Stable isotopes reveal evidence of predation by ship rats on seabirds on the Shiant Islands, Scotland

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Summary

1. Introduced predators are a major threat to native island populations, yet direct evidence of predation is often lacking, especially when it is difficult to detect by traditional dietary methods.

2. Historical declines of nesting seabirds on the Shiant Islands, Outer Hebrides, roughly coincided with the accidental introduction of ship rats *Rattus rattus* in *c*. 1900. Rats have been implicated in declines of seabirds, but the Shiant population is one of two remaining naturalized *R. rattus* populations in Britain, prompting calls for their protection.

3. Live-trapping studies with stable isotopes and gut content analysis were used to investigate whether ship rats prey on Shiant Islands seabirds. Another aim of this study was to determine whether marine-derived foods subsidize rat populations, permitting higher densities, greater productivity and larger body size than expected from terrestrial resources alone.

4. Comparisons of stable carbon and nitrogen isotopic signatures of rat tissues with those of seabirds, marine invertebrates, marine algae and land-based foods revealed that seabirds and other marine prey were the primary source of protein for rats living in colonies or near the shore. These results were corroborated by gut content analysis, and suggest a greater role for active predation of seabirds by rats than has previously been apparent at this locality.

5. Seabird colonies and especially coastal areas supported higher numbers of rats than more inland habitats. Coastal and colony-dwelling rats were more active reproductively and were larger than those living inland.

6. Although rats are capable of surviving solely on terrestrial foods, their ability to use marine prey may buffer populations during lean times, i.e. outside the seabird nesting season, and may in part explain their success and status as pests on islands world-wide. Overall, this work reveals the value of stable isotopes in identifying predation by exotic species, but also underscores potential uncertainties inherent in all diet-based methods in distinguishing predation from scavenging.

Key-words: gut content analysis, Hebrides, introduced predators, marine subsidies, *Rattus rattus*.

Journal of Applied Ecology (2002) **39**, 831–840

Introduction

Introduced predators pose a significant threat to the conservation of native animal populations world-wide (Mooney & Drake 1984; Manchester & Bullock 2000). Island populations are especially vulnerable to exotic predators because dispersal opportunities are limited and because many such insular populations evolved in the absence of natural enemies. This is particularly true for seabirds, which must return to land to raise their young, often nesting on islands where terrestrial predators are generally absent (Atkinson 1985). Population declines and extinctions of nesting colonies have been attributed to the arrival of exotic predators, notably feral cats *Felis catus* (L.), foxes *Vulpes* sp., *Alopex* sp. and rats *Rattus* sp. (Moors & Atkinson

1984). Programmes to control or eradicate exotic pests have successfully restored some native populations (Moors & Atkinson 1984; Jackson 2001; Donlan, Tershy & Croll 2002), but these efforts are expensive, difficult logistically and sometimes controversial.

One such case is that of the black or ship rat *Rattus rattus* (L.) on the Shiant Islands, in the Outer Hebrides off north-western Scotland (McDonald, Hutchings & Keeling 1997). Rats are thought to have arrived on these small islands around 1900 as a result of a shipwreck (Haswell-Smith 1996). Ship rats were common throughout Great Britain until the introduction of the larger Norway or brown rat *Rattus norvegicus* (Berkenhout) in the early 18th century, and were common in sea ports and major cities until the late 1800s; thereafter, improved rodent control and sanitation measures dramatically reduced commensal populations (Twigg 1992; Harris *et al*. 1995). Transient populations persist in larger cities and ports but the Shiant Islands population is one of only two remaining naturalized populations in Britain. Ship rats, because of their low numbers and restricted distribution, are listed as endangered in Britain (Morris 1993), yet they are roundly considered a pest and categorized as a harmful naturalized species under Schedule 9 of the 1981 Wildlife and Countryside Act.

The presence of rats on the Shiant Islands represents a potential threat to large nesting populations of seabirds, which includes *c*. 80 000 pairs of Atlantic puffins *Fratercula arctica* (L.), 13 000 pairs of common guillemots *Uria aalge* (Pontoppidan), 11 000 pairs of razorbills *Alca torda* (L.) and smaller colonies of northern fulmars *Fulmarus glacialis* (L.), black-legged kittiwakes *Rissa tridactyla* (L.) and several gull species (*Larus* spp.; Brooke 1972, 1973; Lloyd, Tasker & Partridge 1991). Rats have been implicated in the historical declines of puffins and other seabirds on the Shiant Islands and elsewhere in Britain (Lockley 1953; Harris 1984; Lovegrove, Williams & Williams 1994). Key *et al*. (1998) found feathers in faeces of Shiant Islands rats, but suggested that this mostly reflected scavenging of birds killed by gulls. Both Key *et al*. (1998) and McDonald, Hutchings & Keeling (1997) questioned whether rats actively preyed upon large numbers of seabirds, and argued that the Shiant Islands rat population was of sufficiently unique scientific value to warrant protection from eradication.

Predation in general is rarely observed directly, and reports of seabird predation are often based on the presence of feathers and bones in faecal pellets (McDonald, Hutchings & Keeling 1997; Key *et al*. 1998). However, faecal and gut content analyses underestimate consumption of eggs and nestlings, which are highly digestible. Traditional methods are also inadequate for evaluating the importance of seabirds in rat diets. This is necessary to estimate the degree to which rats depend on seabird prey and hence affect seabird populations. In contrast, recent advances in analysis of stable isotopes (Peterson & Fry 1987) have demon-strated the utility of this technique for studying trophic interactions, particularly at the land–ocean interface (Hobson 1987; Stapp, Polis & Sánchez Piñero 1999). Unlike conventional methods, which provide a record of diet from one to a few meals, the isotopic composition of consumer tissue is an integrated measure of the contributions and assimilation of different food sources over time. Bias associated with differential digestibility is less important than in faecal and gut content analysis, although selective metabolism, storage and isotope fractionation of nutrients from different sources can complicate the interpretation of isotope signatures (Gannes, O'Brien & Martínez del Rio 1997; Hobson & Stirling 1997). Hobson, Drever & Kaiser (1999) and Drever *et al*. (2000) recently used stable isotope analysis to show that small mammals, including *R. norvegicus*, prey on seabirds and their eggs.

Carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) are the most widely used isotope ratios for identifying diet sources. Carbon isotopes are particularly useful in coastal environments because they permit distinction between the consumption of marine vs. terrestrial prey (Peterson & Fry 1987). Nitrogen isotopes are used to determine diet source and also trophic position, because N isotope values tend to increase predictably by 3–5‰ between successive levels of consumers in a food chain (Schoeninger, DeNiro & Tauber 1983; Minagawa & Wada 1984). Additionally, body tissues differ in their metabolic activity (DeNiro & Epstein 1978), therefore it is possible to analyse multiple tissues to estimate an animal's diet over a range of time scales. In diet-switching experiments of gerbils *Meriones unguiculatus* (Milne-Edwards) turnover rates of C were highest in liver, with a half-life of 6·4 days, intermediate in muscle and brain tissue (27·6–28·2 days) and longest in tissues such as hair (47·5 days), bone and connective tissue (Tieszen *et al*. 1983). Similarly, Hilderbrand *et al*. (1996) described rapid C and N turnover rates for blood plasma (half-life = 4 days) and red blood cells (28 days) of black bears *Ursus americanus* (Pallas). Hobson & Clark (1992) reported a half-life of 173·3 days of C in bone of Japanese quail *Coturnix japonica* (Temminck & Schlegel) and suggested that analysis of bone collagen C may provide the best measure of lifetime integration of diet. Tieszen *et al*. (1983) advocated combining isotopic analysis of tissues spanning a range of turnover rates with traditional methods such as faecal or gut content analysis to establish an animal's complete dietary history.

This study evaluated the role of ship rats as predators of nesting seabirds on the Shiant Islands. Gut content and stable isotope analysis were used to compare the diets of rats captured in seabird colonies with those living in inland areas and near the ocean shore. Rats in coastal habitats reportedly eat littoral prey (Drummond 1960; Pye & Bonner 1980; Navarrete & Castilla 1993), which provides a plentiful source of protein and energy year-round. It was hypothesized that marine resources, i.e. seabirds and littoral prey, subsidize rat populations,

allowing them to attain high population densities locally and to persist on the Shiant Islands during periods when terrestrial resources are less available. It was also predicted that, as a consequence of the high nutritive quality of marine foods and increased crowding, subsidized rats would reach larger body size and would prolong breeding activity relative to rats that depend solely on land-based foods.

Study area

The Shiant Islands (57°54′N, 6°22′W) lie in The Minch, approximately 8 km south of Lewis and 21 km north of Skye (Fig. 1). The group consists of three main islands, two of which (Eilean an Tighe, 54 ha, and Garbh Eilean, 88 ha) are connected by a narrow cobble bar. The third island, Eilean Mhuire (31 ha), is 0·6 km east of Garbh Eilean. The islands have remained largely uninhabited since 1901 (Haswell-Smith 1996).

The islands are recognized as a site of special conservation interest by Scottish Natural Heritage (SNH).

Access to the interior of the islands, and especially Garbh Eilean, is restricted by the presence of steep cliffs of columnar basalt, which rise as high as 150 m above the sea. Cliffs also form the eastern coast of Eilean an Tighe but the island slopes more gently on the western side, forming grassy terraces strewn with boulders and ruins of stone walls and buildings. Evidence of rats (faeces, runways, burrows) was found in these ruins, among boulder piles, along cliffs and among rock walls. Fulmars, kittiwakes and guillemots nest in cliffs on all the islands but the largest seabird colonies are located on Garbh Eilean, in a large boulder field and grassy slopes beneath the northern and eastern cliffs. Brooke (1972) estimated that puffins occupied approximately 59 000 burrows in these areas in 1970, counting 1150 razorbills and 440 shags *Phalacrocorax aristotelis* (L.) among the boulders in the same year
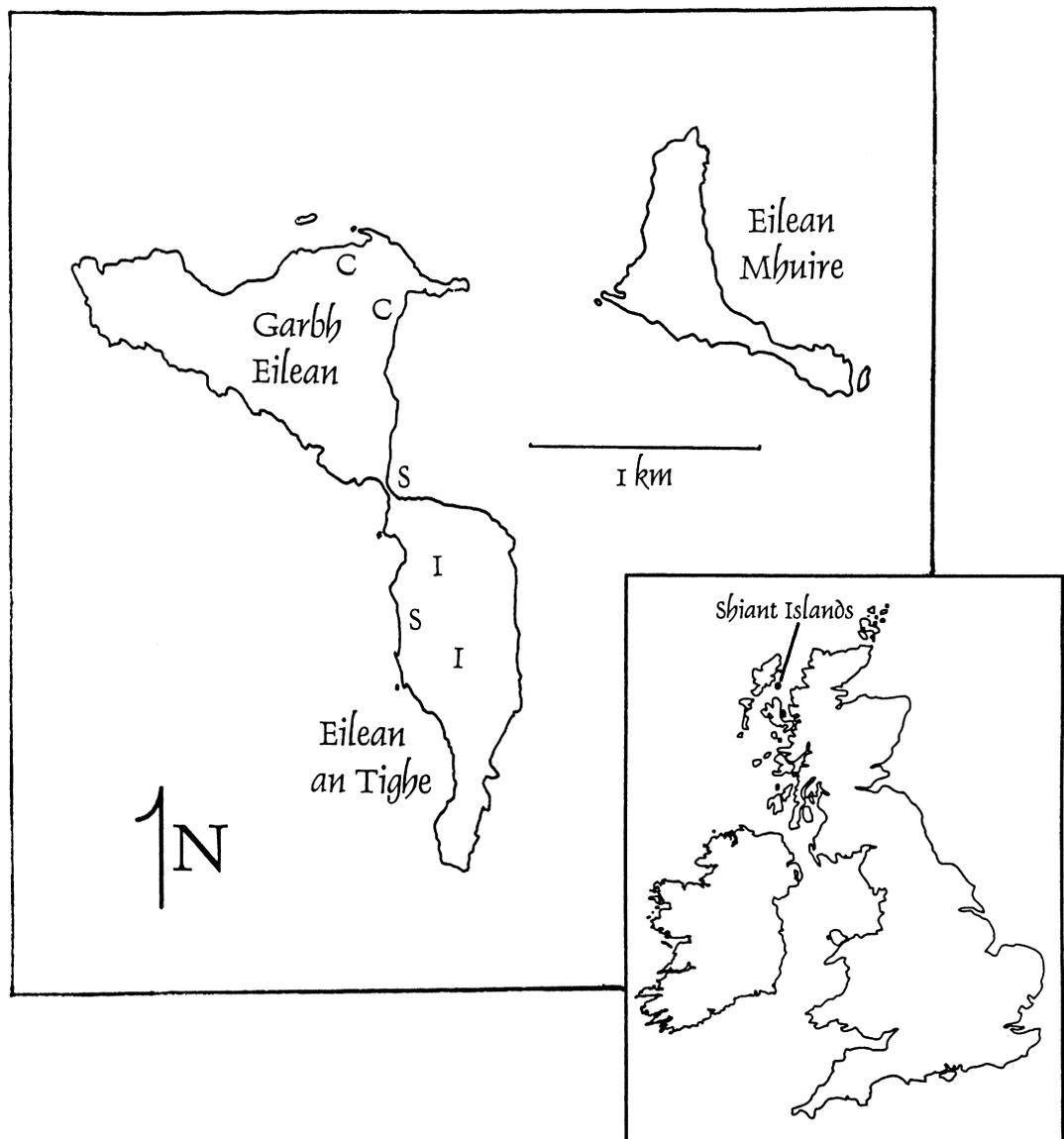

Fig. 1. Map of the Shiant Islands, Outer Hebrides, Scotland, showing the location of trapping sites in seabird colonies (C), near shore (S) and inland (I).

(Brooke 1973). Smaller groups of herring gulls *Larus argentatus* (Pontoppidan) and greater *Larus marinus* (L.) and lesser black-backed gulls *Larus fuscus* (L.) nest primarily near the cliff tops. Ship rats and domestic sheep *Ovis aries* (L.) are the only resident land mammals, although otters *Lutra lutra* (L.) are occasional.

Methods

Field work was conducted during a single visit to the islands from 22 to 28 August 2000. Although rats are present on Eilean Mhuire (Key *et al.* 1998; Maclennan, Ferguson & Buxton 2000) all work was conducted on Eilean an Tighe and Garbh Eilean. Rats were trapped at six different sites, representing three habitat types (Fig. 1). Traps were placed along stone walls and ruins and among loose boulders > 200 m from the western shore of Eilean an Tighe to sample inland habitats. Shore trapping areas were < 50 m from the sea on Eilean an Tighe. One site was on the western coast; the other was along the narrow gravel bar connecting the two islands. Seabird colony sites were located on Garbh Eilean. One site was located on a steep grassy slope riddled with puffin burrows, and the second site was at the edge of the boulder field.

Groups of 8 to 12 Tomahawk cage traps ($41 \times 13 \times 13$ cm) (Tomahawk, Wisconsin, USA) were baited with peanut butter and set in pairs of transects for two nights at each site. Traps were opened in the late afternoon and checked and closed each morning. Captured individuals were weighed, measured and marked with a coloured felt marker to distinguish recaptures from new individuals. A sample of 14–16 rats from each habitat type was killed by injection with a mixture of sodium pentobarbitone (Pentoject, 4 ml; Animalcare Ltd, York, UK) and local analgesic (procaine hydrochloride, Willcaine, 1 ml; Arnolds Veterinary Products Ltd, Shrewsbury, UK) to collect tissue samples for stable isotope analysis and to examine gut contents. Each rat was dissected and a small piece of liver and thigh muscle and two toes (for bone tissue) were placed in separate vials containing 70% ethanol. The stomach and intestines were then removed and washed and the contents were examined in the field. Recognizable food items were placed into broad diet categories; no attempt was made to quantify percentage composition by volume of different foods. Animal capture, handling and euthanasia procedures followed UK Home Office guidelines approved by the Biology Department at the University of York, UK.

Samples of potential food items of rats were also collected for stable isotope analysis. Leaf material from terrestrial plants and marine algae were gathered and dried in envelopes. Invertebrates were collected by hand and by pitfall trapping and stored in 70% ethanol. SNH staff and the landowner collected seabird tissues during a population survey in June 2000. Tissues included muscle tissue from carcasses of four razorbill chicks, neck muscle from four adult Atlantic puffins

killed by gulls, and solid contents of the discarded eggs of one Atlantic puffin, razorbill, lesser black-backed gull and northern fulmar, which were stored in separate vials containing ethanol. Resident seabird species differed in their diets and isotopic signatures (Hobson, Piatt & Pitocchelli 1994) were used with the aim of determining which species were most susceptible to rat predation. Although insufficient numbers of tissue samples from all breeding species could be safely and efficiently salvaged at the time of the June survey, the samples collected reflected the relative abundance of ground-nesting species on the islands and were judged to be representative of seabird prey available to rats.

Vials containing animal tissue were frozen upon returning to the laboratory. Samples were oven-dried at 50 °C for 24 h, ground by mortar and pestle to homogenize the material, and placed in tin capsules. Collagen was not separated from bone taken from toes of rats, therefore isotopic values of bone C included both organic and inorganic fractions. Lipids were also not extracted from samples. The presence of lipids, which are depleted in ^{13}C (DeNiro & Epstein 1978; Tieszen *et al.* 1983), may result in uncharacteristically low δ^{13}C values, and tissues with a high proportion of lipids would be more sensitive to this source of error. Comparisons of C isotope ratios of tissues containing lipids with those of the same tissues from which lipids had been extracted, however, suggested that the resulting bias may be relatively small (< 2‰). δ^{13}C values of bone collagen of six deer (*Odocoileus* sp.) were 0·53‰ lower (more negative) than those of collagen with lipids removed (Chisholm *et al.* 1983), a difference that was not statistically significant (paired-t = 1·28, P = 0·255; calculated from Chisholm *et al.* 1983, table 3). Liden, Takahashi & Nelson (1995) reported slightly larger differences (0·8–1·8‰) in δ^{13}C values of collagen and lipid-free collagen from bones of two pigs (*Sus* sp.) and two foxes (*Alopex* sp.). Comparing δ^{13}C values of avian egg constituents, Hobson (1995) found a mean difference of 1·64‰ between whole and lipid-free yolk (n = 5 avian species; calculated from Hobson 1995, table 2). Additionally, the amount of isotope fractionation between diet and rat tissue may have been different for the different tissues but there were no data to determine the presence or magnitude of such variation. For these reasons, and because of the high variability in isotopic signatures of some potential prey items, estimates of the relative contributions of different foods to rat diets using a multiple-source mixing model were not attempted (cf. Ben-David *et al.* 1997) but instead this study sought to identify qualitatively the distinct differences in isotopic signatures and, hence, diets among rats from different habitats and their possible use of seabird prey.

Samples were analysed for stable C and N isotope ratios using a Europa Hydra 20–20 isotope ratio mass spectrometer at the University of California Davis Stable Isotope Facility (Davis, CA). Isotopic composition was

Table 1. Comparisons of trap success, demography and standard morphological traits among ship rats *Rattus rattus* captured near shore, in seabird colonies, and in inland areas of the Shiant Islands, Outer Hebrides. Values are means ± 1 standard error. Morphological measurements are from adult rats, with sample size given in parentheses. Entries with different letters (head and body length) are significantly different from one another (ANOVA with Tukey HSD test, $P < 0.05$)

Variable	Shore	Colony	Inland
Trap success (no. per 100 trap-nights)*	79·17 ± 4·18 (28/36)	81·25 ± 0 (26/32)	37·50 ± 16·72 (18/48)
% Juvenile	17·86	15·38	0
% Male	57·14	61·54	66·67
% Reproductive (adults)	56·52	36·36	33·33
% Black colour phase (vs. brown)	67·86	57·69	44·44
Weight (g)	226·1 ± 9·2 (17)	211·7 ± 11·9 (15)	207·7 ± 15·3 (7)
Head and body length (mm)	184·4 ± 2·4a (17)	175·9 ± 3·7ab (14)	169·7 ± 6·4b (7)
Tail length (mm)	237·3 ± 7·9 (11)	231·9 ± 3·6 (13)	206·0 ± 19·6 (6)
Hind foot (mm)	38·2 ± 0·7 (17)	38·9 ± 0·3 (15)	36·6 ± 1·5 (7)
Ear (mm)	24·5 ± 0·2 (16)	25·3 ± 0·3 (14)	24·9 ± 0·6 (7)

*Numbers in parentheses are the total number of individuals captured/total number of trap-nights, with $n = 2$ sites of each type, trapped for two nights.

expressed as the ratio of the heavy to light isotope relative to a standard, using delta (δ) notation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where X is ^{13}C and ^{15}N, R is the corresponding ratio ^{13}C/^{12}C and ^{15}N/^{14}N, and the units are parts per thousand (‰). The laboratory standard for estimating δ^{13}C was beet sucrose (−23·83‰ vs. PeeDee Belemnite, calibrated against NIST 22 at −29·73‰), and for δ^{15}N ammonium sulphate (1·33‰ vs. air, calibrated against IAEN1 and IAEN2; D. Harris, University of California, Davis, CA, personal communication). Isotopic values of 42 standard samples analysed concurrently with tissue samples deviated by 0·04% and 1·50% from the laboratory standards for δ^{13}C and δ^{15}N, respectively (mean ± standard deviation: δ^{13}C = −23·82 ± 0·05‰; δ^{15}N = 1·31 ± 0·10‰; $n = 42$).

Results

Capture success, expressed as the number of individuals captured per 100 trap-nights, was much higher at shore and colony sites than at inland sites (Table 1). Differences among the three habitat types were marginally non-significant ($F = 6·19$, d.f. = 2, 3, $P = 0·086$) but shore and colony sites combined had higher capture success than inland sites ($t = −4·05$, d.f. = 4, $P = 0·016$). Although transects covered roughly the same amount of area in each habitat (130–180 m), trapping effort was too low to calculate meaningful estimates of population density. However, rats more readily entered traps in colony areas (night 1 capture success = 81·25%) and near shore (66·67%) than farther inland (8·33%), and new individuals quickly replaced those culled for

tissue samples from shore and colony sites. Differences in capture success were therefore assumed to reflect qualitative differences in the abundance of rats among habitat types. Populations also tended to differ demographically among habitats: juvenile rats were only captured at shore and colony sites, and a greater proportion of adult rats captured near shore were judged to be in breeding condition (swollen testes, evidence of lactation or pregnancy) than in colony and inland areas (Table 1). Sex ratio was similar across habitat types. Body size of rats also differed among habitat types. Adult rats captured in inland areas were consistently smaller than those in the other two habitats for most measurements, and were significantly smaller in body length, the most meaningful measurement of overall size, than those near shore ($F = 3·68$, d.f. = 2, 35, $P = 0·035$; Table 1). Individuals of both brown and black colour phases were captured at all sites but black morphs made up a greater proportion of rats captured near shore and in colonies than in inland areas (Table 1).

Gut contents revealed that rats living near shore consumed a broader variety of food items than those from other habitats (Table 2). Marine prey were found in guts of 44% of rats collected near shore, and included seabird feathers, fish scales and muscle tissue of molluscs (e.g. periwinkles *Littorina* sp. and dog whelks *Nucella* sp.). Only plants and exoskeletal remains of insects (presumably adult carabid beetles or caterpillars) were found in the guts of rats from colony and inland areas. Most (74%) rats consumed leaf material, which was too finely chewed to be identified in the field. No seabird remains were found in the guts of rats from colonies, which was not surprising given that the nesting season had ended a few weeks earlier

Table 2. Percentage occurrence of food items in guts of ship rats of the Shiant Islands. Sample size is given in parentheses

Variable	Shore (16)	Colony (16)	Inland (14)
Seabird feathers	12·5	0	0
Marine invertebrates	31·25	0	0
Fish scales	18·75	0	0
Plants	31·25	100	92·86
Terrestrial arthropods	25	18·75	57·14
Rat hair	43·75	0	21·43

Table 3. *F*-ratios from analysis of variance tests to determine differences in stable C and N isotope signatures of tissues (liver, l; muscle, m; bone, b) of ship rats collected in three different habitat types (shore, S; colony, C; inland, I) on the Shiant Islands. In all cases, $n = 10$ samples of each tissue from each habitat and d.f. = 2, 27. Order of letters indicates decreasing levels of isotopic enrichment. Letters joined by underlining were not significantly different from one another (Tukey HSD multiple comparison test; $P \leq 0.05$; NS = not significant). *F*-ratio significance values: *$P \leq 0.05$; **$P \leq 0.0001$

	Carbon ($\delta^{13}C$)		Nitrogen ($\delta^{15}N$)	
	F	Tukey HSD	*F*	Tukey HSD
(a) Differences among tissues				
Shore	3·43*	NS	0·4	NS
Colony	16·12**	b m l	3·94*	l b m
Inland	23·32**	b l m	0·08	NS
(b) Differences among habitats				
Liver	38·46**	S C I	119·53**	C S I
Muscle	56·89**	S C I	103·12**	C S I
Bone	35·26**	S C I	86·16**	C S I

(M. de L. Brooke, Cambridge University, Cambridge, UK, personal communication) and that few seabird carcasses were found.

Rat tissues differed in their stable C and N isotope signatures. $\delta^{13}C$ values of bone were consistently more enriched than those of liver and muscle, but were significantly different from liver and muscle $\delta^{13}C$ only at inland sites, and from liver $\delta^{13}C$ only at colony sites (Table 3). On average, $\delta^{15}N$ varied little among tissues collected in inland and shore areas (Table 3), suggesting that rats in these areas fed at the same trophic level over time. In contrast, liver $\delta^{15}N$ of rats from colony areas was enriched relative to muscle and, to a lesser degree, bone, which suggested a slight shift in trophic position of colony rats over time.

Differences in isotope signatures among habitat types were highly significant for all rat tissues (Table 3). The order of the $\delta^{13}C$ and $\delta^{15}N$ values was always the same across tissues, with rats from colony areas having the highest $\delta^{15}N$ values, those from shore areas having the highest $\delta^{13}C$ values, and rats from inland areas having significantly less enriched values for both $\delta^{13}C$ and $\delta^{15}N$. Rats from shore and colony areas had similar $\delta^{13}C$ for muscle and bone, but liver $\delta^{13}C$ for shore rats was significantly enriched compared with that of colony rats.

The distinct diets of rats from the three habitat types were clear when the isotope signatures of rats and their potential prey were plotted together (Fig. 2). Assuming a step-wise trophic shift in $\delta^{15}N$ of 3–5‰ between consumers (Schoeninger, DeNiro & Tauber 1983), rats captured in colonies derived most of their protein from seabirds ($\Delta\delta^{15}N$, defined as the difference between mean $\delta^{15}N$ values of a consumer and a potential food source, for rat and seabird tissues = 17·12–11·90 = 5·22‰). The enriched $\delta^{13}C$ values of bone and muscle, the tissues with the longest metabolic turnover times (Tieszen *et al.* 1983; Hobson & Clark 1992), suggested that consumption of seabirds occurred during or prior to the 2000 nesting period. Bone and muscle $\delta^{13}C$ values of rats differed significantly from those of adult seabirds ($F = 8.27$, d.f. = 2, 21, $P = 0.002$) but were similar to $\delta^{13}C$ values of egg and chick tissue ($F = 3.80$, d.f. = 2, 22, $P = 0.081$), which suggested that rats ate primarily eggs and chicks and not adults. Interestingly, the depleted $\delta^{13}C$ and enriched $\delta^{15}N$ values of liver from colony rats were consistent with a slight increase in consumption of plants or their insect herbivores. Grass (*Holcus lanatus* L.) fertilized by seabird guano had significantly higher $\delta^{15}N$ ($t = 100.90$, d.f. = 8·0, $P < 0.0001$) than the same plants growing outside the colony (Fig. 2). Because there is little evidence of consistent N fractionation between herbivores and their plant foods (Stapp, Polis & Sánchez Piñero 1999), increased consumption of guano-fertilized plants or their insect herbivores would be expected to result in lower $\delta^{13}C$ and higher $\delta^{15}N$ than a diet of seabirds.

The isotopic signatures of shore-dwelling rats indicated that littoral prey were an important source of protein, although the depleted $\delta^{13}C$ values relative to intertidal organisms suggested they also consumed some terrestrial foods (Fig. 2). Of the prey items collected, the most likely foods were marine isopods and woodlice ($\Delta\delta^{15}N = 2.98$–3·27‰), periwinkles ($\Delta\delta^{15}N = 5.03$‰) and amphipods ($\Delta\delta^{15}N = 5.62$‰). Rats from the two shore areas apparently had somewhat different diets: rats captured on the gravel bar, where capture rates were highest, had significantly higher bone and liver $\delta^{15}N$ (*t*-tests, $P < 0.05$) than those from the rocky shelves of the western coast. Combined with the large amount of hair found in guts of shore rats (Table 2), this result revealed the possibility of cannibalism, as was suggested by Atkinson (1949) and Goulding (1996), especially in areas of high population densities. The diet of inland rats was distinct from that of the other populations, but it was difficult to discern food composition based on isotopic signatures (Fig. 2). This may represent inadequate sampling of potential prey items from terrestrial habitats or consumption of prey such as slugs, caterpillars and woodlice, which have extremely variable signatures. At this latitude, both colony and inland plants use C_3 photosynthesis, as evidenced by their depleted $\delta^{13}C$ values, which clearly
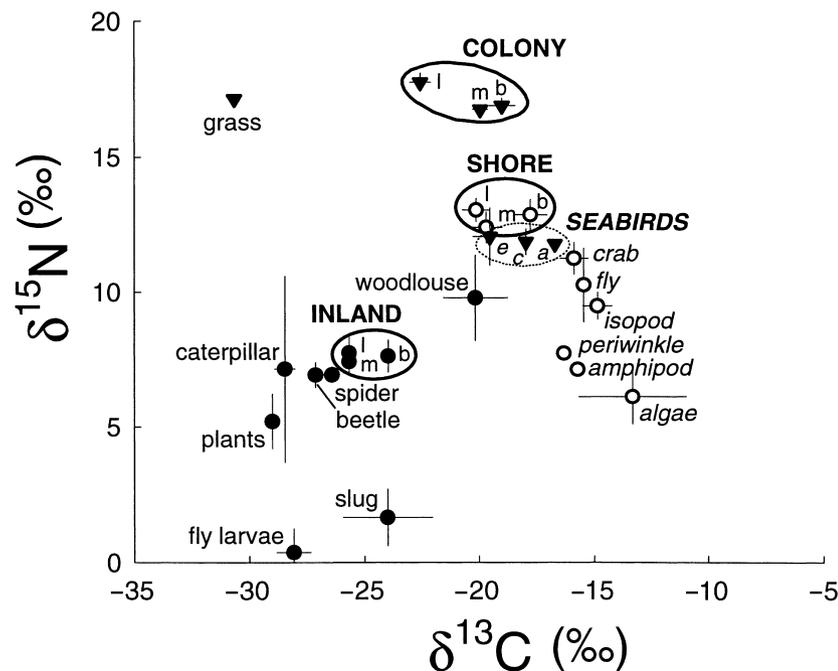
Fig. 2. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic signatures of tissues of ship rats and potential terrestrial and marine foods on the Shiant Islands. Values are means ± 1 standard error. Samples were collected at two sites near shore (open circles), in inland areas (filled circles) and in seabird colonies (filled triangles). Solid ellipses encircle signatures of bone (b), muscle (m) and liver (l) tissues of ship rats ($n = 10$) from each area. Seabird tissues (dashed ellipse; $n = 4$ each) were egg (e) of puffin, fulmar, gull and razorbill, muscle of razorbill chicks (c) and neck muscle of adult puffins (a). Other potential food items (n): plants, mean of seven species [*Festuca ovina* (L.), *Deschampsia flexuosa* (L.), *Molinia caerulea* (L.) (three each); *Holcus lanatus* (L.) (five inland, five colony); *Cochlearia officinalis* (L.), *Armeria maritima* (Willdenow), *Potentilla anserina* (L.), two each]; algae, mean of three genera (*Fucus, Ascophyllum, Enteromorpha*; three each); intertidal and littoral invertebrates [crab, *Carcinus* sp. (3); periwinkle, *Littorina* sp. (3); marine isopod, *Ligia oceanica* (L.) (3); unidentified kelp fly (3); unidentified amphipod (3)]; and samples of unidentified species of slug (3), fly larvae (3), woodlouse (3), caterpillar (3), Carabidae beetle (4), and cursorial spider (4).

distinguishes them from food items derived directly from the sea (Fig. 2).

Discussion

Stable isotope analysis revealed that ship rats on the Shiant Islands obtain much of their protein from marine-derived foods, including seabirds and littoral invertebrates. Rats living in colonies clearly use seabird tissues for tissue growth and development. Key *et al.* (1998) found quills and feathers in 42–68% of the rat faeces they examined from the Shiant Islands but downplayed the role of rats as predators, suggesting that rats mostly scavenged birds killed by gulls. Although the results from this study cannot distinguish predation from scavenging, $\delta^{13}C$ values of rat tissues were more similar to those of eggs and chicks than adult seabirds, which, for burrow-nesting species such as puffins, would be less vulnerable to gull predation for most of their development. Rats are known to kill and eat adults of small-bodied species of seabirds, but in most cases predation by rats tends to be focused on eggs and young when these are available (Atkinson 1985). Scavenging of addled eggs and dead nestlings cannot, however, be ruled out. Peak egg-laying by puffins, razorbills and guillemots on the Shiant Islands typically occurs in late May, with chicks and fledglings

present from June until late July (guillemots, razorbills) and mid-August (puffins; M. de L. Brooke, personal communication). The similarity between $\delta^{13}C$ values of rat tissues with the highest metabolic turnover rates (liver and muscle; Tieszen *et al.* 1983) and those of eggs and chicks suggests that some scavenging probably occurred because these prey would not usually be abundant for most of the period for which these tissues would be expected to be reflective of diet (with half-lives of 6 and 28 days for liver and muscle C, respectively, assuming similar turnover rates for rats and captive gerbils; Tieszen *et al.* 1983). Even for gerbils, however, complete turnover of liver C did not occur until 84 days after source diets had been switched, during which time liver samples had $\delta^{13}C$ values that were intermediate between the two diet endpoints (Tieszen *et al.* 1983). It therefore seems likely that C isotopic signatures of rats reflect consumption of seabird tissues taken during the recently completed nesting season. Note, however, that because rat and seabird samples were only collected over a single season, this study could not address potential interannual variation in the consumption of seabird tissue.

Little evidence of seabirds was found in the guts of rats, which was not surprising given the scarcity of seabirds at the time of this study. McDonald, Hutchings & Keeling (1997) similarly found little evidence of seabird

remains in rat faeces collected in May, prior to the onset of egg-laying and hatching of most birds. Stable isotope analysis therefore complemented traditional methods of diet analysis (e.g. gut content analysis) by revealing the importance of seabirds as a seasonal food resource. Moreover, differences in isotope signatures among tissues of colony rats demonstrated the switch in rat diets from seabirds to terrestrial foods after the nesting season, which was apparent in guts of rats as well. Both techniques also showed the importance of marine prey in the diet of rats living near shore, although gut contents provided more detailed corroborative information on the diversity of foods eaten by these rats, which included littoral invertebrates, terrestrial arthropods and plants, and marine and land-based carrion. In contrast, rats living farther inland consumed exclusively terrestrial foods, which corroborates results of previous diet studies based on faeces (Goulding 1996; McDonald, Hutchings & Keeling 1997; Key *et al.* 1998; Maclennan, Ferguson & Buxton 2000).

Although rats clearly are capable of surviving on land-based foods, the results from this study suggest that marine resources subsidize insular rat populations, permitting higher densities than would be possible based on terrestrial resources alone. Populations with access to marine prey attained higher population densities, and individuals tended to be larger and exhibited greater reproductive activity, than those living farther inland. Two of the three past surveys of the Islands rat population also reported higher abundance or activity and larger body size of rats in and near seabird colonies than in other areas (Key *et al.* 1998; Maclennan, Ferguson & Buxton 2000). Rats on the Shiant Islands are also larger than mainland populations, which typically weigh < 200 g (Macdonald & Barrett 1993). This was particularly true of rats captured near shore, which were also more aggressive and vocal than those captured in other habitats.

Whereas seabirds are a rich but ephemeral food resource to rats, littoral and supralittoral prey represent a critical source of nutrients and energy that is available year-round. The extent to which coastal populations of rats act as dispersal sources for the remainder of the islands is not known, but the availability and quality of marine resources may buffer the Islands populations during periods when seabirds are absent and terrestrial foods are less plentiful. Marine subsidies support high insular and coastal densities of small mammals and other consumers in the Sea of Cortez, Mexico (Case 1975; Rose & Polis 1998; P. Stapp & G. A. Polis, in press) and elsewhere (Nilsson 1977; Bengston & Block 1983; Drever *et al.* 2000), and may in part explain the persistence and widespread distribution of small omnivorous mammals on islands worldwide. The ability of introduced rats to take advantage of a broad range of resources, including marine-based foods, undoubtedly has contributed to their success on islands, usually with disastrous consequences for

native vertebrate populations (Atkinson 1985). These problems have been compounded when cats have been introduced to control rats and mice, because cats are particularly effective seabird predators (Moors & Atkinson 1984). Thus, in such cases the availability of marine foods may have significant direct and indirect effects on seabirds as well as terrestrial populations: directly, by subsidizing rat populations over the winter months, and indirectly, by allowing the persistence of a consistent prey base (rats) for more effective seabird predators (cats) to ensure survival of predators during periods when seabirds are absent.

There are no records of the ecological consequences of the arrival of rats on the Shiant Islands, aside from their reputed effects on seabirds. The results presented here suggest a greater role for active predation by rats than has been argued previously, but the historical and current impact of the presence of rats on Shiant Islands seabirds remains unresolved. Lockley (1953) described at length instances of declines or extinctions of puffin colonies that he attributed to the arrival of rats, principally *R. norvegicus*, on islands. Harris (1984), however, reported that the Shiant Islands seabird colony stabilized after the declines of the first half of the century, even though rats still thrived on the islands. A recent survey (2000) of the colonies suggests that seabird populations have continued to be stable and may even have increased since the early 1970s (M. de L. Brooke, personal communication).

Although rat predation and other local factors may hasten the demise of a given colony, Harris (1984) concluded that the decrease in puffin numbers observed throughout the North Atlantic in the early 1900s was more likely to have been the result of regional changes in the marine environment, particularly the availability of fish prey. Historical accounts suggest that the introductions of rats were most detrimental for small colonies (e.g. St Margaret's, Cardigan Islands, UK) or for preventing the recovery of once-large colonies decimated by other mortality sources such as pollution or hunting (e.g. Preistholm, Lundy and Ailsa Craig, UK; Lockley 1953; Lovegrove, Williams & Williams 1994), or for colonies of smaller species of burrow-nesting seabirds. The presence of rats on the Shiant Islands probably limits opportunities for the establishment and growth of breeding populations of such small-bodied burrow-nesting seabirds [e.g. British storm petrels *Hydrobates pelagicus* (L.); McDonald, Hutchings & Keeling 1997] that are particularly susceptible to predation by rats (Atkinson 1985). Additional studies to quantify the rate of nest predation vs. scavenging, e.g. to monitor burrows remotely and to estimate egg and fledgling survival, are needed to clarify the role of rats as seabird predators. Because of the large size and current stability of the Shiant Islands populations, however, it was concluded that rat predation probably does not represent a significant threat to most resident seabirds, and at present there are no plans to implement a control programme (D. Maclennan, SNH, personal

communication). This provides researchers with a unique opportunity to study the ecology of a naturalized rat population in isolation from other rodents and largely in the absence of human control measures (McDonald, Hutchings & Keeling 1997), and to understand better the mechanisms by which rats and seabirds coexist in an extreme high-latitude insular environment.

Overall, the results of this project demonstrate the increasing utility of stable isotope analysis for elucidating trophic linkages across habitat and ecosystem boundaries (Stapp, Polis & Sánchez Piñero 1999) and for identifying food-web consequences of the spread of invasive and exotic species. The effects of invasive species may be direct, as in the case of introduced predators of seabirds and other native prey (Vander Zanden, Casselman & Rasmussen 1999), or manifest via complex indirect interactions, such as spillover predation and apparent competition (Roemer, Donlan & Courchamp 2002). When combined with conventional techniques for quantifying diet and detailed investigation of predator–prey interactions, stable isotope analysis can be a powerful tool for determining the potential impact of invasive species on native communities.

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