

Isotopic niche mirrors trophic niche in a vertebrate island invader

Marlenne A. Rodríguez M. · L. Gerardo Herrera M.

Received: 4 January 2011 / Accepted: 17 July 2012
© Springer-Verlag 2012

Abstract Caution for the indiscriminate conversion of the isotopic niche into ecologic niche was recently advised. We tested the utility of the isotopic niche to answer ecological questions on oceanic islands. We compared the isotopic niches of black rats (*Rattus rattus*) on two islands in the Gulf of California, Mexico: Farrallón de San Ignacio (FSI) and San Pedro Mártir (SPM). Both islands maintained several species of marine birds, but FSI is devoid of terrestrial vegetation and SPM has several species of terrestrial plants. We tested the hypothesis that rats on FSI have a narrower trophic niche due to its lower diversity of food items. We predicted a smaller variance in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of rat muscle on FSI, and a lower use of marine birds as food on SPM. We also examined stomach contents of rats on both islands to validate the isotopic information. Variances in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of black rats were lower on FSI, and the contribution of marine birds to the diet of rats was smaller on SPM. Stomachs in most rats collected on FSI contained only one or two types of food items, mostly marine birds and terrestrial

invertebrates. In contrast, stomachs with only one type of food item were rare on SPM, and in most cases they contained three or more food types. Our findings showed that isotopic variance is a good approximation for trophic niche when comparing populations with access to an assemblage of preys with contrasting biological and isotopic diversity.

Keywords Black rats · Feeding habits · Island ecology · *Rattus rattus* · SIAR

Introduction

Hutchinson concept of ecological niche has been fundamental for stable-isotope ecologists interested in studying trophic relationships (Hutchinson 1957; Bearhop et al. 2004; Newsome et al. 2007; Semmens et al. 2009). Hutchinson defined ecological niche as an n-dimensional space of resources available to organisms. Groups of food items available to organisms often differ in stable-isotope signatures and one can visualize the resource space as an area with isotopic values as coordinates (δ -space; Newsome et al. 2007). However, the use of isotopic niche as a proxy for trophic niche can be deceptive (Flaherty and Ben-David 2010), and empirical studies probing the utility of this approach are scant. Closed systems, such as lakes and islands, are ideal to test the potential of this technique (Bearhop et al. 2004). For example, an experimental study that manipulated variance of isotopic values in the food web of a freshwater lake (Syväranta and Jones 2008), and a comparison of several creeks with varying levels of fragmentation (Layman et al. 2007), suggest that isotopic variance can reflect feeding niche breadth.

We evaluate the use of the isotopic niche to infer trophic niche in populations of black rats (*Rattus rattus*) on

Communicated by Stuart Bearhop.

M. A. Rodríguez M.
Instituto de Ecología, A.C., Carretera Antigua a Coatepec 351,
El Haya, Xalapa, VER 91070, Mexico

Present Address:
M. A. Rodríguez M.
Grupo de Ecología y Conservación de Islas, A.C., Avenida
Moctezuma 836, Zona Centro, Ensenada, BC 22800, Mexico

L. G. Herrera M. (✉)
Estación de Biología de Chamela, Instituto de Biología,
Universidad Nacional Autónoma de México, Apartado Postal 21,
San Patricio, JAL 48980, Mexico
e-mail: gherrera@ibiologia.unam.mx

two islands with contrasting diversity of food resources in the Gulf of California, Mexico: Farrallón de San Ignacio (FSI) and San Pedro Mártir (SPM). FSI is a small islet devoid of terrestrial vegetation and SPM is an island with several species of terrestrial plants. Trophic chains on FSI are thus mostly dependant on the input of allochthonous sources (e.g., shore rack and marine birds), whereas, on SPM, food webs are maintained by both allochthonous and autochthonous sources. We tested the hypothesis that black rats on FSI have a narrower trophic niche due the lower diversity of food items on the island. We use two approaches to test the hypothesis. First, we compared the variation among individuals of isotopic values on rat muscle on the two islands to test the prediction that the rat population on FSI has a smaller variance in C and N stable-isotope values than on SPM. Variance in isotopic ratios among individuals is one of the simplest measures of trophic niche width in a consumer population (Bearhop et al. 2004). The method assumes that, in a system when prey types differ in isotopic composition, individual variation in isotope ratios reflects the diversity of the diet of the predator population. Measurements of individual isotopic variation in consumers have been used to compare trophic niches of introduced and native species (Olsson et al. 2009), and to contrast individual and population trophic niches (Vander Zanden et al. 2010; Matich et al. 2011).

The isotope niche might be deceptive if one of the populations compared has access to food resources with a wider spectrum of isotopic values (Newsome et al. 2007). To correct for the distribution of isotopic values of food items, comparative studies of niche width must transform the δ values into dietary proportions of different isotopic sources using mixing models (p-space; Newsome et al. 2007). In addition to comparing δ -space between rat populations, we compare the p-space to test the prediction that marine birds contribute to a lower extent to the diet of black rats on SPM than on FSI. We base this prediction on previous work that indicates that predation on native fauna is lower where the diversity of dietary alternatives is higher (Donlan and Wilcox 2008). We complement the stable-isotope analysis (SIA) with dietary information derived from the examination of stomach contents.

Materials and methods

Study site

The study was conducted in 2007 on two islands in the Gulf of California in northwestern Mexico: Farrallón de San Ignacio (FSI; 25°26'N, 109°22'W) and San Pedro

Mártir (SPM; 28°23'N, 112°19'W). SPM and FSI are part of the Islas del Golfo de California Protected Area. FSI (17 ha, 0–140 m asl) is located 27 km off the coast of Sinaloa; this island has no vegetation and its fauna is represented by five species of breeding marine birds (red-billed tropicbird *Phaethon aethereus*, brown booby *Sula leucogaster*, blue-footed booby *S. nebouxii*, Heermann's gull *Larus heermanni*, and yellow-footed gull *L. livens*; Mellink et al. 2002; González-Bernal et al. 2002). Other vertebrates on FSI are two species of lizards (western whiptail *Aspidoscelis tigris* and tree lizard *Urosaurus ornatus*; González-Bernal et al. 2001) and one gecko (Sonoran leaf-toed gecko *Phyllodactylus homolepidurus*); there are no native terrestrial mammals. SPM (267 ha, 0–300 m asl) is located ~60 km off the coast of Sonora. Vegetation on SPM is composed of 25 species of plants, including a cardon (*Pachycereus pringlei*) forest. Vertebrate fauna on SPM includes 53 species of terrestrial birds, 38 species of marine birds, 4 species of reptiles, and 3 species of bats (Grismer 2002; Frick 2007). Eight species of marine birds breed on SPM, of which *S. leucogaster*, *S. nebouxii*, *P. aethereus*, and brown pelican *Pelecanus occidentalis* are present in large numbers (Tershy et al. 1992; Tershy and Breese 1997). SPM and FSI were used to extract guano in the nineteenth century, and were invaded by black rats presumably when this industry was active. Similarly to other islands, black rats affected the species composition and reproductive performance of native fauna on FSI and SPM (Tershy et al. 1992; Tershy and Breese 1997).

Collection of samples

Field work was conducted on FSI and SPM in April and July. During each period, we placed 15 Tomahawk traps in 2–3 transects on the coast and inland of each island. The traps were separated by 20 m, and they were baited with peanut butter during 1–3 consecutive nights. The coast sites were located next to breeding colonies of *L. heermanni* on FSI (0 m asl), and of *S. leucogaster*, *S. nebouxii* and *L. heermanni* on SPM (0–10 m asl). The inland sites were located close to breeding colonies of *S. leucogaster*, *S. nebouxii* and *L. heermanni* on FSI (~100 m asl), and of *S. leucogaster*, *S. nebouxii* and *P. occidentalis* on SPM (~200–250 m asl). There were breeding colonies of marine birds on both islands during all sampling periods with some slight variation in species composition. In April and July, nesting *S. leucogaster* and *S. nebouxii* were the most abundant marine birds on both islands with a large, patchy colony of *P. occidentalis* on SPM in April. The distance between coast and inland sites was ~200 m on FSI, and 400–500 m on SPM. Individuals of *R. rattus* captured in the traps were euthanized with sodic pentobarbital injected

directly into the heart according to the Norma Oficial Mexicana NOM-033-ZOO-1995 (humane sacrifice of wild-life and domestic animals). We collected muscle samples from 52 black rats on FSI (April: $n_{\text{coast}} = 12$, $n_{\text{inland}} = 14$; July: $n_{\text{coast}} = 11$, $n_{\text{inland}} = 15$) and from 42 black rats on SPM (April: $n_{\text{coast}} = 12$, $n_{\text{inland}} = 10$; July: $n_{\text{coast}} = 8$, $n_{\text{inland}} = 12$), and they were dried in the field for C and N SIA. Mean life of C and N in rat muscle is ca. 31–36 and 41–45 days, respectively (Kurle 2009); SIA thus reflects the integrated diet of the animal in the 2–3 months prior to sample collection. Stomachs collected from individuals in July were examined with a compound microscope to determine the frequency of different food categories. We collected samples of potential food sources at each island to provide an isotopic baseline. Accordingly, we collected marine (mostly Gastropoda and Decapoda; $n_{\text{FSI}} = 12$, $n_{\text{SPM}} = 8$) and terrestrial invertebrates (mostly Coleoptera; $n_{\text{FSI}} = 18$, $n_{\text{SPM}} = 19$), egg yolk and muscle samples from corpses of adult and young marine birds (*S. nebuoxii*, *S. leucogaster*, *L. heermanni*, *L. livens*, and *P. occidentalis*; $n_{\text{FSI}} = 10$, $n_{\text{SPM}} = 9$), muscle from fish regurgitated by marine birds ($n_{\text{FSI}} = 3$, $n_{\text{SPM}} = 3$), sea algae ($n_{\text{FSI}} = 3$, $n_{\text{SPM}} = 5$), and vegetative structures of terrestrial plants using the Crassulacean acid metabolism pathway (CAM plants; *P. pringlei*; $n_{\text{SPM}} = 5$) or the C₃–Calvin cycle pathway (C₃ plants; mostly globe mallow *Sphaeralcea hainesii*, wild cucumber *Veseyanthus insularis*, and Baja California fig *Ficus palmeri*; $n_{\text{SPM}} = 14$) at sites where traps were placed.

Stable-isotope analysis

SIA were conducted at the Department of Biology of the University of Miami. Samples were dried in a digital oven (Imperial V; Lab-Line) at 50 °C during 24 h and powdered with a mortar. Because tissues with a high lipid content might be depleted in ¹³C (DeNiro and Epstein 1978; Tieszen et al. 1983), we placed the powdered samples in a 2:1 chloroform–ethanol mixture during 5 h to extract the lipids (Major et al. 2007). Samples were then dried again, and one subsample of each (1 mg for animal tissues, 5 mg for plant tissues) was placed into 3.5 × 5-mm tin cups. Samples were combusted in a EurovectorTM (GV Instruments, Manchester, UK) elemental analyzer. Resultant gases were separated and analyzed in a GV IsoprimeTM (GV Instruments) continuous-flow isotope ratio-mass spectrometer for stable-C and N isotope ratios on the same sample. We used two laboratory standards (egg albumen) for every five unknowns in sequence. Stable-isotope ratios were expressed in δ -notation as parts per thousand (‰) deviations from the international standards Peedee belemnite marine limestone (C) and air (N) according to the equation

$$\delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000,$$

where X was ¹³C or ¹⁵N, and R was the corresponding ratio ¹³C:¹²C or ¹⁵N:¹⁴N. Based on several hundred replicates of laboratory standards, we estimated laboratory measurement error to be ± 0.1 ‰ for C and N.

Diet reconstruction

We used the SIAR (stable-isotope analysis in R) package (Parnell et al. 2010) to determine the proportions of different food sources in the diet of black rat populations on each island. The output produces a range of solutions regarding the proportional contribution of each food to the diet for each population based on every individual rat sample. We considered only food items that appeared at least in two rat stomachs (e.g., marine invertebrates were thus not considered). For rats on FSI, we considered marine birds, marine fish, marine algae, and terrestrial invertebrates as potential food sources. In the case of rats from SPM, we considered marine birds, marine fish, marine algae, terrestrial invertebrates, and C₃ and CAM plants. The model incorporates sources of uncertainty in isotope composition and element concentration of food sources, and in the value of trophic enrichment factors (TEF; e.g., the difference in isotopic signature between the source and the consumer as the food is incorporated into the tissues). We considered mean (\pm SD) of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, % C, and % N of each food source, and the mean (\pm SD) of TEF for animal and plant food sources. For plant food, we used TEF values derived from mice fed corn and wheat (1.2 ± 0.3 and 3.1 ± 0.2 ‰ for C and N, respectively), and, for animal food, we used TEF values obtained in mice fed fish, cane sugar, and soy oil (1.9 ± 0.5 and 2.0 ± 0.5 ‰ for C and N, respectively). The C TEF value for the fish-based diet was obtained using the C isotope value of fish instead of the value for the bulk diet because most carbon synthesized into new tissue is derived from dietary protein (Arneson and MacAvoy 2005). We present mean (\pm SD) contribution of each food source to the diet of black rats.

Statistical analyses

We conducted a three-way analysis of variance (ANOVA) with sex, month, and zone of collection as factors to test sexual, temporal, and geographic variations in stable-isotope composition of rat muscle. Separate ANOVAs were conducted for rat $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at each island. We compared variance in isotopic values of rats using Levene's tests for homogeneity of variance for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values at each island. All analyses were conducted in

Table 1 Food items found in stomach of back rats in coast and inland sites on Farallón de San Ignacio (FSI) and San Pedro Mártir (SPM)

Data represent the number of stomachs in which remains of each food item were found. *Marine fish* is fish regurgitated by marine birds

| | FSI | | SPM | |
|---------------------------|-------|--------|-------|--------|
| | Coast | Inland | Coast | Inland |
| Marine birds | 10 | 13 | 9 | 10 |
| Marine algae | 5 | | 2 | |
| Marine fish | 1 | 2 | 2 | 2 |
| Marine invertebrates | 1 | | | 1 |
| Terrestrial invertebrates | | 7 | 1 | 7 |
| Terrestrial plants | | | 6 | 10 |
| Stomachs examined | 11 | 15 | 10 | 12 |

STATISTICA version7 (StatSoft, Tulsa, OK, USA) and significance was accepted at $\alpha = 0.05$.

Results

Stomach contents

We examined the food content of 24 stomachs from FSI and 22 from SPM in July. Remains from marine birds were the food items most frequently found in the stomachs from both islands at coastal and inland sites (Table 1). The main difference between islands was the presence of remains of terrestrial vegetation on SPM but not on FSI (Table 1). On both islands, remains of terrestrial invertebrates were more frequently found at the inland sites, whereas remains of algae were more frequently found at coastal sites (Table 1). Stomachs from FSI had only 1 ($n = 10$) or 2 food items ($n = 14$), in contrast to SPM where most stomachs had a mixture of 3–4 ($n = 9$) or 2 items ($n = 10$), and stomachs with only 1 item were rare ($n = 3$).

Isotopic signatures of prey types

Isotopic values of food sources revealed contrasting isotopic pictures at each island (Fig. 1). The minimum–maximum range of $\delta^{13}\text{C}$ (-17.1 to -13.2 ‰) and $\delta^{15}\text{N}$ (16.1 – 22.3 ‰) mean values from FSI was smaller than from SPM ($\delta^{13}\text{C}$: -23.9 to -13.3 ‰; $\delta^{15}\text{N}$: 16.5 – 32.8 ‰).

Isotopic signatures of black rats

There were significant differences in $\delta^{13}\text{C}$ values of rat tissues from FSI between months ($F_{1,44} = 14.5$, $P < 0.001$) and zones ($F_{1,44} = 17.7$, $P < 0.001$), but the effect of sex and of all the interactions was not significant ($F_{1,44} < 1.3$, $P > 0.20$); the same pattern was found for $\delta^{15}\text{N}$ values (month: $F_{1,44} = 17.2$, $P < 0.001$; $F_{1,44} = 8.9$, $P = 0.004$; sex and all interactions: $F_{1,44} < 2.2$, $P > 0.15$).

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were more positive in April and at inland sites (Table 2). In contrast, on SPM, there were no significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between months ($\delta^{13}\text{C}$: $F_{1,34} = 0.2$, $P = 0.59$; $\delta^{15}\text{N}$: $F_{1,34} = 2.3$, $P = 0.13$), zones ($\delta^{13}\text{C}$: $F_{1,34} = 3.4$, $P = 0.08$; $\delta^{15}\text{N}$: $F_{1,34} = 3.1$, $P = 0.08$), or sexes ($\delta^{13}\text{C}$: $F_{1,34} = 0.05$; $P = 0.82$; $\delta^{15}\text{N}$: $F_{1,34} = 0.01$, $P = 0.91$), and none of the interactions were significant ($P > 0.05$). We compared variance in isotopic values of rats pooling all the data from each island because the differences between months and sites on FSI, although statistically significant, were very small for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Table 2). Variance of $\delta^{13}\text{C}$ values were significantly different (Levene's test for homogeneity of variance: $F_{1,118} = 39.1$, $P < 0.001$): variance on FSI (0.35) was lower than on SPM (1.8). This difference reflects the minimum–maximum range of $\delta^{13}\text{C}$ values found at each island (FSI: -15.1 to -17.6 ‰, SPM: -14.2 to -19.8 ‰). A similar picture emerged for the variance of $\delta^{15}\text{N}$ values: variance on FSI (1.05) was dramatically lower than on SPM (13.8; $F_{1,118} = 62.1$, $P < 0.001$). Minimum–maximum range of $\delta^{15}\text{N}$ values was narrower on FSI (19.7–21.1 ‰) compared to SPM (21.6–35.3 ‰).

Diet reconstruction

Results from SIAR showed that marine and terrestrial sources of food contributed almost equally to the diet of the rat population on FSI whereas the rat population on SPM depended predominantly (70 %) on terrestrial sources of food (Fig. 2). Marine birds contributed to a larger extent to the diet of the rat population on FSI (35 %) than on SPM (8 %), where terrestrial invertebrates (25 %), C_3 (27 %), and CAM plants (18 %) predominated. SIAR showed that algae on SPM contributed to a larger extent than marine birds to the diet of rats (11 %), but this item rarely appeared in the stomachs examined (Table 1). However, even after eliminating algae from SIAR, the projected contribution of marine birds increased modestly (11 %),

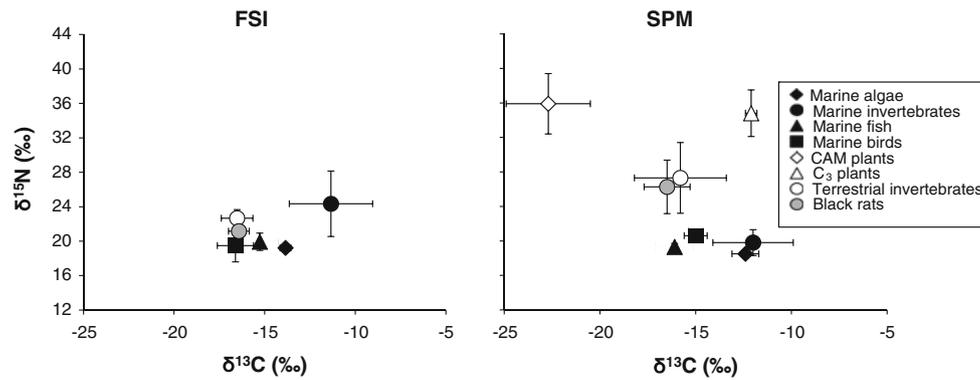


Fig. 1 Mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of black rats (*Rattus rattus*) and their potential food sources on two islands in the Gulf of California: Farallón de San Ignacio (FSI) and San Pedro Mártir

and rat diet was still conformed predominantly of terrestrial sources of food (79 %).

Discussion

In general, our study showed that the isotopic niche measured in δ - and p-spaces matched the expected ecological niche of black rat populations on each island. As predicted, the isotopic width was larger and the contribution of marine birds as food was lower in the rat population that inhabited the island with a higher diversity of food sources. In the following sections, we discuss dietary patterns of black rats on each island, the conservation implications of our findings, and the contribution of our study to the use of the isotopic niche to approach ecological questions.

Dietary patterns of black rats on SPM and FSI

Black rats on FSI and SPM fed on sea birds as evidenced by data from stomach contents and SIA, but they showed a generalist feeding behavior that included other food items. Almost all stomachs that were collected on SPM (86 %) and FSI (88 %) contained sea bird remains that indicated that most individuals fed on this item a few hours before their collection. Several other items were also found in stomachs of black rats collected on both islands indicating a generalist diet. A generalist feeding diet has been reported previously for black rats and other introduced rats, and it is considered one of the keys of their success in invading insular ecosystems. For example, SIA revealed that the diet of *R. norvegicus* varies widely on an Alaska island and that this rat feeds on sea birds where they are more readily available (Major et al. 2007). Stomach content analysis showed that black rats feed on a wide variety of food items and SIA suggested that they are important predators of breeding sea birds on a Caledonian

(SPM). Values for food sources were corrected by the appropriate trophic fractionation value (Arneson and MacAvoy 2005)

island (Caut et al. 2008). Revision of stomach contents and SIA demonstrated that black rats have a generalist feeding habit and that they feed on resident colonial sea birds on a subantarctic island (Quillfeldt et al. 2008). Other studies also support these conclusions (Clark 1982; Hobson et al. 1999; Stapp 2002; Cassaing et al. 2007; Pisanu et al. 2011).

Dietary patterns of black rats and island characteristics

We hypothesized that black rats on FSI would have a narrower trophic niche due to its lower diversity of potential food items. We predicted a more diverse diet and a lower importance of marine birds as food on the island with a higher diversity of food sources. Our first prediction was supported by the finding of a higher variance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the SPM black rat population. This isotopic pattern was validated by the finding of remains of only one or two food sources in most stomachs of rats collected on FSI, in contrast to SPM where most stomachs contained three or four items and stomachs with only one item were rare. Interestingly, isotopic values of black rats on FSI varied with location with respect to bird colonies but not on SPM. The difference in coastal and inland mean values on FSI, although statistically significant, was very small for both elements (0.4 ‰ for $\delta^{13}\text{C}$ and 0.6 ‰ for $\delta^{15}\text{N}$) and of low biological importance. A previous study showed that *R. norvegicus* differed in C and N isotope composition at different sites to a much larger extent on an island several times bigger than FSI and SPM (Major et al. 2007). Black rats on FSI and SPM probably forage throughout the island, but isotopic variance on SPM suggests that, although they overlap in their spatial foraging grounds, there is long-term dietary inter-individual partition. For example, some individuals collected from coastal sites on SPM had isotopic signals suggesting a strong dependence on terrestrial sources and vice versa.

Table 2 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (mean \pm SD ‰) values of black rats collected on Farallón de San Ignacio (FSI) and San Pedro Mártir (SPM) islands in the Gulf of California, Mexico

| | April | | July | | Coast | | Inland | | Males | | Females | |
|-----|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ |
| FSI | -16.0 ± 0.5 (26) | 21.7 ± 0.6 | -16.7 ± 0.5 (26) | 20.5 ± 1.1 | -16.6 ± 0.4 (23) | 20.8 ± 1.1 | -16.2 ± 0.6 (29) | 21.4 ± 0.9 | -16.5 ± 0.3 (36) | 21.1 ± 1.1 | -16.2 ± 0.5 (16) | 21.4 ± 0.9 |
| SPM | -16.3 ± 0.26 (22) | 26.8 ± 3.5 | -16.6 ± 0.27 (20) | 25.5 ± 2.3 | -16.1 ± 1.2 (20) | 25.5 ± 2.5 | -16.8 ± 1.1 (22) | 26.9 ± 3.4 | -16.3 ± 1.2 (20) | 26.4 ± 3.1 | -16.6 ± 1.2 (22) | 26.1 ± 3.1 |

Muscle samples were collected in coastal and inland sites on each island. Numbers in parentheses are sample sizes

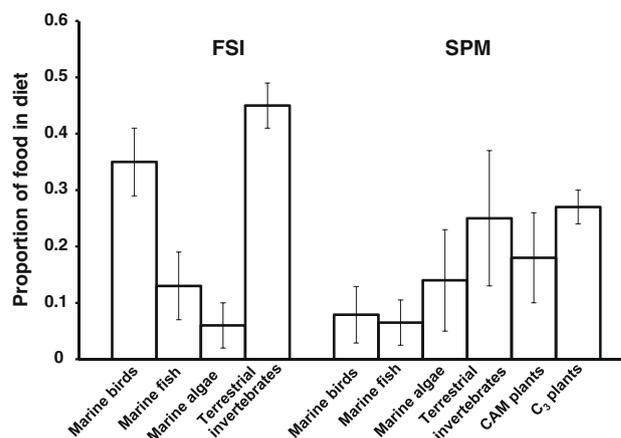


Fig. 2 Contribution of food sources to the diet of black rats on two islands in the Gulf of California: Farallón de San Ignacio (FSI) and San Pedro Mártir (SPM). Values were calculated using SIAR (stable isotope analysis in R; Parnell et al. 2010) and represent the mean value (\pm SD) of the range of potential solutions regarding the contribution of each food type to the diet. The analysis included only food items that appeared in at least two stomachs examined in each rat population (e.g., marine invertebrates were not included on either island)

Our second prediction was supported by the SIAR diet reconstruction that indicated that marine birds represented up to 35 % of the diet of black rats on FSI and only 8 % on SPM. The reconstructed diet of rats on FSI was predominantly composed of marine birds and terrestrial invertebrates, the two food items most frequently found in stomachs in this population. In contrast, SIAR diet reconstruction of rats on SPM suggested that terrestrial invertebrates and plants were the most important food sources. Use of alternative food sources in the SPM rat population was supported by the diversity of items found in most stomachs. Our SIAR might have underestimated the importance of marine birds in favor of items that were rarely found in stomachs (e.g., algae). However, even when we eliminated algae from SIAR of SPM rats, the contribution of marine birds to their diet was still much lower than on FSI.

Conservation implications

A previous study showed that the negative impact of introduced rats on native sea fauna increases on islands that have a low diversity of alternative preys (Donlan and Wilcox 2008). Our findings are in line with this finding, but provide the first direct evidence that diet of introduced rodents is less varied and probably more dependent on sea birds on islands with a lower diversity of alternative preys. In the fall of 2007, black rats were extirpated from SPM and FSI and this action is already showing positive effects for sea bird reproduction. For example, only 2 years after

rat extirpation, the survival of chicks and nest occupancy of *P. aethereus* on FSI increased by 20 and 60 %, respectively, and nesting *S. cravieri* were reported for the first time in 16 years on SPM (Castillo-Guerrero et al. 2009). Our findings suggest that there are significant differences in the impact of introduced fauna on sea birds as islands get less biologically diverse. The impact of introduced rodents on other native insular taxa (e.g., mammals, reptiles, invertebrates) might operate by the same rules.

Isotopic niche and ecological questions

Recent simulation models warn that the isotopic niche might misrepresent trophic ecology when foraging behavior of consumers and habitat-derived isotopic differences are ignored (Flaherty and Ben-David 2010). For example, specialist populations might show wider isotopic niches than generalist populations. Our study showed that isotopic niche was a good measure of trophic niche in two generalist populations with contrasting access to food sources. The use of this approach was possible because isotopic diversity of food sources was directly related to the diversity of food items offered in the two habitats. These results encourage the use of the isotopic niche to measure trophic niche when certain circumstances are met, and add to a growing number of studies (Layman et al. 2007; Syväranta and Jones 2008) that have proved the utility of the isotopic niches to answer ecological questions.

Acknowledgments We thank Carolina Valdespino, Vinicio Sosa, Alberto González and Enriqueta Velarde for their advice and help in the development of this study, Alfonso Aguirre and Araceli Samaniego from Conservación de Islas for their wonderful support, Ricardo González and Jorge Villavicencio for their assistance in the field work, and Donald L. Phillips and Richard Inger for their comments on the manuscript. The Consejo Nacional de Ciencia y Tecnología supported our work with a research grant to L.G.H.M. (#43343), and a scholarship to M.A.R. Sampling and landing permits were granted by the Wildlife General Direction (DGVS) of the Environment Ministry (SEMARNAT), and the Interior Ministry (SEGOB), respectively. We finally thank to the regional offices of the Islas del Golfo de California Natural Protected Area from the Comisión Nacional de Áreas Naturales Protegidas in Sonora and Sinaloa for allowing us the access to the islands.

References

- Arneson LS, MacAvoy SE (2005) Carbon, nitrogen, and sulfur diet-tissue discrimination in mouse tissues. *Can J Zool* 83:989–995
- Bearhop S, Adam CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. *J Anim Ecol* 73:1007–1012
- Cassaing J, Derré C, Moussa I, Cheylan G (2007) Diet variability of Mediterranean insular populations of *Rattus rattus* studied by stable isotope analysis. *Isot Environ Health Stud* 43:197–213
- Castillo-Guerrero JA, González Gómez R, Vizcaíno E, Guevara MA, Latofski M, Ventura J, Leal M (2009) Monitoreo de aves post-erradicación de ratas (*Rattus rattus*) en las islas Farallón de San Ignacio y San Pedro Mártir en el Golfo de California, México, 2009. Technical report
- Caut S, Angulo E, Courchamp F (2008) Dietary shift of an invasive predator: rats, seabirds and sea turtles. *J Appl Ecol* 45:428–437
- Clark DA (1982) Foraging behavior of a vertebrate omnivore (*Rattus rattus*): meal structure, sampling, and diet breadth. *Ecology* 63:763–772
- DeNiro M, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42:495–506
- Donlan CJ, Wilcox C (2008) Diversity, invasive species and extinctions in insular ecosystems. *J Appl Ecol* 45:1114–1123
- Flaherty EA, Ben-David M (2010) Overlap and partitioning of the ecological and isotopic niches. *Oikos* 119:1409–1416
- Frick W (2007) Influences of island characteristics on community structure and species incidence of desert bats in near-shore archipelago, Baja California. PhD dissertation, Oregon State University, Corvallis
- González-Bernal MA, Mellink E, Payán-Esquerria C (2001) *Cnemidophorus tigris* y *Urosaurus ornatus*. *Herpet Review* 32:192–193
- González-Bernal MA, Mellink E, Fong-Mendoza JR (2002) Nesting birds of Farallón de San Ignacio, Sinaloa, México. *Western Birds* 33:254–257
- Grismer LL (2002) Amphibians and reptiles of Baja California, including its pacific islands and the islands in the sea of Cortes. University of California Press, Los Angeles
- Hobson KA, Drever MC, Kaiser GW (1999) Norway rats as predators of burrow-nesting seabirds: insights from stable isotope analyses. *J Wildl Manag* 63:14–25
- Hutchinson GE (1957) Concluding remarks: cold spring harbor symposium. *Quant Biol* 22:415–427
- Kurle CM (2009) Interpreting temporal variation in omnivore foraging ecology via stable isotope modeling. *Funct Ecol* 23:733–744
- Layman CA, Quattrochi JP, Peyer CM, Allgeier JE (2007) Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecol Lett* 10:937–944
- Major HL, Jones IL, Charette MR, Diamond AW (2007) Variations in the diet of introduced Norway rats (*Rattus norvegicus*) inferred using stable isotope analysis. *J Zool* 271:463–468
- Matich P, Heithaus MR, Layman CA (2011) Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. *J Anim Ecol* 80:294–305
- Mellink E, Orozco-Meyer A, Contreras B, González-Jaramillo M (2002) Observations on nesting seabirds and insular rodents in the middle Sea of Cortés in 1999 and 2000. *Bull Southern Calif Acad Sci* 101:28–35
- Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. *Front Ecol Environ* 5:429–436
- Olsson K, Stenroth P, Nyström P, Granéli W (2009) Invasions and niche width: does niche width of an introduced crayfish differ from a native crayfish? *Freshw Biol* 54:1731–1740
- Parnell A, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. *PLoS One* 5:e9672
- Pisanu B, Caut S, Gutjahr S, Vernon P, Chapuis JL (2011) Introduced black rats *Rattus rattus* on Ile de la possession (Iles Crozet, Subantarctic): diet and trophic position in food webs. *Polar Biol* 34:169–180
- Quillfeldt P, Schenk I, McGill RAR, Strange IJ, Masello JF, Gladbach A, Roesch V, Furness RW (2008) Introduced mammals coexist with seabirds at New Island, Falkland Islands: abundance, habitat preferences, and stable isotope analysis of diet. *Polar Biol* 31:333–349

- Semmens BX, Ward EJ, Moore JW, Darimont CT (2009) Quantifying inter- and intra-population niche variability using hierarchical Bayesian stable isotope mixing models. *PlosOne* 4:e6187
- Stapp P (2002) Stable isotopes reveal evidence of predation by ship rats on seabirds on the Shiant Islands, Scotland. *J Appl Ecol* 39:831–840
- Syväranta J, Jones RI (2008) Changes in feeding niche widths of perch and roach following biomanipulation, revealed by stable isotope analysis. *Freshw Biol* 53:425–434
- Tershy BR, Breese D (1997) The birds of San Pedro Martir island, Gulf of California. Mexico. *Western Birds* 28:96–107
- Tershy BR, Breese D, Angeles-P A, Cervantes-A M, Mandujano-H M, Hernández-N E, Córdoba-A A (1992) Natural history and management of Isla San Pedro Martir, Gulf of California. Report to conservation International-Mexico, Guaymas
- Tieszen LL, Boutton TW, Tesdahl KG, Slade NA (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia* 57:32–37
- Vander Zanden HB, Bjorndal KA, Reich KJ, Bolten AB (2010) Individual specialists in a generalist population: results from a long-term stable isotope series. *Biol Lett* 6:711–714