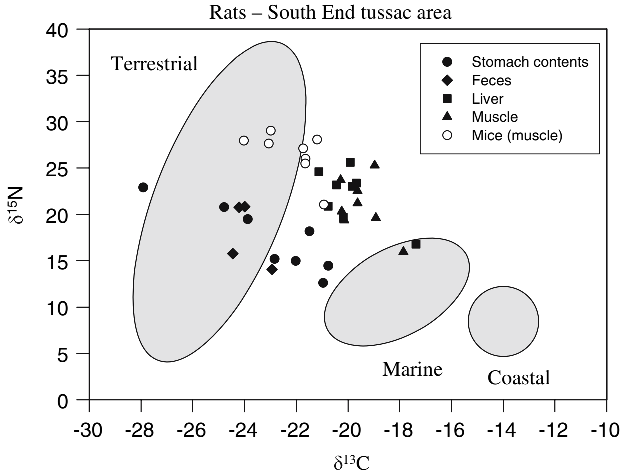

Fig. 7 Carbon and nitrogen stable isotope ratios for ship rats from the South end tussac area, New Island. The background data, indicated in *grey shades*, correspond to the data given in Fig. 4

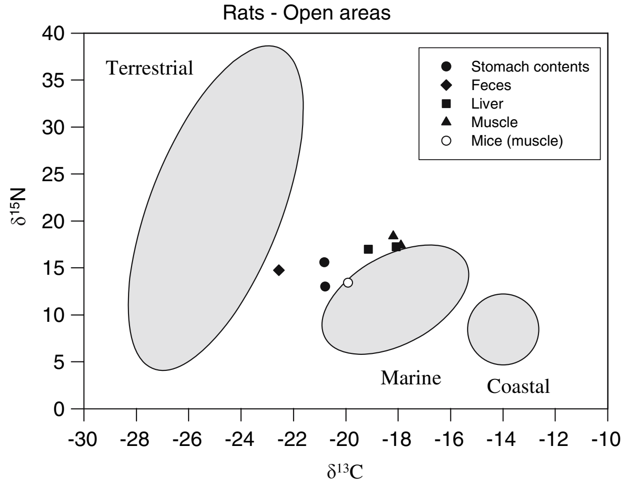

Fig. 9 Carbon and nitrogen stable isotope ratios for ship rats from open areas of New Island. The background data, indicated in *grey shades*, correspond to the data given in Fig. 4

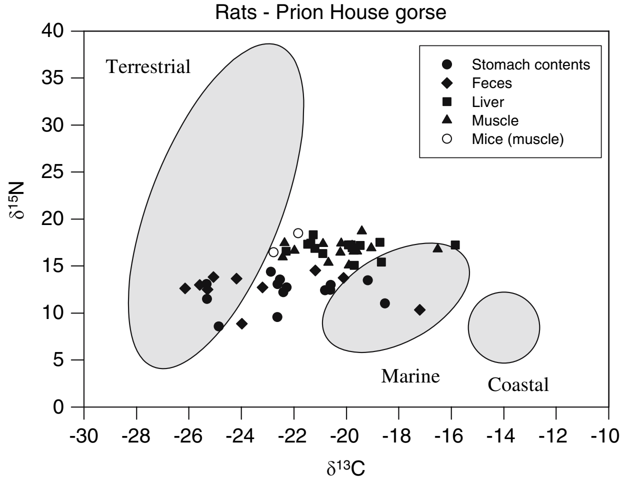

Fig. 8 Carbon and nitrogen stable isotope ratios for ship rats from the "Prion house" gorse line, adjacent to dense prion nesting areas. The background data, indicated in *grey shades*, correspond to the data given in Fig. 4

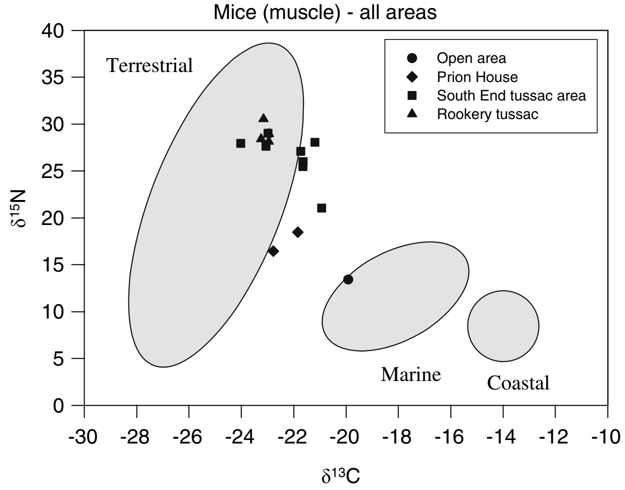

Fig. 10 Carbon and nitrogen stable isotope ratios for muscle samples of house mice from different areas of New Island. The background data, indicated in *grey shades*, correspond to the data given in Fig. 4

rats and mice. In contrast, areas providing cover in the form of the native tussac grass or introduced gorse contained higher numbers of both species of rodents. New Island has a small number of introduced feral cats, which prey mainly on rats, mice and rabbits (Matias 2005). Predators are also found among the birds of New Island, such as the Falkland skua, short-eared owl *Asio flammeus* and red-backed hawk *Buteo polyosoma*. Other potential predators are the striated caracara and the crested caracara. Areas of cover may therefore be preferred because they offer protection for the rodents from predation. Choice of a habitat providing refuge is an integral component of predator-avoidance behaviour, and if a habitat has few refuges or a low complexity and animals feed only near refuge (e.g. Orrock et al. 2004), then they will have access to less food. In such habitats, rodents may suffer non-lethal effects of the perceived predation risk such as lower growth rates and delayed reproduction, as has been shown experimentally for house mice (Arthur et al. 2004).

The abundance of rats in areas of cover at New Island, on the other hand, was not related to the presence of small burrow-nesting seabirds, as one area of relatively high rat density (Settlement Rookery Tussac) has no or very few nests of prions (personal observation). Moreover, although the present study included the time of rockhopper penguin and imperial shag incubation and hatching, very little evidence was found in the rat diet for an interaction between the rats and penguins. The present data therefore suggest

Table 8 Carbon and nitrogen stable isotope analysis of stomach and contents as well as liver and muscle tissue, of house mice at New Island

Isotope data (‰)	Rookery Tussac ($n = 4$)	South End Tussac area ($n = 7$)	Gorse areas ($n = 2$)	Open areas ($n = 1$)	
Gut content					
δ^{13}C	−23.7 ± 0.8	−23.3 ± 0.4			Wilk's $\lambda = 0.910$, $P = 0.685$
δ^{15}N	23.0 ± 0.8	24.4 ± 1.3			
Liver					
δ^{13}C	−22.0 ± 0.2	−22.3 ± 0.5		−19.1	Wilk's $\lambda = 0.192$, $P = 0.007$
δ^{15}N	29.2 ± 0.6	26.7 ± 1.1		13.8	
Muscle					
δ^{13}C	−23.1 ± 0.1	−22.2 ± 0.4	−22.3 ± 0.5	−19.9	Wilk's $\lambda = 0.078$, $P < 0.001$
δ^{15}N	29.0 ± 0.5	26.4 ± 1.0	17.4 ± 1.0	13.4	

Stable isotope data are given (mean and standard error), and the final column describes results from Multivariate ANOVA tests for differences between areas

Table 9 Within-individual correlation of isotope ratios of four sample types of house mice (*Mus musculus*) at New Island

Sample type	Liver	Muscle
Carbon		
Gut contents	0.418*	0.167
Liver	–	0.782***
Nitrogen		
Stomach contents	0.851***	0.699***
Liver	–	0.667**

GLM were used to control for the effect of area, but for readability we give only the effect size (eta squared value) of pairwise correlations between sample types

* denotes significance values of $P < 0.05$, while ** denotes significance values of $P \leq 0.01$ and *** $P \leq 0.001$

that the rats prefer the Settlement Rookery Tussac for cover and as a food source, and not for the proximity to seabirds. In line with this, Igual et al. (2006) found that Cory's shearwaters breeding in burrows of vegetated slopes were more vulnerable to predation by ship rats than birds breeding in open, rocky habitat.

This has consequences when it comes to management actions, as an important part of the cover is provided by gorse, introduced as an ornamental plant in the settlement, but which is now also found in remote sites of the island. It is thus important to remove this vegetation, and a program aimed at 50% reduction is currently underway.

Inter-annual variability and population responses of rats

During the first two seasons of trapping, more than 130 rats were trapped and killed, approximately half of them females. This appeared to cause a significant demographic impact. We observed a change in the size distribution from normal to bimodal and a change from equal sex ratio to strongly male-biased sex ratio over the study period. The observed change may be a population response to a decrease in density. Mice and rats have the potential to self-regulate their density through social interactions, termed spacing behaviours, that include territoriality, pre-saturation dispersal, breeding inhibition and various forms of social mortality (e.g. Singleton and Hay 1983). After an induced sudden drop in density, such as imposed control, rodent populations have an acute ability to recover rapidly (Drummond 1970). Population responses to decreased density may be the result of compensatory mechanisms such as density-dependent mortality and fecundity, i.e. changes in breeding, survival and recruitment. A decrease in density through removal of individuals may result in a reduction in inter-specific or intra-specific competition for food resources, and may promote a higher breeding capacity of the remaining animals, with increased pregnancy rates and

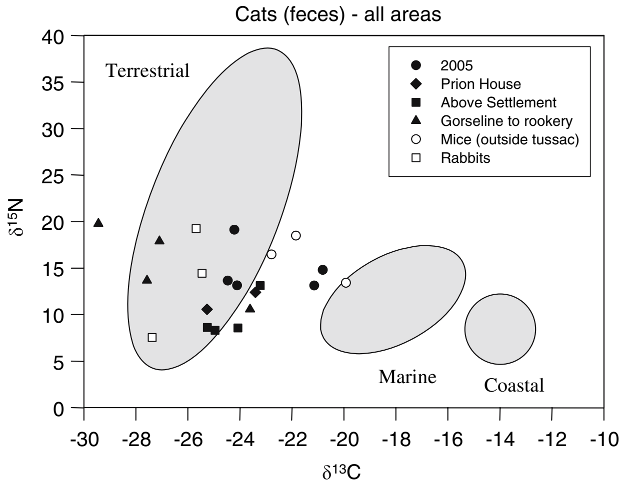

Fig. 11 Carbon and nitrogen stable isotope ratios for cat faecal samples from different areas of New Island. The background data, indicated in *grey shades*, correspond to the data given in Fig. 4

litter sizes (e.g. Davis and Christian 1958; Montgomery 1981), and high rates of survival of adults or juveniles in the population (Gliwicz 1981; Montgomery 1981; Gundersen et al. 2001). Further, density-dependent dispersal also can be important through immigration (e.g. Sullivan 1979; Montgomery et al. 1997). As a response to removal, studies of rodents found population compensation through immigration of smaller, younger animals (e.g. Brown and Tuan 2005) and by commencing reproduction earlier (e.g. Schieck and Millar 1987; Krebs et al. 1976). Further, some studies show that more males colonized the removal area than females (e.g. Schieck and Millar 1987).

Thus, the demographic change we observed is typical for a population response to a decrease in density, but very strong compared to other studies. The delay in the response (detectable from the third season) suggests that the pattern is caused by changes in breeding parameters rather than by immigration. The fact that such a strong response was caused by the removal of ca. 70 animals in the first season and 60 animals in the second season suggests that the total population is probably relatively small.

Diet of rats

Similar to other studies on rats (e.g. Major et al. 2007), the present data indicate a high plasticity of rat diet. We found tussac to be an important source of food and shelter for rats, similar to other sub-Antarctic islands (e.g. Pye et al. 1999). Diet analyses carried out between mid-November 2002 and mid-January 2003 showed that tussac grass was the singlemost important food source, occurring in identifiable form in nearly half of the samples. In particular young rats fed extensively on tussac (Fig. 3), whereas older rats also took many mice and possibly young rats, as suggested by the presence of hairs in over a third of the stomachs of all ages combined, and about half the stomachs of adult ship rats. The presence of maggots in a number of stomachs indicates that scavenging is also important.

One concern has been the influence of the rats on the population of thin-billed prions at New Island, as this species probably has its most numerous breeding population here. During the incubation period of the thin-billed prions, rats had a mixed diet, with plants occurring in 80% of the samples and animal items in 51%. Only five stomach contents (8% of animal items or 3% of total samples) contained traces of ingested birds, three feathers and two yolks.

However, data collected during the chick-rearing period of thin-billed prions in different years consistently indicated that the amount of animal tissue taken strongly increased later in the season (Table 5) and dead and/or alive prion chicks may become an important part of the rat diet during their nestling period. This was supported for some areas using stable isotope methods (see below).

We compared the diet of rats trapped in different areas, and found strong differences among areas. While rats in three of four areas had a diet with marine as well as terrestrial content, rats of the Settlement Rookery tussac area consumed a high proportion of terrestrial food. Among all areas sampled at New Island, this area consistently had the highest density of ship rats as well as house mice over three seasons (Fig. 1), and thus the terrestrial food web appears fully sufficient to maintain these populations. Rats would appear to take marine food opportunistically to supplement their diets.

Because body tissues differ in their metabolic activity, it is possible to analyse multiple tissues to estimate an animal's diet over a range of time scales. Turnover times for different animals somewhat vary, and it is recommended that when turnover rates are unknown for the species in focus, then turnover rates obtained from another species close in body size, taxonomy and ecology is possibly used for the measured species (Dalerum and Angerbjorn 2005). The small mammals best studied in this respect are gerbils *Meriones unguiculatus*. In diet-switching experiments with gerbils Tieszen et al. (1983) found that liver had high turnover rates of carbon stable isotopes, with a half-life of about 1 week, while they were much longer in muscle tissue (ca. 4 weeks).

We analysed individual consistency of diet in ship rats using stomach contents and faeces (representing the last few meals, but also representing a relatively depleted isotope signature in comparison with diet) and liver and muscle tissue (representing diet over a period of several weeks). Rats showed a high consistency between liver and muscle isotope ratios, and thus were specialized in prey types for a time of several weeks. The lower rates of correlation between the isotope ratios of the last few meals (stomach contents, faeces) and longer-term ratios found in liver and muscle underpins the opportunistic feeding behaviour of rats in the short term. Consistent with this, we found a wide range of isotope ratios in rat diet (e.g. Fig. 5).

Most rats in our study showed a mixed diet, but in two of the three areas, we found individuals specialized on marine-derived food (in total 4 of 34 rats or 12%). Prions were the most frequently encountered item of marine food in the diets. Among the potential sources of marine foods, other than prions, are food items lost by imperial shags when harassed by skuas. Fish are found occasionally in areas with regular flight routes of imperial shags, and this may explain the fish found in one stomach of a rat in the Settlement Rookery tussac, which is situated on the top of a vertical cliff. Skuas also chase adult prions, and dead adults with wounds or half eaten are found occasionally. In busy nights at the colony, prions often collide with each other and regurgitated crustaceans are found on the ground in the morning. Further sources of marine food other than prions may be regurgitated by Magellanic penguins, especially of lobster krill *Munida gregaria*. Along the shoreline, we observed occasional beaching of krill, lobster krill, marine isopods or squid. Thus, there is a range of potentially available marine food sources.

The present study also demonstrates that individual rats use different dietary strategies both within and between areas and habitats. This may partly depend on their size and sex. For example, we found that during the austral spring, adult rats consumed a larger proportion of animal diet than juvenile rats. Further studies of rat diets could focus on the causes of the individual differences observed during the chick-rearing period of prions.

Diet of mice

Feral house mice on sub-Antarctic islands typically feed on seeds and insects (Copson 1986; Crafford 1990; Chown and Smith 1993). Recent studies of house mice at Gough Island (Cuthbert and Hilton 2004), however, suggested that mice might have a larger influence on seabird populations than previously recognized. Therefore, an analysis of marine versus terrestrial contents in the diet of mice at New Island seemed desirable, and the stable isotope approach appropriate.

We found that dietary differences among individual mice persisted for several weeks, indicating some specialisation. Most mice had a terrestrial diet, a few had a mixed marine and terrestrial diet and one mouse from an open area grouped with the marine data for muscle isotope ratios, indicating a specialisation of this latter mouse in marine-derived food. Unfortunately, the gut content of this mouse was not sampled. The gut contents of all other mice showed no overlap with prion tissue according to the isotope ratios, indicating that none had recently consumed prion tissue.

Diet of cats and indirect effects of rabbits

The diet of cats inferred from the stable isotope ratios was broadly comparable to an analysis using visual contents (Matias 2005) which also found that other introduced mammals were the main prey of feral cats at New Island. The isotope ratios in faeces were consistent with rodents and rabbits as the chief prey of cats at New Island, both appearing about equally important. Cat faeces overlapped in their δ^{13}C values with prion chick red blood cells for 13% of scats, which we interpreted as the maximum frequency of scats containing prions as their main item. In comparison, Matias (2005) found a similar number (12.8%) in the settlement area, but greater frequencies of occurrence in other areas (up to 57% in a small sample from Rookery Hill, a dense prion nesting area). Rabbits, mice and rats were the chief prey of cats identified by visual analysis of scats (Matias 2005). While not yielding the same detail in prey identification, the stable isotope method can be used to trace prey of which little remains in the scats would be visible. For example, Matias (2005) found that the rabbits taken by cats were small individuals. However, large individuals would not be consumed whole and would therefore leave traces with the isotope method, but not with the visual analysis. On the other hand, Matias (2005) found 2–3 individual preys in each scat on average; thus our method may have overlooked some prion remains when they were minor in weight compared with other prey.

The influence of cats on the population of prions is estimated to be very small, due to the small number of cats present on the island in comparison to the large population of prions, and also due to the abundance of other prey like rabbits. However, recent studies have drawn attention to the possibility of a hyperpredation effect (Courchamps and Caut 2005). This occurs when one or several prey species (in this case, mice and rabbits) introduced into an environment in which a predator has also been introduced (in this case cats) sustain high predator numbers, such that local prey, less adapted to high levels of predation, could suffer a population decline and possibly even extinction. Such a process has consequences when it comes to management actions, as the introduced prey plays a key role that is not always obvious. Predators are often perceived as having the most deleterious effects on invaded ecosystems (Courchamps and Caut 2005), and consequently control programs more often target them, sometimes neglecting the introduced prey. Yet, through a hyperpredation effect, introduced prey may have an indirect impact on indigenous prey. In parts of New Island, rabbits also compete for space with prions for digging burrows. Thus, rabbits should also be taken into account when considering the possibility of eradicating introduced mammals.

Coexistence with seabirds and conclusions

New Island is the only place in the Falkland archipelago where the ship rat is found. All current eradication programs in the Falkland Islands are directed against the Brown or Norway rat *Rattus norvegicus*, which is a larger, more ferocious species. We have no evidence of the latter species at New Island.

The breeding colony of thin-billed prions has coexisted with introduced ship rats and feral house mice for about 100 years according to available records. The present data suggest that the coexistence has been possible due to the rat population of New Island being relatively small and restricted mainly to areas providing cover, and probably due to the absence of Norway rats.

It has been pointed out that the coexistence of introduced rodents and seabirds at New Island may be due to predator swamping in this highly seasonal environment (Catry et al. 2007), and this is supported by the small population sizes indicated by the present data. Over-winter survival may be an important factor regulating the rodent populations, as the food may become scarce during that period, and New Island has no winter-nesting seabirds. The absence of sheep and cattle over the past 30 years may also be a contributing factor. In several studies on introduced rodents on islands, winter-nesting seabirds were affected much more than summer-nesting birds (e.g. Brothers 1984; Cuthbert et al. 2004). In addition, tussac as an important source of food and shelter for rats is restricted to few areas on New Island and thus, predator survival in winter may be low at present, but possible changes need to be taken into account. Sub-Antarctic ecosystems have been found to respond sensitively to variation in ambient temperature (e.g. Chapuis et al. 2004), which have increased across several parts of the Antarctic and sub-Antarctic for the past 50 years (e.g. Smith 2002; Turner et al. 2005). Climate change may lead to more favourable conditions for reproduction (e.g. Ferreira 2006) or over-winter survival of rodents or less favourable conditions for thin-billed prions (see Quillfeldt et al. 2007a, b), which may influence the relative numbers of prions and rodents and thus may disrupt the apparent present equilibrium.

The diet analyses also indicate that during the incubation period, the interaction between rodents and thin-billed prions is minimal. However, an impact of rats has been described on the survival of prion chicks in the South End tussac area (Catry et al. 2007). Thin-billed prion chicks may be vulnerable to predation by rats shortly after hatching (MacKay et al. 2001), although in a study plot in an open area, but close to the settlement gorse line where rats occur, no predation on hatchlings was observed (e.g. Quillfeldt et al. 2003). The reports of prion hatchling mortality of MacKay et al. (2001) refer to the South End tussac area, where 1,660 trap nights resulted in a total of only 16 rats caught. Further, the rats in the South End Tussac area that were found with down feathers in their stomach contents weighed only 33–72 g; thus were immatures and possibly thus more likely to scavenge than to kill a pre-fledging prion weighing about 150 g. There have been reports of small rodents killing surprisingly large prey, but only when it is relatively immobile, as in the case of 35 g mice killing albatross chicks weighing >10 kg (Cuthbert et al. 2004). In the second half of February, when the present samples were collected, prion chicks are mobile except when poorly fed and hypothermic.

While from the ship rats' point of view live or dead prions may be an important food source, in terms of the prion population, the predation by rats, mice and cats seems to have a negligible influence. One reason for this lack of influence is that the number of introduced predators at New Island is relatively low, but also because in such a large population of prions (with 2 million pairs), even a small percentage of mortality would create a massive amount of dead animal tissue to be scavenged.

Except for the cases when maggots were observed in the stomach contents, neither visual analysis of stomach contents nor the stable isotope data could reveal whether the prions observed in the stomach contents of rats or the marine foods traced in tissue isotope signatures were preyed upon or scavenged, but we may extrapolate from data on chick mortality.

In total, we followed 213 Thin-billed prion chicks over four breeding seasons 2003–2006 in a study plot in an open area (close to the Settlement gorse line). The main causes of chick mortality were environmental factors, the most important being starvation (18 chicks or 8.5%), followed by nest flooding (2 chicks or 0.9%) and overheating (1 chick or 0.5%). Predation by striated caracaras was observed for 8 chicks (3.8%), while we observed only one probable case of predation by a rodent (*Rattus rattus* or *Mus musculus*) in 2005. In both 2005 and 2006, prion chicks were not well fed towards the end of the breeding season, and some chicks died of starvation when close to fledging age in both years, coinciding with the time of sample collection (4 of 74 chicks in 2005 (Quillfeldt et al. 2007b) and 1 of 39 chicks in 2006 (P. Quillfeldt, unpublished data).

Thus, the number of chicks which died from causes other than predation in our study plot was considerably higher than the number of chicks preyed upon by rodents (21 vs. 1 case), and the number of chicks preyed upon by caracaras was also higher than the number of chicks preyed upon by rodents (8 vs. 1 case). This indicates that although prions appear to be an important food source for rats in certain areas, they may be obtained mostly by scavenging. This is supported by the fact that maggots are found regularly with prion remains in stomach contents of rats. Also, thin-billed prion chicks in the South End tussock were observed to be vulnerable to predation by rats shortly after hatching (MacKay et al. 2001), but stomach samples in February 2001, when predation was not noted in that area, also contained prion feathers and maggots.

At present, prions are virtually absent in the area of the Rookery tussac where the highest density of rats is observed, and in other tussac areas their breeding success is lower than in open areas (Catry et al. 2007). However, there is insufficient evidence to show that rodents are responsible for the apparent lower breeding success of prions in tussac habitats on New Island. Other tussac islands, such as Bird Island (SW Falklands), where rodents are absent and prions breed in large numbers, are an example where prions nest in much greater density in areas containing more friable soils than in the dense tussac peat.

According to our data, the impact of predation by introduced mammals on the large population of thin-billed prions at New Island appears to be small. We observed the chief cause of chick mortality to be starvation, followed by predation by native predators, while predation by rodents is only occasionally observed. The unique set of introduced mammals at New Island would appear to be mainly dependent on the terrestrial food web, while using marine-derived food as an opportunistic supplement to their terrestrial diet.

Since the removal of sheep, the vegetation cover of New Island has changed from a sparsely covered terrain to a dense growth of vegetation. Ground nesting species such as Falkland pipits *Anthus corredera grayi*, long-tailed meadowlarks *Sturnella loyca falklandica* and Falkland thrushes *Turdus f. falcklandii* are now common breeders. Black-throated finches *Melanodera m. melanodera*, tussac birds *Cinclodes a. antarcticus* and black-chinned siskins *Carduelis barbata* and grass wrens *Cistothorus platensis falklandicus* breed in smaller numbers. Dark-face ground tyrants *Muscisaxicola macloviana* are also common breeders. The main influence on their increase and breeding is a direct result of removing stock, but is also an important indicator that rodents have little impact on these species at New Island.

One ground-nester, the Cobb's wren *Trogolodytes cobbi* is absent from New Island in the breeding season, but sometimes observed in winter. However, this species is also absent from several rat-free islands, two examples being South Fur Island and South Jason Island. It is also very uncommon on Beauchêne Island where it appears to be restricted to specific habitats. The absence of this species from New Island may therefore be due to unsuitable habitat, and care should be taken in the often generalized assumption that rodents are solely the reason for its absence from some islands.

The present information therefore suggests:

1. there is no urgency for eradication of rodents at New Island; however, close monitoring of the present equilibrium is required,
2. short-term measures of control may not be effective, because the populations have strong compensatory responses,
3. although the current population of thin-billed prions is not at risk from predation in their main habitat (open areas), the eradication of rodents from the island would potentially make more habitat available to the thin-billed prions and other ground nesting birds,
4. if any eradication is considered in the future, it may need to include all introduced mammals (rats, mice, rabbits and cats) because little information exists on interrelationships and the possible effects of partial removal of invasive species.

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