

Reports

Ecology, 98(4), 2017, pp. 903–908
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Testing the niche variation hypothesis in a community of passerine birds

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Abstract. The niche variation hypothesis (NVH) predicts that populations with broader niches should exhibit greater between-individual diet variation or individual specialization (IS) relative to populations with narrower niches. Most studies that quantify population niche widths and associated levels of IS typically focus on a single or few species, but studies examining NVH in a phylogenetically informed comparative analysis among species are lacking. Here we use nitrogen isotope ($\delta^{15}\text{N}$) analysis to measure population niche widths and IS in a single bird community composed of 12 passerine species representing different foraging guilds. We found support for the NVH at the interspecific level; species with broader population niche widths were comprised of more individual specialists. Moreover, our results suggest that this relationship is influenced by foraging guild; specifically, omnivores have higher degrees of IS for a given population niche width than insectivores. Finally, the levels of IS among passerine species, in contrast to population niche width, were associated with their relatedness, suggesting that the potential phylogenetic effect on the prevalence of IS is higher than previously recognized.

Key words: *community ecology; individual specialization; isotopic niche; niche variation hypothesis; passerines; stable isotopes.*

INTRODUCTION

The study of variation in resource use among individuals within populations has been the focus of research in diverse fields of ecology over the past decade (e.g., Bolnick et al. 2003, Araújo et al. 2011). This attention resulted from the realization that individuals often consume a small subset of the resources utilized by their population, a phenomenon known as individual diet specialization (Bolnick et al. 2003). Such variation plays a pivotal role in shaping population niche width (Van Valen 1965, Roughgarden 1972, Bolnick et al. 2003), which is an important source of diversification that has implications for adaptation and speciation.

The niche variation hypothesis (NVH; Van Valen 1965) proposed that an increase in population niche width is related to higher incidences of individual specialization (IS). Accordingly, it would be expected

that populations with broader dietary niches should exhibit greater among-individual variation in resource use relative to those populations with narrower niches (Van Valen 1965). Empirical and theoretical studies testing NVH have shown mixed support (e.g., Díaz 1994, Meiri et al. 2005, Costa et al. 2008, Bolnick et al. 2010, Santoro et al. 2011, Hsu et al. 2014). The first multiple taxa evidence of the NVH emerged only recently, when Bolnick et al. (2007) performed a meta-analysis largely focused on intraspecific patterns in distantly related species such as three-spine sticklebacks (*Gasterosteus aculeatus*), Eurasian perch (*Perca fluviatilis*), *Anolis* lizards (*Anolis sagrei*), and intertidal gastropods (*Nucella* spp.), but also included an interspecific comparison of niche components in four sympatric Brazilian savannah frog species (*Adenomera* sp., *Eleutherodactylus* sp., *Leptodactylus fuscus*, and *Proceratophrys* sp.).

Several approaches have been used to quantify dietary IS (Bolnick et al. 2003). Some studies attempt to directly measure IS by quantifying among individual diet variation via direct observation or analysis of gut/stomach contents (e.g., Tinker et al. 2008, Araújo et al. 2009,

Manuscript received 15 July 2016; revised 27 January 2017; accepted 1 February 2017. Corresponding Editor: Matthew L. Forister.

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Bolnick et al. 2010); while others have used a more indirect method by measuring the amount of phenotypic variation in a trait that is related to food utilization (e.g., Díaz 1994, Hsu et al. 2014). Measurement of morphological variation within populations has been the most widely used approach to quantify IS, but has also been criticized because diet variation among individuals could be related to other traits such as behavior, and/or physiology (Bolnick et al. 2003). Recently, stable isotope analysis (SIA) has been used to quantify IS (Araújo et al. 2007, Newsome et al. 2009, 2015, Vander Zanden et al. 2010, Elliott Smith et al. 2015), and is especially useful for examining individual-level dietary variation over temporal scales (months to years) required to accurately evaluate IS that is often impractical using traditional proxies like scat/stomach content analysis or observation.

To test the NVH, we quantified the relationship between IS and population niche width using a phylogenetically informed analysis of isotope-based niche metrics in a community of 12 passerine bird species in central Chile. Passerines are well-suited animal models for studying IS because they are a diverse group of related consumers that occupy multiple trophic levels from granivores to insectivores (Ramirez-Otarola et al. 2011). The species studied here were collected from a single community during a single season (winter) to constrain possible environmental effects (Hsu et al. 2014). IS was quantified with Roughgarden's index (Roughgarden 1972) using nitrogen ($\delta^{15}\text{N}$) isotope values in tissues differing in their isotopic incorporation rates that we used to estimate seasonal variation in individual's diets over time (Bearhop et al. 2004). In agreement with the NVH, we expected that increases in population niche width would correspond to higher levels of IS. We also predicted that variation in both of these niche metrics would have a phylogenetic basis. Our study provides one of the few community-level examinations of the NVH among closely related consumers.

METHODS

Non-reproductive adult individuals belonging to 12 species of passerine birds were captured with mist nets in winter (July–August) in central Chile (33°31'S, 70°50'W). The study site is characterized by a Mediterranean climate with most precipitation falling in the cold winter months and relatively high temperatures and low precipitation in summer. Birds captured in this study (Table 1) have a broad spectrum of dietary habits (Ramirez-Otarola et al. 2011). After capture, birds were weighed with an electronic balance (± 0.1 g), euthanized, and transported to the laboratory where we collected a subsample of their first primary feather, muscle, and liver tissue for isotope analysis.

While stable isotope analysis does not typically identify diet items to the species level, it is a useful proxy for measuring individual- and population-level components of

dietary variation that define IS (Newsome et al. 2009, 2012, 2015, Bond et al. 2016). One effective approach for quantifying within-individual dietary variation, which is far more difficult to estimate than population level diet variation, is to analyze tissues that represent different time periods in the annual life cycle (Matich et al. 2011, Hanson et al. 2015, Bond et al. 2016). Nitrogen isotope ($\delta^{15}\text{N}$) values have been widely used to characterize trophic level (Post 2002), and here we use those values to assess IS because it reliably tracks foraging guild. We measured $\delta^{15}\text{N}$ values of tissues that have different isotopic incorporation rates (liver, muscle, and feather) that were collected from each individual to quantify niche components necessary to estimate population niche width and IS (Bearhop et al. 2004, Vander Zanden et al. 2010). While previous meta-analyses have identified small ($\sim 1\%$) differences in $\delta^{15}\text{N}$ trophic discrimination factors among bird tissues (Caut et al. 2009), the application of corrections to account for such tissue-specific discrimination did not impact our results. To test this we subtracted 1‰ from measured feather $\delta^{15}\text{N}$ values to directly compare them to liver and muscle $\delta^{15}\text{N}$ values (Caut et al. 2009) and then analyzed the data set using the statistical methods described below. Thus, we only report results of statistical analyses of measured $\delta^{15}\text{N}$ values that were not corrected for tissue-specific discrimination.

In birds, complete isotopic turnover of liver occurs in ~ 2 – 3 weeks, whereas muscle integrates diet over the past ~ 2 – 3 months prior to collection (Hobson and Clark 1992, Carleton et al. 2008, Bauchinger et al. 2010). In contrast, the isotopic composition of metabolically inert feathers represents diet during the short period (weeks) of molt (Bearhop et al. 2004, Martínez del Rio et al. 2009), which occurs during the austral summer (December–January) for the species examined in this study (Pyle et al. 2015). Thus to characterize the birds' diets for an extended period of time, we assume liver and muscle samples from birds captured in July–August represent resources assimilated during the austral winter, and feathers reflect diet from the previous summer molting period.

We removed surface contaminants on feathers by rinsing them in a 2:1 chloroform:methanol solution. Liver and muscle samples were ground into a fine powder, lipid extracted with petroleum ether in a Soxhlet apparatus at 40–60°C for 24 h, and then freeze dried. Approximately 0.5–0.6 mg of dried tissue was weighed into tin capsules and $\delta^{15}\text{N}$ values were measured with a Costech 4010 elemental analyzer (Valencia, California, USA) coupled to a Thermo Scientific Delta V isotope ratio mass spectrometer (Bremen, Germany) at the University of New Mexico Center for Stable Isotopes (Albuquerque, New Mexico, USA). Stable isotope results were expressed as δ values, $\delta^{15}\text{N} = 1000 \times [(R_{\text{sample}}/R_{\text{standard}}) - 1]$, where R_{sample} and R_{standard} are the $^{15}\text{N}/^{14}\text{N}$ ratios of the sample and standard, respectively, where the standard is atmospheric N_2 . δ values are expressed as parts per thousand or per mil (‰). Analytical precision was quantified via repeated measurements of internal laboratory reference

TABLE 1. Results of population niche width (TNW), within-individual component (WIC), between-individual component (BIC), and individual specialization (IS) for each passerine species.

Species	Family	FG	<i>n</i>	TNW (‰ ²)	WIC (‰ ²)	BIC (‰ ²)	IS
<i>Diuca diuca</i>	Thraupidae	G	12	3.39	1.72	1.67	0.51
<i>Sporaga barbata</i>	Fringilidae	G	14	2.32	1.57	0.75	0.68
<i>Phrygilus fruticeti</i>	Thraupidae	G	13	2.86	1.61	1.25	0.56
<i>Anairetes palurus</i>	Tyrannidae	I	7	1.86	1.30	0.57	0.70
<i>Troglodytes aedon</i>	Trogloditidae	I	13	4.74	1.91	2.83	0.40
<i>Xolmis pyrope</i>	Tyrannidae	I	9	4.01	2.50	1.51	0.62
<i>Leptasthenura aegithaloides</i>	Furnaridae	I	11	5.43	2.70	2.73	0.50
<i>Scelorchilus albicollis</i>	Rhinocryptidae	I	11	1.32	1.00	0.32	0.76
<i>Zonotrichia capensis</i>	Emberizidae	O	13	3.14	1.25	1.89	0.40
<i>Sturnella loyca</i>	Icteridae	O	7	1.45	0.95	0.49	0.66
<i>Mimus thenca</i>	Mimidae	O	11	4.62	1.16	3.46	0.25
<i>Pteroptochos megapodius</i>	Rhinocryptidae	O	10	1.91	1.43	0.48	0.75

Note: Species were classified by foraging guild (FG) as follows: granivores (G), insectivores (I), and omnivores (O).

materials, which was $\pm 0.2\%$. As a control for the quality of feather keratin, muscle, and liver tissues we measured the weight percent carbon-to-nitrogen concentration ([C]:[N]) of each sample and compared them to the theoretical [C]:[N] ratios for pure protein.

To quantify IS among species, Roughgarden (1972) distinguished two components of the niche, which when added are equal to the population or total niche width (TNW): (1) the within-individual component (WIC) that reflects the average of resource variability utilized by individuals and (2) the between-individual component (BIC) that represents the between-individual variation in average resource use. Considering TNW as the total variance of resources consumed by the population, IS can be represented by the WIC:TNW ratio, which increases from 0 to 1 as individuals consume a higher proportion of those resources utilized by the entire population (see Roughgarden 1972, 1974, Bolnick et al. 2002). In contrast to other metrics used to measure niche breadth, the WIC:TNW ratio uses the diet of the entire population as a proxy for resource availability; individuals' diets are compared with those from the population instead of with the environment, and thus, estimates of the abundance of resources available in the environment are not required (Bolnick et al. 2002).

To test the NVH, we first produced a non-phylogenetic least-squares regression (OLS) between the dependent variable IS and TNW. We then tested the NVH and accounted for relatedness with a phylogenetic generalized least squares analysis (PGLS; Revell 2010) through a molecular phylogeny describing the topology and branch lengths of the 12 passerine species (Appendix S1; Fig. S1); see Appendix S1 for more details about the PGLS analysis.

We used a Monte Carlo procedure to test if the observed relationship between IS and TNW could be explained by a null model in which IS was generated by individuals stochastically sampling a limited set of prey from a shared prey distribution (Bolnick et al. 2007,

Araújo et al. 2009). To generate the null model, $\delta^{15}\text{N}$ values for all individuals in each species were considered as an undifferentiated pool representing the population diet. Each individual was then reassigned to a random diet drawn from the population diet (Bolnick et al. 2007, Araújo et al. 2009). The degree of IS was calculated using 10,000 random resampling estimates and we then regressed the mean resampled IS against the observed TNW to evaluate whether the null model produced a negative relationship between WIC:TNW (IS) and population niche width (TNW). Thus, the NVH is supported only if the observed slope is significantly steeper than the slope generated by the null model. The resampling procedures were performed in the RInSp package in R (Zaccarelli et al. 2013) and the regression analysis in JMP statistical software (SAS Institute, Cary, North Carolina, USA). We then calculated the residuals of the observed linear relationship between IS and TNW for each foraging guild (Fig. 1) and tested for differences in the levels of IS (obtained from the residual analysis) and TNW between omnivores and insectivores via a permutation test (10,000 permutations) implemented in R (R Core Team 2016).

Last, to explore whether population niche widths, degrees of IS, population niche components (WIC and BIC), and mean $\delta^{15}\text{N}$ of all tissues ($\delta^{15}\text{N}_{\text{mean}}$) were associated to relatedness, we quantified the phylogenetic signal of each variable using the Bloomberg's *K* statistic (Blomberg et al. 2003, see Appendix S1).

RESULTS

The number of samples utilized for each species, the population niche width, their components (WIC and BIC), the degree of IS, and the isotopic composition ($\delta^{15}\text{N}_{\text{mean}}$) are reported in Table 1 and Appendix S1: Table S2. We observed >400% variation in TNW (range 1.32–5.43) and ~300% variation in IS (range 0.25–0.76) among species. In accordance with the NVH, we observed

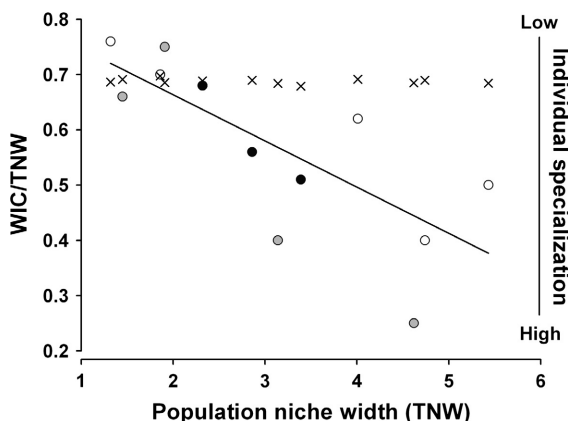


FIG. 1. Relationship between individual specialization (WIC/TNW) and population niche width (TNW). The empirical results of passerine birds from different dietary habits are shown with colored circles: black circles, granivores; gray circles, omnivores; white circles, insectivores. Population niche width (TNW in $\%^{2}$) and the within-individual component (WIC in $\%^{2}$) was quantified with muscle, liver and feather $\delta^{15}\text{N}$ data. The fitted line is $y = 0.84 - 0.09x$, which described the model of the observed data considering the phylogenetic effect. Crosses represent the null model estimated from resampled individual specialization (IS) obtained from individuals reassigned to random diets selected from the population diet and the observed TNW.

a positive relationship between IS (indicated by lower WIC/TNW ratios) and population niche width (Fig. 1, OLS, $R^2 = 0.55$, $P = 0.003$). The Monte Carlo procedure to test for stochastic sampling effects revealed that the observed significant negative slope between WIC/TNW and TNW was much steeper than that generated from random resampling, which did not yield a significant negative or positive relationship (crosses, Fig. 1). The permutation tests revealed that omnivore species had higher levels of IS in comparison to insectivores ($P = 0.04$), whereas TNW did not differ between these foraging guilds ($P = 0.47$).

The effect of population niche width on IS remained significant ($P < 0.01$, Fig. 1) when including phylogenetic data in a PGLS model that used a Brownian motion model of evolution ($\lambda = 1$). When we compared the Brownian PGLS model to a model with $\lambda = 0$ that assumes trait evolution is unrelated to phylogeny, the likelihood ratio test (LRT) revealed that the addition of phylogenetic data significantly increased the likelihood ($P < 0.001$, Fig. 1). The phylogenetic signal estimated via Bloomberg's K statistic revealed that IS and BIC variation was associated with relatedness (Appendix S1: Table S1). In contrast, WIC, TNW, and $\delta^{15}\text{N}_{\text{mean}}$ did not exhibit a significant phylogenetic signal (Appendix S1: Table S1).

DISCUSSION

We found support for the niche variation hypothesis (NVH) in a comparative phylogeny-based analysis of

a passerine bird community in central Chile. Our community-level analysis shows that species with broader population niche widths were comprised of more individual specialists. Specifically, we found that omnivores have higher levels of IS than insectivores at a given population niche width (TNW), even though these two foraging guilds had a similar range in TNW (Fig. 1). It has been proposed that ecological opportunity in the form of resource diversity promotes IS (Van Valen 1965, Roughgarden 1974, Araújo et al. 2011, Layman et al. 2015). Thus, a plausible explanation for the observed difference in IS between foraging guilds is that omnivores have a high degree of ecological opportunity since they consume resources that span multiple trophic levels in comparison to insectivores or granivores. In contrast, the similar range in TNW observed between insectivores and omnivores suggests that insectivores are consuming insects that occupy multiple trophic levels given that our niche components were estimated with $\delta^{15}\text{N}$ values that are sensitive to trophic level.

In theory, dietary IS is maintained within populations because traits associated with capture and processing of a particular resource result in decreased procurement efficiency of another resource (Bolnick et al. 2003, Estes et al. 2003, Araújo et al. 2009). For example, successful capture of one resource type may depend on using specific search and handling strategies, which may result in limited neural capacity to retain other search images or capture behaviors (Bolnick et al. 2003). Such trade-offs create inertia against switching diets, and thus help maintain IS (Araújo et al. 2009). Omnivorous species by definition consume a more diverse set of resources in comparison to insectivores and granivores, but more importantly the wide range in the macromolecular composition and quality of the food items omnivores consume may create physiological trade-offs associated with resource digestion and assimilation. For example, an omnivorous population of Rufous-collared sparrows showed a large degree of individual variation in the activity of a digestive enzyme related to protein consumption (aminopeptidase-N), which in turn was associated with the percentage of insects in the natural diet (Sabat et al. 1998). Such physiological trade-offs may promote IS when animals primarily consume vegetal or animal prey, preventing individuals from becoming omnivores that consume resources from all trophic levels without incurring a cost in digestive efficiency. Thus, our results suggest that IS is not necessarily dependent on the number of prey species consumed, but instead on behavioral and physiological characteristics (e.g., handling skills, assimilation efficiency) that combine to enhance foraging success on a particular set of resources (Newsome et al. 2015). We realize that these patterns are based on only a dozen species in this passerine community, however, to our knowledge, our data set is the largest available for a closely related group of sympatric taxa (Appendix S1: Fig. S1).

Only a few studies have examined the contributions of both ecological and genetic factors on the prevalence of IS (Svanbäck and Eklov 2006, Agashe and Bolnick 2010, Araújo et al. 2011, De León et al. 2012), and none have studied more than a few species in a single community. While our results show that ecological traits such as foraging guild contribute to IS, our data also suggest that IS and the amount of between-individual variation in diet (BIC) is related to phylogenetic relatedness in this passerine community. This is expected since our phylogenetic analysis showed that species belonging to a particular foraging guild were more closely related to each other than species belonging to a different guild; for example, all granivores are in the infraorder Passeridae, whereas all insectivores are in the infraorder Tyranidae (Appendix S1: Fig. S1).

While dietary habits (i.e., foraging guilds) and IS appear to have a phylogenetic component, TNW and other trophic niche related traits (WIC and $\delta^{15}\text{N}_{\text{mean}}$) diverged among closely related species. It has been suggested that relatedness can promote divergence in trophic niche traits to avoid interspecific competition as species undergo character displacement (Larson et al. 2010, Wiens et al. 2010); such that related co-occurring species usually exhibit spatial or temporal differentiation in micro-habitat or resource use (Ackerly et al. 2006). Thus, while the degree of IS appears to be conserved among closely related species, changes in trophic niche position ($\delta^{15}\text{N}_{\text{mean}}$) in concert with TNW are expected to avoid interspecific competition, thus promoting species coexistence. Furthermore, this phylogenetic pattern suggests that to share similar degrees of IS, changes in the TNW of closely related species should be accompanied by changes of similar direction and magnitude in WIC. While disentangling the causes for these evolutionary differences are beyond the scope of this study, our results offer insights into the evolution of niche components through comparison of both ecological and evolutionary aspects of individual specialization at the community level.

Our results suggest that similarities in the degree of IS among foraging guilds and related taxa may have important implications for community assembly that influences species composition and trophic structure. Identifying which ecological and evolutionary factors are the most important drivers of IS within populations is needed to better understand how this important source of ecological variation is promoted and maintained.

ACKNOWLEDGMENTS

We thank Andrés Sazo for assistance in field work and two anonymous reviewer for their valuable comments on an earlier version of this manuscript. Funding was provided by FONDECYT Grant No 1120276 and No 1160115 to P. Sabat and FB0002-2014 to F. Bozinovic. Birds were captured with permits from SAG, Chile (No. 840/2012). All protocols were approved by the institutional Animal Care Committee of the University of Chile.

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