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Dietary segregation between two cohabiting species of sparrows revealed with stable isotope analysis

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Abstract: Fox Sparrows (*Passerella iliaca* (Merrem, 1786)) and Song Sparrows (*Melospiza melodia* (A. Wilson, 1810)) cohabit on many islands along the Pacific coast of North America, and previous studies suggest that they rely on similar prey types. We used $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis on blood collected from breeding adults of both species in each of two habitats on Triangle Island, British Columbia, Canada, to test the hypothesis that the two species exhibit a consistent pattern (direction) of dietary segregation in different habitat types. Both $\delta^{13}C$ and especially $\delta^{15}N$ values differed between habitats, indicating that the two habitats were isotopically distinct. As predicted, $\delta^{15}N$ values differed consistently between the two species in the two habitats, averaging ~1.5‰ higher in the smaller Song Sparrow than in the larger Fox Sparrow in both. We infer that Song Sparrows included more animal matter and less plant matter in their diets than Fox Sparrows, and suggest that fixed traits related to body size might underlie the dietary (trophic) differences. In contrast, $\delta^{13}C$ values did not differ between species. We conclude that dietary segregation could help to facilitate the widespread cohabitation of these two species of sparrows.

Key words: cohabitation, dietary segregation, Fox Sparrow, *Melospiza melodia*, *Passerella iliaca*, Song Sparrow, stable isotopes.

Résumé : Les bruants fauves (*Passerella iliaca* (Merrem, 1786)) et les bruants chanteurs (*Melospiza melodia* (A. Wilson, 1810)) cohabitent dans de nombreuses îles de la côte du Pacifique de l'Amérique du Nord, et des études antérieures laissent croire qu'ils dépendent de types de proies semblables. Nous avons analysé les isotopes stables du carbone et de l'azote ($\delta^{13}C$ et $\delta^{15}N$) de sang prélevé d'adultes reproducteurs des deux espèces dans deux habitats distincts de l'île Triangle, en Colombie-Britannique (Canada) afin de vérifier l'hypothèse voulant que les deux espèces présentent un patron (direction) cohérent de ségrégation alimentaire dans différents types d'habitats. Les valeurs de $\delta^{13}C$ et particulièrement de $\delta^{15}N$ variaient selon l'habitat, indiquant que les deux habitats sont différents sur le plan isotopique. Comme prévu, les valeurs de $\delta^{15}N$ présentaient des différences cohérentes entre les deux espèces dans les deux habitats, les valeurs du bruant chanteur, le plus petit des deux oiseaux, étant en moyenne de ~1,5 ‰ supérieures à celles du bruant fauve dans les deux habitats. Nous en concluons que le régime des bruants chanteurs comprend plus de matière animale et moins de matière végétale que celui des bruants fauves et postulons que des caractères fixes liés à la taille du corps pourraient sous-tendre ces différences alimentaires (trophiques). En revanche, les valeurs de $\delta^{13}C$ des deux espèces étaient semblables. Nous concluons que la ségrégation alimentaire pourrait faciliter la cohabitation à grande échelle de ces deux espèces de bruants. [Traduit par la Rédaction]

Mots-clés : cohabitation, ségrégation alimentaire, bruant fauve, *Melospiza melodia*, *Passerella iliaca*, bruant chanteur, isotopes stables.

Introduction

There is a wide variety of mechanisms that might enable potential competitors to cohabit (Chesson 2000). These mechanisms include frequency-dependent predation (Holt 1977), temporal segregation in the period of peak resource use (Kotler et al. 1993), and dietary segregation associated with differences in morphology (Leyequién et al. 2007) and feeding behavior (Page et al. 2005).

Here, we consider dietary segregation. On Triangle Island, British Columbia, Canada, Fox Sparrows (*Passerella iliaca* (Merrem, 1786)) and Song Sparrows (*Melospiza melodia* (A. Wilson, 1810)) are the two most abundant songbirds and the only breeding species of Emberizidae (Carl et al. 1951; Vermeer et al. 1976). In fact, the two sparrows cohabit on many islands along the Pacific coast of North America (Campbell et al. 2001). The larger Fox Sparrow is dominant to the smaller Song Sparrow in interspecific encounters for food (Smith et al. 1980), but general accounts of nesting habits and diets suggest that their use of available resources could overlap to a large extent. In particular, both species feed primarily on insects, fruits, and seeds while breeding, and on islands both consume amphipods taken in the intertidal zone (Arcese et al. 2002; Weckstein et al. 2002).

In this study, we test the hypothesis that cohabiting Fox Sparrows and Song Sparrows will exhibit a consistent pattern (direction) of dietary segregation in different habitat types. Stable carbon ($\delta^{13}C$) and especially stable nitrogen ($\delta^{15}N$) isotope analysis have proven useful tools to index niche (diet) breadth in comparative studies (Bearhop et al. 2004), because $\delta^{15}N$ values tend to increase with trophic level, while $\delta^{13}C$ gauges the source of nutrients, e.g., marine vs. terrestrial (Hobson and Welch 1992). Therefore, we collected blood from breeding Fox Sparrows and Song Sparrows in each of two isotopically distinct habitats on Triangle Island, and compared $\delta^{13}C$ and $\delta^{15}N$ values between habitats and species. Because body size can be an important determinant of diet in sparrows, through its influence on the efficiency with seeds of different sizes are handled (Pulliam 1985), we also took a suite of morphological measurements on all of the birds that we bled. Lacking simple a priori reasons to predict the magnitude or

Table 1. Mean (95% confidence interval) morphometric measurements of 15 adult Fox Sparrows (*Passerella iliaca*) and 13 adult Song Sparrows (*Melospiza melodia*) on Triangle Island, British Columbia.

Measurement	Song Sparrow	Fox Sparrow
Mass (g)	27.5 (0.36)	41.7 (0.80)
Wing chord (unflattened; mm)	66.9 (0.61)	80.2 (0.62)
Tarsus (mm)	24.3 (0.22)	26.5 (0.31)
Head + bill (mm)	33.9 (0.19)	35.7 (0.18)
Culmen (nostril to tip; mm)	9.4 (0.14)	9.5 (0.13)
Exposed culmen (mm)	13.1 (0.19)	13.4 (0.21)
Bill depth (mm)	5.9 (0.08)	7.3 (0.10)
Bill width (mm)	4.8 (0.06)	5.8 (0.10)

Table 2. Sources of variation in $\delta^{15}N$ and $\delta^{13}C$ values in the blood of adult Song Sparrows (*Melospiza melodia*) and Fox Sparrows (*Passerella iliaca*) in two habitat types (higher elevation sites on top of Puffin Rock, sites at sea level) on Triangle Island, British Columbia.

Isotope	Source	Sum of squares	df	F	P
$\delta^{15}N$	Species	9.63	1	6.64	0.01
	Habitat	75.75	1	52.19	<0.001
	Species × habitat	0.27	1	0.18	0.67
	Error	34.83	24	—	—
$\delta^{13}C$	Species	0.23	1	0.25	0.62
	Habitat	8.10	1	8.92	0.006
	Species × habitat	2.50	1	2.76	0.11
	Error	21.78	24	—	—

direction of interspecific variation, we predicted simply that $\delta^{13}C$ and $\delta^{15}N$ values would differ between Fox Sparrows and Song Sparrows.

Materials and methods

Our study took place on Triangle Island (50°52′N, 129°5′W) from 12 June to 5 July 2005. We set mist nets in two habitats ~0.8 km apart. The first habitat was in well-drained sites situated in a narrow band above gravel beaches and immediately below steep sea slopes. These areas were dominated by herbaceous vegetation (grasses, ferns, forbs) and tall (1.5–2 m) salmonberry (*Rubus spectabilis* Pursh). Two seabirds, Cassin's (*Ptychoramphus aleuticus* (Pallas, 1811)) and Rhinoceros (*Cerorhinca monocerata* (Pallas, 1811)) auklets, bred in burrows on the sea slopes but not in the areas where we set mist nets. We sampled in this habitat on 12 occasions for a total of 20.4 h. The second habitat was in flat, higher elevation sites (~100 m) atop Puffin Rock, in areas dominated in roughly equal proportions by tufted hairgrass (*Deschampsia cespitosa* (L.) P. Beauv), licorice fern (*Polypodium glycyrrhiza* D.C. Eaton), and short (<1 m), wind-pruned salmonberry. Cassin's Auklets and Leach's Storm-Petrels (*Oceanodroma leucorhoa* (Vieillot, 1818)) bred densely in burrows immediately beneath the mist nets. We sampled in this habitat on four occasions for a total of 10.3 h. We expected the $\delta^{15}N$ baseline to be higher atop Puffin Rock than in beachtop areas, due to nitrification by seabirds, and that this difference would be maintained through to consumers (Croll et al. 2005).

Song Sparrows and Fox Sparrows were the only species caught in any of the nets. All captured birds were aged (adult or juvenile), checked for evidence of breeding (brood patches in females, cloacal protuberances in males), then weighed with a 100 g spring scale (±1 g). We also took a series of linear measurements: lengths of (1) tail and (2) unflattened wing chord (both with a small ruler; ±1 mm), (3) tarsus, and (4) culmen (both exposed and nostril-to-bill tip), (5) bill width, (6) bill depth, and (7) head + bill (maximum distance from the back of the head to the tip of the bill) (the remaining measurements with vernier calipers; ±0.1 mm). We then took ~150 μL of blood from the brachial vein of breeding birds and immediately placed the blood in 70% ethanol; by sampling only breeders, we excluded nonterritorial, transient individuals. Prior to release, we clipped a single tail feather to avoid resampling the same individuals.

Samples were analysed at the Stable Isotope in Nature Laboratory at University of New Brunswick. Approximately 0.2 mg of dried, powdered sample was loaded into tin capsules and combusted in a Carlo Erba NC2500 elemental analyzer; resultant gases were delivered via continuous flow to a Finnigan Mat Delta XP mass spectrometer. Isotope ratios are reported relative to international standards for carbon (Peedee Belemnite Carbonate) and nitrogen (atmospheric N$_2$, AIR) according to $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X is the heavier isotope (^{13}C or ^{15}N) and R is the ratio of heavy to light isotopes ($^{13}C/^{12}C$ or $^{15}N/^{14}N$). Isotope values were corrected using International Atomic Energy Agency standards for all runs: CH6 (–10.4‰ ± 0.2‰, mean ± SD), CH7 (–31.8‰ ± 0.1‰), N1 (0.4‰ ± 0.2‰), and N2 (20.3‰ ± 0.1‰). One standard deviation

of sample repeats within runs were $\delta^{13}C < 0.7$‰ and $\delta^{15}N < 0.8$‰, and an internal laboratory standard (bovine liver) yielded values of –18.6‰ ± 0.1‰ ($\delta^{13}C$) and 7.2‰ ± 0.2‰ ($\delta^{15}N$).

Given that the expected half-life for stable isotopes in the blood of a sparrow-sized bird is ~20 days (Carleton and Martínez del Rio 2005), and that both Fox and Song sparrows were present when we arrived on Triangle Island in late March, stable isotope values in blood collected in June and July should reflect local dietary inputs exclusively. We used a two-way ANOVA to assess variation in $\delta^{15}N$ and $\delta^{13}C$ values in relation to species, habitat, and their interaction. We were unable to include sex as a factor because we caught no male Fox Sparrows on Puffin Rock. However, there was no indication that isotopic values differed between male and female Song Sparrows in the two habitats: in a two-way ANOVA, parameter estimates ± 95% confidence intervals (CIs) for $\delta^{15}N$ was –0.13‰ ± 0.51‰ and for $\delta^{13}C$ was –0.34‰ ± 0.45‰, with values in both cases lower in females than in males. Likewise, isotopic values did not differ between male and female Fox Sparrows in beachtop areas: in a one-way ANOVA, parameter estimates ± 95% CIs for $\delta^{15}N$ was 0.19‰ ± 0.58‰ and for $\delta^{13}C$ was 0.43‰ ± 0.52‰, higher in both cases in females.

Results

We caught totals of 9 female and 4 male Fox Sparrows, and 4 female and 11 male Song Sparrows, all of which were breeding. The ratio of adult Fox Sparrows to Song Sparrows did not differ significantly (Fisher's exact test, $P > 0.1$) between sites at low (10:7) and at higher (3:8) elevation, although with small sample sizes the power of that test to detect a difference was low. Based on 95% CIs around mean values, Fox Sparrows were larger than Song Sparrows in all body parts except culmen length (Table 1). We also caught and immediately released six juvenile Fox Sparrows and five juvenile Song Sparrows, including at least one of each species in both habitats.

Using a two-way ANOVA, we found that both $\delta^{15}N$ and $\delta^{13}C$ stable isotope values in sparrow blood differed between habitats (Table 2), with both being higher atop Puffin Rock (Fig. 1). As predicted, $\delta^{15}N$ values differed between Fox Sparrows and Song Sparrows, with no species × habitat interaction (Table 2): in both, $\delta^{15}N$ values averaged ~1.5‰ higher in Song Sparrows than in Fox Sparrows (Fig. 1). The two sparrows did not differ in $\delta^{13}C$ values (Table 2, Fig. 1).

Discussion

As predicted by the hypothesis that the two species will exhibit a consistent pattern (direction) of dietary segregation in different habitats, mean $\delta^{15}N$ values in the blood of breeding Song Sparrows averaged ~1.5‰ higher than those in breeding Fox Sparrows in each of two isotopically distinct habitats; for a perspective, it is generally accepted that $\delta^{15}N$ values increase by ~3.4‰ from one trophic level to the next (Minagawa and Wada 1984). Thus, the

Fig. 1. Bivariate plot showing the mean (±95% confidence intervals) $\delta^{15}N$ and $\delta^{13}C$ values in blood of adult Song Sparrows (*Melospiza melodia*) (solid symbols) and Fox Sparrows (*Passerella iliaca*) (open symbols) captured in mist nets in beachtop (circles) and Puffin Rock (triangles) habitats on Triangle Island, British Columbia. Numbers beside symbols are sample sizes.
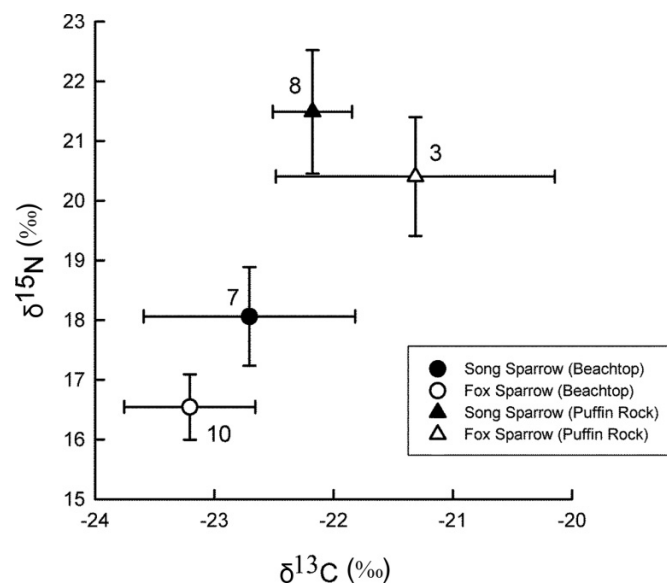
smaller Song Sparrows tended to feed at a higher trophic level than the larger Fox Sparrows, perhaps consuming more animal matter and less plant matter. The consistency between habitat types may indicate that traits related to body size, such as the ability to handle seeds of a particular size (Pulliam 1985), were an important (fixed) factor underlying the dietary segregation, and that habitat features did not appreciably alter that relationship. But whether Fox Sparrows and Song Sparrows differ in fundamental niches (i.e., the dietary differences are intrinsic) or in realized niches (i.e., the differences result from active competition between them) remains unanswered.

Recently, Beaulieu and Sockman (2012) used stable isotope analysis to show that smaller Lincoln's Sparrows (*Melospiza lincolni* (Audubon, 1834)) fed at a lower trophic level than larger White-crowned Sparrows (*Zonotrichia leucophrys* (J.R. Forster, 1772)), but only following an increase in the abundance of potential competitors late in the breeding season. Results of that study, in combination with ours, suggest that trophic relations between cohabiting sparrows can be both static and dynamic, and need not be determined solely by size—which itself had an inconsistent effect on relative trophic level in the two studies.

The $\delta^{15}N$ values were unusually high on Triangle Island compared with terrestrial biomes, whereas the $\delta^{13}C$ values were unusually low. This is the normal situation on large seabird colonies, however, where vast quantities of marine-derived nutrients are delivered to the system in guano (Croll et al. 2005). The strong and unequal ammonification of the two habitats in this study leaves $\delta^{15}N$ a useful indicator of nutrient sources to consumer diets within each habitat type, but not a reliable indicator of relative trophic level when comparing between habitats (Drever et al. 2000). Why $\delta^{13}C$ values were higher atop Puffin Rock is less clear, and in fact, we might have expected the opposite pattern if sparrows breeding just above beaches consume marine food, such as amphipods, with higher $\delta^{13}C$ values than terrestrial sources. Regardless, for our purposes, what was important was that the two habitats were isotopically distinct.

Dietary segregation and mechanisms that facilitate the coexistence of potential competitors has long been an important topic in ecological research (MacArthur 1972; Siepielski and McPeek 2010). Our simple study provides quantitative evidence that two species of sparrows exhibit similar patterns of dietary segregation in different habitats, and suggests that body size differences might play a role in niche (trophic) segregation (Pulliam 1985; Leyequién et al. 2007). Dietary segregation is thought to be an important mechanism which facilitates the cohabitation of species that could potentially compete with one another if food is limiting (Chesson 2000), and we conclude that dietary differences might enable Fox Sparrows and Song Sparrows to cohabit widely on islands along the Pacific coast of North America (Campbell et al. 2001).

Acknowledgements

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