The Interplay of Ecological Opportunity and Adult Foraging Strategies in Juvenile Sparrow Individual Specialization

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Abstract

Temporal variation in resource availability, amplified by global change, may have strong impacts on species breeding at temperate and high latitudes that cue their reproduction to exploit seasonal resource pulses. This study examines how resource availability (ecological opportunity) and parental care influence niche partitioning between and within age classes in the rufous-collared sparrow, which provides extensive parental care. We hypothesized juveniles would exhibit narrower niches focused on high-quality resources compared to adults, regardless of ecological opportunity. We used stable isotope analysis to quantify individual and population niches in juveniles and adults across the breeding season in two cohorts experiencing contrasting resource landscapes. Contrary to our initial hypothesis, juveniles exhibited greater individual specialization and smaller total niche widths during periods when resource availability was high in comparison to periods of low ecological opportunity. Interestingly, niche characteristics of adults remained stable across seasons despite a shift in trophic level, highlighting their potential role in providing a consistent diet for their young. These findings reveal a dynamic interplay between ecological opportunity, parental care, and individual specialization, with important implications for understanding population resilience under variable resource scenarios. The study also suggests that adult sparrows adapt their provisioning strategies based on ecological opportunity, potentially buffering offspring from environmental fluctuations. Understanding age-specific responses to resource variation is crucial for predicting species responses to ecological conditions, particularly in regions like central Chile where seasonal resource limitation is expected to become more variable in response to climate change.

Introduction

Global change is expected to increase variation in the availability of resources (Jia et al., 2019), and within-population variability in resource use may increase its resilience to environmental change (Ramos et al., 2020; Riverón et al., 2021). Trophic niche differences between age classes have been a key focus of population-level research, while more recently, individual specialization, where individuals utilize narrower resource ranges than their population, has gained interest (Costa-Pereira et al., 2018). These kinds of variation may be driven by the same mechanisms that underlie resource partitioning among species to reduce competition (Keast, 1977; Maiorana, 1978; Svanbäck and Bolnick, 2005). For example, individual specialization can occur within a single age class, reducing intraspecific competition and enhancing a population's resilience to fluctuations in resource availability. Furthermore, the diversification of ecological roles promoted by individual niche differentiation can contribute to ecosystem stability (Araújo et al., 2011; Bolnick et al., 2011). Additionally, individual specialization can mitigate the costs of transitioning between different resources due to functional trade-offs in which generalist individuals experience decreased exploitation efficiency when using a wide range of resources. Consequently, high levels of individual specialization would enable individuals to allocate energy towards other essential functions that enhance fitness such as reproduction (Bolnick et al., 2003; Araújo et al., 2011; Maldonado et al., 2019).

In general, it can often be assumed that parents feed their offspring a diet as diverse as what they consume, leading to similar resource use and no niche partitioning between adults and juveniles. In birds, parental decisions about how to allocate food to their nestlings are strongly influenced by nestling behavior, parental sex, life history traits, and the nutritional needs of their offspring, which require high-quality food to rapidly grow and enhance their probability of survival (Alonso et al., 2012; Raya Rey et al., 2012; Beaulieu and Sockman, 2014). It has been suggested that protein intake is higher at early ages due to the

predominance of anabolic reactions caused by the formation of new tissues (Kyriazakis and Oldham, 1993). This is consistent with studies on the overlap of population niches among different age classes, which show that juveniles occupy higher trophic levels compared to adults (Hobson, 1993; Hammerschlag-Peyer et al., 2011). Several studies have reported niche partitioning between adults and juveniles, as well as differences in individual specialization among age classes due to disparities in foraging abilities, morphology (*i.e.* body mass, bill length), or social status (Durell, 2003; Hall et al., 2021). (Sword and Dopman, 1999; Frédérich et al., 2010; Vander Zanden et al., 2013; Hall et al., 2021). For example, in western sandpipers (*Calidris mauri*) adults and juveniles differed in individual specialization levels because juveniles have less experience in handling prey, shorter bills, and lower body mass (Hall et al., 2021). A common feature in these studies, however, is that they report differences between adults and juveniles in species that have little or no parental care or in juveniles that can forage independently (Durell, 2003; Hall et al., 2021). Moreover, these studies have not considered resource variation as a potential explanatory variable, despite its well-documented influence on both niche breadth and niche partitioning (Finke and Snyder, 2008; Araújo et al., 2011; Stephens et al., 2019).

Our hypothesis is that ecological opportunity modulates niche partitioning in both adults and juveniles through the influence of seasonal resource availability on parental behavior (prey selection). In species with significant parental care, we expect parents to select high-quality food to ensure their brood's survival even if it results in more competition with other adults during periods of low food availability (Beaulieu and Sockman, 2014). Thus, juveniles should exhibit narrower niches focused on high-quality prey occupying higher trophic levels that contain high protein contents, and lower degrees of individual specialization compared to adults independent of environmental shifts in resource availability. On the contrary, adults are expected to have higher levels of individual specialization during conditions of high resource availability when ecological opportunity is enhanced (Hall et al., 2021). No studies

have examined how parental care, specifically the provisioning of food from parents to offspring, affects niche partitioning both between and within age classes under contrasting levels of ecological opportunity.

To assess these hypotheses, we studied the rufous-collared sparrow (*Zonotrichia capensis*) that provides parental care while chicks are in the nest and during the post-fledging period as juveniles learn to forage independently (Miller and Miller, 1968; Tubaro, 1990). To compare niche partitioning between and within age classes, we exploited the species' capability to generate multiple broods within a single breeding season, allowing for two distinct cohorts of nestlings and adults to experience contrasting ecological opportunity. We used isotope-based estimates of dietary variation, an effective approach to quantify individual specialization via estimates of individual and population isotopic variance by analyzing consumer tissues that reflect diet over different timescales (Matich et al., 2011; Hanson et al., 2015; Bond et al., 2016; Maldonado et al., 2017). Nitrogen isotope ($\delta^{15}N$) values have been widely used to characterize trophic level and food-chain length (Post, 2002) and here we measured $\delta^{15}N$ values of blood plasma, red blood cells, and claw tips collected from each individual as a proxy of dietary variation to quantify individual and total trophic niches of juveniles and adults throughout the breeding season (Bearhop et al., 2004; Vander Zanden et al., 2010).

Materials and Methods

Fieldwork and Tissue Collection. We captured rufous-collared sparrows (*Zonotrichia capensis*) with mist nets in Quebrada de la Plata (33°31'S 70°50'W) in central Chile in spring (November 2020) and summer (January 2021). We categorized captured individuals into adults (N_{spring} =16, N_{summer}= 20) or juveniles (fledglings; N_{spring}= 12, N_{summer}=8) according to plumage characteristics described in (Miller and Miller, 1968). The study site is characterized by a Mediterranean climate with cool wet winters and relatively

hot dry summers (Di Castri and Hajek, 1976). In addition, at this site the availability of insects and plants varies seasonally being highest in spring and lowest in winter; summer values also are lower than in spring (Lopez-Calleja, 1995).

Parental care in this species extends from hatching until complete independence at 40 days old, with both parents actively feeding the chicks. Fledglings start self-feeding at 18 days old and achieve independence by four weeks, although they may still receive food from parents until day 40 (Miller and Miller, 1968; Tubaro, 1990). Individuals captured during November in spring would correspond to late September broods, while those captured in late January (summer) would correspond to early December broods, ensuring that both broods were raised under markedly different ecological conditions.

Immediately after capture, individuals were placed in a bird-holding bag (Ecotone, Poland), weighed to the nearest 0.1 g on a digital scale, and a ~50µl blood sample was collected from the brachial vein using heparinized microhematocrit capillary tubes. We then sampled claw tips, which were placed in an Eppendorf tube. All samples were stored frozen in liquid nitrogen prior to preparation for stable isotope analysis. All tissue samples were dried at 80°C, homogenized, and ~0.5–0.6 mg of each sample was loaded into tin capsules for stable isotope analysis.

Resource Availability. The rufous-collared sparrow is an omnivorous species that routinely consumes both plants and insects (Lopez-Calleja, 1995). We first examined seasonal variation in available resources in our study site. To measure plant availability, we established five permanent 1m^2 quadrats distributed across the study area in which we identified cover percentage of living herbaceous species during both seasons: mid-September and mid-November for spring and mid-December and mid-January for summer. We also collected leaf and seed samples of 12 plant species during the spring; seed samples of 6 species were collected during the summer since live plant cover was

absent in our study quadrats. This collection allowed us to characterize the (baseline) $\delta^{15}N$ composition required to estimate relative trophic level (see below).

We sampled terrestrial arthropods with Barber pitfall traps filled with water and biodegradable detergent (Southwick, 1978) placed every 1 m along five linear transects of 10 m distributed across the study area and collected after 24 h (Jaksic and Lazo, 1999). We counted and identified the collected arthropods to the lowest taxonomic resolution in the laboratory.

We measured the density of arthropods for each transect and sample day by quantifying the number of individuals collected divided by the number of Barber pitfall traps. Density of plant resources was measured by the total percent cover of living plants at each sample quadrant. We then estimated the mean density of each assemblage for each season and its confidence interval by bootstrap procedure with 10,000 iterations. Resource diversity was estimated by quantifying the Hill numbers for the plant and arthropod assemblages (Chao et al., 2014). Seasonal species richness and Shannon diversity index were calculated by using sample-size-based rarefaction and extrapolation estimation of the Hill numbers of order q equal to 0 and 1, respectively. The estimates were based on species abundance, measured as the percent cover of living plant species and number of individuals within each arthropod morphotype (Chao et al., 2014; Hseih et al., 2019). All estimations were performed with the package iNEXT (Hseih et al., 2019).

Stable Isotope Analysis. We measured $\delta^{15}N$ values in blood plasma, red blood cells, and claw tips of juvenile and adult individuals to quantify niche characteristics in seasons associated with high (spring) and low (summer) resource availability. Although many tissues can be compared to construct a time series of isotopic variation, blood plasma, red blood cells, and claws can be easily collected in the field without sacrificing animals (Podlesak et al., 2005; Carleton et al., 2008). $\delta^{15}N$ values of claw tips integrate dietary

inputs over ~6 weeks prior to sample collection, while blood plasma and red blood cells integrate diet over ~1-2 and ~3-4 weeks prior to collection, respectively (Hobson and Clark, 1992; Carleton et al., 2008; Hahn et al., 2014). Young birds initiate the post-juvenile molt either at the time of independence or within about 10 days thereafter (Miller and Miller, 1968). Therefore, fledglings had not achieved total independence or had only recently done so at the time of capture. This implies that the variance in diet composition based on analysis of these three tissues, with the most recent one reflecting diet integrated over 7 days prior to capture, represents the diet of juvenile individuals during the parental care period when they had not yet achieved foraging independence.

Nitrogen isotope ($\delta^{15}N$) values of sparrow tissues were measured on a Costech 4010 elemental analyzer coupled to a Thermo Finnigan Delta Plus XP isotope ratio mass spectrometer at the University of New Mexico Center for Stable Isotopes (Albuquerque, NM). Stable isotope data are expressed in delta (δ) notation as parts per thousand (‰) according to the equation, $\delta^{15}N = (R_{sample} / R_{standard} – 1) X 1000$, where R represents the ratio heavy to light isotopes ($^{15}N/^{14}N$) of the sample relative to the international reference standard, respectively. Measured $\delta^{15}N$ values were calibrated relative to AIR with certified reference materials. Within-run estimates of analytical precision were obtained by measurements of an internal laboratory reference material and yielded a precision (SD) ≤ 0.2‰.

Total Niche Width and Individual Diet Specialization. To quantify the total niche width and degree of individual diet specialization between age groups and seasons, we modified the Roughgarden index for use with tissue $\delta^{15}N$ data (Roughgarden, 1972; Maldonado et al., 2017, 2019). Roughgarden used a simple framework to quantify individual diet specialization: the total niche width (TNW) of the (adult or juvenile) population is the sum

of two components: (1) the within-individual component (WIC) which reflects the average of the variability of resources used by individuals, and (2) the between individual component (BIC) that represents the between-individual variation in the average use of resources. The degree of individual diet specialization is reflected in the WIC/TNW ratio where low ratios close to zero indicate a higher prevalence of specialization within an age class, indicating a generalist population composed of individual specialists that each use a small subset of the total niche width.

Trophic Level. We calculated the relative trophic level (TL) of each individual as follows (Post, 2002): $TL=(1 + (\delta^{15}N_{bird} - \delta^{15}N_{producers}) / \Delta^{15}N)$, where the $\delta^{15}N_{bird}$ represents the mean isotopic signature of the three tissues, $\delta^{15}N_{producers}$ correspond to the baseline isotopic signature of the primary producers and $\Delta^{15}N$ is the trophic discrimination enrichment factor. We used a mean trophic discrimination of 2.48‰, which is the mean value of collagen (claws), blood, and plasma tissues for birds (Caut et al., 2009), and a baseline $\delta^{15}N$ value of 3.47‰ estimated for plant samples from the study site.

Statistical Analysis. To assess for differences in individual diet specialization between juveniles and adults against a null model, we employed a non-parametric Monte Carlo procedure with 10,000 iterations to derive p-values. Notably, the null model characterizes the trophic niche of either juveniles or adults as being comprised of generalist individuals who forage randomly across the entire niche of their respective age classes (Bolnick et al., 2002). This Monte Carlo procedure is implemented in the R package RInSp (Zaccarelli et al., 2013). To evaluate whether significant differences exist in TNW, BIC, WIC, and WIC/TNW between juveniles and adults, we utilized a Monte Carlo permutation procedure. To calculate a p-value, the observed mean difference in WIC/TNW between juveniles and adults was compared against the mean differences generated from 10,000 random

permutations of juvenile-adult groups. We then used a one-way Analysis of Variance (ANOVA) followed by Tukey's post hoc test to assess potential differences in trophic levels between the two age classes across seasons. Finally, we estimated the isotopic niche overlap between juveniles and adults in both seasons by calculating the overlapped areas relative to each pair of $\delta^{15}N$ kernel density estimations using the overlapping R package (Pastore, 2018; Pastore and Calcagnì, 2019). To determine if the estimated area of overlap was significantly different from what would be expected by chance, we conducted a permutation test with 10,000 random combinations of the $\delta^{15}N$ values and compared the estimated overlap area with the $CI_{0.95}$ of the permuted data.

Results

The percent of living plant cover decreased from 86% (CI: 82.1–90.1%) in spring to 0% during the summer. A total of 27 herbaceous plant species were available during spring, with an estimated Shannon diversity ($D^{q=1}$) of 4.5 (CI: 4.3–5.3). Conversely, no significant differences were observed in arthropod density (d) between seasons; d= 20.7 (CI: 9.7–37.7) in spring and d = 15.2 (CI: 9.4–22.6) in summer. Shannon diversity was also non-significant: $D^{q=1}$ = 11.255 (CI: 10.89 – 11.97) for spring and $D^{q=1}$ = 12.43 (CI: 11.94 – 13.64) for summer (See Supplementary Materials). However, the taxonomic richness of arthropods was significantly higher in spring ($D^{q=0}$ = 132.00, CI: 120.94 – 143.06) than in summer ($D^{q=0}$ = 81.00, CI: 73.60 – 88.40).

Individual diet specialization and total niche width (TNW) varied significantly between seasons for juveniles but not for adults (Figure 1, Table 1). Juveniles exhibited higher degrees of individual diet specialization in spring than in summer, while TNW was higher in summer than in spring. In contrast, adults maintained a consistent degree of individual diet specialization and TNW across seasons. Notably, adults showed a decrease in trophic level in summer relative to spring, while juveniles maintained a consistent trophic level

between seasons (Table 2). The amount of niche overlap between juveniles and adults varied from 0.595 in spring to 0.390 in summer (Table 3).

Discussion

This study provides valuable insights into the trophic niche structure and individual diet specialization of juveniles and adults in a species with substantial parental care during periods that differ in ecological opportunity. Contrary to our expectations, we found that ecological opportunity influences both total niche width (TNW) and the degree of individual diet specialization in juveniles (Table 1). However, adults show no change in these niche characteristics over the breeding season despite a shift in their trophic level (Table 2).

Previous studies (Lopez-Calleja, 1995) and our findings show that ecological opportunity is highest in spring because of higher arthropod richness and higher plant cover and diversity. The greater availability of resources enables adults to specialize their resource use for them and their offspring. Consequently, both age groups were primarily composed of individual specialists exhibiting nearly identical degrees of individual diet specialization and trophic levels. The high overlap found between juveniles and adults further indicates the similarities in niche characteristics between these two groups during this season (Table 3).

Following the same rationale and according to the niche variation hypothesis, we expected that faced with a reduction in food resources, the total niche width and degree of individual diet specialization should decrease in both age groups. In contrast to this prediction, the prevalence of individual diet specialization only decreased in juveniles in summer by means of a slight increase of WIC and a broadening of their total niche width (Table 1). Our explanation is that juveniles require a protein-rich diet for development, which in turn compels adults to provide food to maintain juvenile requirements under conditions of low resource availability, even at the expense of their own ability to specialize. This explanation aligns with optimal foraging theory, suggesting that parents

feed their offspring with additional less preferred food items when resources are scarce, which results in a wider TNW and more generalist foraging behavior observed in juveniles during the summer relative to spring. The seasonal shift from specialists to generalists observed for juveniles can also result from parents becoming less selective. Under reduced resource availability, parents are likely compelled to be less selective in their prey choice to minimize predation risk associated with an increase in search time. This change in selectivity would allow them to reduce provisioning rates without compromising nutritional delivery to their offspring (Skutch., 1949).

The TNW and WIC of adults were similar across seasons, but this age class occupied a lower trophic level in summer relative to spring. This resulted in a significantly lower amount of dietary overlap between juveniles and adults during the summer (Table 3). This suggests that adults may be inherently more flexible in resource selection because they are not constrained by the same nutritional requirements as developing nestlings. These conditions enable adults to persist during periods of relative resource scarcity while prioritizing the delivery of higher trophic level prey items to their nestlings during critical periods of their growth and development.

In conclusion, the results of this study highlight a dynamic interplay between ecological opportunity and individual diet specialization, with significant implications for understanding species resilience to environmental variation (Bolnick et al., 2003; Araújo et al., 2011). Notably, our study reveals that adult sparrows adapt their parental care strategies in response to seasonal fluctuations in resource availability. The dichotomy in resource use between age groups illustrates the complex strategies species employ to ensure survival and reproductive success. For juveniles, the shift towards generalism in times of resource scarcity may be imperative to survival, ensuring adequate nutrient intake for growth and development. In contrast, an adult population's ability to maintain niche width but alter trophic position underlines a strategic flexibility that likely minimizes

intraspecific competition and optimizes resource utilization across the population. Ultimately, this study underscores the importance of considering age-specific responses to fully understand the ecological and evolutionary mechanisms governing niche partitioning and individual diet specialization within populations. In Mediterranean ecosystems like central Chile, climate change projections predict an increase in temperatures and a decrease in annual precipitation (Bozkurt et al., 2017, 2018), therefore the relatively dry resource-limited conditions associated with summer may extend across a larger portion of the reproductive season. Studies like ours that focus on characterizing dietary flexibility and understanding how resource use may shift under these conditions are essential for understanding species response(s) to ongoing environmental change.

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Table 1: Estimated within-individual component (WIC), between-individual component (BIC), total niche width (TNW), and individual specialization (WIC/TNW) of adults and juveniles individual rufous-collared sparrows captured during summer and spring. Units of WIC, BIC, and TNW are ‰^{2}; sample sizes are noted in parentheses.

	Spring		Summer	
	Juveniles (11)	**Adults** (16)	**Juveniles** (8)	**Adults** (20)
WIC	0.252^a	0.436^a	1.924^b	0.566^a
BIC	0.958^a	1.665^a	1.482^a	2.980^a
TNW	1.210^a	2.101^a	3.405^b	3.546^a
WIC/TNW	0.208^a	0.207^a	0.565^b	0.160^a
Trophic Level	2.36^a	2.57^a	2.54^a	2.0^b

Different superscript letters denote significant differences ($P < 0.05$) among groups.

Table 2. Results of Analysis of Variance (ANOVA) assessing changes in trophic level among sparrow age (juveniles and adults) and season of tissue collection (spring and summer).

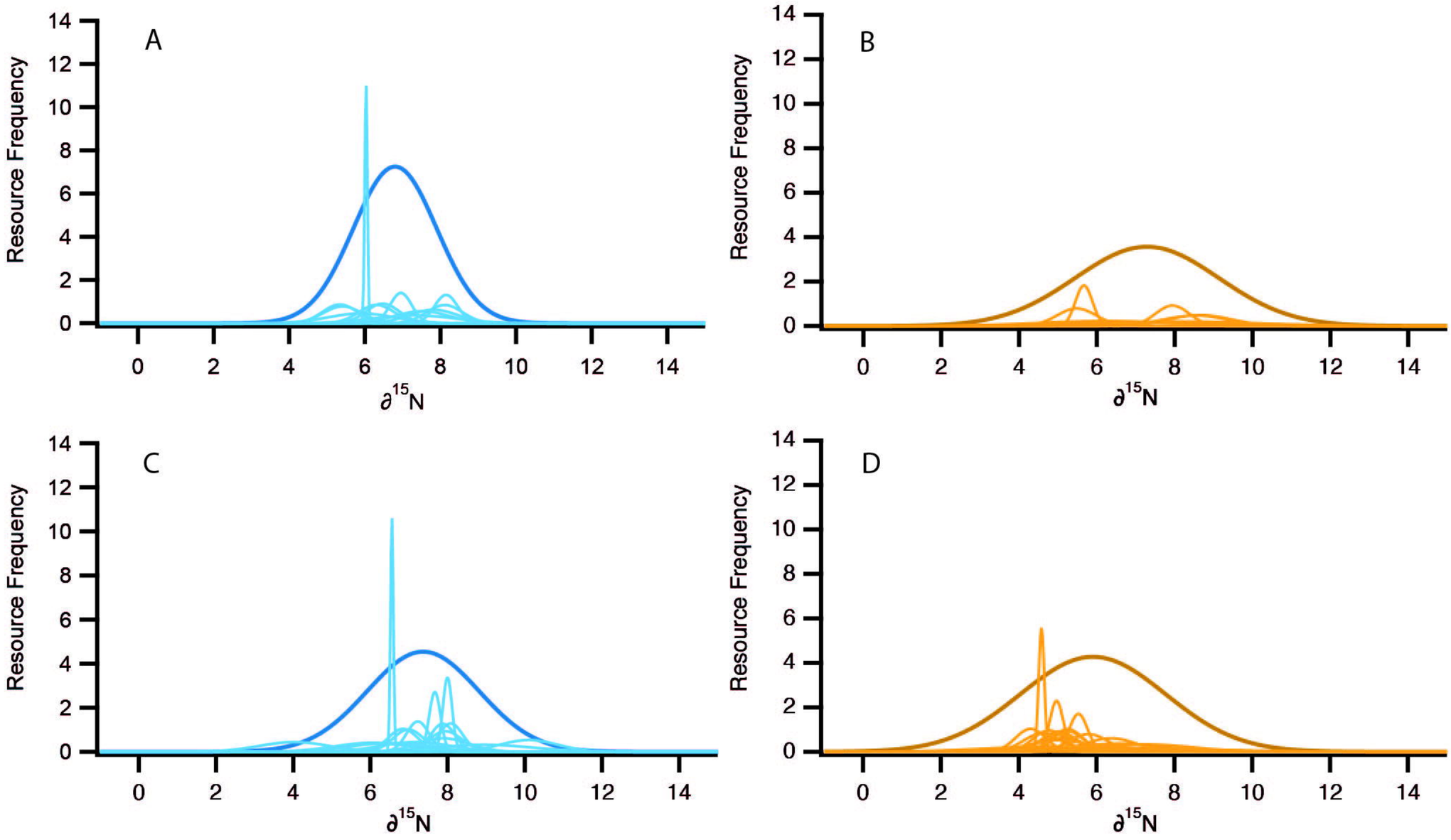
	Df	Sum Sq	Mean Sq	F value	Pr(>F)
factor(age)	1	0.22	0.22	0.64	0.43
factor(season)	1	1.45	1.45	4.20	0.04*
factor(age) : factor(season)	1	1.67	1.67	4.83	0.03*
Residuals	51	17.66	0.35		

*P<0.05

Table 3: Estimated isotopic niche overlap between juveniles and adults in both seasons using $\delta^{15}N$ kernel density estimates. Permuted quantiles were calculated with a confidence interval of 0.95.

Group 1	Group 2	Overlap	Permuted Quantiles	
			Low 95%	High 95%
J_{Spring}	J_{Summer}	0.593	0.534	0.884
J_{Spring}	A_{Spring}	0.595	0.572	0.866
J_{Spring}	A_{Summer}	0.308	0.574	0.894
J_{Summer}	A_{Spring}	0.489	0.511	0.851
J_{Summer}	A_{Summer}	0.390	0.492	0.890
A_{Spring}	A_{Summer}	0.206	0.641	0.910

Figure 1: Distributions with thin lines correspond to individual niches for sparrows captured in the spring (blue) and summer (yellow) of juveniles (A and B) and adults (C and D) generated from $\delta^{15}N$ values of blood plasma, red blood cells, and claw tips. Distributions with thick lines represent the corresponding total population niche width (TNW), which were scaled equally for the four populations enabling direct comparison.


A
B
C
D
Resource Frequency
∂15N
0
2
4
6
8
10
12
14