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Foraging habitat and diet of Song Sparrows (*Melospiza melodia*) nesting in farmland: a stable isotope approach

J. Girard, A. Baril, P. Mineau, and L. Fahrig

Abstract: Agricultural intensification has been linked to declines in farmland and grassland bird populations in Europe and in North America. One factor thought to be behind these declines is reduced invertebrate food abundance in the breeding season, leading to reduced reproductive success. However, little is known about foraging habitat or diet of farmland birds in North America. We used stable isotopes to study foraging habitat and diet of Song Sparrows (*Melospiza melodia* (A. Wilson, 1810)), a common hedgerow-breeding bird, by collecting claw clippings of Song Sparrow nestlings from farms in eastern Ontario, Canada. Mean values of δ^{13}C and δ^{15}N were compared between claws and invertebrate food sources from adjacent land-cover types, using a Bayesian mixing model. The portion of nestling diet that came from seminatural and forage habitats was higher than expected, based on the proportion of seminatural and forage cover at the nest. This was particularly evident at nests with low seminatural cover, where hedgerows were the only noncrop habitat. The most important food sources for Song Sparrow nestlings were hoppers (Auchenorrhyncha) and caterpillars (Lepidoptera). Management actions to increase invertebrate abundance in hedgerows may benefit Song Sparrows and other farmland birds with minimal impact on crop yield.

Key words: *Melospiza melodia*, Song Sparrow, stable isotope, agriculture, carbon, nitrogen, claw, hedgerow.

Résumé : L'intensification de l'agriculture a été liée au déclin de populations d'oiseaux des terres agricoles et des prairies en Europe et en Amérique du Nord. Un des facteurs à l'origine de ce déclin serait une diminution de l'abondance de la nourriture invertébrée durant la période de nidification, menant à une diminution du succès de reproduction. Cela dit, les connaissances sur les habitats d'alimentation et le régime alimentaire des oiseaux des terres agricoles en Amérique du Nord sont limitées. Nous avons fait appel aux isotopes stables pour étudier l'habitat d'alimentation et le régime alimentaire du bruant chanteur (*Melospiza melodia* (A. Wilson, 1810)), un oiseau répandu qui nidifie dans des haies, en prélevant des rognures de griffes d'oisillons de bruants chanteurs dans des fermes de l'est de l'Ontario (Canada). Les valeurs moyennes du δ^{13}C et du δ^{15}N des griffes et de sources de nourriture invertébrées provenant de différents types de couverture terrestre sur place ont été comparées à l'aide d'un modèle bayésien de mélange. La part du régime des oisillons provenant d'habits semi-naturels et fourragers était plus grande que ce qui aurait été prévu à la lumière des proportions des couvertures semi-naturelle et fourragère au site de nidification. Cela était d'autant plus évident pour les nids caractérisés par une faible couverture semi-naturelle, où les haies constituaient le seul habitat non agricole. Les sources de nourriture les plus importantes pour les oisillons de bruants chanteurs étaient des auchénorrhynches et des chenilles (lépidoptères). Des mesures d'aménagement visant à accroître l'abondance d'invertébrés dans les haies pourraient être bénéfiques aux bruants chanteurs et à d'autres oiseaux des terres agricoles sans pour autant avoir un grand impact sur le rendement des cultures.

Mots-clés : *Melospiza melodia*, bruant chanteur, isotope stable, agriculture, carbone, azote, griffe, haie.

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Introduction

Over the past half century, agricultural practices have intensified through the use of chemical pesticides and fertilizers, increased field sizes, farm specialization, destruction of edge and boundary features, and drainage of land among others (reviewed by Tscharntke et al. 2005). This has increased agricultural productivity (Robinson and Sutherland 2002; Green et al. 2005), but has also led to declines in biodiversity on farmland (Benton et al. 2002, 2003; Robinson and Sutherland 2002). Consequently, farmland and grassland bird populations have declined in Europe and in North America (Fuller et al. 1995; Siriwardena et al. 1998; Donald et al. 2001; Murphy 2003; Sauer et al. 2011).

One of the factors thought to contribute to farmland bird declines is a reduction in invertebrate food abundance, which is important for feeding nestlings (Campbell and Cooke 1997; Newton 2004). Long-term use of pesticides and reduction in diversity of land uses within farmed areas (e.g., simplification of crop rotation, reduction in mixed farming, loss of semi-natural habitat within farmland; Wilson et al. 1999; Robinson and Sutherland 2002) has reduced invertebrate abundance in farmland (Aebischer 1990; Campbell and Cooke 1997; Wilson et al. 1999; Robinson and Sutherland 2002; Newton 2004). Farmland birds breeding at nest sites with lower nestling food abundance or higher insecticide applications can show reductions in nest success including reduced fledgling success and reduced nest survival (Brickle et al. 2000; Boatman et al. 2004; Britschgi et al. 2006). Reduced food abundance has been linked to population declines in Grey Partridges (*Perdix perdix* (L., 1758)) (Potts 1986) and is suspected to be a factor in declines in a number of other species (Campbell and Cooke 1997; Boatman et al. 2004; Britschgi et al. 2006).

The detailed understanding of how farmland birds in Europe (particularly in the UK) are affected by reductions in invertebrate food abundance are underpinned by extensive knowledge of both the diet and the foraging habitat of these birds (e.g., Hill 1985; Stoate et al. 1998; Wilson et al. 1999; Moreby and Stoate 2001; Morris et al. 2001; Southwood and Cross 2002; Holland et al. 2006). For example, diet studies of Grey Partridge juveniles were critical in demonstrating the link between herbicide use and population declines (Green 1984; Potts 1986). Foraging habitat and diet of farmland birds have received much less attention in North America than in Europe. North American farmland breeding birds are known to use crop fields, hay fields, and boundary features, such as hedgerows, for foraging (Best et al. 1990; Boutin et al. 1999; Puckett et al. 2009). Boutin et al. (1999) surveyed birds in corn, soybean, apple orchards, and vineyards in southern Ontario and found that of 14 species observed within field centers and in edges adjacent to crop fields, most species were observed in edges more than expected based on habitat availability. The only detailed North American study of foraging habitat use within crop fields we are aware of was carried out by Rodenhouse and Best (1994). They showed that Vesper Sparrows (*Pooecetes gramineus* (Gmelin, 1789)) nesting in corn and soybean fields forage most often within 1 m of weedy or unplanted areas and prefer fields with crop residue over bare fields, presumably due to increased food abundance.

We studied foraging habitat and diet in Song Sparrows (*Melospiza melodia* (A. Wilson, 1810)) breeding in hedgerows and fencerows using stable isotope analysis. Unlike foraging observations, which provide information only on habitat use, or ligatures or fecal analysis, which provide a snapshot of diet items, and may be biased against certain food types, stable isotope analysis provides information on food sources that have been incorporated into an animal's tissues over time (Hobson and Clark 1992; Hobson and Bairlein 2003; Pearson et al. 2003; Bearhop et al. 2003). Stable isotope analysis is suited to studying foraging habitat and diet where habitats and food sources have different isotopic signatures (Gannes et al. 1997; Phillips and Gregg 2001). We have previously shown that carbon and nitrogen stable isotopes can be used to distinguish between invertebrates captured in crop fields and those captured in hedgerows and hay fields in our study area (Girard et al. 2011). In this study, we (*i*) test the null hypothesis that nestling food is obtained from crop fields and from semi-natural and forage habitats in proportion to local habitat availability and (*ii*) determine which invertebrate taxa are most important in the diet of Song Sparrow nestlings in hedgerow nests. Stable isotope analysis has been infrequently used in passerine nestlings, so we also provide evidence to validate this methodology.

Materials and methods

Study sites

This study was carried out at 12 sites on dairy and arable farms in eastern Ontario, Canada, where each site consisted of a continuous hedgerow and the adjoining fields. Farms were located between the towns of Navan (45°25′15.68″N, 75°25′36.28″W) and Embrun (45°16′26.29″N, 75°16′30.04″W), south east of Ottawa. The dominant crop rotation is field corn (*Zea mays* L.) and soybean (*Glycine max* (L.) Merr.), but hay and wheat (genus *Triticum* L.) are also common. Hedgerows varied from grassy strips with occasional shrubs to fully treed hedgerows. Hedgerows were selected to avoid deep ditches and areas of permanent water.

Study species

Song Sparrows were selected for this study, as they are widespread and abundant in farmland across North America (e.g., Best et al. 1995; Freemark and Kirk 2001; Jobin et al. 2001; Sykes and Hannon 2001; Puckett et al. 2009). Their use of field edges for foraging, together with their relatively high abundance in these areas, led Boutin et al. (1999) to rate Song Sparrows as high risk for pesticide exposure. Song Sparrow populations in the study region (lower Great Lakes – St. Lawrence plain) have shown a long-term pattern of decline (1966–2009: –0.6% change/year, 95% CI: –0.9% to –0.4%, $n = 167$; Sauer et al. 2011).

During the breeding season, Song Sparrows eat primarily invertebrates (Arcese et al. 2002). Song Sparrows forage primarily on the ground, although we also observed them gleaning invertebrates from leaves and bark, and occasionally hawking for flying insects (J. Girard, personal observation). Based on ligature samples of nestling food from three Song Sparrow nests, we found that nestling food is highly variable and includes hoppers (Auchenorrhyncha; 22 individuals, hoppers include leafhoppers, plant hopers, froghoppers, etc.), true spiders (Araneae; 8 individuals), caterpillars (Lepidoptera; 2 individuals), unidentified larvae (2 individuals), beetles (Coleoptera; 2 individuals), bees or wasps (Hymenoptera; 1 indi-

vidual), true bugs (Heteroptera; 1 individual), and flies (Diptera; 1 individual) (J. Girard, unpublished data). Because of the small number of samples obtained and the high taxonomic variability of the invertebrates in the samples, we did not use these data to create a prior distribution for the Bayesian mixing model described below.

Nest searching

Nest searching was carried out in 2006–2008 between mid-May and early August. Nests were found primarily by flushing females off the nest, as well as by observing adults and by chance. Once a nest was found, it was monitored every 3–4 days, on average, until success or failure of the nesting attempt was established.

Nestling samples

To obtain $\delta^{13}C$ and $\delta^{15}N$ values from nestlings, we collected claw samples from 81 nestlings in 28 nests in 2006 and 2007. Samples were collected by clipping approximately 2 mm from the middle claw of each foot, when the nestling was 5 or 6 days old. Claw samples were cleaned with methanol, cut into very small pieces, and approximately 0.3–0.4 mg was weighed into a tin capsule for stable isotope analysis.

Animal care and sampling protocol was approved by the National Wildlife Research Centre and the Ontario region of the Animal Care Committee of Environment Canada (project no. 06X06P50).

Invertebrate sampling

Invertebrate samples were collected from 59 nests, including the 28 nests from which claws were collected. Sampling was carried out in the hedgerow and in adjoining fields, within a 35 m radius of each nest, which approximates the mean territory size of Song Sparrows in these study sites (J. Girard, unpublished data). Samples were collected using pitfall traps, a D-Vac suction sampler (model 122; D-Vac Company, Ventura, California, USA; Dietrick et al. 1959) and by hand (Fig. 1). See Girard et al. (2011) for a full description of invertebrate sampling methods. Samples were always collected between hatching and fledging of the nestlings, and generally when the nestlings were between 5 and 8 days of age. Note that many of the invertebrate samples analysed here were previously analysed by Girard et al. (2011) in a different context. This does not include data on invertebrates captured in wheat fields or data on sap beetles and beetle larvae that were not presented previously. In addition, previously used data on invertebrates captured in field edges are not included here.

In the laboratory, invertebrates were sorted and identified to family (beetles) or to order or suborder (all other invertebrates). Based on abundance in trapping samples and presence in ligature samples (see above), we selected seven taxa for further analysis: caterpillars (Lepidoptera larvae; $n = 39$ samples used in stable isotope analysis), crickets (Ensifera; $n = 35$), adult ground beetles (Carabidae; $n = 129$), beetle larvae (Coleoptera larvae; $n = 10$), hoppers (Auchenorrhyncha; $n = 80$), sap beetles (Nitidulidae; $n = 65$), and true spiders (Araneae; $n = 158$)). Invertebrates were either freeze-dried (2006) or oven-dried at 60 °C for at least 48 h until dry (2007, 2008), then crushed into a fine powder, and approximately 1 mg was weighed into a tin capsule for isotope analysis.

Fig. 1. Layout of pitfall traps used to sample invertebrates, showing a single nest site with four hedgerow traps and four traps in each adjacent field. Circles represent pitfall trap locations used in all years (2006–2008), whereas triangles represent pitfall trap locations used only in 2007 and 2008. D-Vac samples were collected twice in each field between the rows of traps, at least 10 m into the field and 10 m apart. Invertebrate samples were also collected by hand from shrubs and trees in the hedgerow. Adapted from Girard et al. (2011) and reproduced with permission of Écoscience, vol. 18, issue 2, pp. 98–109, © 2011 Écoscience, Université Laval, Québec, Que., Canada. Carbon and nitrogen stable isotope ratios differ among invertebrates from field crops, forage crops, and noncropped land uses.
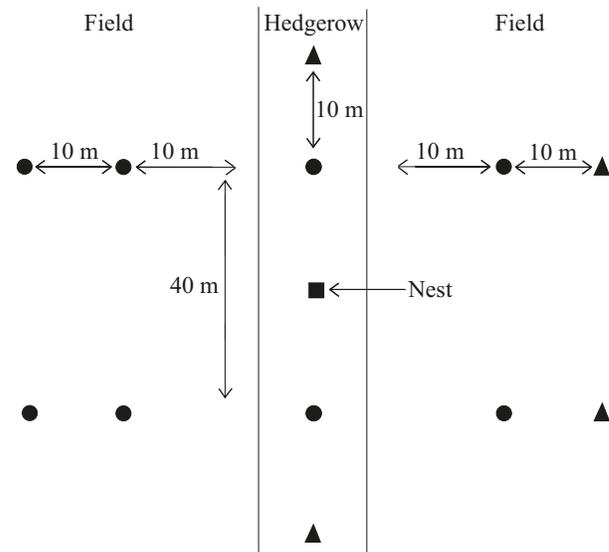
Isotope analysis

Samples and standards were loaded into an elemental analyser (Vario EL III; Elementar Analysen systeme, Hanav, Germany), which was interfaced to an isotope ratio mass spectrometer (Conflo II, Delta XP Plus Advantage; Thermo Finnigan, Bremen, Germany). The data are reported in delta notation, defined as $\delta = [(R_{sample} - R_{standard})/R_{standard}] \times 1000$, where R is the ratio of the abundance of the heavy to the light isotope. $\delta^{15}N$ is reported as permil (‰) vs. AIR and $\delta^{13}C$ is reported as permil (‰) vs. V-PDB and normalized to internal standards calibrated to international standards. Analytical precision (SD for repeated measurement of internal standard C-55 within runs) was better than 0.2‰ for invertebrate $\delta^{13}C$ and $\delta^{15}N$ and better than 0.45‰ for claw $\delta^{13}C$ and $\delta^{15}N$. Ninety-one out of 524 invertebrate samples were duplicated (difference (mean ± SD) between sample and duplicate; $\delta^{13}C$: 0.24‰ ± 0.23‰; $\delta^{15}N$: 0.22‰ ± 0.21‰) and 11 of 86 claw samples were duplicated ($\delta^{13}C$: 0.11‰ ± 0.08‰; $\delta^{15}N$: 0.23‰ ± 0.21‰). All samples were analysed at the G.G. Hatch Laboratories at the University of Ottawa.

Land cover

We used 2008 aerial photographs of eastern Ontario to digitize landscape structure around each site (DRAPE 2010). Land uses within 100 m of each nest were added to the digitized map in two categories—crop cover (corn, wheat, and soy) and seminatural and forage cover (alfalfa, hay,

pasture, hedgerow, riparian, and verge; hereafter seminatural cover)—to reflect expected differences in stable isotope values of invertebrates. Maps were then used to quantify land uses at 35 and 100 m radii at each nest. The 35 m radius reflects the mean territory radius of Song Sparrows nesting on these study sites (J. Girard, unpublished data). The larger scale accounts for long-distance foraging trips regularly made by Song Sparrows (J. Girard, personal observation). Crop cover and seminatural cover were strongly correlated at each scale (100 m: $\rho = -0.95$, $p < 0.001$, 35 m: $\rho = -0.99$, $p < 0.001$) and crop cover was highly correlated between scales ($\rho = 0.85$, $p < 0.001$).

Statistical analyses

We used a Bayesian mixing model to estimate the contributions of the different invertebrate food sources to the diet of the nestlings (siar package in R; Parnell et al. 2010). This model incorporates input variability and outputs a probability density function (PDF) for each food source, representing the probable contribution of each food source to the consumer tissue (Moore and Semmens 2008; Parnell et al. 2010). Because all the food sources in this study were invertebrates with similar C:N ratios (Table S1),[1] we did not correct for differing C:N ratios among food sources (Post et al. 2007).

A discrimination factor was used to account for changes in isotopic ratio between food source and consumer. Discrimination factors can vary with species, tissue, and diet, and using inaccurate discrimination factors can strongly affect the outcomes of mixing models (e.g., Cherel et al. 2005; Caut et al. 2009; Hussey et al. 2010). We could not find discrimination factors for claws of any bird species in the literature, so instead we used a discrimination factor for tail feathers of juvenile (23–26 days old) Song Sparrows ($\delta^{13}C$: 0.2‰ $\pm$ 0.58‰ (mean $\pm$ 1 SD); $\delta^{15}N$: 2.74‰ $\pm$ 0.31‰; Kempster et al. 2007). Tail feathers emerge at approximately 6 days in Song Sparrows (Jongsomjit et al. 2007), so the feathers incorporate material laid down at the age at which claw samples were collected. Discrimination factors are not affected by growth in young Song Sparrows (Kempster et al. 2007), so we made no correction for any difference in growth rate between our 6-day-old chicks and the juveniles from which the discrimination factor was obtained.

To test our null hypothesis that nestling diet is obtained from local land-cover types in proportion to their availability, we created a mixing model in which the food sources represented invertebrates captured in crop fields (corn, soybean and wheat) and those captured in hedgerows and hayfields (hereafter seminatural habitats). Because not all invertebrate taxa were captured at every nest and different numbers of nests were sampled in different fields, invertebrate $\delta^{13}C$ and $\delta^{15}N$ were first averaged by field or section of hedgerow and then by cover type. All sap beetles were included as a single food source, as they have relatively high values of $\delta^{13}C$ and $\delta^{15}N$, which do not differ between crop fields and hedgerow and hayfields, probably owing to their specialization as crop pests (Nout and Bartelt 1998; Dowd 2000). The inputs to the mixing model were the mean claw $\delta^{13}C$ and $\delta^{15}N$ value from each nest, the mean and SD of each food source, and the mean and SD of the discrimination factor.

The mixing model was run for each nest individually, and then the PDF for crop sources and for seminatural sources were summed to give a distribution of proportion of diet from crop sources and from seminatural sources at each nest. A paired t test was used to compare the median proportion of diet from crop sources and from seminatural sources at each nest. A paired Wilcox test was used to compare the median proportion of the diet from seminatural habitats with the proportion of seminatural cover at each nest. Finally, we used a linear regression to test whether the median proportion of Song Sparrow nest diet from seminatural habitats increased with the proportion of seminatural land cover at each nest, and used a Student's t test to test whether this relationship differed from the 1:1 relationship predicted if diet is obtained from seminatural habitats in proportion to their availability close to the nest.

To determine which invertebrate taxa are most important in the diet of nestling Song Sparrows, we ran a second mixing model using the seven invertebrate groups as potential food sources. We then took the median value of the PDF for each food source at each nest and averaged across nests to compare the importance of different food sources to nestling diet. A Kruskal–Wallis test followed by a Nemenyi–Damico–Wolfe–Dunn post hoc test (Hollander and Wolfe 1999) was used to test for significant differences among food sources.

If food sources entering a mixing model vary in lipid content, a bias can be introduced, because lipids are more depleted in ^{13}C than other tissues (DeNiro and Epstein 1978). Using $\delta^{13}C$ values from food sources with high lipid levels could lead to erroneous results because claws have low lipid content. Lipids contain little or no nitrogen, so if lipid content is variable among food sources, then we would expect a negative relationship between C:N ratio and $\delta^{13}C$ across food sources. We used a Pearson's correlation to test for such a relationship.

Because we analysed whole invertebrates, bias could also be introduced into the mixing model if invertebrate exoskeleton is not assimilated by nestlings, and the exoskeleton has different $\delta^{13}C$ or $\delta^{15}N$ values from soft body parts of invertebrate food sources. The chitin in invertebrate exoskeletons is derived from excretory ammonia (Webb et al. 1998 and references within), which generally has a lower $\delta^{15}N$ than the diet. Chitin has a relatively high C:N ratio of about 6.9, so if the presence of chitin in our food sources is influencing $\delta^{15}N$, then we would expect to see a negative relationship between C:N ratio and $\delta^{15}N$ value. We tested for this relationship using a Pearson's correlation.

All tests were carried out in R (R Development Core Team 2010).

Validation of methodology

Do $\delta^{13}C$ and $\delta^{15}N$ values of nestling claws reflect diet?

Claws have rarely been used as a tissue to study diet in passerines (Bearhop et al. 2003; Gagnon and Hobson 2009; Robb et al. 2011). Claws are made of keratin, which is metabolically inactive, so stable isotope values of keratin do not change once it has grown (Caumette et al. 2007). However,

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[1]Supplementary materials (Tables S1–S3 and Figs. S1A–S6B) are available with the article through the journal Web site (http://nrcresearchpress.com/doi/suppl/10.1139/z2012-103).

keratin is continually deposited at the tip of the claw (Ethier et al. 2010), so the claw could integrate isotope values of diet over time. Rapid growth in nestlings should ensure that claws collected at 5 or 6 days represent isotopic values of nestling food. Nevertheless, it is possible for young chicks to reflect the isotopic value of maternal input from the egg rather than of the diet (Sears et al. 2009). A laboratory-based diet switch study was outside the scope of the current study. However, we were able to test the validity of using claws to represent nestling diet in two ways. First we compared claw values with four un-hatched eggs, collected from nests in this study. If claws were reflecting isotope value of the egg, then we would expect them to be enriched in $\delta^{13}C$ and $\delta^{15}N$ compared with the eggs because of standard fractionation processes. Eggs were homogenized and freeze-dried, then lipids were extracted using 2:1 ratio of DCM to methanol. Both the lipid-extracted and the raw samples were then tested for $\delta^{13}C$ and $\delta^{15}N$ values as described above.

Secondly, we compared the $\delta^{13}C$ and $\delta^{15}N$ values of claws from Song Sparrows with those of Brown-headed Cowbirds (*Molothrus ater* (Boddaert, 1783)) raised in the same nests. Brown-headed Cowbirds are obligate brood parasites, and once an egg is laid in a host nest, all parental care is provided by the host birds (Lowther 1993). If $\delta^{13}C$ and $\delta^{15}N$ values of nestling claws reflect diet and not the egg, claws of Brown-headed Cowbirds and Song Sparrows from the same nests are predicted to have very similar values. Claws were collected from three Brown-headed Cowbirds at approximately 6–7 days of age and treated as described above for claws of Song Sparrows.

Validity of discrimination factor

Discrimination factors are often tissue specific. Because no discrimination factors are available for claw material, we used a discrimination factor generated for feathers ($\delta^{13}C$: 0.2‰ ± 0.58‰ (mean ± 1 SD); $\delta^{15}N$: 2.74‰ ± 0.31‰; Kempster et al. 2007). To test whether this discrimination factor is appropriate, we reran our mixing model based on predicted feather stable isotope values instead of claw values. Predicted values were generated by regressing mean claw values against mean feather values for four nests where both tissues were collected from dead nestlings ($\delta^{13}C$: $F_{[1,2]} = 104.2, p = 0.009$, $R^2 = 0.98$; $\delta^{15}N$: $F_{[1,2]} = 198.3, p = 0.005, R^2 = 0.99$) (Figs. S1A, S1B, Table S2).[1]

Validity of food sources

Mixing models work best when food sources are well separated (Gannes et al. 1997; Phillips and Gregg 2001). Here we contrast invertebrates captured in seminatural habitats, dominated by C3 plants, and crop fields. Corn is a C4 plant and is therefore expected to have a high $\delta^{13}C$ value compared with C3 plants, which include most other plants, trees, and cool-season grasses (DeNiro and Epstein 1978). Feeding experiments have consistently shown that invertebrates raised on C4 food sources have higher $\delta^{13}C$ values than those raised on C3 sources (e.g., Tallamy and Pesek 1996; Ponsard et al. 2004; Gratton and Forbes 2006), so a clear difference in $\delta^{13}C$ is expected between invertebrates captured in the corn fields and the C3-dominated seminatural habitats. For example, Latendresse (2004) showed significantly higher values of $\delta^{13}C$ of invertebrates captured in corn fields compared with those captured in adjacent forests or at the field–forest boundary. To create the crop food source, we combined invertebrates captured in corn fields, soybean fields, and wheat fields, even though soybean and wheat are C3 plants and have much lower $\delta^{13}C$ values than corn. This is based on our previous work, where invertebrates captured from corn and soybean fields all have relatively high $\delta^{13}C$ and $\delta^{15}N$, and are indistinguishable using these isotopes, probably because of the regular rotation of these crops (Girard et al. 2011). Wheat fields in this study area are also grown in rotation with corn, and invertebrates captured in wheat fields also had high $\delta^{13}C$ and $\delta^{15}N$ values. Previous studies have not directly compared the stable isotope values of invertebrates from rotational farm fields. However, Haubert et al. (2009) showed the $\delta^{13}C$ of fatty acids from spiders captured in corn and soybean fields was not strongly affected by crop type. We tested for differences in $\delta^{13}C$ and $\delta^{15}N$ among taxa and cover types using a nested ANOVA analysis where cover type was nested in taxon.

Results

Mean $\delta^{13}C$ and $\delta^{15}N$ were always higher for the food sources collected in crop habitats than those from seminatural habitats and were also significantly different among taxa (nested ANOVA; $\delta^{13}C$—taxon: $F_{[3,149]} = 19.7, p < 0.001$; land cover nested in taxon: $F_{[4,149]} = 18.0, p < 0.001$; $\delta^{15}N$—taxon: $F_{[3,149]} = 132.1, p < 0.001$; land cover nested in taxon: $F_{[4,149]} = 5.3, p < 0.001$; Fig. 2A, Table S1[1]). Sap beetles (all habitats combined) had the highest mean $\delta^{13}C$ of any of the food sources.

We found no relationship between mean C:N ratios of food sources and mean $\delta^{15}N$ ($\delta^{15}N$: $r_{[5]} = -0.3, p = 0.5$; Figs. S2A, S2B[1]). There was a strong but nonsignificant relationship between mean C:N ratios of food sources and mean $\delta^{13}C$, but this was entirely driven by the high $\delta^{13}C$ of sap beetles ($r_{[5]} = 0.58, p = 0.2$; Figs. S2A, S2B[1]). The lack of a relationship between C:N ratios and either $\delta^{13}C$ or $\delta^{15}N$ suggests that neither differential lipid content of food sources nor presence of exoskeleton in food samples was a factor in the results of our mixing models.
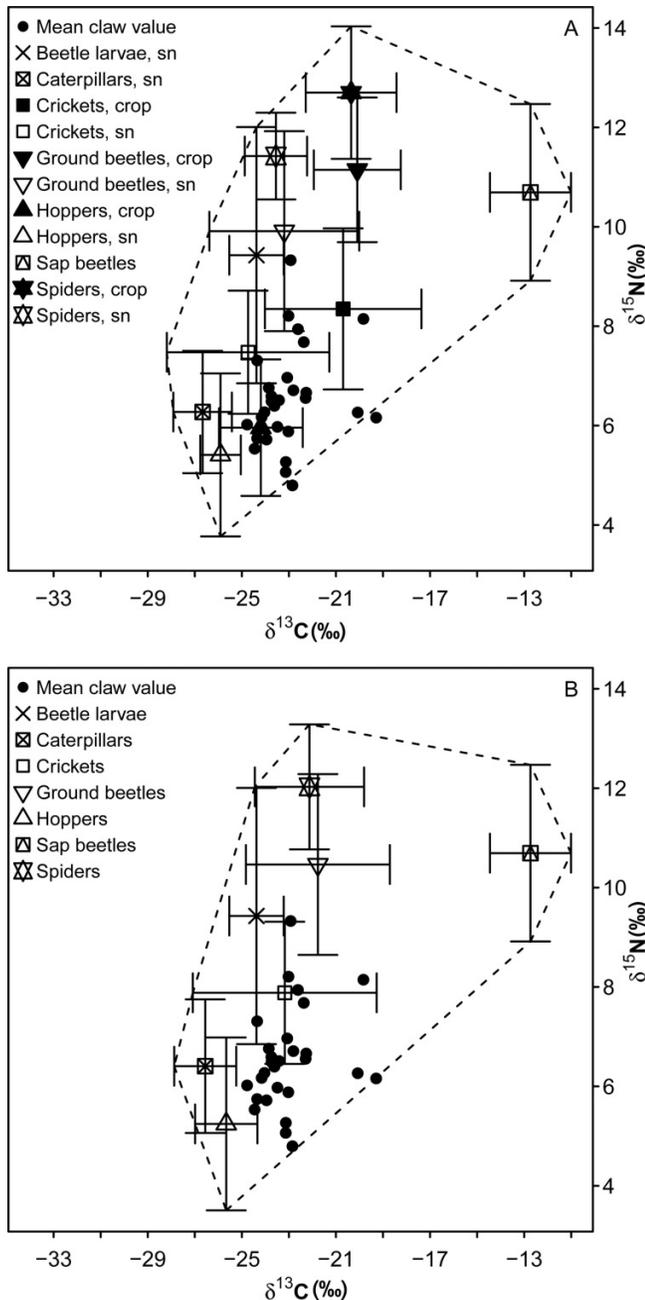
Foraging habitat

Mean claw values for 2 of the 28 nests fell outside of the mixing polygon, represented by the area encompassed by the food sources and their standard deviations (Fig. 2A, Table S3[1]). All the mean predicted feather values except one fell within the mixing polygon (Fig. S3A).[1]

The median proportion of diet obtained from seminatural habitats at each nest was significantly greater than the median proportion of diet obtained from cropped habitats (seminatural habitats: 0.61 ± 0.07 (mean ± 1 SD); cropped habitats: 0.39 ± 0.07; paired t test, $t_{[27]} = 8.0, p < 0.0001$). However, credibility limits overlapped in all cases (Figs. S4A, S4B).[1]

Contrary to our null hypothesis that nestling diet would come from crop fields and seminatural habitats in proportion to local habitat availability, the mean proportion of diet from seminatural habitats was significantly greater than the proportion of seminatural land cover both within 100 m of the nest (proportion (mean ± 1 SD) of diet from seminatural habitats: 0.61 ± 0.07; proportion of seminatural cover: 0.29 ± 0.24; $V = 9, p < 0.001$), and within 35 m of the nest (proportion of seminatural cover: 0.35 ± 0.24; $V = 25, p < 0.001$). The median proportion of the diet coming from seminatural habi-

Fig. 2. Mean (±1 SD) $\delta^{13}C$ and $\delta^{15}N$ values of claws taken from Song Sparrow (*Melospiza melodia*) nestlings in 28 nests, together with (A) $\delta^{13}C$ and $\delta^{15}N$ values of invertebrate food sources collected from adjacent crop fields (solid symbols) and seminatural and forage habitats (sn, open symbols), and (B) $\delta^{13}C$ and $\delta^{15}N$ values of invertebrate food sources averaged over all habitats. Food sources have discrimination factors added to them to account for the concentration of heavier isotopes at higher trophic levels ($\delta^{13}C$: 0.2‰ and $\delta^{15}N$: 2.74‰; Kempster et al. 2007). The broken lines show the mixing polygon bounded by the food sources entered into the mixing model.

Fig. 3. Relationship between the proportion of seminatural cover within (A) 100 m and (B) 35 m of Song Sparrow (*Melospiza melodia*) nests, and the median proportion of the diet of nestlings estimated to come from seminatural habitats. The broken line shows the 1:1 relationship expected if nestling food is obtained from seminatural habitat in proportion to local habitat availability.
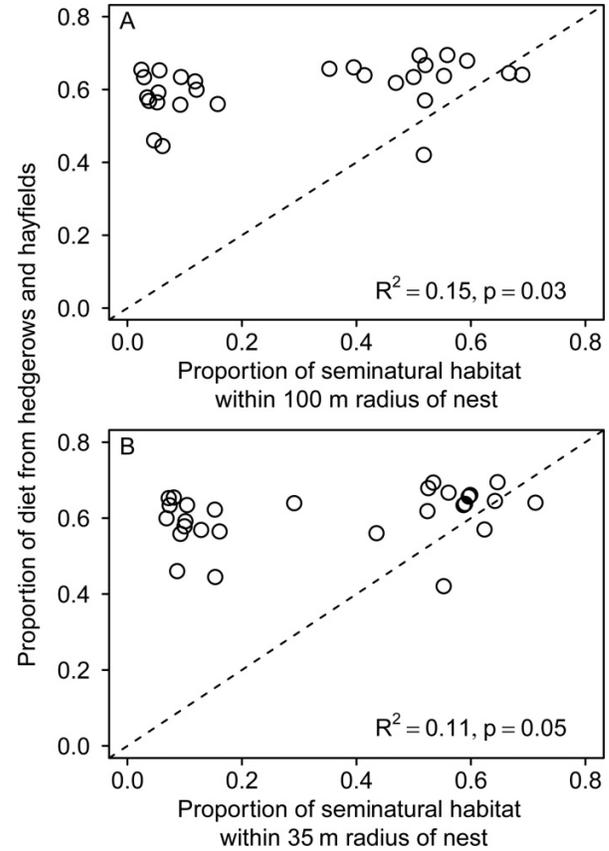
scale but was only marginally significant ($F_{[1,26]} = 4.26$, $p = 0.05$, $R^2 = 0.11$; Fig. 3B). At both scales, the slope of the relationship was significantly less than the 1:1 relationship that we predicted (100 m: $t_{[26]} = -16.6$, $p < 0.001$; 35 m: $t_{[26]} = -16.9$, $p < 0.001$).

Nestling diet

Hoppers had the highest mean contribution to nestling diet, but the proportion of hoppers in the diet was not significantly higher than that of caterpillars (Figs. 2B, 4). The taxa that made the lowest contributions to the diet were the sap beetles, ground beetles, and spiders. The mixing model based on predicted feather values had very similar results and the top four food groups were identical to the mixing model based on mean claw values (Figs. S3B, S5).[1]

Do $\delta^{13}C$ and $\delta^{15}N$ values of nestling claws reflect diet?

If stable isotopes of nestling claws were reflecting the egg rather than the diet, we expected $\delta^{13}C$ and $\delta^{15}N$ values of claws to be either higher than or close to egg values. Instead, claw values were depleted in $\delta^{13}C$ and $\delta^{15}N$ compared with eggs in the direction of the invertebrate food sources (Fig. 5). In addition, $\delta^{13}C$ and $\delta^{15}N$ of Brown-headed Cowbirds and Song Sparrows from the same nest are similar, especially

tats did increase slightly with the proportion of seminatural habitat within 100 m of the nest ($F_{[1,26]} = 5.88$, $p = 0.03$, $R^2 = 0.15$; Fig. 3A). The same pattern was observed at the 35 m

Fig. 4. Median estimated proportion of diet from invertebrate food sources for 28 Song Sparrow (*Melospiza melodia*) nests. Error bars are ±1 SD. Letters indicate significant differences at $p < 0.05$ (Kruskal–Wallis, $\chi^2_{[7]} = 143.62$, $p < 0.0001$).
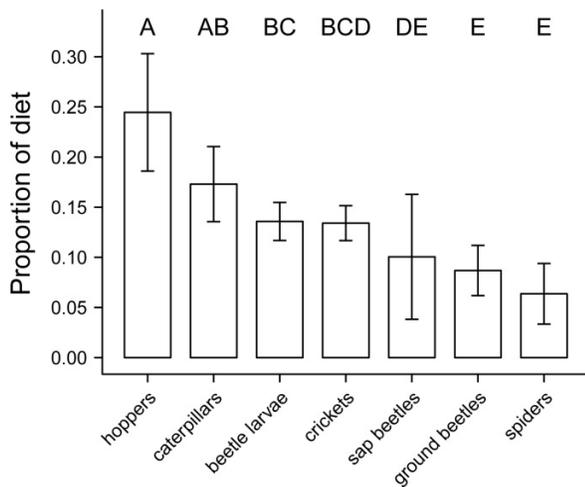

Fig. 5. δ¹³C and δ¹⁵N values for Song Sparrow (*Melospiza melodia*) eggs and claws, together with δ¹³C and δ¹⁵N values of invertebrate food sources. Values from four nests are highlighted; we analysed an egg and two claws from nest 774, an egg and two claws from nest 785, and an egg only from each of nests 916 and A6. Grey circles show values of Song Sparrow claws from nests from which only claw material was analysed. No discrimination factor is applied.
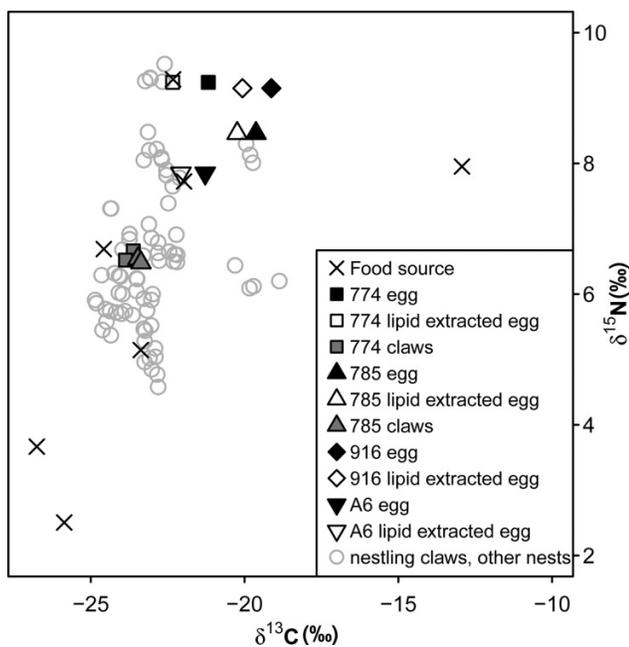

Fig. 6. δ¹³C and δ¹⁵N values for eggs and claws of Song Sparrow (*Melospiza melodia*; SOSP) and Brown-headed Cowbird (*Molothrus ater*; BHCO) nestlings. Values from three nests are highlighted; we analysed, a cowbird claw and two sparrow claws from nest 774, a cowbird claw and two sparrow claws from nest 915, and a single cowbird claw and a single sparrow claw from nest 787. Grey circles show values of Song Sparrow claws from nests from which only claw material was analysed. No discrimination factor is applied.
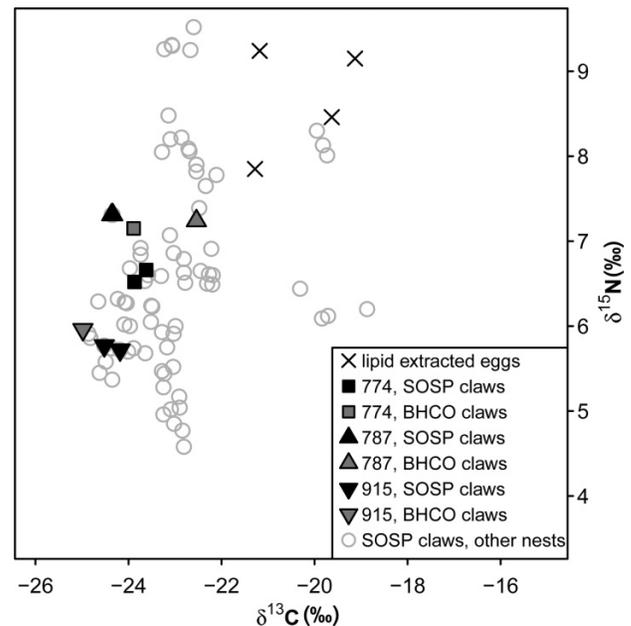
claw δ¹⁵N (Figs. S1A, S1B),[1] but this did not result in a large change in the location of the nestling values in the mixing polygon relative to the food sources (Figs. S3A, S3B).[1]

The results of the mixing model based on mean feather values were very similar to those based on mean claw values, showing that the proportion of diet from seminatural habitats was significantly greater than the proportion of seminatural land cover both within 100 m of the nest (proportion (mean ±1 SD) of diet from seminatural habitats: 0.62 ± 0.07; proportion of seminatural cover: 0.29 ± 0.24; $V = 9$, $p < 0.001$), and within 35 m of the nest (proportion of seminatural cover: 0.35 ± 0.24; $V = 14$, $p < 0.001$; Figs. S6A, S6B[1]).

Discussion

We used stable isotope analysis to show that the diet of nestling Song Sparrows is not obtained randomly with respect to local habitat amounts. Instead, a higher proportion of diet comes from seminatural habitats than expected based on habitat availability. We also found that hoppers and caterpillars make up the largest proportion of nestling diet.

We suggest two nonmutually exclusive hypotheses for why Song Sparrows obtain more food from seminatural habitats: habitat choice and food availability. Although Song Sparrows use a wide range of habitats, they are most closely associated with shrubs adjacent to moist or wet ground (Arcese et al. 2002). Watts (1990) studied sparrow assemblages in winter and showed that Song Sparrows favoured weedy or woody cover over mown areas and faced relatively high predation

compared with the differences between Song Sparrow nestling claws and eggs (Fig. 6).

Validity of discrimination factor

The mean feather δ¹³C tended to be lower than mean claw δ¹³C, and mean feather δ¹⁵N tended to be higher than mean

rates in open areas compared with Savannah Sparrows (*Passerculus sandwichensis* (Gmelin, 1789)). Therefore, Song Sparrows might simply be predisposed to forage preferentially in the greater cover provided by hedgerows and, in spring at least, by hayfields compared with more open cropland.

Alternatively, the disproportionate amount of nestling diet from seminatural habitat could be due to higher invertebrate abundance in these habitats. Several studies from Europe have shown higher abundance of invertebrates in hedgerows than in crop fields (e.g., Thomas et al. 1991; Thomas and Marshall 1999; Varchola and Dunn 2001; Meek et al. 2002; Brickle and Peach 2004; Grüebler et al. 2008), presumably because of a combination of lower disturbance, reduced pesticide inputs, and greater plant biomass and diversity. Invertebrate abundance in hayfields varies depending on management (e.g., Vickery et al. 2001; Hoste-Danyłow et al. 2010), but is expected to be higher than in crop fields early in the season because of higher plant biomass. Data on invertebrate biomass from fields included in this study were inconclusive, with relative invertebrate biomass measured using a D-Vac suction sampler being higher in hedgerow and hayfields than in crop habitats, but invertebrate biomass from pitfall traps not differing among land uses (J. Girard, P. Mineau, and L. Fahrig, unpublished data). Given the propensity of Song Sparrows to use shrubby habitat and the likelihood of increased food abundance in seminatural habitat compared with crop fields, it is probable that both these factors play a role in driving the pattern of disproportionate provision of nestling food by seminatural habitats.

Hedgerow habitat in particular seems to be important to nesting Song Sparrows: at the nests with less than 7% seminatural cover ($n = 9$; Figs. 3A, 3B), hedgerows comprised at least 90% of seminatural habitat available and therefore provided the majority of nestling food. Hedgerow density has declined in eastern Canada, as hedgerows and fencerows are removed to increase field size (Boutin et al. 2001). Management actions to stop hedgerow removal and to increase invertebrate abundance and diversity in hedgerows, such as sowing wild flower mixtures (Thomas and Marshall 1999; Meek et al. 2002) or actions to reduce drift of pesticides into hedgerows (reviewed by Maudsley 2000), could benefit Song Sparrows and potentially other farmland breeding birds.

The proportion of nestling diet coming from seminatural habitats increased slightly with proportion of local seminatural cover. This relationship was stronger at the 100 m scale than at the 35 m territory scale, suggesting Song Sparrows travel outside their territories to forage. If Song Sparrows nesting in areas with lower seminatural cover are forced to travel farther to obtain enough food, then they will spend more time away from the nest, which has been shown to lead to reduced nest survival in Song Sparrows (Rastogi et al. 2006).

Hoppers and caterpillars were the most important food sources for Song Sparrow nestlings. Hoppers and caterpillars may provide a good food source for young nestlings because of their small size and soft bodies. In reviewing Song Sparrow diet, Arcese et al. (2002) mention hoppers and caterpillars as food items for adults, but although caterpillars are mentioned in nestling diet, hoppers are not listed as being an important food item for nestlings. However, the importance of hoppers in the mixing model results agrees with the dominance of hoppers in the few ligature samples that we obtained from nests in

the study (see Materials and methods). It is possible that hoppers, which are pests of alfalfa and soybeans (Baute 2002), are more prevalent in the diet of Song Sparrow nestlings in farmland habitats than in other habitats.

We made two key assumptions in this analysis: (1) nestling claw material reflected nestling diet and not egg material and (2) the discrimination factor that we used accurately reflected the change in isotopic values between the food sources and the claw material. Two lines of evidence suggest that nestling claw material reflects diet and not the egg. Firstly, claws had lower values of $\delta^{13}C$ and $\delta^{15}N$ than eggs, closer to the values of the majority of the food sources that we analysed (Fig. 5). If the $\delta^{13}C$ and $\delta^{15}N$ values of claws depended on the egg, rather than nestling diet, then we would have expected either no difference in $\delta^{13}C$ and $\delta^{15}N$ between egg and chick Paszkowski et al. 2004) or that $\delta^{13}C$ and $\delta^{15}N$ would be enriched in claws compared with eggs (Gladbach et al. 2007; Klaassen et al. 2004). Secondly, Song Sparrow claw $\delta^{13}C$ and $\delta^{15}N$ values were similar to Brown-headed Cowbird nestlings raised in the same nests, i.e., nestlings with different mothers, but the same diet (Fig. 6). Since we cannot show how similar or different Brown-headed Cowbird and Song Sparrow eggs are, this does not provide strong evidence that nestling claws do not reflect the egg. However, the similarity in isotope values of nestlings of different species raised in the same nest does suggest that $\delta^{13}C$ and $\delta^{15}N$ in nestling claws reflects their diet as nestlings. Although this is not conclusive evidence, we believe this shows that the influence of the egg on $\delta^{13}C$ and $\delta^{15}N$ of nestling claws is minimal and does not strongly affect our results.

We also assumed that the discrimination factor we used, which was generated from the feathers of juvenile Song Sparrows, accurately reflects the change in stable isotope values between food sources and nestling claws. Both the tissue type and age class are known to affect discrimination factors (Cherel et al. 2005; Caut et al. 2009; Hussey et al. 2010). However, the similarity in results obtained when the model was run on either claws or feathers suggests the feather discrimination factor was adequate in this case.

The use of stable isotope analysis of nestling tissues to examine diet and foraging habitat is becoming more common in seabirds, which cover vast distances on a single foraging trip (e.g., Ainley et al. 2003; Gladbach et al. 2007; Williams et al. 2007; Harding et al. 2008; Hedd et al. 2010; Browne et al. 2011). However, we know of only two examples of studies that have used this technique in landbirds. Koenig et al. (2008) used stable isotope analysis of blood samples from nestling and adult Acorn Woodpeckers (*Melanerpes formicivorus* (Swainson, 1827)) to compare nestling and adult diets, and Kosciuch et al. (2008) used stable isotope analysis of feathers from nestling Brown-headed Cowbirds to distinguish between cowbirds raised in grassland and shrubland nests. Using claws to sample nestlings is less invasive than taking a blood sample, or collecting feathers while nestlings are still growing, and shows potential for learning about nestling diet in situations where food sources differ in stable isotope values. However, more research is needed into discrimination factors for nestling claws.

Managing farmland for both agricultural productivity and to maintain bird populations requires understanding how birds

use different cover types and resources. We have demonstrated how stable isotope analysis can be used to assess the foraging habitat and diet of farmland nesting birds, and have shown the importance of seminatural habitats, and in particular hedgerows, to Song Sparrows nesting in farmland. Management actions to stop hedgerow destruction and to increase invertebrate abundance in hedgerows may benefit Song Sparrows and other farmland birds.

Acknowledgements

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