

One meadow for two sparrows: resource partitioning in a high elevation habitat

Michaël Beaulieu · Keith W. Sockman

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Abstract Resource partitioning is the basis of the coexistence of sympatric species and has therefore received much attention in ecological studies. However, how variation in environmental conditions (and particularly natural variation in resource availability) can influence resource partitioning in free-ranging animals is not well understood. In the present study, we addressed the hypothesis that natural changes in the availability of food resources affect food partitioning between sympatric species. To do so, we examined temporal changes in the plasma isotopic signature ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of syntopic Lincoln's sparrows *Melospiza lincolnii* and white-crowned sparrows *Zonotrichia leucophrys*, in parallel with seasonal changes in habitat maturity and food availability from spring to early summer. We found no apparent trophic segregation between Lincoln's and white-crowned sparrows when resources were scarce in spring. But, interestingly, as resource availability and the number of breeding birds increased, Lincoln's

sparrows showed lower $\delta^{15}\text{N}$ values than white-crowned sparrows, as they consumed more prey from lower trophic levels and less prey from higher trophic levels. This feeding divergence between sympatric species may be explained (1) by a change in foraging preferences and opportunities for Lincoln's sparrows and (2) by the abundance of competitors that increased faster than resources, thus promoting interspecific competition and trophic segregation. These results provide clear evidence that trophic segregation is dynamically tied to variation in environmental conditions, which are therefore fundamental to consider when examining resource partitioning between co-existing species.

Keywords Bird · Community structure · Montane environment · Resource partitioning · Seasonal changes

Introduction

The coexistence of sympatric species is traditionally viewed as being possible through the use of distinct niches (Schoener 1974; Chesson and Huntly 1997). Shelters, breeding sites, and food resources are usually involved in resource partitioning. For food resources, partitioning (i.e. trophic segregation) can result from different foraging capacities and requirements between sympatric species or from interspecific competition. Competition may occur through (1) interference (one species actively repels another from a given resource) and (2) exploitation (by exploiting a resource, a species decreases its availability for sympatric species). Resource partitioning may also occur between individuals from the same species. For instance, males and females, obliged to coexist at least during breeding, may share the same habitat by exploiting

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M. Beaulieu (✉) · K. W. Sockman
Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, USA
e-mail: mbeaulie@email.unc.edu

K. W. Sockman
e-mail: kws@unc.edu

Present Address:
M. Beaulieu
Faculty of Biology, University of Freiburg,
Department of Evolutionary Biology and Animal Ecology,
Hauptstr. 1, 79104 Freiburg, Germany

K. W. Sockman
Curriculum in Neurobiology, University of North Carolina at Chapel Hill, Chapel Hill, USA

different foraging locations and resources (e.g., Forero et al. 2005; Bearhop et al. 2006).

Despite the large number of studies examining resource partitioning in animals, the factors underlying this partitioning still remain poorly documented. One factor expected to affect resource partitioning is resource availability; low availability of shared resources, associated with high demand by coexisting organisms of different species, promotes interspecific competition, may exclude one species from using these resources, and therefore may increase interspecific segregation (hypothesis 1; Schoener 1974; Dhondt 2010). On the other hand, an increase in resource availability may be associated with the emergence in the environment of new prey that only one species is able to exploit, therefore increasing interspecific segregation (hypothesis 2). One way to examine these hypotheses is to investigate how the relationship between resource availability and resource partitioning varies between habitats providing different amounts of resources or within one habitat showing temporal changes in resource availability. For the second alternative, high-latitude and high-elevation environments, characterized by large and quick changes in environmental conditions between seasons, are of particular interest.

Stable isotope analysis has become a standard method to examine the use of ecological niches by animals (Kelly 2000; Newsome et al. 2007; Inger and Bearhop 2008). Considering that animals are made of what they eat, their isotopic signature reflects the isotopic signature of their prey. For instance, C_3 and C_4 plants use different enzymes to fix atmospheric CO_2 during photosynthesis. In contrast to the small discrimination against ^{13}C by phosphoenolpyruvate carboxylase in C_4 plants, discrimination against ^{13}C by the enzyme RuBisCO in C_3 plants is much larger. Fractionation by phosphoenolpyruvate carboxylase is ca. 4.4 ‰ and fractionation by RuBisCO is ca. 29 ‰. Consequently, the $^{13}C:^{12}C$ ratio (expressed as $\delta^{13}C$) is much lower in C_3 plants (range: -35 to -21 ‰) than in C_4 plants (range: -14 to -10 ‰). These differences in primary producers' $\delta^{13}C$ values translate to differences in the $\delta^{13}C$ values in consumers at higher trophic levels (Kelly 2000). However, there may still be slight differences between the $\delta^{13}C$ values of consumers and those of primary producers: in consumers, lipids are depleted in ^{13}C (about 1–2 ‰ below the diet), whereas bones, integuments, and muscles are slightly enriched in ^{13}C (about 1–2 ‰ over the diet; Kelly 2000). This enrichment is even more important for ^{15}N (about 3 ‰ over the diet); as trophic level increases, the proportion of ^{15}N also increases so that the $^{15}N:^{14}N$ ratio (expressed as $\delta^{15}N$) indicates the trophic position of the consumer (Kelly 2000). Additionally, the isotopic signature of an organism reflects its feeding ecology over a certain period of time, depending on the duration of isotope incorporation into the biological tissue

under consideration; tissues with a faster turnover (e.g., plasma) reflect a shorter time-span than slowly-renewed tissues (e.g., bones). One can therefore examine temporal variation in the feeding ecology of animals by measuring stable isotopes (1) from the same tissue over time, (2) from tissues with different isotopic incorporation rates, or (3) from tissues with progressive growth (Dalerum and Angerbjörn 2005). Using these approaches simultaneously in sympatric species can consequently highlight differences in the feeding ecology of these species and how they share resources over time within the same habitat.

In this study, we examined temporal changes in the partitioning of dietary resources in two syntopic *Emberizidae* species, the Lincoln's sparrow (*Melospiza lincolni*) and the white-crowned sparrow (*Zonotrichia leucophrys*), who often coexist in subarctic and subalpine habitats in North America during the breeding season (Ammon 1995; Chilton et al. 1995). The omnivorous diet of these closely-related species and the pronounced seasonality of their habitat make this simple vertebrate community an excellent system for examining how natural variation in environmental conditions can affect resource partitioning between sympatric species. Towards this end, we repeatedly measured the adult individuals' plasma isotopic signature from spring to early summer. We also examined the isotopic signature of their young to determine if trophic segregation was also apparent in the prey items delivered by adults to their offspring. Finally, as the location where sparrows nest and forage is likely to affect their diet (if the territories of both species differ and contain different subsets of food resources), we also examined their nesting distribution.

Materials and methods

Fieldwork was conducted from late May to late July 2010 in a meadow located in the Rocky Mountains close to Molas Pass (37.74°N, 107.69°W), Colorado, USA, at an elevation of 3,250 m (see Sockman 2008, 2009 for details of the study system). Here, we focus on the period from late May to early July when vegetation changes from its winter to its summer stage and the sparrows of interest breed. The subalpine 20-ha study site is mostly composed of low-lying willows (*Salix glauca*, *S. wolfii*). Also nesting and foraging in this meadow are fox sparrows (*Passerella iliaca*) and Wilson's warblers (*Wilsonia pusilla*). There are only 1–3 fox sparrows and about 20 pairs of Wilson's warblers on the meadow each year (compared to the ~200–250 Lincoln's and white-crowned sparrows). Moreover, Wilson's warblers are obligate insectivores. Thus, the omnivorous songbird community on the meadow is composed almost exclusively of Lincoln's and white-crowned sparrows.

Environmental data

In late May, deciduous foliage remains leafless. Leaves appear progressively throughout June. To quantify habitat maturation, every week (from 31 May to 4 July 2010), we took a RAW digital picture from a rock outcrop overlooking the meadow. Habitat maturation was then analyzed as described and validated by Sockman (2009) but with different software (Adobe Photoshop CS5; Adobe, San Jose, CA, USA). Briefly, the green component (reflecting the appearance of leaves) of each pixel of the same six areas in the meadow was quantified relative to the red and the blue components (Villafuerte and Negro 1998). To estimate food availability, we collected arthropods every week (from 31 May to 4 July 2010) in six traps positioned across the meadow. Each trap was made of a yellow plastic tub filled with water and detergent and placed about 1 m above the ground (see Sockman 2009). Once collected, arthropods were stored in 70 % ethanol, then dried (10 days at 60 °C) and counted. We used the number of collected arthropods as an index of the probability that birds would encounter them on the meadow.

Nest location and breeding data

On this study site, Lincoln's and white-crowned sparrows almost always nest on the ground or slightly (<0.5 m) elevated in vegetation. Every day during the field season, five people searched for sparrow nests for 3 or 4 h each. Nests were found at four different stages: (1) before egg-laying, (2) during clutch completion, (3) during incubation, and (4) after hatching. We recorded their GPS coordinates, checked them daily (except during the first 7 days of incubation to limit disturbance) and noted each breeding event (egg laying, clutch completion, hatching) until chicks were 8 days old (i.e., just before they left the nest). Estimating the clutch initiation date depended on when we had found the nest. For nests found during egg-laying, we assumed that one egg was laid per day to determine the date of clutch initiation. For nests found during incubation, we subtracted the number of eggs minus one and the mean incubation period [calculated from nests of known incubation period in this study site in 2010; Lincoln's sparrows: 12.62 ± 0.38 day (mean \pm SE, $n = 13$), white-crowned sparrows: 12.17 ± 0.31 day (mean \pm SE, $n = 6$)] from the hatching date. Finally, for nests found at the chick stage, the age of the chicks was estimated according to their development (eye opening, appearance of feathers) so that the hatching date and the clutch initiation date could be estimated.

Bird capture and blood sampling

Every day from 4 to 28 June 2010, we captured birds using 50 seed-baited trapping stations placed throughout the meadow [shortest distance between two traps: 42.4 ± 1.7 m (mean \pm SE)] and for which GPS coordinates were known. After 28 June 2010, we captured birds with mist nets. We sexed each bird using cloacal inspection, and then we marked unbanded Lincoln's sparrows with a US Geological Service identification band and a unique combination of colored plastic bands (white-crowned sparrows were not banded).

We chose to measure isotopic ratios in birds' plasma as this tissue is quickly renewed, thus allowing us to examine quick changes in the isotopic signature of the birds between early June and early July. We collected blood (50–100 μ L) from the wing vein with a heparinized capillary tube (Natelson blood collecting tubes, Fisherbrand®; Fisher Scientific, Pittsburgh, PA, USA). Because, in songbirds, the incorporation of ^{13}C and ^{15}N into blood plasma lasts <1 week (Podlesak et al. 2005; Carleton et al. 2008; Tsahar et al. 2008), we let at least 5 days pass between two consecutive blood samplings from the same birds. We did not take blood from white-crowned sparrows that we had previously bled (as indicated by a small hematoma around the wing vein). Once collected, blood was transferred into Eppendorf tubes, held on ice for a few hours and centrifuged (7,000 rpm, 9 min). Plasma was then separated from red blood cells and frozen until analysis. We also bled chicks when they were 8 days old to measure their isotopic signature.

Isotopic analysis

We collected potential prey items for sparrows and froze them until isotopic analyses. These included plant material [seeds from willows ($n = 5$) and dandelions (*Taraxacum* sp., $n = 5$)], and arthropods [spiders (*Araneae*, $n = 7$) and the following insects ($n = 43$): flies (*Brachycera*, $n = 6$), crane flies (*Nematocera*, $n = 6$), damselflies (*Zygoptera*, $n = 7$), ladybugs (*Coccinellidae*, $n = 6$), caterpillars (*Lepidoptera*, $n = 9$), ants (*Formicidae*, $n = 4$) and grasshoppers (*Caelifera*, $n = 5$)]. It is important to note that the diet of omnivorous birds such as Lincoln's and white-crowned sparrows may include many more prey species than those that we collected. For instance, sparrows may preferentially target other plants (e.g., Nebraska sedge *Carex nebrascensis*, which is the primary ground cover on the meadow), or other ground arthropods over the aerial arthropods that we collected. Moreover, these prey species were not collected regularly across the season. Therefore,

we urge caution in interpreting the results of the analyses including the isotopic signature of these prey species (e.g., calculation of the proportion of prey in the diet of birds; see “Data analysis”).

After the field season, prey and plasma samples were freeze dried over night, homogenized, and loaded in tin cups for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses. Isotopic assays were carried out at Duke Environmental Stable Isotope Laboratory (Duke University, NC, USA). Results are expressed as the standard δ notation (‰) relative to Pee Dee belemnite for $\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$. The mean difference between two standards of acetanilide within the same assay was 0.16 ± 0.04 ‰ for $\delta^{15}\text{N}$ and 0.08 ± 0.03 ‰ for $\delta^{13}\text{C}$ (mean \pm SE, $n = 9$ assays) and the mean difference between two measurements of standard acetanilide in different assays was 0.07 ± 0.02 ‰ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (mean \pm SE, $n = 9$ assays).

Data analysis

To examine habitat maturation, we used a mixed effects linear regression with photograph nested within area of the meadow as a random coefficient on date, the proportion of green as the dependent variable, and date expanded into a dummy variable set with 28 June (the date with the highest mean value of green) omitted as the date against which all other dates were independently contrasted. Arthropod abundance was also examined with a mixed effects linear regression using the dummy variable date as described above, trap nested within date as a random intercept, and the number of arthropods as the dependent variable.

To analyze the nesting distribution of both species, we divided the study site, ranging from 37.742 to 37.748°N and from 107.687 to 107.694°W, into 42 0.001° (latitude) \times 0.001° (longitude) plots (Fig. 1). The overlap coefficient between the nesting distributions of the two species was calculated following the formula given by Horn (1966):

$$C = 2 \sum_{i=1}^n (A_i \times B_i) / \left(\sum_{i=1}^n A_i^2 + \sum_{i=1}^n B_i^2 \right)$$

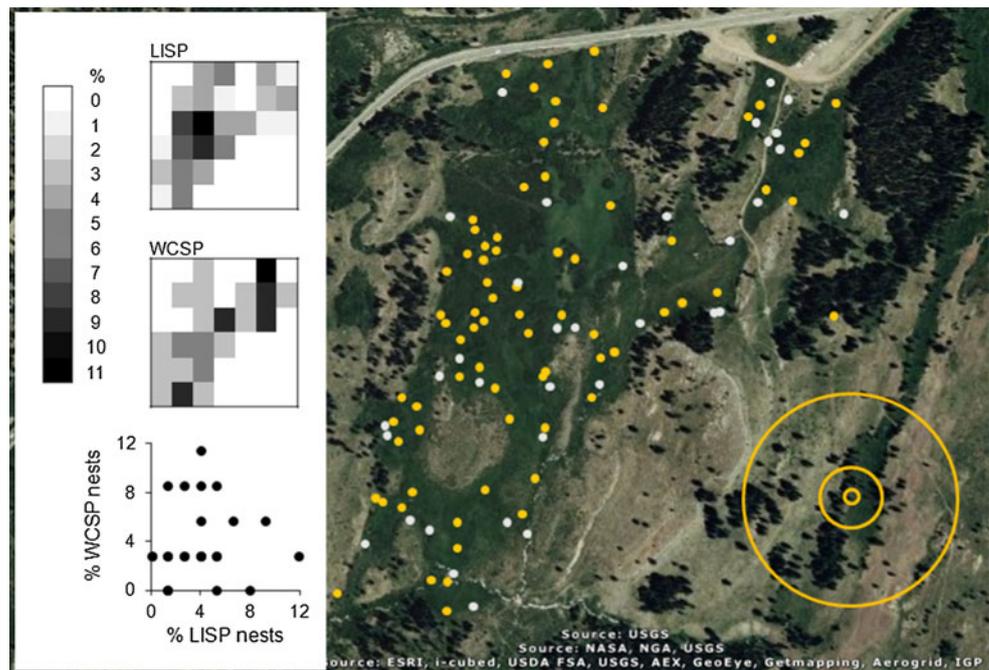
where n is the number of plots and A_i and B_i are the proportions of Lincoln’s sparrow nests and white-crowned sparrow nests found in plot i , respectively. The coefficient is 0 if there is no overlap between both species and 1 when both species have the exact same spatial distribution. To determine if the nesting distribution of one species was related to the nesting distribution of the other, we also carried out a Spearman correlation between the abundance of each species in each plot (not including 16 plots in which neither of the species was present). For 93 Lincoln’s sparrows captured with the seed-baited traps, the

individual’s nest was identified a posteriori. The “nest to trap” distance was then calculated using ArcGIS Explorer (Environmental Systems Research Institute, Redlands, CA, USA). On average, this distance was 56 ± 4 m (mean \pm SE) and was used as a proxy for the typical foraging distance of birds (Fig. 1). We estimated the level of potential competition by counting the number of nests in a circle with a radius of 120 m around each nest (as birds from different nests were assumed to forage about 60 m away from their nest, we considered all the nests located within 120 m around one’s nests as potential competitors). To compare levels of potential competition between both species, we used a Poisson regression because count data typically show a Poisson distribution. Focal species was a fixed factor, and the number of surrounding (i.e., within 120 m) nests of either species, the number of surrounding Lincoln’s sparrow nests and the number of surrounding white-crowned sparrow nests were each a dependent variable in separate analyses.

The ordinal date of clutch initiation was compared between species with a general linear model. As predation rate can affect resource partitioning (Chase et al. 2002), we also checked that predation rate was similar for both species by comparing the proportions of nests depredated with a Chi-square test. A nest was considered depredated when it was found prematurely empty after previously containing eggs or chicks. We used the number of chicks at 8 days to estimate breeding success (including the nests that were depredated), and we compared breeding success between species with a general linear model.

For isotopic analyses, we analyzed plasma samples in 5-day bins. Most of the samples in each bin were collected on the day indicated. However, some were collected either the day before or the day after (to have sufficient sample size in each bin). In total, we collected 131 plasma samples from adult Lincoln’s and white-crowned sparrows. Because we had few individuals with repeated measures, we analyzed only one sample per individual, selecting samples ($n = 106$) that best balanced our sample sizes across dates ($n = 6$ – 14 for each species, for each date). As the amount of plasma that we were able to collect was very small, we did not remove lipids from samples. This may be a problem since lipids are depleted in ^{13}C and consequently plasma rich in lipids show lower $\delta^{13}\text{C}$ values (Post et al. 2007). However, the ratio C:N is a strong predictor of lipid content in animal samples (Post et al. 2007). Therefore, we added this ratio as a covariate in the statistical tests where $\delta^{13}\text{C}$ was the dependent variable to correct for differences in the lipid content of samples. To compare $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios between both species, we used a general linear model with species and sex as fixed factors. We included date as a fixed factor, but unlike our analyses above, this time, based on preliminary examination of the data, we modeled it as a

Fig. 1 The study meadow and location of Lincoln’s sparrow (*Melospiza lincolni*) nests (*LISP*, yellow symbols) and white-crowned sparrow (*Zonotrichia leucophrys*) nests (*WCSP*, white symbols). The inset represents the relative distribution of each species in the meadow divided in 0.001° plots and the relationship between the distributions of both species. The three concentric circles represent the maximal (205 m), mean (56 m) and minimal (11 m) foraging ranges of Lincoln’s sparrows (color figure online)



continuous variable. We also included all interactions as fixed factors. Even though the diet of sparrows may include other prey species than those collected in the field and assuming the isotopic signature of the prey was constant over time (see “Discussion”), we estimated the proportions of each prey in the diet of sparrows at the beginning and the end of the season, by using a mixing model for Stable Isotope Analyses in R (SIAR v4; Parnell et al. 2010). We used for these analyses the following trophic enrichment factors (TEF) for bird plasma (mean ± SE): $-0.08 \pm 0.38 \text{ ‰}$ for $\delta^{13}\text{C}$ and $2.82 \pm 0.14 \text{ ‰}$ for $\delta^{15}\text{N}$ (Caut et al. 2009). We ran the analyses twice: once without combining sources, and once after combining sources based on isotopic similarities. Sources were combined according to their isotopic similarity (Fig. 2): crane flies, ants, and caterpillars were combined into “Insect 1”, and ladybugs, damselflies, and flies were combined into “Insect 2”. To examine whether the proportions of prey followed the same order in Lincoln’s and white-crowned sparrows, we conducted Pearson correlations between the median proportions of prey in their respective diet.

To compare the isotopic signature of Lincoln’s and white-crowned sparrow chicks, we took into account only nests with three or four chicks that survived from hatching to 8 days (43 chicks from 12 Lincoln’s sparrow broods and 17 chicks from five white-crowned sparrow broods). We used a mixed effect linear regression with chick nested within brood as a random intercept and species as a fixed factor. We did not compare the isotopic signatures of adults and chicks since blood of adults and chicks was collected at different times (adults: 7 June–2 July 2010, chicks: 2–27

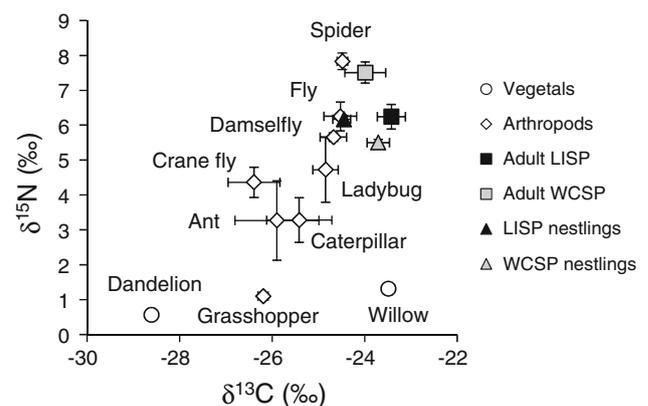


Fig. 2 Isotopic signature (mean ± SE) of potential prey living on the meadow, of adult sparrows in early July and of chicks. (*LISP* Lincoln’s sparrow, *WCSP* white-crowned sparrow)

July), which is likely to confound this comparison. Finally, we conducted a mixing model for Stable Isotope Analyses in R to compare the proportions of prey in the diet of the chicks of the two species. We conducted these analyses by using the same TEF as in adults and after correcting them because of the potential effects of growth on nitrogen-use efficiency that may be responsible for ^{15}N depletion in growing chicks. For this correction, we subtracted 0.2 ‰ from the ^{15}N TEF of adults and 0.3 ‰ from the ^{13}C TEF of adults (Sears et al. 2009).

When necessary, the normality of data was checked with Kolmogorov–Smirnov tests. Statistical analyses were conducted in Stata IC 10.1 for the Macintosh (Stata, College Station, TX, USA). Results are expressed as means ± SE.

Results

Environmental data

During our study, the proportion of green on the meadow, reflecting the growth of leaves, significantly changed with time, overall increasing between 31 May and 28 June 2010 ($z = -14.81$, $P < 0.001$), remaining stable between 21 and 28 June 2010 ($z = -0.65$, $P = 0.518$) and slightly decreasing during the first week of July ($z = -5.82$, $P < 0.001$; Fig. 3a). Even though arthropod abundance was more variable, it followed the same trend, increasing between 6 and 28 June 2010 ($z = -4.40$, $P < 0.001$) and remaining stable between 28 June and 5 July 2010 ($z = -0.65$, $P = 0.515$; Fig. 3a).

Nest abundance and location

Lincoln's sparrow nests were over twice as abundant as white-crowned sparrow nests in the meadow (76 vs. 35 nests, respectively). The overlap coefficient between the nesting distributions of both species was 0.66. We found no evidence that the spatial distributions of the two species were correlated, as the number of Lincoln's sparrow nests in a plot was not related to the number of white-crowned sparrow nests in the same plot ($r_s = 0.169$, $P = 0.410$; Fig. 1). On average, white-crowned sparrows had about two (15 %) surrounding nests fewer than Lincoln's sparrows ($z = -2.68$, $P = 0.007$; Fig. 4a). This was because white-crowned sparrows had two surrounding Lincoln's sparrow nests fewer than Lincoln's sparrows ($z = 9.928$, $P = 0.002$; Fig. 4b). In contrast, the number of surrounding white-crowned sparrow nests was statistically indistinguishable between white-crowned sparrow and Lincoln's sparrows ($z = 0.135$, $P = 0.713$; Fig. 4c).

Breeding parameters

The date of clutch initiation could be determined for 64 Lincoln's sparrow nests and 23 white-crowned sparrow nests; the other nests, found with eggs, were depredated before clutch completion or hatching. On average, Lincoln's sparrows initiated clutches 4 days earlier than white-crowned sparrows (20 June \pm 0.88 and 24 June \pm 1.47 days, respectively; $z = 2.03$, $P = 0.043$; Fig. 3b). Similarly, the hatching date of the first egg followed the same trend (7 July \pm 0.89 and 10 July \pm 1.52 days, respectively; $z = 1.84$, $P = 0.066$). The predation rate (61 % in Lincoln's sparrows and 66 % in white-crowned sparrows; $\chi^2_1 = 0.274$, $P = 0.601$) and the breeding success (1.07 \pm 0.17 chick/nest in Lincoln's sparrow and 0.88 \pm 0.24 chick/nest in white-crowned sparrow; $z = -0.89$, $P = 0.374$) were similar in both species.

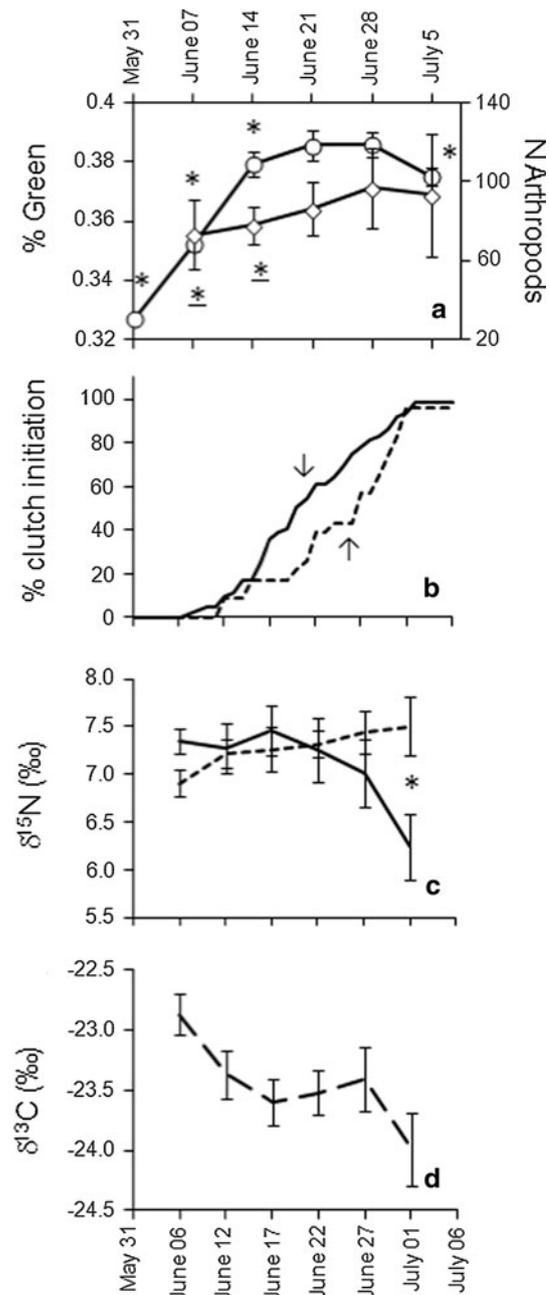


Fig. 3 Percentage of green in the meadow as a measure of habitat maturity (circles, $n = 6$ areas in the meadow for each data point, **a**), and abundance of arthropods (diamonds, $n = 6$ arthropod traps for each data point, **a**), percentage of clutch initiations (**b**) and changes in $\delta^{15}\text{N}$ (**c**) and $\delta^{13}\text{C}$ values (**d**) with time in Lincoln's sparrows (solid lines, $n = 6$ –9 birds for each data point) and white-crowned sparrows (short-dash lines, $n = 6$ –14 birds for each data point) or in both species combined (long-dash line). In (**a**), asterisks indicate where independent contrasts with values on June 28 resulted in P values < 0.05 (% green: simple asterisks, arthropod abundance: underlined asterisks). In (**b**), the arrows indicate the mean date of clutch initiation for each species. In (**c**), the asterisk indicates a significant difference between species for a given date based on post hoc analyses. Notice that the time intervals for (**a**) are slightly different from the time intervals for the other figures

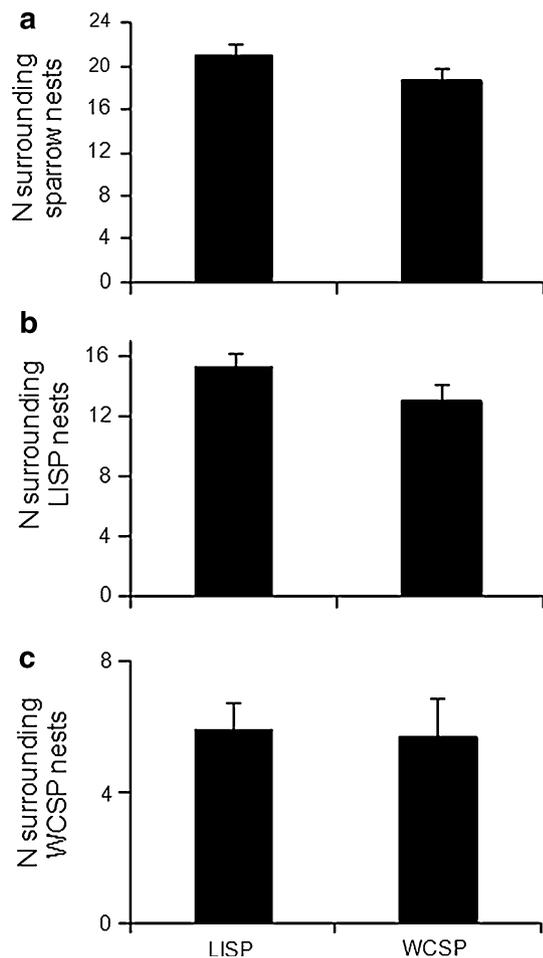


Fig. 4 Number of sparrow (a), Lincoln's sparrow (b) and white-crowned sparrow (c) nests surrounding Lincoln's sparrow (*LISP*, $n = 76$) and white-crowned sparrow (*WCSP*, $n = 35$) nests

Isotopic ratios

Overall, white-crowned sparrows had higher $\delta^{15}\text{N}$ values than Lincoln's sparrows ($z = 2.94$, $P = 0.003$). This was because $\delta^{15}\text{N}$ values in white-crowned and Lincoln's sparrows changed differently with time (species \times date interaction: $z = -3.01$, $P = 0.003$). We had the a priori interest in whether or not the date(s) at which Lincoln's and white-crowned sparrows diverge corresponded to the dates of peak food availability. Therefore, as a post hoc approach, we examined whether the species differed in their $\delta^{15}\text{N}$ values for each individual date on which we collected samples. Lincoln's and white-crowned sparrows initially had similar $\delta^{15}\text{N}$ values (each $P > 0.088$ from early to late June) but Lincoln's sparrows exhibited lower $\delta^{15}\text{N}$ values than white-crowned sparrows in early July ($z = -1.05$, $P = 0.006$; Fig. 3c). Males and females had similar $\delta^{15}\text{N}$ values ($z = 1.04$, $P = 0.298$) and we found no evidence for a reliable sex \times date ($z = -1.10$,

$P = 0.270$), sex \times species ($z = -0.93$, $P = 0.353$) or sex \times date \times species interaction ($z = 0.99$, $P = 0.321$).

$\delta^{13}\text{C}$ values were not reliably different between species ($z = -0.18$, $P = 0.859$) or between sexes ($z = -0.96$, $P = 0.335$) and tended to decrease with time ($z = -1.74$, $P = 0.082$), similarly in both species (species \times date interaction: $z = 0.17$, $P = 0.864$; Fig. 3d). None of the other interactions in the model was reliable (all $P > 0.339$).

Our mixing models for stable isotopic analyses in SIAR without or after combining insect sources showed the same trends concerning the diet of birds, but lower residual variance values, reflecting better fit for the model, were found after combining prey (Table 1). The results of that model showed that at the beginning of the season, the proportions of prey in the diet of Lincoln's sparrows were highly and positively correlated with the proportions of prey in the diet of white-crowned sparrows ($r = 0.976$, $P = 0.001$), suggesting that the most consumed prey species in Lincoln's sparrows were also the most consumed species in white-crowned sparrows (and vice versa; Fig. 5). However, this relationship disappeared in early July ($r = 0.421$, $P = 0.406$). From Fig. 5, it appears that this was due to a decrease in the proportion of prey from higher trophic levels (spiders) associated with an increase in the proportion of plant material (willow seeds) in the diet of Lincoln's sparrows. In contrast, white-crowned sparrows maintained constant the proportion of spiders and willow seeds in their diet.

In contrast to the comparisons between the adults of the two species, white-crowned sparrow nestlings tended to exhibit lower $\delta^{15}\text{N}$ values ($z = -1.85$, $P = 0.065$) than Lincoln's sparrow nestlings and had higher $\delta^{13}\text{C}$ values ($z = 1.98$, $P = 0.048$; Fig. 2). Our mixing models for stable isotopic analyses in SIAR, without or after correcting TEF because of the growth of chicks, gave similar proportions of prey in the diet of birds, but lower residual variance values, reflecting better fit for the model, were found without correcting TEF (Table 2). This model revealed higher contribution of plant material (willow seeds) in the diet of white-crowned sparrow nestlings than in the diet of Lincoln's sparrow nestlings (Fig. 5).

Discussion

Lincoln's and white-crowned sparrows highly overlap within the same habitat during the breeding season in subalpine or subarctic environments. This coexistence may be facilitated by a flexible partitioning of food resources in relation with changing environmental conditions. Indeed, by examining the isotopic signature of Lincoln's and white-crowned sparrows over time from spring to summer, when resource conditions change in a high-elevation

Table 1 95 % high density region values for residual variance [standard deviation (*SD*)] from SIAR models for adult Lincoln's sparrows (*Melospiza lincolni*) (*LISP*) and white-crowned (*WCSP*) sparrows (*Zonotrichia leucophrys*) in June (6 June 2010) and July (1 July 2010)

	Sources	SD $\delta^{15}\text{N}$		SD $\delta^{13}\text{C}$	
		Low 95 %	High 95 %	Low 95 %	High 95 %
LISP June	Not combined	0.00	0.61	1.29	4.24
	Combined	0.00	0.62	1.04	3.68
LISP July	Not combined	0.01	1.96	0.36	3.28
	Combined	0.02	1.97	0.00	2.28
WCSP June	Not combined	0.00	0.62	1.60	4.48
	Combined	0.00	0.64	1.35	4.04
WCSP July	Not combined	0.00	1.74	0.94	4.34
	Combined	0.00	1.76	0.83	4.14

Calculations were carried out with all the different sources (not combined), and after combining some sources together based on isotopic similarity (combined). Lower residual variance values reflect better fit for the models

meadow, the present study shows that the trophic ecology and the partitioning of food resources between these two sympatric sparrow species vary with respect to the season.

We found, however, a clear decoupling between seasonal changes in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. This may result from different $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ variability in prey species in our study site. To compare the different feeding strategies that organisms could adopt in a certain habitat through stable isotope analyses, one preliminary condition is that predators have the possibility to forage on prey with variable isotope values (Newsome et al. 2007). In our study site, potential prey species exhibited a low $\delta^{13}\text{C}$ variance (2.76) compared to $\delta^{15}\text{N}$ variance (6.38; Fig. 2). Therefore, even if Lincoln's and white-crowned sparrows adopted different feeding strategies, this would not necessarily be reflected by differences in their plasma $\delta^{13}\text{C}$ values. In contrast, as $\delta^{15}\text{N}$ values were more variable between prey species, a change in the feeding habits of birds was more likely to be reflected by their plasma $\delta^{15}\text{N}$ values.

Lincoln's and white-crowned sparrows shift their diet from primarily plant material (with low $\delta^{15}\text{N}$ values) in winter to arthropods (with high $\delta^{15}\text{N}$ values) in summer (Morton 1967; Raley and Anderson 1990; Ammon 1995). This dietary change is expected to be reflected by an increase in birds' plasma $\delta^{15}\text{N}$ values. However, $\delta^{15}\text{N}$ values did not significantly increase in white-crowned sparrows throughout the breeding season (although there was a trend; Fig. 3c) while they decreased in Lincoln's sparrows. Based on the isotopic values measured in birds and in potential prey species, we estimated how the proportions of prey changed with time in the diet of sparrows, with a mixing model for stable isotopic data. The results of this model have to be considered with caution, as (1) we probably did not sample all the prey species on which the birds could feed, and (2) the isotopic signature of primary producers and arthropods may have also changed with time

in the meadow. For instance, $\delta^{13}\text{C}$ ratios are higher in growing leaves at bud burst than in mature leaves (Helle and Schleser 2004; Li et al. 2007), and $\delta^{13}\text{C}$ ratios decrease in plants with increasing temperatures (O'Leary 1981). This should be reflected by a decrease in the $\delta^{13}\text{C}$ values of organisms feeding on these plants and may explain why $\delta^{13}\text{C}$ values in both sparrows (feeding on plant material and arthropods eating plant material) tended to decrease in spring when leaves became more and more mature and temperatures rose. Despite these caveats, the results of our mixing models were still in agreement with the intuitive hypothesis that lower $\delta^{15}\text{N}$ values in Lincoln's sparrows could be attributed to a higher contribution of prey from low trophic levels and/or a lower proportion of prey from higher trophic levels. Indeed, our mixing model suggested that Lincoln's sparrows increased the proportion of plant material (willow seeds) in their diet, while they decreased the proportion of arthropods from higher trophic levels. In contrast, in white-crowned sparrows, the consumption of plant material and the consumption of spiders remained constant.

Three non-exclusive hypotheses may explain the contrasting feeding strategies observed between the two sympatric species (Fig. 6): (1) Lincoln's and white-crowned sparrows changed their foraging behavior because their feeding preferences/requirements diverged (Lincoln's sparrows targeted plant material while the opposite was observed in white-crowned sparrows), (2) a new niche opportunity (here willow seeds), preferentially used by Lincoln's sparrows, appeared with seasonal changes, and (3) white-crowned sparrows, which previously shared resources (in particular, prey from high trophic levels) with Lincoln's sparrows when their requirements were low (early spring), outcompeted Lincoln's sparrows at a time when breeding requirements increased for both species.

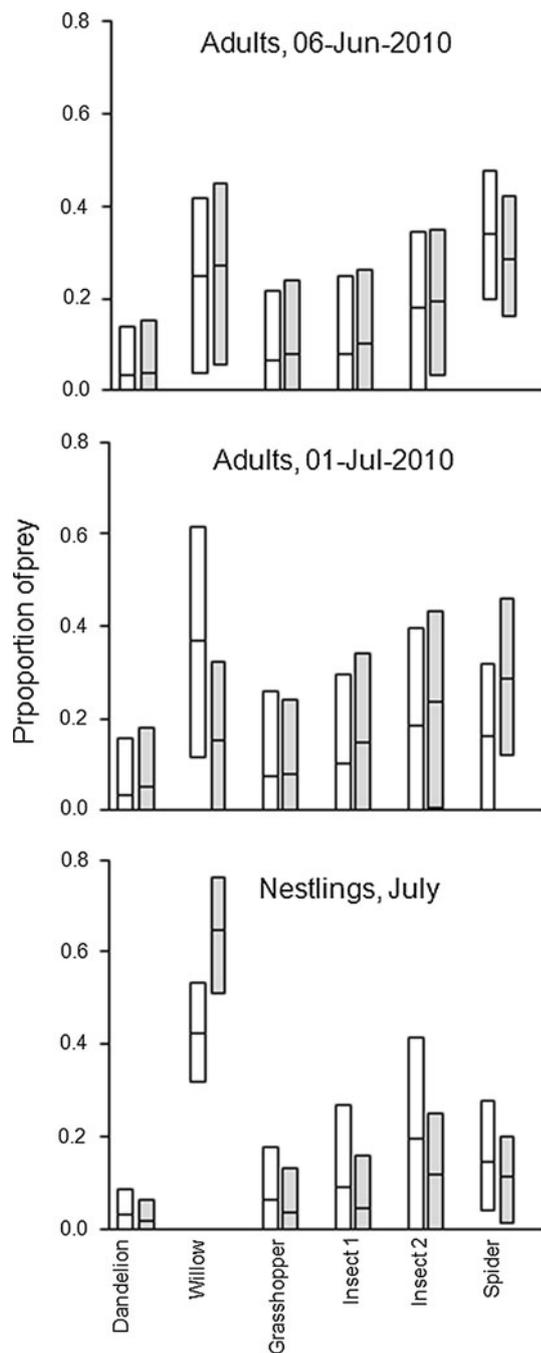


Fig. 5 a Proportions of prey in the diet of adult Lincoln's sparrows (LISP, white bars) and white-crowned sparrows (WCSP, gray bars) in early June and early July, and of nestlings in July. The bars show the credibility intervals at 95 % and the median given by SIAR. Some insect sources were combined into two categories (*Insect 1* and *Insect 2*) because of isotopic similarities

Concerning the third hypothesis, it is indeed possible that the total demand for food resources increased more rapidly than the increase in food available in the meadow, as reflected by stable arthropod abundance in early summer while the number of breeding birds was still increasing

(Fig. 3). At that time, resources were likely to be more and more valuable for birds, hence promoting interspecific competition (Peiman and Robinson 2010). Our study did not consider the presence of Wilson's warblers on the meadow, as they are obligate insectivores whereas Lincoln's and white-crowned sparrows are omnivorous. However, it is important to note that their presence may have made the competition for insect resources even more important between Lincoln's and white-crowned sparrows, as they must also have reduced overall insect availability. Considering sparrows and the fact that the bigger species is usually dominant over the smaller one (Leyequien et al. 2007; Zeng and Lu 2009), white-crowned sparrows would be expected to be able to outcompete smaller Lincoln's sparrows if interference competition occurs between both species. The fact that white-crowned sparrows had fewer Lincoln's sparrow surrounding nests than Lincoln's sparrows indeed suggests that white-crowned sparrows partially prevented Lincoln's sparrows from nesting around their nests and that interference competition for nesting sites may occur between both species. However, interference competition for nesting sites could explain the trophic segregation observed between both species only if white-crowned sparrows had territories containing one subset of resources and Lincoln's sparrows had territories with another subset of resources. This seems improbable as the nesting distributions of the two species highly overlapped and sparrows mostly forage around their nest. For this reason, exploitative competition, rather than interference competition, seems more likely to explain trophic segregation between white-crowned and Lincoln's sparrows. If competition drove this segregation, then it may have forced Lincoln's sparrows to decrease their consumption of prey from high trophic levels and use alternative food sources (willow seeds; Fig. 6) to mitigate interspecific competition when the demand for resources in the meadow was high.

Using willow seeds, a food source that is likely to be more widespread and accessible than arthropods, may explain why Lincoln's sparrows were more successful than white-crowned sparrows in terms of nest abundance than white-crowned sparrows. This would suggest that white-crowned sparrows are not as efficient as Lincoln's sparrows at exploiting willow seeds. Still, additional data are necessary to distinguish between the possibility of competition, the appearance of a new niche opportunity or changing foraging preferences as the driving force behind resource segregation between Lincoln's and white-crowned sparrows. Towards this end, it would be interesting to investigate whether the dietary change observed in early July in Lincoln's sparrows also occurs in other meadows where white-crowned sparrows are less abundant or absent.

Considering nestlings, it is surprising that in both species they had lower $\delta^{15}\text{N}$ ratios than adults, as they would

Table 2 95 % high density region values for residual variance [standard deviation (SD)] from SIAR models for Lincoln's (*LISP*) and white-crowned (*WCSP*) nestlings

	TEF	SD $\delta^{15}\text{N}$		SD $\delta^{13}\text{C}$	
		Low 95 %	High 95 %	Low 95 %	High 95 %
LISP	General	0.19	0.90	0.69	1.21
	Corrected	0.23	0.92	0.74	1.22
WCSP	General	0.00	0.48	0.50	1.41
	Corrected	0.00	0.48	0.65	1.83

Calculations were carried out with two different trophic enrichment factors (TEF) for plasma: (1) general TEF from Caut et al. (2009), and (2) after correction of this general TEF, due to the potential effect of growth on TEF (see "Materials and methods"). Lower residual variance values reflect better fit for the models

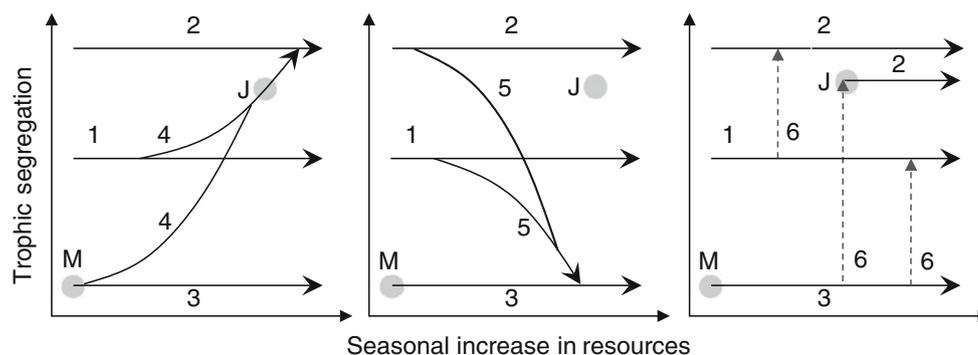


Fig. 6 Hypothetical relationships between the seasonal increase in resources in spring and trophic segregation between sympatric species. The different lines correspond to different situations affecting the relationship between resource availability and trophic segregation: 1 the resources increase at the same rate as the density of consumers, 2 the consumer demand exceeds the available resources and even if resource abundance increases, the abundance of consumers is so high that it results in constant trophic segregation (this may also be because consumers do not exploit the same resources, because of differences

in their foraging capacities or feeding preferences and requirements), 3 resources are so abundant that the density of consumers does not drive trophic segregation, 4 resource abundance increases slower than the abundance of consumers, 5 resource abundance increases faster than the abundance of consumers, 6 one of the consumers shifts to an alternative resource (i.e. increases its niche breadth). The gray disks indicate the results of the present study in late May/early June (*M*) and early July (*J*). The lines explaining our results best are 4 and 6

be expected to be fed with a high proportion of spiders (as usually reported in passerine nestlings; e.g., Arnold et al. 2007), and not with a high proportion of plant material, as found in our study. This may be because the nestlings in our study were sampled when they were 8 days old, while spiders may be important in their diet only during the very first days of growth (Arnold et al. 2007). Interestingly, the trophic segregation between Lincoln's and white-crowned sparrows persisted into the chick-rearing period since nestlings of both species exhibited different isotopic signatures. However, opposite trends were observed between nestlings and between adults: in nestlings, Lincoln's sparrows tended to have higher $\delta^{15}\text{N}$ ratios than white-crowned sparrows whereas in adults, Lincoln's sparrows had lower $\delta^{15}\text{N}$ ratios than white-crowned sparrows in early July (Fig. 2). The results of our mixing model for stable isotope analysis also suggests opposite trends between the diets of adult sparrows in early July and that of their chicks, with white-crowned sparrow nestlings being fed with more plant-material than Lincoln's sparrow nestlings (Fig. 5).

Even though, in our study, isotopic ratios are not directly comparable between adults and nestlings (as blood was collected at different times), it is still tempting to speculate that adult white-crowned sparrows could maintain a stable diet throughout the season by feeding their chicks with more plant material while adult Lincoln's sparrows would use the same prey for self- and chick-feeding. As suggested by their stable isotopic signature across the season, white-crowned sparrow parents may be less tolerant to any change in their diet. This apparent dietary inflexibility may explain the low nest-density of white-crowned sparrows relative to Lincoln's sparrows, as higher nest densities would result in higher intra-specific competition. In order to keep their diet constant, the only possibility for adult white-crowned sparrows may be to nest at low densities and feed their chicks with a diet different from theirs, and characterized by high proportions of plant material. However, high proportions of plant material in the diet of nestlings have been related to low breeding success in another omnivorous passerine, the house sparrow (*Passer*

domesticus; Peach et al. 2008). Consequently, white-crowned sparrows feeding their chicks with more plant material than Lincoln's sparrows might be expected to have fewer chicks. Even though, this trend was observed in our study, it was not particularly reliable from a statistical perspective. This may be because the proportions of plant material in the diet of Lincoln's and white-crowned sparrow nestlings did not sufficiently differ (Fig. 5). Indeed, the impact of plant material on breeding success can only be seen when the proportions of plant material in the diet of nestlings largely differ between nests (Peach et al. 2008).

Overall, our study shows that the relationship between resource availability and resource partitioning is complex, as the demand for resources may outpace resource availability, and new feeding opportunities available for only one of the coexisting species may appear as overall resource availability increases. As resource partitioning appears to be dynamically tied to new environmental conditions, its examination at a single time point would have given an incomplete and misleading snapshot of the actual situation. However, the picture would have been even more complete if we had known the temporal changes in abundance and isotopic signature of each prey species and of different tissues (e.g., leaves, seeds, etc.) from primary producers, across the season. Moreover, white-crowned sparrows appear to be phenologically more sensitive than Lincoln's sparrows to climate changes (Butler 2003). In this context, it would be worthwhile to examine how Lincoln's and white-crowned sparrows, living in climate-sensitive environments, share their habitat when environmental conditions vary from one year to another. For instance, our index of habitat maturity was 20 % lower in the present study than 4 and 5 years earlier in the same study site (Sockman 2009). These differences in environmental conditions may affect each component of the habitat (primary producers, arthropods, birds, and predators of birds). Therefore, it would also be worthwhile to broaden our approach by examining the combined effects of seasonal and annual environmental conditions on resource partitioning in order to better understand how closely related species coexist within the same habitat.

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