

Introduced black rats *Rattus rattus* on Ile de la Possession (Iles Crozet, Subantarctic): diet and trophic position in food webs

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Abstract Rats introduced on islands can affect ecosystem structure and function by feeding on terrestrial plants and both marine and terrestrial animals. The diet and trophic position of *Rattus rattus* introduced on Ile de la Possession (Iles Crozet) was assessed from two sites, according to the presence or absence of a king penguin colony. We used three complementary assays: macroanalyses of the stomach, faecal microhistology, and stable isotope analyses of $\delta^{15}\text{N}/\delta^{13}\text{C}$ in liver. Near the rookery, spermatophytes contributed on average 50% (confidence interval: 23–75) to the diet based on isotopes, mainly consisting in reproductive parts of *Poa* spp., *Agrostis magellanica*, and *Cerastium fontanum* identified in faeces. Terrestrial animal preys were represented by insects that contributed 25% (0–56) in isotopes, dominated in faeces by caterpillars of *Pringleophaga* spp. and adult weevils. Bird remains were found in faeces, forming 18% (6–30) of isotopes. Terrestrial earthworms contributed to 7% (0–21), with chaetae observed in faeces. On the other site, spermatophytes represented 62% (51–73) of assimilated food in rats' livers, mainly formed by Poaceae and *Acaena magellanica*, insects by caterpillars [24% (10–39)], and terrestrial earthworms [13% (2–23)]. Our results suggest that

rats, which were found at the top of terrestrial food chains, may have a direct role on a such simplified ecosystem, by preying on the most abundant and largest body-sized terrestrial invertebrates,—e.g. the keystone species *Pringleophaga* spp.—, and by feeding on both reproductive and vegetative parts of autochthonous and introduced plants. The discrepancies and usefulness of employing both isotopes and faecal analyses are discussed.

Keywords Introduced rodent · *Rattus rattus* · Diet · Stable isotopes · Food web · Subantarctic island

Introduction

Pronounced modification in plant community structure by introduced predators on insular ecosystems, e.g. arctic foxes *Alopex lagopus* in the Aleutian archipelago, has occurred via the reduction in nutrient transport from ocean to land through predation on seabirds (Croll et al. 2005; Maron et al. 2006). Rats introduced on islands are also associated with altered terrestrial communities and modified ecosystem properties (Drake and Hunt 2009; Fukami et al. 2006; Kurle et al. 2008; Mulder et al. 2009; Wardle et al. 2009). Indeed, these rodents are opportunist feeders, and they directly impact terrestrial communities by feeding on plants (Clark 1981; Grant-Hoffman and Barboza 2010; Grant-Hoffman et al. 2010a, b) and animals (Townsend et al. 2006, 2009). The effects of introduced small mammals on insular ecosystems is, however, difficult to assess (Courchamp et al. 2003) primarily because of interactions with other co-introduced species (Bergström et al. 2009; Quillfeldt et al. 2008). On subantarctic islands, however, ecosystems are species-poor and have high rates of endemism, and food chains are mainly detritus based

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(Davies 1973; Smith 1977; Tréhen et al. 1985; Vernon et al. 1998). The negative effects exerted by introduced mice *Mus musculus* on terrestrial communities in the sub-antarctic have been controversially documented (Angel et al. 2009; Chown and Smith 1993; Smith and Steenkamp 1992; Smith et al. 2002; but see van Aarde et al. 2004). Few studies have been devoted to identifying the detrimental effects of introduced black rats *Rattus rattus* on these remote islands (Jouventin et al. 2003; Quillfeldt et al. 2008; Shaw et al. 2005).

The quantitative determination of the diet of omnivorous rodents is difficult in the wild (Hansson 1970). Rats are nocturnal, cryptic rodents, which preclude their study by direct observation; thus, their diet can almost only be determined from stomach and faecal contents (Jordan 2005). Another method based on stable isotope tracers has shown that the isotopic composition of a predator is similar to that of its prey (DeNiro and Epstein 1978, 1981; Tieszen et al. 1983). Stable isotope ratios of carbon usually reflect dietary composition, while stable nitrogen isotope ratios usually indicate the trophic level of the prey item (DeNiro and Epstein 1978, 1981; Minagawa and Wada 1984). These ratios in organ tissues provide a more representative indication of diet history; however, such measures are less time-specific than those obtained by studying intestinal contents because they reflect an integration of all prey items assimilated over a different period of time depending on the tissue analysed (about 1 week to several months; Tieszen et al. 1983). Although the use of stable isotope analysis has advantages over conventional methods in food web studies, the optimal approach is to combine stable isotope analysis with conventional methods that provide a taxonomic resolution of resources (Post 2002; Vander Zanden et al. 1997). Isotopic mixing models are very helpful in providing quantitative indices of food item contributions in a consumer's diet, but they require prior classical diet analyses in order to select the correct potential resource items (Caut et al. 2008a).

As the single introduced mammal species on the sub-antarctic Ile de la Possession, Iles Crozet, for approximately two centuries (Chapuis et al. 1994; Frenot et al. 2005), the black rat offers the opportunity to detect its role on plant and animal communities without confounding effects from other introduced vertebrates. Little attention has been paid to this rodent's influence on native terrestrial ecosystems on this island (but see Jouventin et al. 2003). The purpose of this paper was to evaluate the position occupied by rats in food chains on Ile de la Possession and to discuss their potential effect on terrestrial communities, which can be inferred from the analysis of their diet from two habitats and at two seasons using three complementary assays: stomach and faecal contents, and isotopic signature in organ tissues.

Materials and methods

Sites and populations studied

The climate on Ile de la Possession (46°20'–28'S; 51°39'–52'E) is cold oceanic and is characterised by low amplitudes in mean monthly air temperature (2–3°C in the coldest winter month of July; 7–8°C in the warmest summer month of January), high annual rainfall (on average: 2,400 mm), and strong winds (Carcaillet 1995; Frenot et al. 2001).

In order to create a referenced catalogue of potential food materials to be used for both stomach, faecal, and isotope analyses, several individuals of all plant species were collected at hand. In order to collect the maximum of invertebrate species, pitfall traps were used, and soil quadrats, 20 × 20 cm large by 15 cm deep, were sampled and all below ground invertebrates manually extracted. Additionally, above ground invertebrates, including coastal species, were sought and caught by hand during continuous searches of 5–10 mn. Plants were identified to the species level and invertebrates to species, genus, or family levels by two of us (SG and PV).

Two sites were chosen in the north-eastern part of the island for the analysis of rat diet, according to the presence or absence of king penguins, *Aptenodytes patagonicus*. The first site was located in the Baie Américaine (46°23'24"S; 51°48'08"E). The rat traps were not arranged regularly in a standardised manner but placed according to the presence of traces of rats to increase successful catches. The trapping area could therefore not be precisely calculated, but traps arrangement formed approximately a line of 200 m long, located on average 70 m (approximately 20–130 m) from the high-tide level. The vegetation cover was mainly formed by mosses and two vascular plants, *Agrostis magellanica* and *Sagina procumbens*. Rare species (<10% cover) included *Blechnum penna-marina*, *Lycopodium magellanicum*, *Uncinia compacta*, *Juncus scheuchzeroides*, *Poa cookii*, *P. annua*, *Cerastium fontanum*, *Stellaria alsine*, *Galium antarcticum*, *Pringlea antiscorbutica*, and *Ranunculus biternatus*. The invertebrate community was dominated by earthworms (marine coastal: *Phreodrilus crozetensis*; terrestrial: *Microscolex crozetensis*, *M. enzenspergeri*), spiders (*Myro kerguelensis*, *M. paucispinosa*), and moths (*Pringleophaga crozetensis*, *P. kerguelensis*). Less common species included Coleoptera, such as the endemic ground beetle *Amblystogenium pacificum* and weevils (*Bothrometopus* spp. and *Ectemnorhinus* spp.), and four species of Diptera: *Anatalanta aptera*, *Listriomastax litorea*, *Amalopteryx maritima*, and *Paractora dreuxi*. No other invertebrates were found. The vertebrate community is dominated all year by king penguins, with approximately 10,000–15,000 breeding

individuals. Rare birds that are encountered all year long are kelp gulls *Larus dominicanus* and black-faced sheath-bills *Chionis minor*. Seasonally, this site is settled by low numbers of rockhopper (*Eudyptes chrysocome*) and gentoo (*Pygoscelis papua*) penguins, giant petrels (*Macronectes halli*), subantarctic skuas (*Catharacta skua*), and Kerguelen's terns (*Sterna virgata*). No Procellariid species were observed on this site during our field study, although no specific surveys have been conducted to rule out their presence. Two marine mammals, elephant seals *Mirounga leonina* and Kerguelen's sea lions *Arctocephalus gazella*, are encountered seasonally near the trapping site.

Four km north-west of the Baie Américaine, the second site (46°22'45"S; 51°46'34"E) was located in the Vallée de la Hébé, 1.5 km inland. Traps were placed on a line approximately 500 meters long, along the southern bank of the river. This site is devoid of dense colonial seabird settlement. The vegetation cover was dominated by mosses and by *B. penna-marina*, *Agrostis magellanica* and *Acaena magellanica*. Less predominant species with less than 10% cover were *Azorella selago*, *P. antiscorbutica*, *P. annua*, *G. antarcticum*, *J. scheuchzeroides*, and *R. biternatus*. The invertebrate community was also dominated by earthworms, spiders, and *Pringleophaga* spp. The rarest captured species were *A. pacificum* and weevils. No other invertebrates were found. Few native vertebrates inhabited this site, which was only frequented occasionally by terns and skuas. There was no precise information on the presence of petrels, although there may have been some individuals inhabiting the slopes of the valley several hundred metres from the trapping zone, along with several sooty albatrosses (*Phoebetria palpebrata*).

Stomach and faecal analyses

The rats were captured at both sites in March and November 2007, using 20–30 traps for 2–3 consecutive nights depending on the sites and periods. The rats were killed using isoflurane gas and autopsied in the field. Their digestive tract was removed and placed in 90% ethanol for later analysis.

Only stomachs from adult rats containing over 1 g of wet content were analysed. Their contents were determined under a stereomicroscope (×60) after filtration (mesh 1 mm). Each item, including vegetative or reproductive organs from plants and animal pieces separated according to the order or family level, was estimated visually either from the entire contents or from a sample comprising at least 20% of total weighed wet content. The relative abundance was calculated as the number of pieces of an identified item divided by the total number of pieces of food material, including unidentified parts, counted in

stomach content, expressed in per cent, averaged over all rats.

For each rat, two to three faecal pellets collected in the distal part of the rectum were macerated in water. The residuals of faecal material obtained from washing on a 0.25-mm sieve were mounted on slides. For each rat, 400 fragments, including vascular plant and animal matter, were determined under a microscope (100×) and compared with the epidermal structures of species available (see Hansson 1970; Holechek et al. 1982; Jordan 2005). Plants could be identified to the genus or species level and animals to the family, genus, or species level. Relative abundance of each item was calculated as in stomach.

Isotopic analyses

Samples from livers of captured rats and from potential food items, listed earlier, for each study site were collected for stable isotope analysis during each trapping session. Flesh of *A. patagonicus* and feathers of *L. dominicanus* were also collected on dead birds that were found on the rookery. All samples were fixed in 90% ethanol (Barrow et al. 2008). No materials from faecal or stomach contents were used in isotopic analyses.

All samples were dried at 60°C for at least 48 h and homogenised using a mortar and a pestle. For invertebrates, individuals of the same species were pooled to obtain enough material for isotopic analyses and values at the level specie. Rats' liver and animal preys did not undergo lipid extraction since all samples had consistently low lipid content (C:N <4.0; Post et al. 2007; Ehrich et al. 2010). Aliquots of homogenised sample were packed into tin cups and analysed for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, % carbon, and % nitrogen by a spectrometer from IsoPrime (*MicroMass*) coupled with an analyser EuroEA 3024 (*EuroVector*). Stable C and N isotope ratios are expressed as: $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ for $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$, respectively. Ratios are presented as δ values (‰), expressed relative to the vPDB (Vienna Peedee Belemnite) standard and to atmospheric N_2 for carbon and nitrogen, respectively. Reference materials were IAEA-NBS 21 (graphite -28.13‰) for $\delta^{13}\text{C}$ and the IAEA-N1 (+0.4‰) and IAEA-N2 (+20.3‰) for $\delta^{15}\text{N}$. Ten replicate assays of internal laboratory standards indicated measurement maximum errors (SD) of $\pm 0.15\%$ and $\pm 0.2\%$ for stable carbon and nitrogen isotope measurements, respectively. These ratios were used to illustrate the different foraging sources and trophic levels of each component of terrestrial and marine-coastal communities investigated in our study sites, along with the positioning of rats within these components.

Parnell et al. (2010) developed a package called *SIAR* for solving linear mixing models. This model uses

Bayesian inference to solve for the most likely set of dietary proportions given the isotopic ratios in a set of possible food sources and a set of consumers. The model assumes that each target value comes from a Gaussian distribution with an unknown mean and standard deviation. The structure of the mean is a weighted combination of the food sources' isotopic values. The weights are made up dietary proportions (which are given a Dirichlet prior distribution) and the concentration dependencies given for the different food sources. The standard deviation is divided up between the uncertainty around the discrimination corrections and the natural variability between target individuals (more information see Jackson et al. 2008; Moore and Semmens 2008; Parnell et al. 2010). Throughout this paper, mean dietary proportions from isotope analyses will be followed by their confidential interval, noted C.I.

The model calculates the range of all possible source contributions for systems where the number of potential sources is greater than $n + 1$, n being the number of isotopes. Isotopic models typically use the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each type of diet, corrected for the discrimination factor of the consumer (the increase in consumer isotopic ratio compared with its diet, noted ΔN and ΔC). Discrimination factors depend on several sources of variation (e.g. taxa, site, tissue; see review Caut et al. 2009). Previous laboratory work showed significant relationships between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of diets and the corresponding ΔN and ΔC of the different tissues of rats fed on these diets (Caut et al. 2008a). We calculated for the rat liver, the diet-dependent discrimination factors corresponding to each potential rat diet item.

Data analysis

Due to small sample sizes, comparisons of relative abundance of diet items from stomach and faeces contents were made using nonparametric statistics (Siegel and Castellan 1988) using the Mann–Whitney U -test for median comparison for unpaired samples, the Wilcoxon T -test for matched paired samples, and the Spearman correlation coefficient ρ_s .

We performed factorial ANOVAs to test the effect of period and study site on isotopic ratios of different groups including rat liver, plants and insects. The sample size of the group of species formed by earthworms was not sufficient for statistical analysis because we pooled individuals to have enough material for isotopic analysis. Dependent variables were either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ of each group, and independent variables were months and study sites. Computations were performed with STATISTICA 6.0 (StatSoft Inc 2001, <http://www.statsoft.com>) and R 2.8.1 (R Development Core Team 2010, <http://www.r-project.org/>).

Results

Stomach and faecal analyses

Among the 61 rats captured, both stomach contents and rectal droppings could be analysed from 47 adult individuals; the number of rats analysed for each combination of month and site ranged from 10 to 15 (Table 1). Relative abundance of flowering plants in the stomach contents ranged between $32 \pm 7\%$ and $69 \pm 7\%$ (mean \pm SE), and animal prey abundances ranged between $22 \pm 8\%$ and $51 \pm 7\%$, mostly represented by moth larvae, with adult weevils the next most common prey item. Spiders were found infrequently (13 pieces total in five rats).

Relative abundance of bryophytes in faeces were ~ 3 to ~ 5 fold greater than in stomachs, except in November on Baie Américaine. The relative abundance of bryophytes in faeces was significantly correlated ($n = 47$, $\rho_s = 0.788$, $P < 0.01$) with the relative abundance of caterpillars in stomachs.

After excluding counts of the bryophyte, relative abundance of plant or animal materials were of the same magnitude in stomach and faeces, except on Baie Américaine (Fig. 1) where relative abundance of reproductive parts of dicotyledons was increased by ~ 3 to ~ 5 fold in faeces compared to stomachs. Neither earthworms nor land snail shells were found in the macroscopic analyses of stomach contents.

Micro-histological analysis of faeces showed the ingestion of a large variety of the predominantly available food items according to site and month (Table 2). These analyses included rectal droppings from two additional adult rats that had empty stomachs. Grasses were the most consumed plant on both sites at both seasons. Reproductive parts or seeds of Caryophyllaceae (*C. fontanum*) were eaten in March, especially at Baie Américaine. Vegetative parts of *A. magellanica* were more consumed in the Vallée de la Hébé in both seasons than in the Baie Américaine. To a much lesser extent, rats had eaten pteridophytes (*B. pennamariana*), lycopodiophytes (*L. magellanicum*), Cyperaceae (*U. compacta*), Rubiaceae (*G. antarcticum*), and Brassicaceae (*P. antiscorbutica*). The introduced Caryophyllaceae *S. procumbens* was consumed only at a very low level on Baie Américaine.

The animal diet consisted mostly of caterpillars of *Pringleophaga* spp. and larvae and adults of weevils. Aphids were found in March and November in rats from Baie Américaine. Earthworm chaetae were frequently found throughout the study period on both sites. Feathers and pieces of birds' skin were also regularly observed in rats from Baie Américaine, but only exceptionally in rats from the Vallée de la Hébé. Interestingly, we detected the presence of elephant seal skin (moult) in a rat in November

Table 1 Comparison of the relative abundance (mean in %, \pm SE) in food items identified in stomachs and faeces of rats

Site	Baie Américaine				Vallée de la Hébé			
	March		November		March		November	
Month								
N of rats	15		10		10		12	
Compartment	Stomach	Faeces	Stomach	Faeces	Stomach	Faeces	Stomach	Faeces
N items (Mean \pm SE)	266 \pm 33	599 \pm 63	153 \pm 31	841 \pm 80	276 \pm 44	430 \pm 7	363 \pm 41	899 \pm 115
Bryophytes	9 \pm 4	27 \pm 6	9 \pm 2	9 \pm 1	17 \pm 6	49 \pm 4	11 \pm 2	56 \pm 5
Monocotyledons								
Reproductive parts	30 \pm 8	19 \pm 5	38 \pm 9	28 \pm 9	7 \pm 3	~1	9 \pm 3	4 \pm 1
Vegetative parts	4 \pm 2	5 \pm 1	6 \pm 3	3 \pm 2	5 \pm 2	3 \pm 1	11 \pm 2	10 \pm 2
Dicotyledons								
Reproductive parts	3 \pm 2	14 \pm 4	<1	3 \pm 1	<1	2 \pm 1	–	<1
Vegetative parts	8 \pm 3	5 \pm 4	22 \pm 9	20 \pm 7	18 \pm 7	16 \pm 6	20 \pm 4	8 \pm 2
Undetermined plants	10 \pm 4	11 \pm 3	3 \pm 1	17 \pm 6	2 \pm 1	4 \pm 2	~1	3 \pm 1
Total (Spermatophytes)	55 \pm 9	54 \pm 6	69 \pm 7	71 \pm 7	32 \pm 7	27 \pm 6	42 \pm 7	26 \pm 4
Oligochaeta	–	~2	–	3 \pm 1	–	~1	–	3 \pm 1
Arachnida	–	–	<1	–	–	–	<1	–
Lepidoptera	19 \pm 6	7 \pm 1	6 \pm 3	1 \pm 1	45 \pm 7	22 \pm 4	30 \pm 7	10 \pm 3
Coleoptera	8 \pm 3	2 \pm 1	8 \pm 4	8 \pm 4	2 \pm 1	~1	17 \pm 5	5 \pm 2
Birds (feathers)	8 \pm 6	4 \pm 3	6 \pm 6	7 \pm 7	<1	<1	<1	–
Undetermined animals	~1	4 \pm 4	1 \pm 1	~1	3 \pm 3	<1	<1	<1
Total (animals)	36 \pm 9	19 \pm 4	22 \pm 8	20 \pm 7	51 \pm 7	24 \pm 3	47 \pm 8	18 \pm 2

2007 and the consumption of the introduced Thysanopterid *Apterothrips secticornis* by a rat in March on Baie Américaine.

No seasonal shift was detected in the consumption of grasses on Baie Américaine, while in Vallée de la Hébé, rats ate more inflorescences in November than in March. Rats shifted their consumption of *C. fontanum* on both study sites from vegetative parts in November towards floral parts in March. A seasonal shift of animal prey was also observed at both study sites with an increase in relative abundance of caterpillars in the diet between November and March and a marked increase in consumption of both weevil adults and earthworms in November, in the Vallée de la Hébé.

Isotopic analysis

Conventional diet analyses allowed prey types to be identified and used as inputs to isotopic models (see Tables 2 and 3). Site was the major factor affecting the carbon and nitrogen isotopic values for each class (Table 4). The site effect was significant ($P < 0.05$; Table 5) only for $\delta^{15}\text{N}$ in all different classes (liver of rats, insects, and plants). For $\delta^{13}\text{C}$, site was significant for the liver of rats and for insects. The interaction between period and site was never significant for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. In summary, these results showed significant differences between sites but not

between periods. Therefore, we choose to group the two periods for SIAR isotopic model analysis. Conventional diet analyses and observations allowed the selection of the different prey as inputs for isotopic models (see Table 4).

At Baie Américaine, plants, including only spermatophytes, represented more than half (50% [C.I.: 23–75]) of the assimilated food in rats' livers, based on isotopic signals. Insects, including Lepidoptera and Coleoptera, represented 25% [0–56]. Seabirds including king penguins and Dominican gulls isotopes represented 18% [6–30], and terrestrial earthworms *Microscolex* spp. represented 7% [0–21]. In the Vallée de la Hébé, plants represented 62% [51–73] of assimilated food in rats' livers; insects, 24% [10–39]; and terrestrial earthworms *Microscolex* spp., 13% [2–23].

Rats occupied the top of the food chains involving preys of terrestrial origins with lower values in carbon isotopes compared to coastal or marine species (Fig. 2a). Rats were close to spiders *Myro* spp. and the wingless fly *A. aptera*, which were also highly positioned in terrestrial food chains. At an intermediate level, polyphagous insects such as *Pringleophaga* spp. and weevils, as well as earthworms *Microscolex* spp. and the Carabid beetle, *A. pacificum*, were found, followed by spermatophytes and bryophytes at the lowest nitrogen levels. Overall, the $\delta^{15}\text{N}$ level was higher in Baie Américaine (Fig. 2a) than in the Vallée de la Hébé (Fig. 2b). The large standard error on the Curculionidae

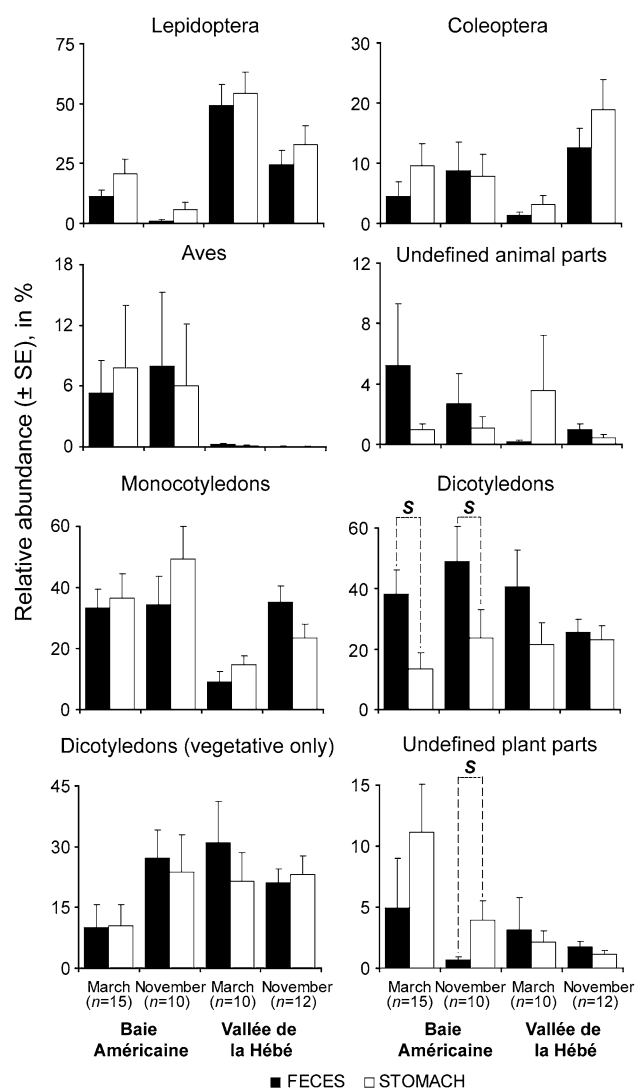


Fig. 1 Comparison of relative abundance in food items between faeces and stomach analysis. Bryophyte material has been excluded from these analyses. Significant ($P < 0.05$) Wilcoxon T^+ -tests are indicated with 'S' above histogram bars

nitrogen isotope ratio in the Vallée de la Hébé was due to the small number of individuals analysed over the study period ($n = 4$).

Discussion

The differences observed in diet quantification between stomach and faecal contents from rats on Ile de la Possession are consistent with previously known sources of errors in using such methods (Hansson 1970; Jordan 2005). Microhistological analyses from faecal samples, however, allowed an accurate recovery of many invertebrates, even soft-bodied ones such as earthworms, (Dickman and Huang 1988; Goszczynski et al. 2000; Wroot 1987); these analyses

also facilitated very precise botanical identifications (Holechek et al. 1982), as in the case where the diversity in available number of plant species is reduced (Chapuis et al. 2001; Le Roux et al. 2002). Soft parts of some plant species may, however, have been highly digested, like those of *G. antarcticum*, and subsequently underestimated. The main discrepancy between the two methods arose from missing pieces of the small seeds of *C. fontanum* in stomachs, due to the large mesh used to filter stomach contents. Difference in mesh size may also explain the discrepancy in bryophyte counts between stomach and faeces. Using smaller mesh to do microhistological analyses of stomach content (see Clark 1981) would have been an appropriate method to avoid this bias, but this may have posed another problem: the overestimation of unfragmented materials. However, relative abundances of most prey types from macroscopic analysis of stomach and microhistological analysis in faeces were similar. Apart from the fact that analysis of stomach contents allows the most precise identification of animal preys, our results encourage the use of microhistological analyses of faecal content to study the diet of black rats. Such analysis may offer the advantage of monitoring rodent populations without killing individuals.

According to faecal analyses, plant materials formed the bulk of the diet of rats in both habitats. The direct influence of introduced rodents on vegetation communities has been largely underestimated (Mulder et al. 2009; Phiri et al. 2009). Based on our results, there is evidence of a balanced influence between the detrimental effect of feeding on small autochthonous species (*G. antarcticum*, *U. compacta*, *A. magellanicum*; see also Copson 1986; Grant-Hoffman et al. 2010a, b; Shaw et al. 2005) and the potential benefit of limiting introduced species such as *C. fontanum* or *P. annua* through the consumption of both reproductive and vegetative parts. The positive relationship between mosses and caterpillars suggests that passive ingestion of bryophytes occurred while rats were feeding on caterpillars, but we cannot exclude that rats ate mosses that were highly represented in the vegetation of our study sites. Indeed, mosses are eaten by various small mammals living in cold environments, such as lemming species in the Arctic (Prins 1981). We found no trace of mycophagy, which is a rare feeding behaviour observed in rats (Johnston 2002).

The lack in detecting seasonal shift in plant food using isotope analyses, as for inflorescences of grasses on the Vallée de la Hébé, may have been due to the fact that assimilation processes for such food materials may not be as important as those of animal preys, due to temporal differences in tissue assimilation and to tissue composition (Caut et al. 2008a). Such a lowered assimilation processes of plant materials is also in accordance with the great discrepancies observed in trophic levels between plants and

Table 2 Seasonal comparison of the diet quantified as relative abundance calculated from faecal analyses

Site	Baie Américaine			Vallée de la Hébé		
	March	November	T^+	March	November	T^+
Month	15	11		10	13	
Number of rats						
Mean (\pm SE) number of identified items	397 \pm 3	400 \pm 0		394 \pm 7	390 \pm 5	
Plant materials						
Algae	U	4 \pm 4	<1	NS	–	–
Lycopodiaceae <i>Lycopodium magellanicum</i>	V	<1	–	–	–	–
Blechnaceae <i>Blechnum penna-marina</i>	V	–	<1	–	3 \pm 3	\leq 1
Poaceae <i>Poa</i> spp., <i>Agrostis magellanica</i>	R	21 \pm 3	33 \pm 6	NS	2 \pm 1	31 \pm 3
	V	9 \pm 4	4 \pm 4	NS	6 \pm 3	2 \pm 1
Cyperaceae <i>Uncinia compacta</i>	S	1 \pm 1	–	–	<1	–
	V	<1	<1	–	–	–
Caryophyllaceae	S	8 \pm 3	–	–	1 \pm 1	–
<i>Cerastium fontanum</i>	R	9 \pm 4	<1	S	3 \pm 1	<1
	V	<1	6 \pm 4	S	1 \pm 1	2 \pm 1
<i>Sagina procumbens</i>	R	–	1 \pm 1	–	–	–
	V	–	1 \pm 1	–	<1	<1
Rubiaceae <i>Galium antarcticum</i>	R	–	2 \pm 1	–	–	–
	V	2 \pm 1	4 \pm 1	NS	1 \pm 1	\leq 1
Rosaceae <i>Acaena magellanica</i>	U	5 \pm 5	8 \pm 4	NS	25 \pm 10	13 \pm 3
Brassicaceae <i>Pringlea antiscorbutica</i>	S	<1	–	–	–	<1
Undetermined Dicotyledons	R	7 \pm 2	13 \pm 5	S	\leq 2	3 \pm 1
	V	3 \pm 1	5 \pm 2	NS	4 \pm 1	\leq 3
Animal materials						
Oligochaeta	C	3 \pm 1	3 \pm 1	NS	1 \pm 1	6 \pm 2
Coleoptera Curculionidae	Ad	4 \pm 2	8 \pm 4	NS	1 \pm 1	13 \pm 3
Lepidoptera <i>Pringleophaga</i> spp.	L	11 \pm 2	1 \pm 1	S	49 \pm 9	25 \pm 6
Hemiptera Aphididae	L	5 \pm 4	1 \pm 1	NS	–	<1
Thysanoptera <i>Apterothrips secticornis</i>	Ad	<1	–	–	–	–
Aves	F	5 \pm 3	8 \pm 7	NS	<1	–
Mammalia <i>Mirounga leonina</i>	M	–	<1	–	–	–
Total undetermined materials		<1	<1	–	<1	<1

V, vegetative parts; R, floral parts; S, seeds; L, larvae; Ad, adults; C, chaetae; F, feathers or skin; M, moult; U, unidentified parts. Result of the Wilcoxon match-pair T^+ -test is indicated (S: $P < 0.05$; NS: $P > 0.05$)

Table 3 Variation of carbon and nitrogen isotopic values in rats' liver, collected insects, and spermatophytes, according to site and seasons on Ile de la Possession

Site	Baie Américaine				Vallée de la Hébé				
	March		November		March		November		
Materials	n	δ (‰)	n	δ (‰)	n	δ (‰)	n	δ (‰)	
Rats	^{13}C	15	–23.8 \pm 0.4	12	–24.6 \pm 0.3	15	–25.2 \pm 0.2	15	–25.8 \pm 0.2
	^{15}N		12.1 \pm 0.8		12.4 \pm 0.8		6.7 \pm 0.3		7.9 \pm 0.5
Insects	^{13}C	8	–25.7 \pm 0.4	5	–21.0 \pm 2.4	5	–26.2 \pm 0.5	7	–27.6 \pm 1.4
	^{15}N		9.8 \pm 1.0		10.0 \pm 1.1		7.9 \pm 1.0		4.1 \pm 1.6
Spermatophytes	^{13}C	17	–28.8 \pm 0.4	11	–28.7 \pm 0.3	11	–28.6 \pm 0.2	13	–28.5 \pm 0.3
	^{15}N		8.4 \pm 1.8		5.2 \pm 1.0		–1.3 \pm 0.8		–1.4 \pm 1.1

Table 4 Isotopic values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, mean \pm SE $\%$), $\%C$, $\%N$, and C/N ratio for rat livers and the different prey items selected from faecal diet analyses (see also Table 2) for the diet reconstruction with stable isotope analysis calculated at Baie Américaine (BUS) and Vallée de la Hébé (HEBE)

	BUS							HEBE						
	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\%C$	$\%N$	C/N	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\%C$	$\%N$	C/N		
Rats' liver	27	-24.2 \pm 0.1	12.2 \pm 0.1	51.3 \pm 0.1	14.2 \pm 0.1	3.6 \pm 0.0	30	-25.5 \pm 0.1	7.3 \pm 0.3	50.4 \pm 0.3	14.2 \pm 0.2	3.6 \pm 0.1		
Insects ^a	5	-26.7 \pm 0.5	7.9 \pm 0.5	48.7 \pm 1.0	12.4 \pm 0.1	3.9 \pm 0.1	6	-26.8 \pm 0.4	4.6 \pm 1.5	45.8 \pm 1.3	12.0 \pm 0.2	3.8 \pm 0.1		
Oligochaeta ^b	3	-24.4 \pm 0.3	6.6 \pm 0.4	48.0 \pm 0.1	13.4 \pm 0.5	3.6 \pm 0.1	4	-24.4 \pm 0.5	4.2 \pm 2.1	34.1 \pm 4.9	9.2 \pm 1.2	3.7 \pm 0.0		
Spermatophytes ^c	20	-28.7 \pm 0.3	6.4 \pm 1.5	42.0 \pm 0.5	2.3 \pm 0.2	21.7 \pm 2.2	17	-28.8 \pm 0.2	-2.1 \pm 0.6	40.6 \pm 0.5	1.9 \pm 0.2	24.5 \pm 2.1		
Seabirds ^d	4	-19.8 \pm 0.6	9.9 \pm 0.4	48.1 \pm 0.7	14.8 \pm 0.2	3.3 \pm 0.0	-	-	-	-	-	-		

^a *Pringleophaga* spp, *Amblystogenium pacificum* and Curculionidea gen spp

^b *Microcolex luykeni*, *Microcolex enzenspergeri* and *Microcolex crozentensis*

^c Poaceae (*P. annua*, *P. cooki*, *A. magellanica*), Cyperaceae (*U. compacta*), Caryophyllaceae (*C. fontanum*, *S. procumbens*), Rubiaceae (*G. antarcticum*), Rosaceae (*A. magellanica*), Brassicaceae (*P. antisorbatica*)

^d *Aptenodytes patagonicus* and *Larus dominicanus*

Table 5 Factorial analysis of variance exploring the effect of season and site on the variation of carbon and nitrogen isotopic values of rats' liver tissues and potential food material

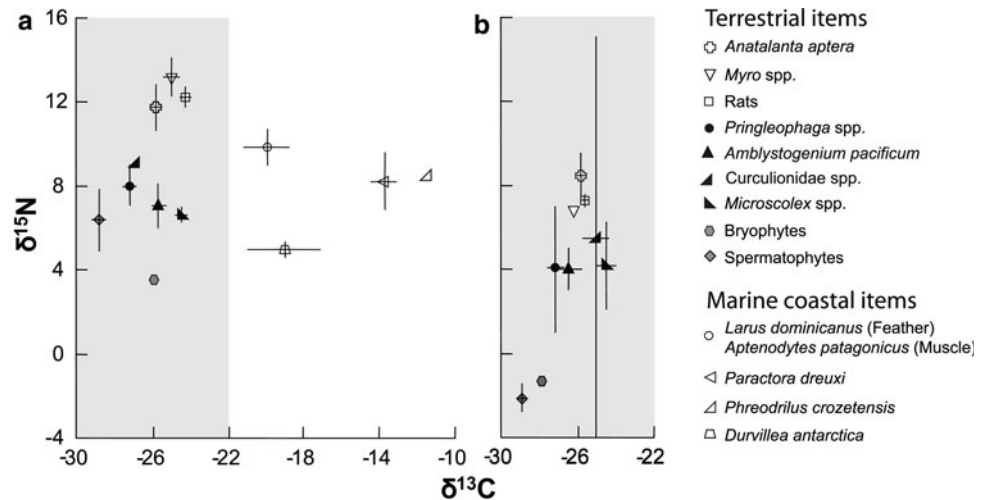
Sources of variation	$\delta^{13}\text{C}$			$\delta^{15}\text{N}$		
	df	F	P	df	F	P
Rats						
Season	1, 53	6.77	0.01	1, 53	1.70	0.20
Site	1, 53	21.07	<0.01	1, 53	80.92	<0.01
Season*site	1, 53	0.32	0.58	1, 53	0.55	0.46
Plants						
Season	1, 55	0.10	0.75	1, 55	1.53	0.22
Site	1, 55	0.14	0.71	1, 55	34.66	<0.01
Season*site	1, 55	<0.01	0.91	1, 55	1.24	0.27
Insects						
Season	1, 24	1.10	0.31	1, 24	2.07	0.16
Site	1, 24	4.81	0.04	1, 24	9.74	<0.01
Season*site	1, 24	3.73	0.07	1, 24	2.56	0.12

invertebrate herbivores and rats on the Vallée de la Hébé. These were found approximately 6‰ distant in $\delta^{15}\text{N}$ level, while one trophic level is expected to increase by ~ 3 – 5 (Peterson and Fry 1987). Moreover, the fragmentation of plant material and their lesser digestibility may produce consequent overestimation in faecal analyses compared to less fragmented pieces of animals, such as insects. Indeed, we regularly observed the entire exoskeleton of *Pringleophaga* sp. in rectal droppings.

Accurate prey identification from faecal analysis revealed seasonal shifts in diet which are consistent with the feeding opportunism of rats according to breeding or winter seasons (Best 1969; Caut et al. 2008b; Clark 1981; Clout 1980; Daniel 1973; Sugihara 1997; Sweetapple and Nugent 2007; Tobin et al. 1994). This situation was specifically observed on the Vallée de la Hébé where rats mainly ate caterpillars in March, representing about 50% of their ingested food, and enlarged the variety of their preys by including weevils and earthworms in November, with all these preys still representing a relative abundance of 44% in the diet. The lack in detecting such a shift using isotope analysis can be explained by the similarity in the different levels of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of the different prey (see Fig. 2). This phenomenon highlights the importance of using traditional diet analyses in complement with isotope analyses as complementary approaches (Caut et al. 2008a), in order to best describe the diet of such a small omnivore.

Black rats were found at the top of food chains in the terrestrial communities investigated both in presence and in absence of seabirds nutrients derived on Ile de la Possession. There was no evidence from stomach analysis that rats ate small-sized arthropods, such as spiders or flightless flies, but rather the evidence suggested that the rats

Fig. 2 Carbon and nitrogen stable isotope ratios (\pm SE) for animals and plants sampled from **a** Baie Américaine and **b** Vallée de la Hébé. Only one sample when no error bars



preferred larger invertebrates, i.e. animals with dry masses greater than ~ 3 mg (see Le Roux et al. 2002), such as caterpillars, earthworms, and the largest species of weevils. This hypothesis is strengthened by the same nitrogen level of either rats, spiders, and flies. If rats had eaten these small arthropods, we would have expected their trophic level to be at an upper bound. Rats mostly fed on caterpillars, most probably of the flightless moth *P. kerguelensis*, which is the largest insect available throughout the year on Ile de la Possession and which is also particularly rich in lipids (Chauvin and Vernon 1981). At Baie Américaine, however, we found the presence of aphids in faeces contents, which indicates that these small Hemipteran insects introduced to Ile de la Possession (Frenot et al. 2005) may have been attractive for rats, as for domestic mice introduced on an island of the subantarctic Kerguelen archipelago (Le Roux et al. 2002).

We found no evidence of foraging by black rats in coastal areas, despite analyses performed on individuals living near the sea border. Both the micropterous fly *P. dreuxi* and the earthworm *P. crozetensis* are the two main species associated with decaying seaweeds accumulating at high water marks (Tréhen et al. 1985). These two potential preys were not found in stomach analysis and did not contribute to rats' diets as inferred from isotopic models, which may have otherwise displaced rats towards higher values of carbon isotope ratios, i.e. placed the rats closer to the isotopic ratios of these preys (Stapp 2002). This is also the case for seabirds as food resources for rats at Baie Américaine. The presence of feathers in the majority of faeces and stomach contents of rats along with the relatively high level of contribution to the isotopic ratio in the rats' livers, but their relatively remote position compared to isotopic ratios found in seabirds, indicate that the rats analysed in our study may have not directly used seabirds as a major food resources but rather scavenged on

dead carcasses (Copson 1986; Quillfeldt et al. 2008). This hypothesis can be drawn from the small difference in $\delta^{13}\text{C}$ level in rats' liver between Baie Américaine and Vallée de la Hébé (see Table 4; Fig. 2), which indicated a slight shift to marine resource. This conclusion must be, however, attenuated because we did not extract lipid from our samples, which may have induced a slight depletion in carbon signal (Ehrich et al. 2010), hence underestimating the amplitude of the shift towards marine resources. However, keeping lipid in our samples is certainly not subject to an important source of error as the carbon to nitrogen ratio C:N, ranging between 3.6 and 3.9, indicates that neither lipid extraction nor normalised correction was truly necessary (but see Ehrich et al. 2010). The fact that we have not detected the presence of smaller birds species, i.e. small burrowing Procellariids, in our study sites, may be the result of the long-term presence of rats for probably over two centuries on the Ile de la Possession (see Chapuis et al. 1994). Indeed, rats are suspected to drive small bird species to extinction (Townes et al. 2006) by preying of eggs or chicks (Innes 2001) or causing long-term disturbances (Jouventin et al. 2003; but see Ruffino et al. 2009). The case of one of the two small terrestrial bird species that inhabit the sites we investigated on Ile de la Possession, the lesser sheathbill *Chionis minor*, must be highlighted, as rat may both directly or indirectly affect their populations, as evocated on Marion Island by Huyser et al. (2000) for the potential negative indirect role of domestic mice.

Introduced black rats on Japanese islands have been found to severely impact land snails (Chiba 2007). On Ile de la Possession, there is only one native land snail species, *Notodiscus hookeri* (Madec and Bellido 2007; Pugh and Scott 2002). This snail was not recovered from our study sites. However, predation by rats on this species has been observed at sites other than those followed in the present study (J. Thévenot pers. com.). These observations deserve

further attention to understand the potential interaction between introduced rats and native land snails.

The main decomposer found in terrestrial communities on Ile de la Possession, the wingless fly *A. aptera* (see Tréhen et al. 1985), was found at the top of the food chains, very close to rats and above seabirds in Baie Américaine and even above rats in absence of dense bird colonies in the Vallée de la Hébé. These patterns are consistent with the coprophagous and necrophagous feeding behaviour of *A. aptera*. However, the rare autochthonous predators in subantarctic terrestrial communities, the spiders *Myro* spp. and the beetle *A. pacificum*, were also found at trophic levels that are not consistent with their feeding behaviour, i.e. flightless flies for spiders (Smith 1977), and earthworms and caterpillars for *A. pacificum* (Davies 1972, 1987), which should have displaced them at an upper level of nitrogen. Our results deserve further attention to the feeding behaviour of these invertebrate predators.

Seabirds are important in marine ecosystems not only as predators but also because they provide substantial organic material and nutrients to nearby habitats (Sanchez-Piñero and Polis 2000). Seabirds often enrich productivity of island ecosystems (Polis and Hurd 1996; Polis et al. 1997) where they roost and spend their long breeding season. Seabirds provide energy and nutrients via their carcasses, feathers, egg shells, and excreta (Sanchez-Piñero and Polis 2000). Nitrogen signatures of both plants and terrestrial consumers were strongly influenced by the presence of seabirds on Baie Américaine on Ile de la Possession, which is in accordance with other patterns observed specifically on subantarctic islands (Erskine et al. 1998; Smith 2008). On the Vallée de la Hébé lacking seabird colonies, plants had much lower ^{15}N than similar plants on Baie Américaine reflecting the contributions of guano-derived N in the soil (Anderson and Polis 1999; Erskine et al. 1998). The ^{15}N values of all the compartments of the ecosystem were enriched directly or indirectly by the presence of seabirds.

Collectively, these results strengthen those from many previous studies that investigated the impact of rodents introduced on oceanic islands and, more specifically, the effect of rats on terrestrial macroinvertebrates, such as lepidopterans and coleopterans (Townes et al. 2009). Taking into account the functional importance of *Pringleophaga* spp. caterpillars as keystone species in subantarctic ecosystems (Klok and Chown 1997) and the roles of weevils as plant eaters and earthworms as decomposers (Chown 1989; Smith 1977; Vernon et al. 1998), a decline in nutrient cycling due to rat predation must affect the dynamics of terrestrial communities. Rats, however, did not displace the expected trophic levels of native dipteran decomposers, or epigeic Arachnid and Carabid predators. Rather, seabird input clearly influenced the overall terrestrial communities in terms of $\delta^{15}\text{N}$ level. Rats seemed not to use seabirds as a

major food resource at our study sites, which is consistent with observed co-habitation between introduced rats and large body-sized seabirds on other islands (Quillfeldt et al. 2008; Ruffino et al. 2009; Townes et al. 2006). Although poorly contributing to food assimilation, the feeding behaviour of rats on both reproductive and vegetative parts of both local and introduced flowering plant species, deduced from faecal analyses, suggests direct balanced effects on plant communities, which is an often neglected issue of the consequences of the role of these small omnivorous rodents introduced onto islands.

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