A comparative isotopic natural history of two native passerines (*Troglodytes cobbi* and *Cinclodes antarcticus*) and the invasive rats (*Rattus norvegicus*) that extirpate them

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Running Title: Invasive rats and native passerines

Abstract

While several studies have shown that invasive rats can have negative effects on island birds through predation (both direct predation and nest predation), other mechanisms for the effects of invasives on island biota have been given less attention. Here we explore another potential mechanism by which invasive rats can affect native island birds: the competitive use of common resources. We used stable isotope analyses to estimate the fraction of marine and terrestrial sources incorporated into the tissues of two species of passerines (*Troglodytes cobbi*, Troglodytidae; and *Cinclodes antarcticus*, Furnariidae) and Norway rats (*Rattus norvegicus*, Muridae) in the Falkland Islands. These two passerines are absent on islands where rats are present. We found significant incorporation of marine resources in the three species, with the highest incorporation in tissues of *T. cobbi*. This species appears to be one of the passerines most reliant on marine sources and the most marine member of the family Troglodytidae. We also used the results of these isotopic analyses to estimate the isotopic niche breadth of each of these species and the isotopic niche overlap among them. *Rattus norvegicus* had a large isotopic niche that overlapped broadly with those of the two passerine species. We propose that different ways of both depicting and estimating isotopic niche widths are complementary rather than alternative. Our results are consistent with the notion that invasive rats might have an impact on these two species of Falkland Island passerines by using common resources, but do not rule out the possibility that part of their effect is through direct predation.

Introduction

Invasive species are detrimental to native island species, communities, and ecosystems (Blackburn *et al.* 2004; Kurle *et al.* 2008; Jones 2010). Rats (*Rattus* spp.) are among the most problematic invasive species, especially for native island birds (Atkinson 1985; Towns *et al.* 2006). The direct effects of invasive rats on native island species (through predation and nest predation) have been well documented (Towns 2009; Traveset *et al.* 2009), while indirect effects (i.e., competition for common resources) have been given less attention. Here we report on the potential indirect effects of invasive rats in the Falkland Islands on native island birds.

The native avifauna of the Falkland Islands includes nine species of passerine birds (Woods and Woods 2006). Historically, there was a native terrestrial mammal in the Falklands (the warrah; *Dusicyon australis*), but this species is extinct, and while there are no extant native terrestrial mammals, several non-native species have been introduced. Norway rats (*Rattus norvegicus*, Muridae; or 'rats') were introduced to the Falklands in the 18th Century and are currently present on about half of the approximately 500 islands in the archipelago (Tabak *et al.* 2015a). The presence of rats is associated with reduced species richness and altered assemblage structure of passerine communities (Tabak *et al.* 2014, 2015b). Rat presence is also associated with a 10-fold reduction in the rate of energy used by passerine communities (Tabak *et al.* in review). The two native passerines that are the most prevalent and abundant on rat-free islands (Tussacbird, *Cinclodes antarcticus*, Furnariidae; and Cobb's wren, *Troglodytes cobbi*, Troglodytidae; henceforth referred to by their generic names: *Cinclodes* and *Troglodytes*) are locally extirpated from islands where rats are present (Tabak *et al.* 2014).

Tabak *et al.* (2014, 2015b) postulated two potentially complementary hypotheses for the seemingly disproportionate effect of rats on *Cinclodes* and *Troglodytes* compared to other passerines in the community. First, because these two bird species are ground nesters (Strange 1992), they might be susceptible to predation by rats, which are responsible for the decline of many island ground-nesting species (Towns *et al.* 2006). Second, rats might compete for the same food sources as these two bird species. *Cinclodes* and *Troglodytes* often feed on the plentiful marine invertebrates on the shoreline edge (Woods and Woods 2006), while Norway rats are generalists with diverse diets (Murray *et al.* 1999). They feed on terrestrial and marine resources (Hobson *et al.* 1999), and hence can have strong effects on the availability of invertebrates used by *Cinclodes* and *Troglodytes*. The effect of rats on *Cinclodes* and *Troglodytes* would be potentially strong if rats deplete the marine resources that appear to explain the high abundance and prevalence of *Cinclodes* and *Troglodytes* in the Falkland Islands (Tabak *et al.* in review). Here we address the question: to what extent does rats' use of marine resources overlap with those of *Cinclodes* and *Troglodytes*? Clearly, documenting the use of a broad range of resources in rats and/or any overlap in resource use with the two species that they affect the most in the Falklands does not address the question of whether their effect is through direct predation. However, our measurements can help to inform whether their effect on these species, and on bird communities in the Falklands (and islands elsewhere), is partially due to their ability to use a broad range of resources.

To examine these questions we measured the stable isotope values of the tissues of birds and rats. Stable isotopes are useful tools to address these questions because marine resources are often enriched in both ^{13}C and ^{15}N relative to terrestrial ones (Sabat *et al.* 2006). Stable isotopes

are powerful tools in ecological studies but they have limitations (Phillips *et al.* 2014). Here we recognize explicitly the limitations that stable isotopes have on the inferences we can make from their measurement. Our analyses were informed by the concept of the "isotopic niche" (Newsome *et al.* 2007), which suggests that stable isotope analyses can be used to investigate questions about an animal's ecological niche, including its width (Bearhop *et al.* 2004), whether this width is the result of intra- or inter-individual differences (Semmens *et al.* 2009), and the overlap in resource use among species (Layman *et al.* 2012). But isotopic niches are not ecological ones (Vander Zanden *et al.* 2010); unlike ecological ones, isotopic niches are "near sighted", they detect whether animals use resources that differ in isotopic value (Newsome *et al.* 2007), but do not detect differences in the taxonomic identity of the resources consumed unless these differences are accompanied by differences in isotopic values (Newsome *et al.* 2012). In our study we investigated the breadth of, and overlap in, the use of marine and terrestrial resources.

Since rats are dietary generalists (Murray *et al.* 1999), we hypothesized that they would have broad isotopic niches. We also hypothesized that if rats use similar resources as *Cinclodes* and *Troglodytes*, we would find high amounts of niche overlap with rats and birds. Evidence supporting our second hypothesis would not explain away the importance of rat predation on these bird species, but it would provide support for the conjecture that competition might play an important role in the extirpation of these species when rats are present.

Methods

Sample collection

Bird, plant, and invertebrate samples were collected in December 2009 from three islands of varying sizes (Carcass Island – 1900 ha – 51.29°S, 60.56°W; Sea Lion Island – 905 ha – 52.43°S, 59.10°W; and Kidney Island – 32 ha – 51.62°S, 57.75°W). Birds were collected using mist nets and approximately 50 µl of blood was drawn from the brachial artery. Blood was smeared onto a glass slide and air-dried. Blood was then scraped into a cryogenic vial and stored frozen. All potential dietary sources (i.e., invertebrate animals and plants) were dried at 65° C in a drying oven and stored frozen. Potential dietary sources were sampled from both marine and terrestrial environments. Materials sampled from intertidal pools and kelp wrack (molluscs, algae, amphipods, and kelp flies (Supplementary Table 1)) were classified as 'marine.' Materials were considered 'terrestrial' if they were collected on terrestrial vegetation (Supplementary Table 1). Marine and terrestrial dietary sources were compared with multivariate analysis of variance (MANOVA) using both δ^{13}C and δ^{15}N as response variables and marine or terrestrial as driving variables. *Cinclodes* and *Troglodytes* are found together on islands, but neither of these species are found on islands where rats are present (Tabak *et al.* 2014, 2015b). Therefore, rats were collected from three islands of similar size to those from which birds were collected (Bleaker Island – 2000 ha – 52.21°S, 58.85°W; Middle Island – 900 ha – 51.40°S, 59.71°W; and Kent Island – 32 ha – 51.43°S, 59.67°W) in February – March 2013. We collected rats using snap traps (VictorPest), removed the *gastrocnemius* muscle, and stored it in 90% ethanol. Before isotope analyses, rat samples were freeze-dried, and then de-lipified by a petroleum ether treatment (Kelly and Martínez del Rio 2010), but none of the other samples were de-lipified.

Samples were ground into a fine powder, weighed ($\approx$ 0.5 mg) on precision scales, and placed in small tin capsules for analysis.

Isotope analyses

δ^{13}C and δ^{15}N values were determined using a Costech elemental analyzer coupled to a Thermo-Finnigan Delta Plus X isotope ratio mass spectrometer. All isotopic analyses were conducted at the University of Wyoming Stable Isotope Facility (UWSIF, Laramie, WY). Isotopic results are expressed as δ values, and the natural abundance of δ^{13}C and δ^{15}N is expressed as a deviation per thousand (‰) with respect to an internationally recognized standard: $\delta = 1000 * [(R_{sample} - R_{standard})/(R_{standard})]$, where R_{sample} and $R_{standard}$ are the ratios of ^{13}C/^{12}C or ^{15}N/^{14}N of the sample and standard, respectively. The analytical error for C was up to 0.3 ‰ for the δ^{13}C and up to 0.5 ‰ N in δ^{15}N analysis. We used bovine liver (δ^{13}C = -17.82 ‰ and δ^{15}N = 6.78 ‰) and blood (δ^{13}C = -17.10 ‰ and δ^{15}N = 5.38 ‰) as references for blood and muscle analyses, chitin (δ^{13}C = -21.66 ‰ and δ^{15}N = 6.59‰) and peptone (δ^{13}C = -15.37 ‰ and δ^{15}N = 5.32 ‰) for invertebrates, and alfalfa (δ^{13}C = -27.52 ‰ and δ^{15}N = 0.21 ‰) for plants and algae. The standard deviation of replicated reference samples in the UWSIF is less than 3‰.

Characterizing the proportion of marine and terrestrial components of diets

Rather than attempting to estimate the individual potential diet components incorporated into each individual's tissues, we established two broad sources of food: marine and terrestrial. We followed Phillips *et al.*'s (2014) advice to sacrifice precision for accuracy to obtain better constrained solutions. To estimate the proportion of these two components in each individual's tissues we used the MixSIAR package (Stock and Semmens 2013). Because we found that
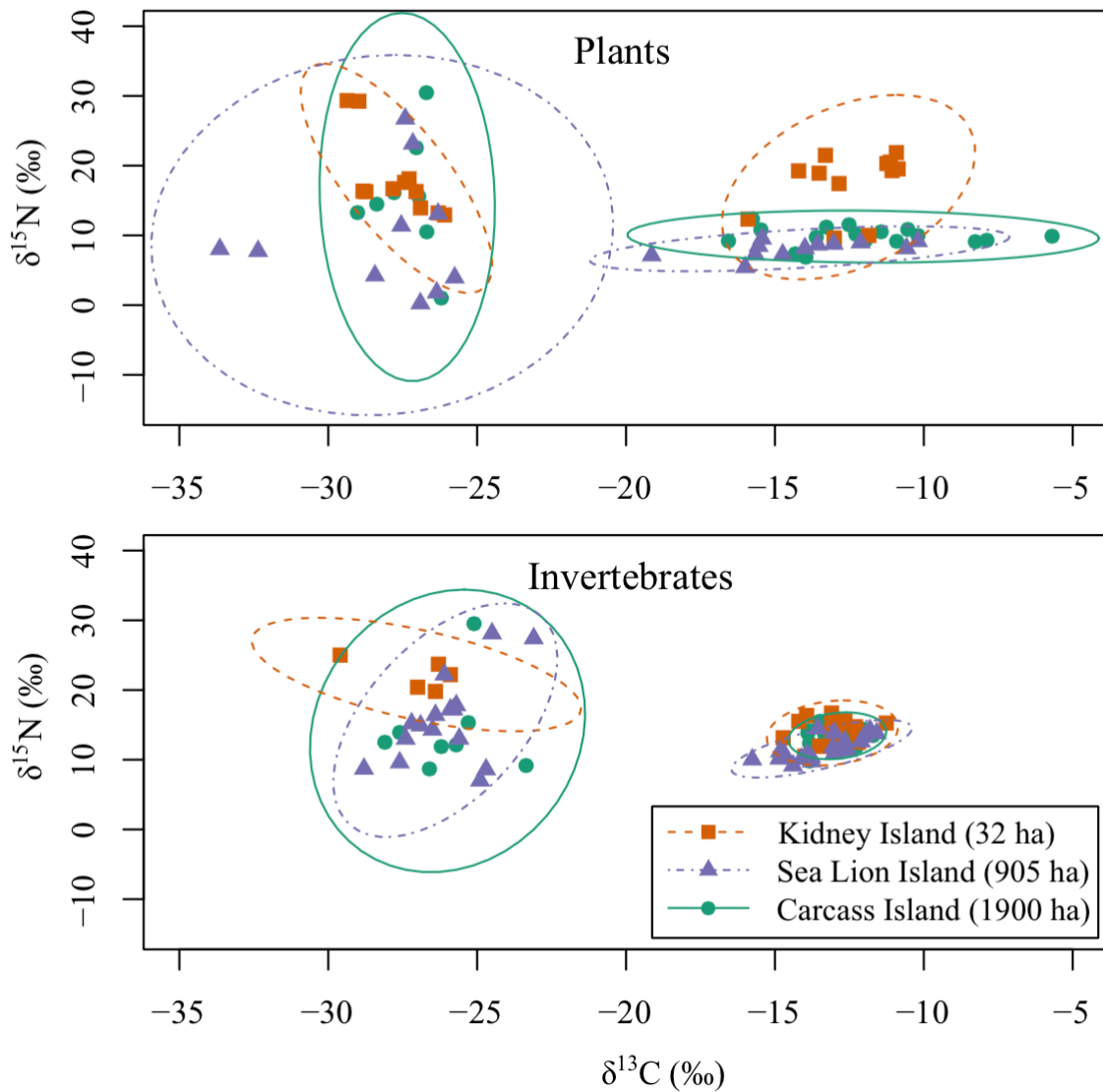
Figure 1: Dietary sources of plants (top) and invertebrates (bottom) were collected from both terrestrial and marine environments. These 95% confidence ellipses for these sources were clearly separated on the $\delta^{13}C$ axes. Marine sources had $\delta^{13}C > -20$ ‰, while terrestrial sources had $\delta^{13}C < -20$ ‰.

carbon clearly separated between the isotopic values of these two resource types whereas those of nitrogen overlapped significantly (Fig. 1), we used only carbon isotopic values to estimate incorporation of marine and terrestrial resources. Indeed the nitrogen isotopic values of marine sources were completely contained within the 95% confidence ellipses of those of terrestrial sources (Fig. 1). We ran Markov chain Monte Carlo (MCMC) simulations with three chains of 10^6 iterations with a burn-in period of 5×10^4, while thinning by 50 iterations. For bird blood we used discrimination values from Carleton and Martinez del Rio (2005; $\Delta^{13}C = 1.5$‰), and for rat muscle we used Caut *et al.*'s (2008) values ($\Delta^{13}C = 0.51$‰). Changing the value of these discrimination rates did not change the inferences of our models significantly. The means and standard errors used to estimate the proportion of marine sources ($\hat{q}$), and therefore also that of terrestrial sources ($1-\hat{q}$), in each individual are shown in Figure 2. We used the averages of invertebrates as potential food sources for birds, as these two species only ingest animal food (Woods and Woods 2006), but used the pooled means of animal and plant sources for rats as these animals are most likely omnivores.

Breadth in the use of marine and terrestrial sources

Several measures have been proposed to quantify the width of isotopic niches, including the area of convex hulls and standard ellipses (Jackson *et al.* 2011). All these useful measurements suffer from the shortcoming of depending on the magnitude of difference in the isotopic values of resources (Newsome *et al.* 2007). If this difference is large, the measurements give a large isotopic niche width value. The Euclidean distances between the isotopic values of resources in "δ space" dictate the width and extent of isotopic niches (Newsome *et al.* 2007). An alternative is to transform raw isotope values into proportions of resources incorporated using

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mixing models (Phillips 2012) and to use classical metrics of niche width and overlap (Flaherty and Ben-David 2010; Willson *et al.* 2010). We used both approaches, which we will argue are complementary rather than alternative. We relied on widely used measurements of niche width (Levins' standardized niche breadth, $\hat{B}_A$; Levins 1968; Hurlbert 1978) and overlap (MacArthur and Levins' overlap, $\widehat{M}_{jk}$; Macarthur and Levins 1967; Pianka 1973; Krebs 2014) to quantify the breadth and degree of overlap in the incorporation of marine and terrestrial resources in birds and rats. We also used the geometrical properties of standard ellipses to infer patterns of resource and habitat use that were not disclosed by the conventional methods used to estimate width and overlap. We emphasize that the values of $\hat{B}_A$ and $\widehat{M}_{jk}$ that we estimated are measures of how evenly animals incorporate marine and terrestrial sources into their tissues, and on how much they overlap in this coarse dimension of their ecological niches. Strictly speaking, $\hat{B}_A$ and $\widehat{M}_{jk}$ are not measures of ecological niche width and overlap. However, although we are cognizant of this caveat, for convenience, we used the terms "isotopic niche breadth" and "isotopic niche overlap" for, $\hat{B}_A$ and $\widehat{M}_{jk}$, respectively.

To characterize the breadth in use of marine and terrestrial resources, we used Levins' standardized measure of niche breadth ($\hat{B}_A$):

$$\hat{B}_A = \hat{B} - 1$$

Where

$$\hat{B} = \frac{1}{\hat{q}^2 + (1 - \hat{q})^2}$$

and $\hat{q}$ is the average posterior proportion of an individual's diet derived from marine sources (Levins 1968; Krebs 2014). The value of $\hat{B}_A$ ranges from zero to one where $\hat{B}_A = 0$ indicates that

an individual's tissues incorporated only marine or terrestrial sources, whereas $\hat{B}_A = 1$ (i.e.,

$\hat{q} = 0.5$) indicates that an individual incorporated 50% marine and 50% terrestrial resources in

its tissues. As an additional estimate of the isotopic niche breadth of each population, we

estimated the Standard Ellipse Area, corrected for small sample size (Jackson *et al.* 2011). To

give a quantitative interpretation to the form of these ellipses, we used Turner *et al.*'s (2010)

eccentricity (E) measure. A value of E equal to 0 indicates a perfectly circular scatter of values in

$\delta^{13}C$ and $\delta^{15}N$ space, whereas a value of 1 describes a perfectly linear relationship. This linear

relationship is an indication of a mixing relationship that includes two distinct sources.

Overlap in the incorporation of terrestrial and marine sources

To estimate overlap in the incorporation of terrestrial and marine sources among islands

and species, we used the method proposed by MacArthur and Levins (1967), where overlap of

the niche of species *j* on that of species *k* ($\widehat{M}_{jk}$) is estimated as:

$$\widehat{M}_{jk} = \frac{\hat{q}_j \, \hat{q}_k + (1 - \hat{q}_j)(1 - \hat{q}_k)}{\hat{q}_j^2 + (1 - \hat{q}_j)^2}.$$

$\widehat{M}_{jk}$ is asymmetrical and varies from 0, when there is no overlap in the incorporation of marine

resources between species *j* and that of species *k*, to 1 when there is complete overlap (Krebs

2014). To examine whether there were reciprocal differences in overlap between species, we

first estimated the average difference in overlap between species *j* and species *k*

$$\overline{M_{Jk} - M_{kJ}} = \frac{\sum_i^m \sum_l^n (M_{jkli} - M_{kjli})}{n+m},$$

where *l* and *i* are the *n* and *m* individuals in each one of these species, respectively. Then we

tested whether this average was significantly different from 0 with one-sample t-tests. We

compared overlap between the two bird species on each of the islands where they coexist, and compared between rats and each bird species on islands of similar size.

Results

Isotopic results

Isotopic values for marine and terrestrial dietary sources differed significantly among plants ($F_{2,68}$ = 379, $p < 0.0001$, Fig. 1), invertebrates ($F_{2,92}$ = 1581, $p < 0.0001$, Fig. 1), and invertebrates and plants combined ($F_{2,163}$ = 1256, $p < 0.0001$, Fig. 1). Although there was no overlap in the $\delta^{13}C$ values of marine and terrestrial potential food sources, the $\delta^{15}N$ values of marine sources were contained within the range and 95% CI ellipses of terrestrial ones (Fig. 1). The 95% CI standard ellipses for the isotopic values of *Troglodytes*, *Cinclodes*, and rats (Fig. 2) had high eccentricity values (> 0.76, Table 1), and in many, albeit not all cases, had high (and significant) R^2_{adj} values indicating two primary resource sources (Table 1). In *Troglodytes* the sign of the slope of the relationships between $\delta^{13}C$ and $\delta^{15}N$ was significantly negative on all islands ($p < 0.001$). The sign of slope of this relationship differed among islands in both *Cinclodes* and rats. In *Cinclodes*, the slope was positive on Carcass Island, negative on Kidney Island, and statistically insignificant on Sea Lion Island (Fig. 2, Table 1). In rats, the slope was positive on Middle Island, but negative on Bleaker and Kent Islands. Below, we consider the meaning and significance of the sign and value of these slopes.

Characterizing the proportion of marine and terrestrial components of diets

In the two bird species, the mean posterior proportion of marine sources incorporated into tissues (*q*) differed among islands (two-way ANOVA, $F_{2,94}$=4.86, $p < 0.001$) and among species
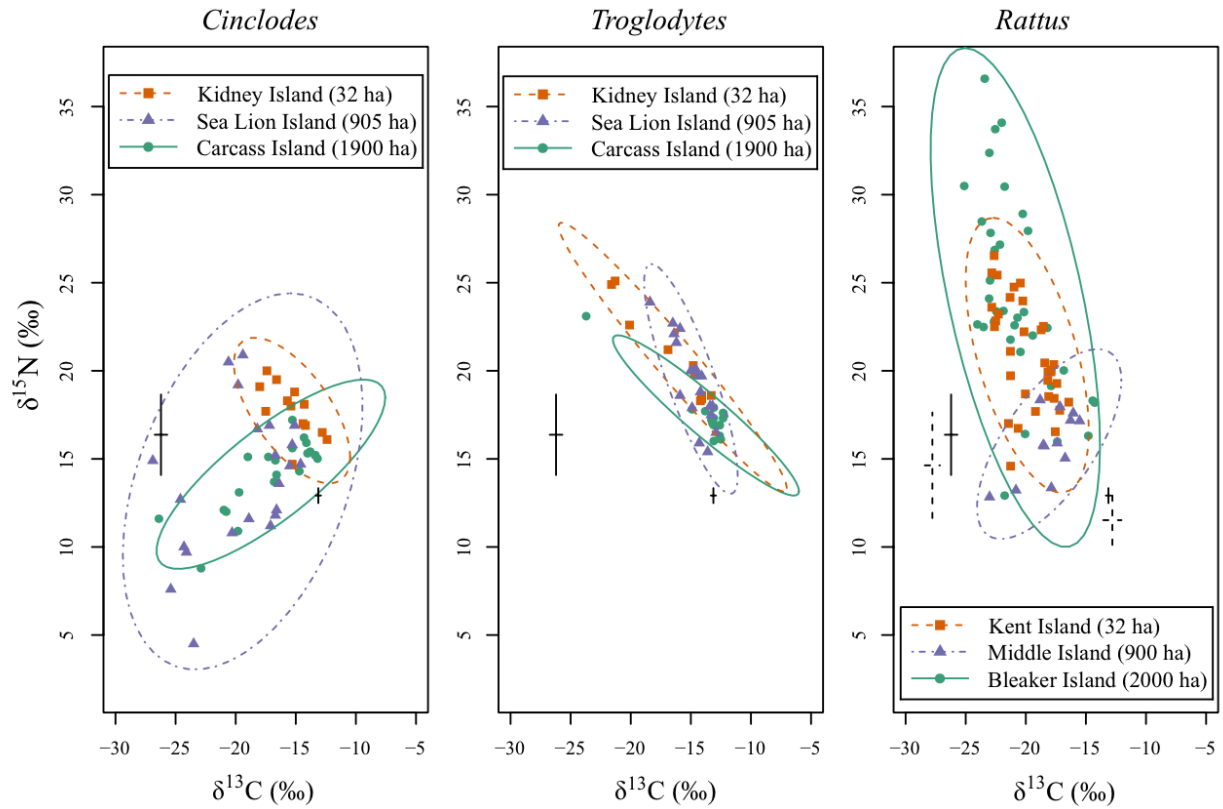
Figure 2: Isotopic values for each species on each island with 95% confidence ellipses. For all species on all islands, ellipses were highly eccentric (eccentricity > 0.75, see Table 1). Error bars represent 95% confidence intervals for isotopic values of potential dietary sources: invertebrates (solid line) and plants (dotted lines).

Table 1: Standard ellipse area, eccentricity, slope, and correlation for each population

Species	Island	Standard Ellipse Area (mean ± 95% CI, ‰)	Eccentricity	Slope relating $\delta^{13}C$ to $\delta^{15}N$ (± 95% CI)	R^2_{adj}
Cinclodes	Carcass	13.5 ± 0.06	0.96	0.46 ± 0.16	0.64**
	Sea Lion	42.4 ± 0.18	0.76	0.43 ± 0.43	0.12
	Kidney	6.4 ± 0.04	0.89	-0.55 ± 0.39	0.35*
Troglodytes	Carcass	5.8 ± 0.03	0.99	-0.56 ± 0.10	0.89**
	Sea Lion	6.4 ± 0.03	0.97	-1.41 ± 0.45	0.69**
	Kidney	7.8 ± 0.05	0.99	-0.78 ± 0.12	0.94**
Rattus	Bleaker	37.7 ± 0.13	0.93	-1.19 ± 0.55	0.33**
	Middle	9.5 ± 0.06	0.90	0.60 ± 0.41	0.40*
	Kent	15.7 ± 0.05	0.88	-0.84 ± 0.45	0.28**

Significance values for linear relationship between $\delta^{13}C$ to $\delta^{15}N$: * indicates $0.05 > p > 0.001$, ** indicates $p < 0.001$.

(two-way ANOVA, $F_{1,94} = 25.48$, p < 0.0001, Fig. 3A), but there was a significant interaction between island and species ($F_{2,94} = 6.78$, p = 0.002). On Carcass and Sea Lion Islands, *Troglodytes* had significantly higher proportions of marine ingredients in their tissues than *Cinclodes* (*a posteriori* Bonferroni-corrected LSD tests, p < 0.05, Figure 3A). On Kidney Island, however, this proportion did not differ significantly between these two species (*a posteriori* Bonferroni-corrected LSD tests, p > 0.1, Figure 3A). Rats differed among islands in the proportion of marine sources incorporated (one-way ANOVA on arcsin, square root-transformed data, $F_{2,77} = 9.54$, p < 0.001). They incorporated similar proportions on Kent and Bleaker Islands, Tukey's HSD p > 0.1), but had significantly higher incorporation of marine sources on Middle Island than on the other two islands (Tukey's HSD, p < 0.05). Because *Troglodytes* and *Cinclodes* were absent from islands with rats, we compared the proportion of marine resources incorporated in rats from all islands with those of the two bird species on all islands. There were significant differences among species in the proportion of incorporated marine sources ($F_{2,176} = 75.10$, p < 0.0001), with rats incorporating the lowest proportion of marine sources in their tissues, *Cinclodes* an intermediate value, and *Troglodytes* the highest value. These values differed significantly from each other for all groups (Tukey's HSD, p < 0.0001, Fig. 3A).

Breadth in the use of marine and terrestrial sources

      The proportion of marine resources incorporated (q), and the breath in the use of marine and terrestrial resources ($\hat{B}_A$) are functionally related. The latter is a symmetrical humped function of $\hat{q}$, with local minima at $\hat{q} = 0$ and 1 ($\hat{B}_A = 0$), and a maximum at $\hat{q} = 0.5$ ($\hat{B}_A = 1$). Species that use marine and terrestrial resources more evenly have higher $\hat{B}_A$ values. In birds, the isotopic niche breadth ($\hat{B}_A$) differed among islands (two-way ANOVA on arcsin, square root-

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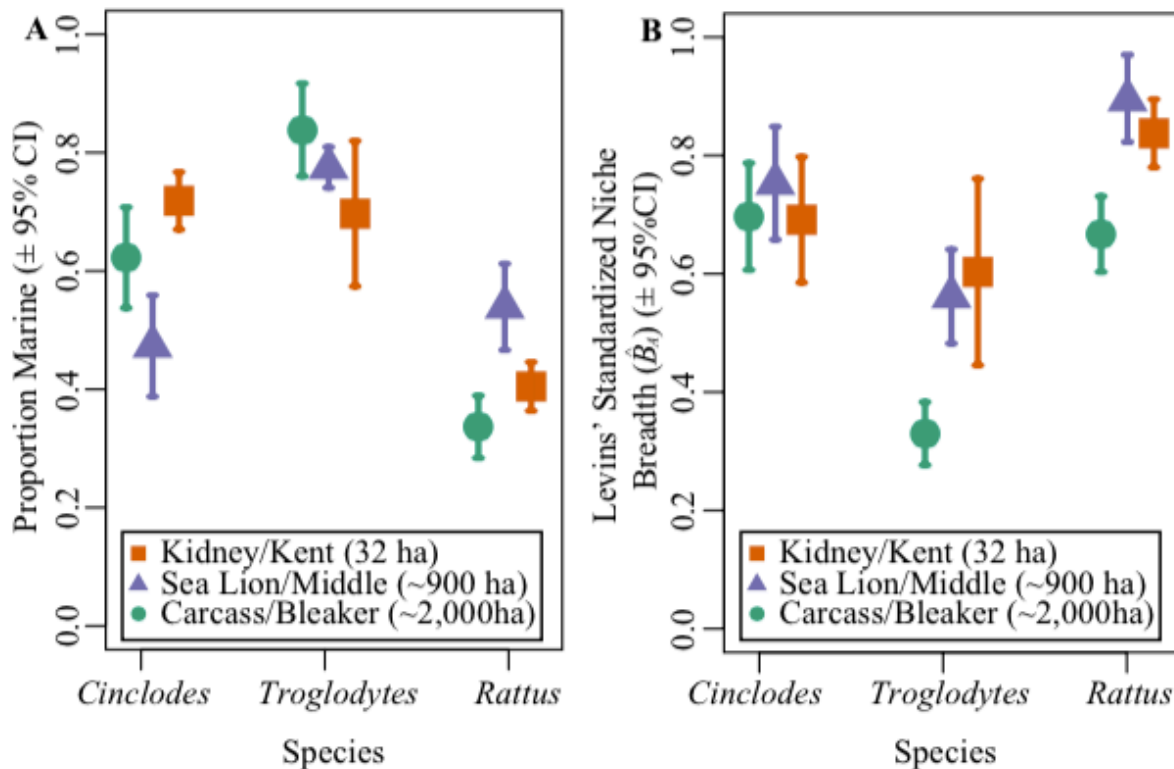
Figure 3: The mean posterior proportion of resources incorporated from marine and terrestrial diets (A) differed among species. *Troglodytes* had the highest proportion marine and *Rattus* had the lowest. Breadth in the incorporation of marine and terrestrial resources was summarized with Levins' standardized niche breadth (B). Niche breadth was the largest for *Rattus*, indicating that their diets were derived from a combination of terrestrial and marine sources.

transformed values, $F_{2,94} = 4.51$, $p = 0.014$) and species ($F_{1,94} = 31.66$, $p < 0.0001$), and there was an interaction between species and island ($F_{2,94} = 3.68$, $p = 0.029$, Fig. 3B). On Carcass and Kidney Islands, *Cinclodes'* $\hat{B}_A$ was higher than that of *Troglodytes* (*a posteriori* Bonferroni-corrected LSD tests, $p < 0.05$, Figure 3B), but on Kidney Island these two species had similar values. For rats, there was a difference in $\hat{B}_A$ among islands ($F_{2,77} = 11.58$, $p < 0.0001$): Middle and Kent Islands had similarly high $\hat{B}_A$ values (Tukey's HSD $p > 0.1$), whereas Bleaker Island had a significantly lower value than that found on these two islands (Tukey's HSD $p < 0.01$). When we compared the values of breadth in the use of marine and terrestrial sources among the three species, we found that there were significant differences in $\hat{B}_A$ among species ($F_{2,176} = 27.18$, $p < 0.0001$). Rats and *Cinclodes* had similarly high $\hat{B}_A$ values (grand mean of $\hat{B}_A \pm SD = 0.77 \pm 0.19$ and 0.71 ± 0.21 for rats and *Cinclodes* respectively, Tukey's HSD $p > 0.1$). *Troglodytes* had the lowest $\hat{B}_A$ value (grand mean of $\hat{B}_A \pm SD = 0.48 \pm 0.21$) and this value differed significantly from that of *Cinclodes* and rats (Tukey's HSD $p < 0.001$).

Overlap in the incorporation of marine and terrestrial sources

On Sea Lion and Carcass Islands, *Troglodytes* incorporated primarily marine resources into its tissues, whereas *Cinclodes* incorporated a more even mixture of marine and terrestrial sources (Fig. 3). Hence, the overlap in the incorporation of marine and terrestrial sources between these two species on these two islands was asymmetrical ($t > 16.5$, $p < 0.001$, Fig. 4): *Cinclodes* incorporated marine sources as well as more terrestrial sources apparently not incorporated by *Troglodytes* (Figs. 2 and 3). In contrast, on Kidney Island, *Troglodytes* and *Cinclodes* incorporated similarly high proportions of marine resources and therefore their resource use overlap values were high and symmetrical (i.e.,
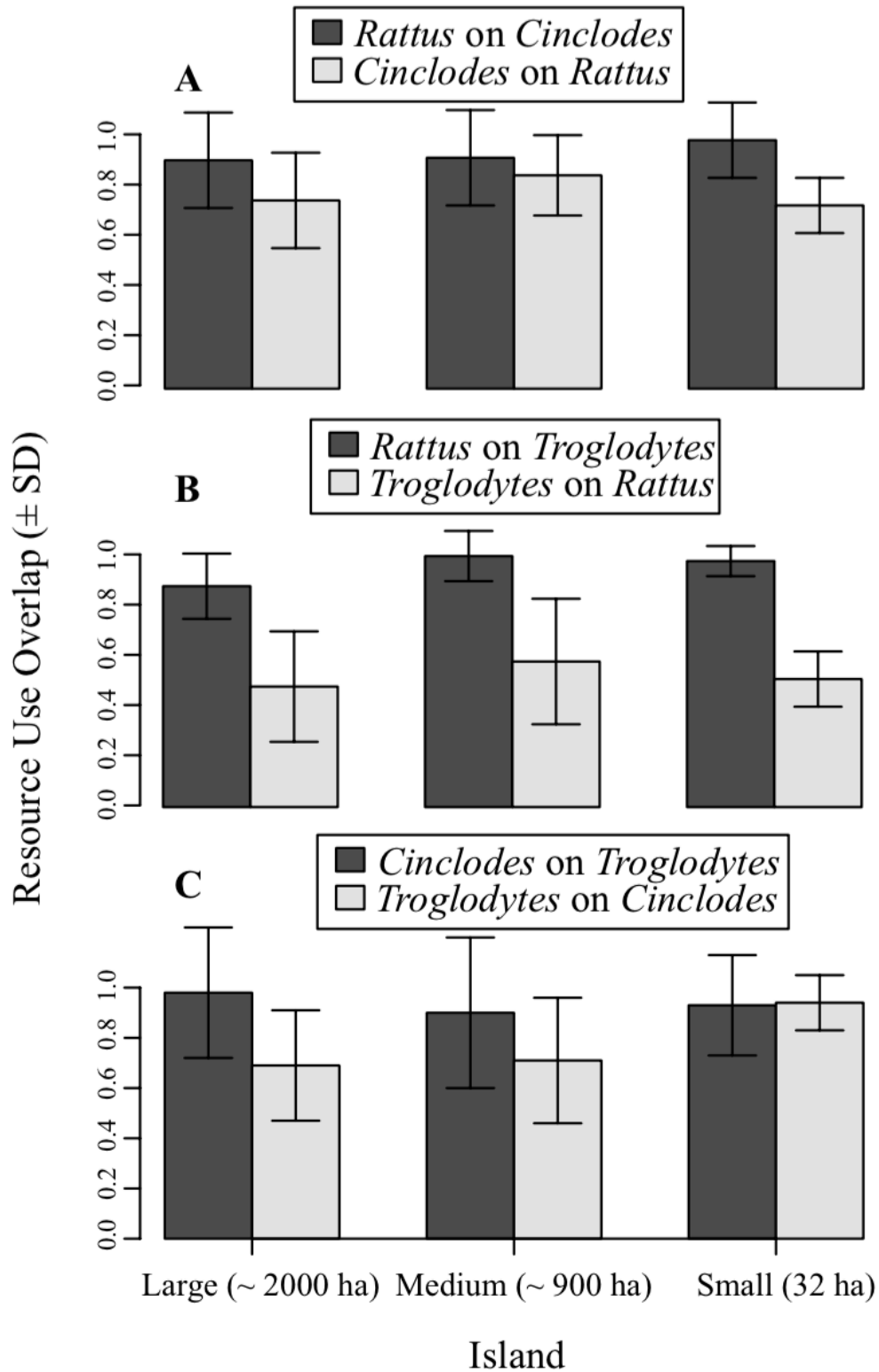
Figure 4: Resource use overlap was asymmetrical and different among species. Rats had high levels of overlap on both bird species (*Cinclode*s and *Troglodytes*, A and B), while birds overlapped less with rats. *Cinclodes* and *Troglodytes* also overlapped in their resource use (C).

$\overline{M_{CinclodesTroglodytes} - M_{TroglodytesCinclodes}}$ did not differ significantly from 0, t < 1.5, p > 0.1).

Rats incorporated marine and terrestrial resources more evenly than both bird species (Fig. 3B).

Consequently, they had high niche overlap with birds ($\widehat{M}_{RatsBirds}$ > 0.8) but because birds

tended to incorporate significantly more marine resources than rats, their overlap with rats was

significantly lower on islands of all sizes (t > 8.2, p < 0.001, Fig. 4).

Discussion

We found that a large fraction of the carbon and nitrogen incorporated into the tissues of

both *Troglodytes* and *Cinclodes* had a marine origin. We also found that rats used both marine

and terrestrial resources, and hence along this dimension, their isotopic niche overlapped

significantly with those of the two passerine species on which they are known to have the

strongest effect. Their use of similar resources provides one potential explanation for the large

effect of rats on these bird species. The interpretation of our results hinges on the metrics that we

used: Levins' niche width ($\widehat{B}_A$), MacArthur and Levins' index of niche overlap ($\widehat{M}_{jk}$), and

standard ellipses and their associated metrics: area and eccentricity. Because these metrics

incorporate a variety of assumptions, and because, to our knowledge, this study is the first to use

$\widehat{B}_A$ and $\widehat{M}_{jk}$ in isotopic ecology, we begin this discussion by considering these assumptions.

Levins, MacArthur, niches, and isotopic ecology

The use of stable isotopes is a potentially powerful complement to the study of ecological

niches (Rader *et al*. in review). Like many other approaches to study ecological niches, stable

isotopes have limitations and shortcomings (discussed in detail by Newsome *et al.* 2007). First,

isotopic analyses provide answers that are relatively coarse and represent only a single

dimension of the ecological niche. Second, depending on the tissue analyzed, isotopic analyses

reveal the isotopic value of the resources incorporated during a single temporal window (Turner

et al. 2010). Using multiple tissues can allow investigating different time intervals (Dalerum and

Angerbjörn 2005), and even changes in resources used through time (Araújo *et al.* 2011). Our

study, however, relied on only two tissues: whole blood for birds and muscle in rats. These

tissues incorporate the isotopic value of resources over a period that spans a few weeks (17-21

days in the case of whole blood and 18-22 days in the case of rat muscle; Arneson *et al.* 2006;

Bauchinger and McWilliams 2009).

In order to overcome some of these limitations, we used three complementary

approaches. To estimate niche width and overlap, we first transformed isotopic values (or data in

δ space) into proportions of marine and terrestrial sources (data in p space; Newsome *et al.* 2007)

using mixing models (Stock and Semmens 2013; Phillips *et al.* 2014). By pooling a variety of

food sources into two broad categories, we lost information, but gained accuracy and hence

confidence in our estimates. We cannot ascertain the taxonomic identity of the marine and

terrestrial resources used by our focal species, but we can be reasonably certain that our

estimates of incorporation of marine and terrestrial carbon sources in tissues are accurate.

Indeed, our posterior estimates of each individual's $\hat{q}$ had narrow credible intervals (range of

95% credible interval size = 0.19 – 0.37). However, our results must be interpreted with the

caveat that within the broad categories of marine and terrestrial resources, each species could

have used different assemblages of taxonomically distinct prey.

The use of $\widehat{B}_A$ and $\widehat{M}_{jk}$ has been criticized because these metrics do not account for resource availability (Hurlbert 1978; Smith 1982). Thus, comparing these values among species that occupy different sites, or that are collected at different times, can be the result of spatial and temporal variation in the availability of different resources (Martinez del Rio *et al.* 2009). In our study, all individuals were captured in roughly the same season (albeit in different years for the rat and bird samples) and all comparisons of isotopic niche metrics between the two bird species were conducted on islands that these species inhabit together (*Cinclodes* and *Troglodytes* were captured at the same time at the same mist net stations and therefore had the same spectra of resource availabilities). When rats are present on an island, they extirpate these two bird species (Tabak *et al.* 2014), and therefore, we can only compare rats and birds from different islands. It is possible that differences between rats and birds are the result of differences in island-specific resource availability. Finally, other metrics for the characteristics of isotopic niches have been proposed (e.g., confidence ellipses). Although these metrics have the shortcoming of depending on the Euclidean distance between sources (Turner *et al.* 2010; Newsome *et al.* 2012) they add information not captured by Levins' niche width metric (or other metrics derived from resource proportion values).

Two marine passerines and a generalist mammal

The large fraction of marine carbon in the tissues of *Troglodytes* (grand mean of 77% of marine resources) makes it one of the most "marine" passerines ever documented (Sabat and Martinez del Rio 2002), and likely the most marine-dependent wren (but see Christie *et al.* 2008). Although, *Cinclodes* also incorporated a significant amount of resources derived from marine environments in its tissues (grand mean of 58%), this proportion was (at least on two

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islands) higher for *Troglodytes*. The relatively low values of isotopic niche width in *Troglodytes* compared to *Cinclodes* indicate higher reliance of this species on marine resources. In addition, on all islands, *Troglodytes* appears to restrict its foraging to the vegetation that fringes the islands' beaches (Fig. 2 and following section). The dependence of *Troglodytes* on marine and island fringe vegetation makes this species an "island specialist." *Troglodytes cobbi* diverged from the House Wren (*Troglodytes aedon*) about one million years ago (Campagna *et al.* 2012) and hence its specialization for life on islands (including large size, stubby wings, and presumably adaptations to a marine diet; Woods and Woods 2006) evolved since this divergence.

The dependence of *Troglodytes* and *Cinclodes* on marine sources appears to be exceptional. The genus *Cinclodes* includes two strictly marine species, *C. nigrofumosus* and *C. taczanowskii* (Sabat and Martinez del Rio 2002), that not only rely almost exclusively on marine resources, but that inhabit the hyper-arid Atacama desert (Sabat *et al.* 2006; Martinez del Rio *et al.* 2009). The dependence of *Troglodytes* and *Cinclodes antarcticus* on marine resources in the Falkland Islands is noteworthy because these islands are considered semi-arid (annual precipitation varies among islands from 300-700 mm).

Isotopic niche breadth depends on how evenly resources are incorporated into animal tissues (Fig. 3). Rats had the most even incorporation of marine and terrestrial resources, and hence the broadest niche. As predicted, along this isotopic niche axis, they were generalists. The capacity to use resources from terrestrial and marine environments can potentially explain a) their success in invading islands (Tabak *et al.* 2015c), and b) their large effect on *Troglodytes* and *Cinclodes* and on energy flow through Falkland Island passerine communities. Tabak *et al.*

(in review) hypothesized that rats' large effect on island ecosystems was the result of their high abundance, use of a wide range of resources, and/or direct predation on birds. In the Falklands, passerine communities on islands in which rats have been eradicated have five-times higher rates of energy use than those on rat-infested islands (Tabak *et al*. in review).

In interpreting the overlap in resource use of rats with that of *Cinclodes* and *Troglodytes*, we offer a caveat about inferring process from pattern. *Cinclodes* and *Troglodytes* do not co-occur with Norway rats. Tabak *et al*. (2015b) inferred that this pattern is the outcome of exclusion of birds by rats. In a similar fashion, because these two bird species and rats are not found together, we cannot determine accurately what their resource use patterns would be were they to co-occur. We are limited to infer from current patterns what the niche overlap might have been when these species co-occurred before the two bird species were extirpated by rats. It is possible that birds could alter their diets (by either restricting their feeding to specific foods or changing to different dietary sources) in the presence of rats to facilitate coexistence with these invaders. Since rats do not co-occur with these bird species, we cannot test this conjecture.

Isotopic niche overlap and the uses of standard ellipses

Overlap in isotopic niche along the marine-terrestrial axis was high for all species pairs, but (as expected) in most cases it was highly asymmetrical. The isotopic niche of the species with narrower isotopic niches (*Troglodytes*) was contained within that of species with broader isotopic niches (*Cinclodes* and *Rattus*, Fig. 4B and C). Furthermore, the isotopic niche of rats overlapped highly with those of birds (Fig. 4A and B). For birds, with the exception of Kidney Island, the isotopic niche of *Troglodytes* was contained within that of *Cinclodes*. We emphasize

that we analyzed a single dimension of the isotopic niche: that represented by the use of marine and terrestrial resources. The shape of standard ellipses, in isotopic space, complements this limited perspective.

In most cases, these ellipses had high eccentricity values and the value of $\delta^{15}N$ was highly correlated with that of $\delta^{13}C$. In addition, on most islands, the slope of the relationship between isotopic values of these two elements was steep (Fig. 2, Table 1). Indeed, these relationships have higher slopes, and even have a different sign, than those that would result from joining the centroids of the isotopic values of marine and terrestrial resources (Fig. 2). How can we reconcile the existence of a steep $\delta^{15}N/\delta^{13}C$ relationship in the isotopic values of animal tissues with the expectation of a flatter one expected from the centroids of the sources? The answer lies in the wide spread of $\delta^{15}N$ values in terrestrial environments (Figs. 1 and 2).

We interpret this large range of values in $\delta^{15}N$ as the result of spatial variation in ^{15}N enrichment. Some terrestrial resources have low $\delta^{13}C$ values because they are sustained by producers with C-3 photosynthesis, but have high $\delta^{15}N$ because they are found in island areas where sea birds and mammals deposit excreta (Ellis *et al.* 2006). These excretions supplement the vegetation of these areas with ^{15}N-enriched nitrogen derived from marine resources (Markwell and Daugherty 2003). Furthermore, the mineralization of some of the uric acid and urea of these excretions leads to additional ^{15}N-enrichment (Jones 2010). We call these resources terrestrial, marine-subsidized resources (TMS). For example, the vegetation that fringes the beaches of Falkland Islands is used as a nesting site by a variety of marine birds including several species of penguin (king penguin *Aptenodytes patagonicus*, gentoo penguin *Pygoscelis*

papua, rockhopper penguin *Eudyptes chrysocome*, macaroni penguin *Eudyptes chrysolophus*, and magellanic penguin, *Speniscus magellanicus*; Woods and Woods 2006) and as a resting site by marine mammals (southern sea lion *Otaria flavescens* and southern elephant seal *Mirounga leonina*; Strange 1992). Thus, the plants and invertebrates of island fringes are likely enriched in ^{15}N relative to those in the islands' interior. TMS sources can explain the very high values of $\delta^{15}N$ and low values of $\delta^{13}C$ for some individuals (especially *Troglodytes* and rats, Fig. 2). For example, some of the rats from Bleaker Island had exceedingly ^{15}N-enriched values and were captured within a permanent rockhopper penguin colony where we hypothesize that the soil was highly enriched in $\delta^{15}N$ as a result of the accumulation of penguin excreta (Supplementary Fig. 1).

We did not sample resources extensively enough to accurately describe the spatial distribution of $\delta^{15}N$ on islands. However, we can combine the isotopic patterns found in animal tissues with natural history observations to generate hypotheses to explain these patterns and qualify the inferences that we made after transforming isotopic data with mixing models. Briefly, we hypothesize that negative slopes indicate that individuals are feeding on habitats that yield resources with marine and/or TMS sources, whereas a positive slope indicates that individuals are feeding from both terrestrial (non-subsidized) and marine sources. A 95% confidence ellipse, which has a slope that does not differ from 0, has a lower eccentricity value, and has a large area indicates that individuals are feeding from resources derived from habitats that have marine, TMS, and terrestrial inputs at the base of the food web.

Ellipses for *Troglodytes* had significantly negative slopes on all islands (Fig. 2, Table 1). Hence, we hypothesize that these birds were primarily using sources with two provenances: marine and TMS. This observation is consistent with the observation that *Troglodytes* inhabits primarily the thick swaths of tussac grass (*Poa flabellata*) that fringe most island beaches in the Falklands (Strange 1992; Woods and Woods 2006). The ellipses for *Cinclodes* had a positive slope on Carcass Island, a negative one on Kidney Island, and a non-significant slope on Sea Lion Island (Fig. 2, Table 1). On the smallest of these three islands, Kidney Island, the ratio of TMS periphery to interior is large (because island size is small) and hence there are few spots not impacted by the transfer of marine subsidies by seabirds and other consumers. In contrast, on the larger Carcass and Sea Lion Islands, seabirds and mammals do not occupy the interior of the islands and it is on these islands that the slopes of *Cinclodes'* 95% confidence ellipses are positive and non-significant. We interpret these slopes to indicate the use of marine and terrestrial (*sensu stricto*) resources on Carcass Island, and broad use of the three types on Sea Lion Island. This interpretation forces us to qualify our estimates of niche overlap derived from $\hat{q}$ values. With the exception of Kidney Island, the overlap values obtained from a single "niche axis" overestimate overlap in resource use, as on the larger islands *Cinclodes* appears to be using terrestrial habitats, and hence resources not used by *Troglodytes*.

The characteristics of the standard ellipses of rats, like those of *Cinclodes*, varied among islands. The slopes were negative on Kent and Bleaker Island (Fig. 2, Table 1), but positive on Middle Island. We hypothesize that rats relied more heavily on marine and TMS resources on the former because there was denser tussac grass cover on these two islands (field observations), which provides protection from predatory birds. Nevertheless, the broad isotopic space occupied

by rats on all islands confirms the notion that they are able to use a wide range of resources (Murray *et al.* 1999), and also supports the hypothesis that their colonization success in islands is due to this ability (Jones *et al.* 2008). Finally, the wide range of resources that rats appear to use is likely a factor in the enormous impact that these animals have on the populations of passerines (Tabak *et al.* 2014, 2015b).

The isotopic niches in δ^{13}C and δ^{15}N space documented here represent a fraction of the isotopic space that a species can potentially occupy. Like other realized niches (*sensu* Hutchinson 1959), they are shaped by a large number of factors including the presence of other species and the availability of resources (Peterson *et al.* 2011). The fundamental isotopic niche is broader and can be defined as the set of all isotopic values that a species can acquire and thus corresponds to all of the isotopically distinct sources on which a species can feed when these resources are available and in the absence of interacting species. The seemingly broad isotopic niche occupied by rats and *Cinclodes* (when all islands are considered together) suggests that these animals have broader "fundamental" isotopic niches than *Troglodytes*. We do not know the extent of these fundamental isotopic niches; however, we can state with confidence that under all conditions investigated in this study, *Troglodytes* uses a more restricted area of isotopic space than *Cinclodes* and rats. This in turn reflects the almost exclusive use of marine resources and TMS at the beach fringes by *Troglodytes* of islands in the Falklands.

Towards a pluralistic approach to the analysis of isotopic data

Our interpretation of 95% confidence ellipses in δ-space as a means of complementing other metrics poses interesting challenges to isotopic ecology. First, it emphasizes the notion that

isotopic methods cannot detect the taxonomic identity of a producer, except in special cases. The $\delta^{15}N$ values of tussac grass, for example, depend on whether the plant grows in areas fertilized by marine birds and mammals or not (Supplementary Table 1). Second, the continuous nature of variation in the isotopic values of some, and perhaps many, resources poses additional challenges. So far, the use of mixing models depends on the ability of researchers to identify discrete resource types that can be used as endpoints in mixing models (Phillips *et al.* 2014). If resources vary continuously, as the $\delta^{15}N$ value of terrestrial resources in the Falkland Islands appears to do, the use of mixing models can be limited.

These challenges diminish neither the power of stable isotopes in ecological studies, nor the usefulness of the concept of the isotopic niche. However, they point to the wisdom of using a plurality of approaches in the analysis of isotopic data. At this stage in the conceptual development of the field, it might be more useful to rely on a variety of complementary approaches that shed light on different aspects of the same phenomenon.

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Supplementary Material
Supplementary Table 1: Isotopic values for potential dietary sources

common name	scientific name	Island	15N
Amphipod	Amphipoda	Carcass Island	12.351
Amphipod	Amphipoda	Carcass Island	12.415
Amphipod	Amphipoda	Carcass Island	13.316
Amphipod	Amphipoda	Carcass Island	13.572
Amphipod	Amphipoda	Carcass Island	13.428
Amphipod	Amphipoda	Carcass Island	14.188
Amphipod	Amphipoda	Carcass Island	14.263
Amphipod	Amphipoda	Carcass Island	11.336
Amphipod	Amphipoda	Carcass Island	11.088
Amphipod	Amphipoda	Carcass Island	14.245
Amphipod	Amphipoda	Carcass Island	14.511
Camel Cricket	Gryllacrididae	Carcass Island	15.3
Camel Cricket	Gryllacrididae	Carcass Island	11.9
Camel Cricket	Gryllacrididae	Carcass Island	8.7
Camel Cricket	Gryllacrididae	Carcass Island	13.9
Camel Cricket	Gryllacrididae	Carcass Island	12.5
Polychaete	Nereidae	Carcass Island	15.5
Tussac Insect	Insecta	Carcass Island	29.5
Terrestrial slug (maybe Ari	Arionidae	Carcass Island	12.1
Hoverfly	Syrphidae	Carcass Island	9.169
Subantarctic Kelp Flies	Helcomyzidae	Carcass Island	9.793
Subantarctic Kelp Flies	Helcomyzidae	Carcass Island	13.512
Subantarctic Kelp Flies	Helcomyzidae	Carcass Island	13.326
Subantarctic Kelp Flies	Helcomyzidae	Carcass Island	14.534
Subantarctic Kelp Flies	Helcomyzidae	Carcass Island	14.343
Subantarctic Kelp Flies	Helcomyzidae	Carcass Island	13.077
Subantarctic Kelp Flies	Helcomyzidae	Carcass Island	14.795
Subantarctic Kelp Flies	Helcomyzidae	Carcass Island	13.664
Subantarctic Kelp Flies	Helcomyzidae	Carcass Island	13.765
Subantarctic Kelp Flies	Helcomyzidae	Carcass Island	14.582
Subantarctic Kelp Flies	Helcomyzidae	Carcass Island	11.883
Subantarctic Kelp Flies	Helcomyzidae	Carcass Island	13.48
Subantarctic Kelp Flies	Helcomyzidae	Carcass Island	14.314
Subantarctic Kelp Flies	Helcomyzidae	Carcass Island	13.832
Amphipod	Amphipoda	Kidney Island	14.173
Amphipod	Amphipoda	Kidney Island	15.579
Amphipod	Amphipoda	Kidney Island	14.766
Amphipod	Amphipoda	Kidney Island	14.741
Amphipod	Amphipoda	Kidney Island	14.468
Camel Crickett	Gryllacrididae	Kidney Island	22.2

Camel Crickett	Gryllacrididae	Kidney Island	23.7
Camel Crickett	Gryllacrididae	Kidney Island	19.8
Camel Crickett	Gryllacrididae	Kidney Island	20.4
Ichneumon wasp	Ichneumonidae	Kidney Island	25
Rock eel	*Austrolycus depressiceps*	Kidney Island	16.7
Rock eel	*Austrolycus depressiceps*	Kidney Island	15.5
Subantarctic Kelp Flies	Helcomyzidae	Kidney Island	12.798
Subantarctic Kelp Flies	Helcomyzidae	Kidney Island	14.073
Dung fly	Scathophagidae	Kidney Island	15.262
Dung fly	Scathophagidae	Kidney Island	13.145
Dung fly	Scathophagidae	Kidney Island	10.513
Snail	*Littorina* spp.	Kidney Island	16.343
Snail	*Littorina* spp.	Kidney Island	12.518
Snail	*Littorina* spp.	Kidney Island	11.951
Snail	*Littorina* spp.	Kidney Island	11.951
Snail	*Littorina* spp.	Kidney Island	13.092
Snail	*Littorina* spp.	Kidney Island	11.632
Amphipod	Amphipoda	Sea Lion Island	11.8
Amphipod	Amphipoda	Sea Lion Island	11.265
Amphipod	Amphipoda	Sea Lion Island	10.902
Amphipod	Amphipoda	Sea Lion Island	11.366
Amphipod	Amphipoda	Sea Lion Island	11.755
Limpet (maybe Nacella)	Patellidae	Sea Lion Island	10.797
Limpet (maybe Nacella)	Patellidae	Sea Lion Island	11.158
Limpet (maybe Nacella)	Patellidae	Sea Lion Island	10.017
Limpet (maybe Nacella)	Patellidae	Sea Lion Island	10.14
Terrestrial slug	Arionidae	Sea Lion Island	22.2
Darwin's black beetle	*Lissopterus quadrinotatus*	Sea Lion Island	14.3
Green spider	*Araneus cinnabarinus*	Sea Lion Island	7
Tussac moth	*Caphornia ochricraspia* or *P*	Sea Lion Island	28.1
Butterfly larvae	Lepidoptera	Sea Lion Island	8.7
Green spider	*Araneus cinnabarinus*	Sea Lion Island	27.4
Camel Crickett	Gryllacrididae	Sea Lion Island	15.2
Camel Crickett	Gryllacrididae	Sea Lion Island	13
Camel Crickett	Gryllacrididae	Sea Lion Island	14.9
Camel Crickett	Gryllacrididae	Sea Lion Island	9.6
Camel Crickett	Gryllacrididae	Sea Lion Island	13
Earthwrom	Moniligastridia	Sea Lion Island	16.4
Earthwrom	Moniligastridia	Sea Lion Island	17.2
Earthwrom	Moniligastridia	Sea Lion Island	17.8
Earthwrom	Moniligastridia	Sea Lion Island	17.2

Earthwrom	Moniligastridia	Sea Lion Island	8.6
Subantarctic Kelp Flies	Helcomyzidae	Sea Lion Island	10.287
Subantarctic Kelp Flies	Helcomyzidae	Sea Lion Island	9.749
Subantarctic Kelp Flies	Helcomyzidae	Sea Lion Island	10.746
Subantarctic Kelp Flies	Helcomyzidae	Sea Lion Island	10.351
Subantarctic Kelp Flies	Helcomyzidae	Sea Lion Island	13.874
Subantarctic Kelp Flies	Helcomyzidae	Sea Lion Island	12.603
Subantarctic Kelp Flies	Helcomyzidae	Sea Lion Island	14.47
Subantarctic Kelp Flies	Helcomyzidae	Sea Lion Island	13.788
Subantarctic Kelp Flies	Helcomyzidae	Sea Lion Island	12.592
Subantarctic Kelp Flies	Helcomyzidae	Sea Lion Island	14.229
Subantarctic Kelp Flies	Helcomyzidae	Sea Lion Island	13.291
Kelp fly	Helcomyzidae	Sea Lion Island	9.153
Kelp fly	Helcomyzidae	Sea Lion Island	10.107
Brown algae	Phaeophyceae	Carcass Island	9.876
Brown algae	Phaeophyceae	Carcass Island	11.523
Brown algae	Phaeophyceae	Carcass Island	11.2
Brown algae	Phaeophyceae	Carcass Island	10.798
Brown algae	Phaeophyceae	Carcass Island	9.711
Brown algae	Phaeophyceae	Carcass Island	9.085
Giant kelp	*Macrocystis pyrifera*	Carcass Island	9.224
Scurvy Grass (Oxalis sp)	Oxalidaceae	Carcass Island	10.517
Scurvy Grass (Oxalis sp)	Oxalidaceae	Carcass Island	14.467
Green algae	Chlorophyta	Carcass Island	9.99
Green algae	Chlorophyta	Carcass Island	10.825
Green algae	Chlorophyta	Carcass Island	12.364
Lessonia algae	*Lessonia* spp.	Carcass Island	9.152
Pig vine	*Gunnera magellanica*	Carcass Island	1.013
Prickly burr	*Acaena magellanica*	Carcass Island	15.589
Red algae	Rhodophyta	Carcass Island	10.492
Red algae	Rhodophyta	Carcass Island	9.28
Rotting kelp	Laminariales	Carcass Island	7.354
Rotting kelp	Laminariales	Carcass Island	6.861
Rotting kelp	Laminariales	Carcass Island	9.202
Sheep sorrel	*Rumex acetosella*	Carcass Island	13.269
Tussac grass	*Poa flabellata*	Carcass Island	22.555
Tussac grass	*Poa flabellata*	Carcass Island	16.123
Tussac grass	*Poa flabellata*	Carcass Island	30.481
Ulva algae	*Ulva lactuca*	Carcass Island	10.161
Brown algae	Phaeophyceae	Sea Lion Island	5.434
Brown algae	Phaeophyceae	Sea Lion Island	8.477

Diddledee	*Empetrum rubrum*	Sea Lion Island	0.242
Green algae	Chlorophyta	Sea Lion Island	7.247
Green algae	Chlorophyta	Sea Lion Island	9.524
Green algae	Chlorophyta	Sea Lion Island	8.663
Giant kelp	*Macrocystis pyrifera*	Sea Lion Island	8.128
Lessonia algae	*Lessonia* spp.	Sea Lion Island	8.983
Lessonia algae	*Lessonia* spp.	Sea Lion Island	8.777
Large brown algae	*Phaeophyceae*	Sea Lion Island	8.149
Mountain berry	*Gaultheria pumila*	Sea Lion Island	13.098
Native woodrush	*Luzula alopecurus*	Sea Lion Island	1.788
Pirickly burr	*Acaena magellanica*	Sea Lion Island	11.386
Red algae	Rhodophyta	Sea Lion Island	8.034
Red algae	Rhodophyta	Sea Lion Island	7.746
Large brown algae	*Phaeophyceae*	Sea Lion Island	7.257
Large brown algae	*Phaeophyceae*	Sea Lion Island	7.12
Sheep sorrel	*Rumex acetosella*	Sea Lion Island	4.237
Small fern	*Blechnum penna-marina*	Sea Lion Island	3.943
Tussac grass	*Poa flabellata*	Sea Lion Island	23.153
Tussac grass	*Poa flabellata*	Sea Lion Island	26.74
Ulva algae	*Ulva lactuca*	Sea Lion Island	9.162
Cinnamon grass	*Hierochloe redolens*	Kidney Island	16.689
Cinnamon grass	*Hierochloe redolens*	Kidney Island	16.294
Green algae	Chlorophyta	Kidney Island	17.429
Iridaea	Gigartinaceae	Kidney Island	21.869
Iridaea	Gigartinaceae	Kidney Island	21.481
Lessonia algae	*Lessonia* spp.	Kidney Island	20.302
Lessonia algae	*Lessonia* spp.	Kidney Island	19.285
Lessonia algae	*Lessonia* spp.	Kidney Island	19.535
Lessonia algae	*Lessonia* spp.	Kidney Island	20.5
Large brown algae	*Phaeophyceae*	Kidney Island	9.388
Large brown algae	*Phaeophyceae*	Kidney Island	9.624
Mountain berry	*Gaultheria pumila*	Kidney Island	13.942
Pig vine	*Gunnera magellanica*	Kidney Island	12.929
Pig vine	*Gunnera magellanica*	Kidney Island	13.217
Rotting kelp	Laminariales	Kidney Island	9.991
Rotting kelp	Laminariales	Kidney Island	12.334
Small fern	*Blechnum penna-marina*	Kidney Island	17.599
Small fern	*Blechnum penna-marina*	Kidney Island	18.113
Tussac grass	*Poa flabellata*	Kidney Island	29.243
Tussac grass	*Poa flabellata*	Kidney Island	29.329
Ulva algae	*Ulva lactuca*	Kidney Island	18.918

Ulva algae	*Ulva lactuca*	Kidney Island	19.25
Wild celery	*Apium australe*	Kidney Island	16.35
Wild celery	*Apium australe*	Kidney Island	16.269

13C	InvertPlant	location
-13.839	Invertebrate	marine
-13.376	Invertebrate	marine
-13.149	Invertebrate	marine
-12.912	Invertebrate	marine
-13.159	Invertebrate	marine
-13.875	Invertebrate	marine
-13.306	Invertebrate	marine
-12.812	Invertebrate	marine
-13.013	Invertebrate	marine
-12.75	Invertebrate	marine
-13.066	Invertebrate	marine
-25.3	Invertebrate	terrestrial
-26.2	Invertebrate	terrestrial
-26.6	Invertebrate	terrestrial
-27.6	Invertebrate	terrestrial
-28.1	Invertebrate	terrestrial
-13.5	Invertebrate	marine
-25.1	Invertebrate	terrestrial
-25.7	Invertebrate	terrestrial
-23.352	Invertebrate	terrestrial
-13.838	Invertebrate	marine
-12.004	Invertebrate	marine
-12.839	Invertebrate	marine
-12.895	Invertebrate	marine
-12.024	Invertebrate	marine
-12.641	Invertebrate	marine
-12.545	Invertebrate	marine
-12.104	Invertebrate	marine
-13.338	Invertebrate	marine
-12.676	Invertebrate	marine
-12.258	Invertebrate	marine
-11.706	Invertebrate	marine
-11.996	Invertebrate	marine
-13.891	Invertebrate	marine
-12.838	Invertebrate	marine
-12.652	Invertebrate	marine
-12.976	Invertebrate	marine
-12.298	Invertebrate	marine
-13.093	Invertebrate	marine
-25.9	Invertebrate	terrestrial

-26.3	Invertebrate	terrestrial
-26.4	Invertebrate	terrestrial
-27	Invertebrate	terrestrial
-29.6	Invertebrate	terrestrial
-13.1	Invertebrate	marine
-14.2	Invertebrate	marine
-12.849	Invertebrate	marine
-12.252	Invertebrate	marine
-11.262	Invertebrate	marine
-14.723	Invertebrate	marine
-13.999	Invertebrate	marine
-13.937	Invertebrate	marine
-12.197	Invertebrate	marine
-13.336	Invertebrate	marine
-13.506	Invertebrate	marine
-13.086	Invertebrate	marine
-12.956	Invertebrate	marine
-12.608	Invertebrate	marine
-12.571	Invertebrate	marine
-13.006	Invertebrate	marine
-12.617	Invertebrate	marine
-13.048	Invertebrate	marine
-14.684	Invertebrate	marine
-14.828	Invertebrate	marine
-15.764	Invertebrate	marine
-14.842	Invertebrate	marine
-26.1	Invertebrate	terrestrial
-26.5	Invertebrate	terrestrial
-24.9	Invertebrate	terrestrial
-24.5	Invertebrate	terrestrial
-28.8	Invertebrate	terrestrial
-23.1	Invertebrate	terrestrial
-27.2	Invertebrate	terrestrial
-25.6	Invertebrate	terrestrial
-26.9	Invertebrate	terrestrial
-27.6	Invertebrate	terrestrial
-27.4	Invertebrate	terrestrial
-26.4	Invertebrate	terrestrial
-25.9	Invertebrate	terrestrial
-25.7	Invertebrate	terrestrial
-25.8	Invertebrate	terrestrial

-24.7	Invertebrate	terrestrial
-14.834	Invertebrate	marine
-13.772	Invertebrate	marine
-13.931	Invertebrate	marine
-13.784	Invertebrate	marine
-13.006	Invertebrate	marine
-12.659	Invertebrate	marine
-13.55	Invertebrate	marine
-11.58	Invertebrate	marine
-12.113	Invertebrate	marine
-11.807	Invertebrate	marine
-12.011	Invertebrate	marine
-14.391	Invertebrate	marine
-14.113	Invertebrate	marine
-5.699	Plant	marine
-12.513	Plant	marine
-13.276	Plant	marine
-15.474	Plant	marine
-13.616	Plant	marine
-8.271	Plant	marine
-11.97	Plant	marine
-26.695	Plant	terrestrial
-28.365	Plant	terrestrial
-10.197	Plant	marine
-10.54	Plant	marine
-15.75	Plant	marine
-10.908	Plant	marine
-26.209	Plant	terrestrial
-26.964	Plant	terrestrial
-11.433	Plant	marine
-7.881	Plant	marine
-14.309	Plant	marine
-13.962	Plant	marine
-16.566	Plant	marine
-29.021	Plant	terrestrial
-27.044	Plant	terrestrial
-27.794	Plant	terrestrial
-26.703	Plant	terrestrial
-12.284	Plant	marine
-16.002	Plant	marine
-15.549	Plant	marine

-26.906	Plant	terrestrial
-15.664	Plant	marine
-15.433	Plant	marine
-13.564	Plant	marine
-10.582	Plant	marine
-12.125	Plant	marine
-13.027	Plant	marine
-13.994	Plant	marine
-26.311	Plant	terrestrial
-26.356	Plant	terrestrial
-27.549	Plant	terrestrial
-33.641	Plant	terrestrial
-32.357	Plant	terrestrial
-14.739	Plant	marine
-19.14	Plant	marine
-28.432	Plant	terrestrial
-25.754	Plant	terrestrial
-27.159	Plant	terrestrial
-27.413	Plant	terrestrial
-10.199	Plant	marine
-27.825	Plant	terrestrial
-27.051	Plant	terrestrial
-12.848	Plant	marine
-10.921	Plant	marine
-13.305	Plant	marine
-11.241	Plant	marine
-11.066	Plant	marine
-10.862	Plant	marine
-11.128	Plant	marine
-13.003	Plant	marine
-13.01	Plant	marine
-26.901	Plant	terrestrial
-26.093	Plant	terrestrial
-26.307	Plant	terrestrial
-11.845	Plant	marine
-15.905	Plant	marine
-27.436	Plant	terrestrial
-27.286	Plant	terrestrial
-28.973	Plant	terrestrial
-29.367	Plant	terrestrial
-13.517	Plant	marine

-14.205	Plant	marine
-28.833	Plant	terrestrial
-28.737	Plant	terrestrial

Supplementary Figure 1: Rockhopper penguin colony where some rat samples from Bleaker Island were collected. We hypothesize that long-term accumulation of penguin excreta from this colony lead to enrichment in $\delta^{15}N$.