

Behavioral niche partitioning reexamined: Do behavioral differences predict dietary differences in warblers?

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Abstract. Behavioral niche partitioning is an important and widely assumed mechanism for the coexistence of ecologically similar species. Here we assessed this mechanism by testing its core assumption, that evolved differences in foraging behavior correspond with differences in resources consumed. We combined data on foraging behavior, available prey, and observed diets of five coexisting species of New World wood warblers (Parulidae), a system that has been foundational to our understanding of behavioral niche partitioning. Consistent with past work, we found that the five species differed markedly in their foraging behavior, enough that some species pairs hardly overlapped at all in foraging microhabitat. In contrast, the birds overlapped highly in diet, while exhibiting small, interpretable differences in resource use. The high overlap resulted mostly from all five species consuming numerous ants, a prey source that moves between microhabitats. To test the prediction that the large differences in foraging behavior explain the small dietary differences, we generated expected diets based on available prey and foraging microhabitat use. Consistent with niche partitioning as a coexistence mechanism, we found that the small dietary differences were explained by a combination of foraging microhabitat and available prey, but this pattern was driven by only a small number of prey taxa. Thus, we found mixed support for behavioral niche partitioning. Our results indicate that foraging behavior among these bird species helps explain subtle variation in diet, potentially facilitating coexistence. However, our results also revealed a weak relationship between foraging behavior and resource partitioning. Consequently, studies that rely solely on foraging behavior may greatly overestimate the degree of niche differentiation leading to erroneous conclusions. Overall, this study calls into question how and why these differences in foraging behavior evolved, and what role if any they play in facilitating coexistence.

Key words: available prey; coexistence; foraging; niche; Parulidae; resource partitioning.

INTRODUCTION

Explaining how ecologically similar species coexist is a central goal in ecology and evolution (Barabas et al. 2016) and essential to understanding the maintenance of diversity (Chesson 2000). Coexistence has often been explained via niche partitioning (MacArthur 1958, Pigot et al. 2018), which is recognized as an important mechanism to maintain species diversity (Levine and Hille Ris Lambers 2009). Although niches can be partitioned along many axes, diet is studied frequently. In his seminal study, MacArthur (1958) concluded that coexisting warblers partition prey as a result of foraging in different parts of conifer trees, a finding that has withstood considerable replication (e.g., Morse 1967; but see Lovette and Hochachka 2006). For more than 50 years, ecologists have routinely used such proxies of resource use, including foraging maneuver (Lack 1976), morphology

(Hiron et al. 2006, Mills 2007, Pigot et al. 2020), and time of day (Albrecht and Gotelli 2001) and across diverse taxa including birds, lizards (Pianka 1974), and arthropods (Albrecht and Gotelli 2001), to explain coexistence.

A potential weakness of much work on coexistence via resource partitioning is the assumption that behavioral and morphological differences, among others, translate directly to differences in resource consumption, or at least impart some form of resource exclusivity, here defined as the individual prey items consumed. Contrary to this, Poulin and Lefebvre (1996) found that prey consumption of migrant birds of different foraging groups were more similar to each other than they were to residents that shared their behavioral foraging niche, and variation in beak shape once assumed to be adapted to partitioned prey resources, appears only weakly related to diet (Navalón et al. 2019). Similarly, Gordon et al. (2019) found that, regardless of foraging guild, desert bats showed high levels of dietary overlap, and Sherry et al. (2016b) concluded that although competing birds did exhibit minor differences in diet, they also showed

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high levels of dietary overlap. Lovette and Hochachka (2006) found that even the warblers featured by MacArthur (1958) do not regularly co-occur at the finest spatial scales, indicating that the observed differences in foraging behavior may not actually permit coexistence.

The risk of using behavior as a dietary proxy is that species that forage differently may nonetheless target the same prey resources via several mechanisms. First, prey may move among microhabitats, making the same individual prey item available to competitors that are separated in foraging location. Thus, two predator species that differ in foraging microhabitat, yet overlap in their consumption of a prey taxon that moves between these microhabitats, may decrease the availability of prey to each other, and thus compete (Wilson 2010). Second, different capture rates may decrease the effectiveness of behavioral niche partitioning (Drenner et al. 1978). For example, foraging on aerial prey may have a lower success rate than on sessile prey, leading to a greater percentage of the diet being composed of sessile prey than would be predicted by behavioral observations. Third, differences in foraging behavior may be unrelated to resource use if diverse behaviors target the same prey species (e.g., catching an insect in flight or gleaning the same insect from a leaf). Because of these factors, it is not enough to simply show that species differ in some way without relating it back to the specific resources used (Wilson 2010) and leads to a fundamental problem with these types of studies. Most if not all species differ in at least some characteristics, but these cannot be taken to show differential resource use, unless one also evaluates the association between the character in question and actual resource use. These problems call for testing the validity of niche proxies in the context of species coexistence.

Migrant New World wood warblers (Parulidae) have a distinguished history in coexistence studies and are generally assumed to coexist via behaviorally mediated dietary niche partitioning (e.g., MacArthur 1958, Lack 1976). These warblers often comprise species-rich communities of ecologically similar species (MacArthur 1958, Lovette and Hochachka 2006), whose foraging behavior is easily quantified. Historically, seminal work on these species, especially Lack's (1976) examination of warblers wintering in Jamaica, found that no two warbler species both share habitats and forage in the same way, leading him to conclude that these species do not compete interspecifically at present, in support of the hypothesis of behavioral niche partitioning as a response to past competition.

Here we combined foraging behavior, available prey, and diet for the first time, to our knowledge, to test rigorously whether differences in foraging behavior correspond with differences in diet. We hypothesized that predator species' differences in foraging behavior lead to consumption of different prey items, thus allowing for coexistence via niche partitioning, and made three predictions: (1) that coexisting species forage differently, via

some combination of microhabitat use, foraging maneuver, and foraging height; (2) that if the available prey also differed among foraging microhabitats, that species should correspondingly differ in their observed diets; and (3) that differences in foraging behavior directly explain differences in diet, i.e., the pairwise species differences in observed diets are explained by pairwise differences in expected diets generated by combining available prey with foraging behavior.

METHODS

Study system

Data were collected in Jamaica during the non-breeding season. Field site and sampling period were selected to maximize niche differences among species by sampling at a time when food should be most limited, late in the dry season, and in a structurally complex habitat to provide opportunity for foraging specialization (Araújo et al. 2011, Sherry et al. 2016b; Appendix S1). We included two native wet-limestone forest sites separated by 35 km: Copse Hill (18.25° N, 77.94° W) from 15 February to 14 March 2017 and the Windsor Research Center (18.36° N, 77.65° W) from 15 to 31 March 2017. Data were collected over short time periods and at the same times and places to control for possible seasonal and spatial turnover in arthropod communities. We included all five species of arboreal, migrant, parulid warblers common in this habitat: American Redstart (*Setophaga ruticilla*), Northern Parula (*Setophaga americana*), Black-throated Blue Warbler (*Setophaga caerulescens*), Black-and-white Warbler (*Mniotilta varia*), and Worm-eating Warbler (*Helmitheros vermivorum*). Several of these species are known to experience winter food limitation (Appendix S1), exacerbating their need to avoid interspecific competition for food.

Data collection

We documented foraging behavior using the methods of Lovette and Holmes (1995; Appendix S1). For all foraging attempts we recorded the maneuver, substrate, and relative height in the canopy. Foraging maneuver was classified as sally strike, hover glean, sally, glean, or flutter chase. Substrate was classified as air, bark, branch tip, or dead leaves. We recorded available arthropod prey from different microhabitats using three methods (Kent et al. 2019; Appendix S1). We sampled arthropods in the branch tips using branch clips, in the airspace using hanging sticky traps, and on bark using collar sticky traps.

Although we conceptually define resource use here based on individual prey items, it is not possible to track individual prey items through the habitat and to their eventual consumer. Thus, here we operationally define resource use in two steps. First we use the observed diets, and then we examine the biology of the prey items that

contributed the most to dietary overlaps. To characterize observed diets, we captured birds in mist nets using play-back starting an hour after sunrise, and typically ending by noon to ensure full stomachs. Stomach contents were obtained by forced regurgitation following the methods of Johnson et al. (2002; Appendix S1). This method was chosen over DNA barcoding as it can give abundance data instead of just presence/absence, and is able to separate potentially important life stages from a foraging perspective, such as larval vs. adult Lepidoptera and winged vs. worker Formicidae. Although this method could theoretically underrepresent soft-bodied insects, in our experience, most soft-bodied taxa had some parts that persist in the gut, such as mandibles of Psocoptera and caterpillars, and wings of Diptera (Sherry et al. 2016b), which often pass intact even into fecal matter (C. M. Kent & T. W. Sherry, *personal observations*). However, the presence of wing scales was often the only evidence of adult Lepidoptera (small moths), making the presence of these easy to detect, but their counts were often limited to presence/absence; and the entirely soft bodies of larval Diptera may have also been undercounted. However, these potential biases are likely inconsequential since they should affect all bird species equally, and do not obscure species differences (see *Results*).

Statistical analysis

We ran all statistical analyses in R v. 3.4.3 (R Core Team 2017). To test the first objective, species differences in foraging microhabitats, maneuvers, and foraging heights were tested using Bayesian categorical mixed models with a random effect of individual bird to account for repeated measures using the package brms v. 2.4.0 (Bürkner 2017). Bayesian methods were selected over frequentist methods due to the difficulty of fitting categorical mixed models in a frequentist framework. All models had uninformative, normally distributed priors with a mean of 0 and a standard deviation of 10, and all models were run with four chains each and 1,000 iterations after a burn-in of 1,000. We treated foraging height as a categorical rather than ordinal variable because there was not a monotonic effect of percent use by height. Potentially important discrete covariates of age class, sex, and study site, as well as the continuous variables of date and time, were included as fixed effects in candidate models. Model selection was performed using Pareto smoothed importance-sampling leave-one-out cross-validation (PSIS-LOO). Significance of species differences was assessed by comparing the model including the effect of species with a null model that did not, using Bayes factors of the alternative hypothesis against the null (BF_{10}). As prey availability for dead leaf clusters was not known, we reran the analysis of microhabitat use by bird species excluding dead leaf clusters and Worm-eating Warbler, the only species to forage heavily there, to estimate the percent use of different microhabitats by species to calculate expected diets.

For the second objective, adequacy of diet sampling from stomach contents was examined with taxa-accumulation curves. To quantify overlap in observed diets, as well as overlap in prey species between microhabitats, we used Pianka's (1974) overlap index and compared them to null expectations using the ra3 algorithm, a permutation test in the package EcoSimR (Gotelli et al. 2015), which randomly switches the number of consumed prey among prey taxa for each bird species. This analysis was carried out primarily for illustrative purposes to understand the level of dietary overlap, and we do not claim to test for or estimate the degree of interspecific competition from niche overlap. Additionally, we did not weight the number of consumed arthropods by the relative abundance of that prey taxon, since we were primarily interested in total dietary overlap, and not the overlap weighted by prey availability. For instance, if high overlap is driven by high consumption of a few common prey taxa by all bird species, interspecific competition could still exist, partially driven by an inability to specialize given the prey distribution. We ran a sensitivity analysis where each prey taxon was removed and the diet overlap recalculated to identify which prey taxa accounted most for overlap patterns. Even if species overlap highly in diet, small but consistent differences among species may still exist as long as overlap is not complete. To visualize variation in prey consumption among bird species, we performed nonmetric multidimensional scaling using Bray-Curtis dissimilarity on prey relative abundance. These differences were tested with a permutational multivariate analysis of variance (PERMANOVA) including site as a covariate and visualized with nonmetric multidimensional scaling (NMDS). Ordination was carried out with the package vegan (Oksanen 2018). Both the Pianka's overlap analysis and PERMANOVA were included, as they test fundamentally different things, with the former quantifying the degree of similarity and the latter testing for subtle dietary differences.

We generated expected diets for each bird species by combining available prey and microhabitat use as predicted from the Bayesian regression models. The predicted values were used instead of the raw data because of high interdependence between foraging substrates within the same foraging bout and a large range in the number of foraging attempts among foraging observations. We included only microhabitat use for this analysis since height in the canopy neither differed among bird species generally nor influenced the arthropod community (Kent et al. 2019), and differences in foraging maneuvers were substantially redundant with microhabitat use. For each of the three microhabitats, we calculated the average relative abundance of each insect taxon in each field site. For each bird species at each site, the relative abundance of each prey taxon expected in the diet was calculated by the average relative abundance of that prey taxon across the three microhabitats weighted by the predicted percent use of that microhabitat. Expected diets were not generated for Worm-eating

Warbler since we lacked data on available prey in dead leaf clusters.

As there are biases associated with any insect sampling method (Kent et al. 2019) as well as sample size limitations for some of the less common bird species, we first validated our estimates of expected diets by comparing them to the observed abundance of each arthropod in the observed diets. This analysis was performed at the level of the individual bird, with each bird’s expected diet being that expected at its field site for its species. We tested negative binomial and Poisson models using the package lme4 (Bates et al. 2015). Candidate models included expected diet, bird species and location, the random effects of individual bird and prey taxa to control for repeated measures, and the log of the total number of prey items identified in the stomach as an offset. The best model was compared to two alternative models: “methods averaged,” where the three sampling methods were averaged together without weighting by behavior, and “clip only,” in which the expected diets were predicted solely using data from branch clips. This was done to ensure the addition of behavioral data did increase the predictability of our expected diets. Both applications of sticky traps were not used in their own separate models because they failed to sample numerous arthropod taxa (see Kent et al. 2019). Additionally, a null model was run containing only the offset and random effects. These four models were compared with AIC, and goodness of fit was assessed by calculating a pseudo R^2 term for the overall model using the methods of Nakagawa et al. (2017) with the package MuMIn (Barton 2018). This analysis was repeated for each bird species individually.

To test the third objective, and having validated the legitimacy of our expected diets (Appendix S4), we next tested whether variation in foraging behavior among bird species leads to differences in diet. We calculated, for each species pair, the difference in the observed abundance and expected relative abundance of each insect taxon in the diet by subtracting bird species 1 from species 2 for both variables. As this analysis pooled individuals from the two sites, the overall expected relative abundance of each prey taxon in the diet was averaged across the two sites weighted by the number of arthropods identified in the stomach contents of that species in each site. We used linear regression to test whether the differences in expected diet predicted the differences in observed diet, but encountered fat-tailed residuals centered at zero with several high-leverage points in all models. Cube root transformation did normalize the data but did not help with leverage. As these points, being the furthest from zero, were the major prey items and/or the most abundantly available taxa, we did not want to diminish their strength as in robust regression. Instead, we used Monte Carlo regression (Gotelli and Ellison 2004), which assumes no frequency distribution, to test whether the slope of the model was significantly greater than expected from random by switching the

response values (difference in observed diet) with the predictor variable (difference in expected diet) and compared the slope of the model against that of 10,000 permutations to obtain a P value.

RESULTS

We observed 613 foraging attempts by 70 individual birds of the five species, and identified 2,429 arthropods in bird stomachs from 71 individual birds (Table 1). In addition, we collected available prey data from 141 branch clips (696 arthropods), 32 hanging sticky traps (1,438 arthropods), and 47 collar sticky traps (822 arthropods). Arthropod accumulation curves for each sampling method began to level off (see Kent et al. 2019 for details), as did those for each bird species, indicating adequate sampling to characterize both available prey and diet.

Behavioral differences

In tests involving all three aspects of foraging behavior, the addition of covariates did not appreciably improve model fit, and thus the best fit model contained only the fixed effect of bird species and random effect of individual. All models showed convergence between chains ($\hat{R} < 1.01$) and unimodal posterior distributions that had converged (Appendix S3). Bird species did not differ in foraging height ($BF_{10} = 0.002$; Appendix S2: Fig. S1); with the only potential difference among all five species being the frequent use of the lowest quartile by Black-throated Blue Warbler. Birds differed in foraging maneuver ($BF_{10} > 10^3$) with Black-and-white Warbler and Worm-eating Warbler almost exclusively gleaning, whereas the three other species also hover-gleaned, and American Redstart used all five maneuvers (Fig. 1A). Bird species differed most in microhabitat use in both the overall test and the test excluding dead leaf

TABLE 1. Sample sizes (N) for foraging behavior and observed diet.

Bird species	Stomach samples	Arthropods identified	Individuals observed foraging	Foraging actions
American Redstart	18	715	21	105
Black-and-white Warbler	6	252	9	141
Black-throated Blue Warbler	17	574	16	209
Northern Parula	18	600	15	91
Worm-eating Warbler	12	288	9	67

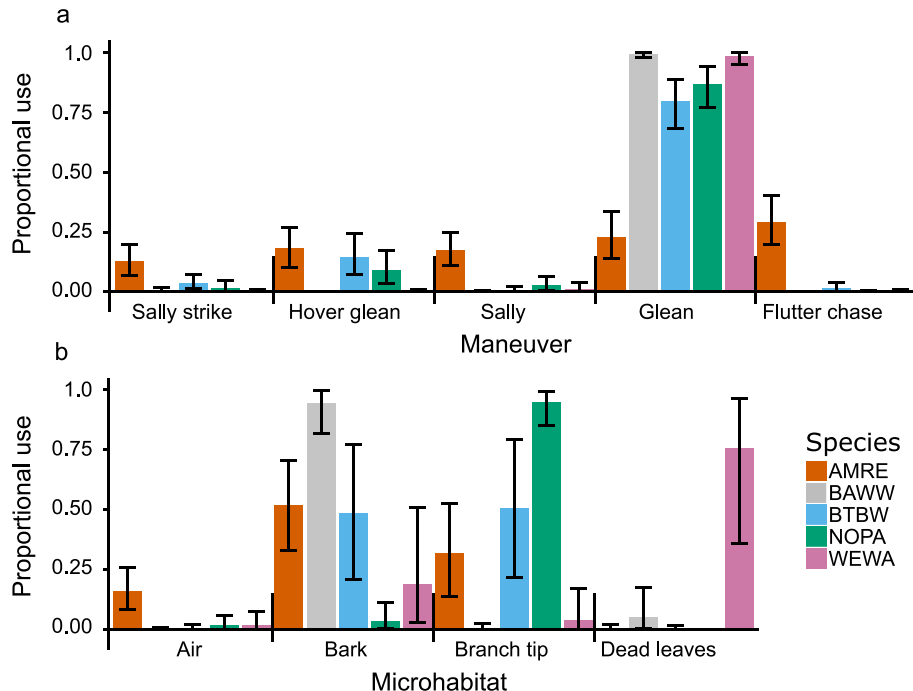


FIG. 1. Fitted estimates (and 95% credibility interval) of proportional use of different foraging behaviors as predicted by a Bayesian mixed-effect categorical regression. (a) Depicts foraging maneuvers by species, with American Redstart being more likely to use a variety of aerial maneuvers compared to the other species. (b) Compares foraging microhabitat use by bird species, in which birds differed strikingly. AMRE, American Redstart; BAWW, Black-and-white Warbler; BTBW, Black-throated Blue Warbler; NOPA, Northern Parula; WEWA, Worm-eating Warbler.

clusters and Worm-eating Warbler ($BF_{10} > 10^3$, $BF_{10} > 10^3$; Fig. 1B, Appendix S2: Fig. S2, respectively). Worm-eating Warbler was the only species to regularly forage in dead leaf clusters, which it did heavily, while the Northern Parula foraged almost exclusively at the branch tips and Black-and-white Warbler on bark substrates. Black-throated Blue Warbler and American Redstart split their foraging between bark and branch tips, with the redstart occasionally using the airspace.

Prey differences

The three microhabitats had low to moderate overlap in available prey, with Pianka's index values of 0.62 between bark and airspace, 0.54 between bark and branch tips, and 0.34 between branch tips and airspace (see Kent et al. 2019 for details on differences in arthropod communities). Most species pairs overlapped highly and significantly in observed diet (Table 2) despite distinct differences among species ($F_{4,65} = 8.74$, $P < 0.001$) with a small effect of site ($F_{1,65} = 3.29$, $P < 0.01$). That is, species have largely overlapping diets, but with small but consistent differences. This is illustrated in the ordination plot, where stomach samples from bird species show some clustering, but nevertheless separate incompletely (Fig. 2). The high level of dietary overlap resulted largely from consumption of Formicidae (Appendix S2: Fig. S3). Examination of intact ant heads in the stomach

contents revealed domination by workers of the same three ant species (*Camponotus capperi*, *Pseudomyrmex simplex*, *Pheidole jamaicensis*); and the size of ants did not differ among these bird species (Rosamond 2018).

Expected and observed differences

We found that expected diets performed well at predicting observed diets for each species, validating our methodology (Appendix S4). Pairwise differences in expected diets (i.e., behavior and available prey) significantly predicted observed differences in diet (i.e., actual resource use) in four out of six species pairs (Fig. 3). In addition, there was a similar trend, albeit not statistically significant, for American Redstart and Black-and-white Warbler. There was no trend for American Redstart and Black-throated Blue Warbler. In each comparison, this pattern was driven by only a small handful of prey taxa and only weakly explained the variance in observed diets, as shown through high-leverage points and small R^2 values.

DISCUSSION

We found that the five warbler species differed in foraging behavior as predicted, especially microhabitat where some species essentially did not overlap, and that these microhabitats overlapped little in available prey.

TABLE 2. Pianka's index of niche overlap in observed diet.

	BAWW	BTBW	NOPA	WEWA
AMRE	0.64*	0.82***	0.67*	0.43
BAWW		0.74**	0.74**	0.51†
BTBW			0.85**	0.55†
NOPA				0.80**

Notes: Asterisks denote significantly higher overlap than predicted from null analysis († $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). AMRE, American Redstart; BAWW, Black-and-white Warbler; BTBW, Black-throated Blue Warbler; NOPA, Northern Parula; WEWA, Worm-eating Warbler.

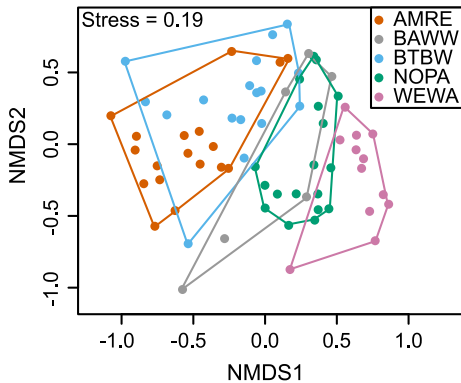


FIG. 2. NMDS biplot with Bray-Curtis dissimilarity on relative abundance depicting the arthropod community found in the stomachs of birds. Points indicate individual stomachs with accompanying minimum convex polygons.

Counter to the assumptions of seminal works involving parulid warblers, our results show high dietary overlap with only small, albeit significant differences among species. Nevertheless, we found that the small dietary differences between species pairs were weakly predicted by foraging behavior and available prey. Results thus confirm, as predicted, that differences in foraging behavior transformed into differences in resource use, and may facilitate coexistence as widely assumed. Nonetheless, since large differences in foraging behavior corresponded with only small differences in resource use, behaviors may need to be more specialized than previously recognized to limit overlap in diet.

Behavioral differences

Consistent with many past studies of these same species, birds were specialized compared to each other in their foraging behavior. We found species varied in their foraging maneuvers, but since the major difference was the use of aerial maneuvers by American Redstarts, this variation was largely reflected in foraging microhabitat, which were all in line with previous knowledge about these species. Worm-eating Warbler was unique in its heavy use of suspended dead leaves (Lack 1976, Greenberg 1987), and both Black-and-white Warbler and Northern Parula foraged mainly on bark (Kricher 2014) and branch tips (Morse 1967) respectively. American Redstarts were unique in their use of the airspace, as well as aerial foraging maneuvers (Lovette and Holmes 1995, Sherry et al. 2016a).

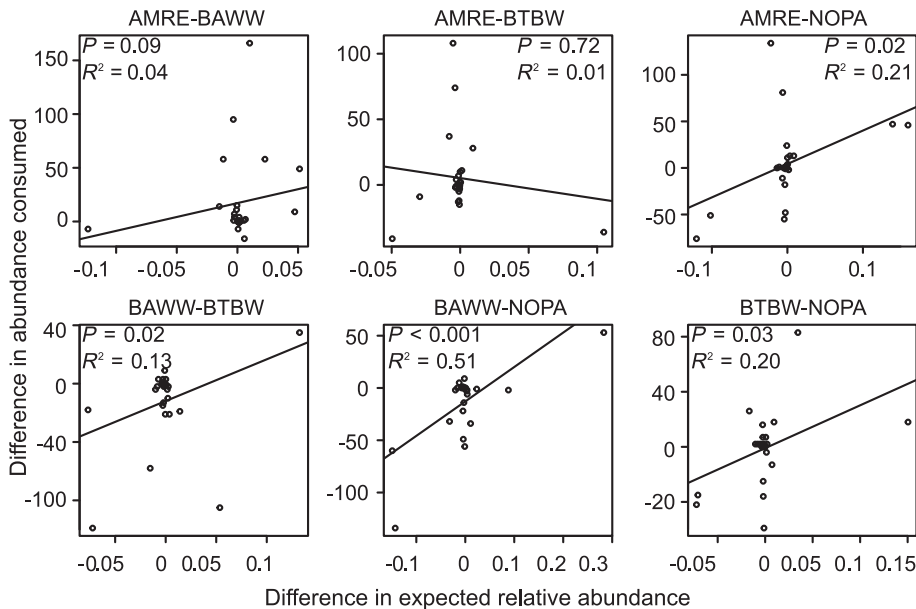


FIG. 3. Differences in expected relative abundance and abundance consumed for each species pair. In interpreting figures, a point more to the right was expected to be consumed more by the second species listed and a point closer to the top was observed to be consumed more by the second species listed. Differences in foraging microhabitat use generally explained differences in observed diets for all species pairs, with the exception of American Redstart and Black-throated Blue Warbler.

Last, Black-throated Blue Warbler divided its foraging between bark and branch tips, similar to redstart, although avoiding the airspace (Lack 1976). In addition, Black-throated Blue Warbler was the only species to use the lowest foraging height quartile regularly (Lack 1976, Holmes et al. 1986), possibly contributing some to behavioral niche partitioning. This striking agreement with past studies, coupled with the consistency of foraging behavior within species and the large number of foraging attempts observed, which led to small credibility intervals for most species, give us high confidence in our estimates of foraging behavior despite some species having fewer individuals sampled.

Prey differences

Our results show that despite the strong differences in foraging microhabitat, birds overlapped highly in resource use (diet). In addition to their comparison to the null model, these overlap values were large compared to previously published results, where a value above 0.6 is often considered high (Gordon et al. 2019); and our values were comparable to those documented by two recent studies that concluded high dietary overlap in their taxa, namely Darwin's finches (e.g. De León et al. 2014; most overlaps around 0.7) and southwestern U.S. desert bats (Gordon et al. 2019; overlaps range from 0.51 to 0.83). Notably, Northern Parula had high diet overlap with Worm-eating Warbler and Black-and-white Warbler, despite almost zero overlap in microhabitat use, and the smallest dietary overlap we detected (0.43 for American Redstart and Worm-eating Warbler) is high considering very limited overlap in their foraging microhabitat. Even with high diet overlaps, all species in the present study showed distinct dietary specializations, a pattern further illustrated through ordination, in which we found a general clustering of stomach content data points by species, although without clear separation.

Although high dietary overlaps alongside large foraging behavioral differences may sound contradictory, this situation is more typical than recognized. These dietary overlaps are consistent with findings from other sites, with similar warbler assemblages (Sherry et al. 2016b, Southwell 2018; C. M. Kent, *unpublished manuscript*). Additionally, Rosenberg (1997) describes diet overlaps > 0.9 for Amazonian dead-leaf foragers, despite distinct differences in foraging habitat, and Poulin and Lefebvre (1996) found that migrant birds, regardless of foraging behavior, consumed broadly similar prey items. As such, these results of high dietary overlap appear to be consistent across both space and time, at least during the non-breeding season. This pattern may help explain why breeding warblers tend not to coexist at small spatial scales (Lovette and Hochachka 2006), indicating that their behavioral specializations may not lead to sufficiently large differences in resource use for local coexistence.

Expected and observed diets

Our expected diets, combining foraging behavior and available prey, performed well at predicting observed diets, explaining a large portion of the variance (Appendix S4). We found that differences in expected diets between species pairs generally predicted differences in observed diets, leading us to conclude that differences in foraging behavior do lead to differences in resource use. Yet, despite large and consistent differences in foraging behavior, and the fact that behavior did well at explaining overall diets, behavior only weakly explained the small amount of dietary variation between species, with the trends being driven by a few prey taxa. That is, while a handful of prey items are uniquely available to certain bird species due to behavioral specializations, all species relied heavily on similar prey items that drove high dietary overlaps, possibly due to foraging pressures (Robinson and Wilson 1998). Given this result, a study based solely on behavior would greatly overestimate dietary separation, necessitating an examination of the nature of the prey resources before concluding that behavioral differences allow for coexistence.

For some prey taxa, especially those that move little, partitioning foraging microhabitats may in theory lead to consumption of different individuals than would be available to other predator species (Wilson 2010). However, this does not seem to be the case in our study, since the dietary overlap was mostly generated by worker ants (Formicidae), a prey taxon in which individuals are moving continuously when outside the nest, and thus likely moving regularly among microhabitats along foraging trails (Powell et al. 2011, Gordon 2012). In theory, this high overlap could be explained through optimal foraging theory, being driven by all species preferentially consuming a high-quality food source (Robinson and Wilson 1998). However, ants are a low quality prey item with little nutritional value (Razeng and Watson 2015) and are not overconsumed compared to availability as this theory would suggest (Fava 2019). This is also not a case of high overlap on a non-limited but low-quality food resource, since Formicidae are likely limited in our system. Populations of arboreal ants in Jamaica are suppressed by insectivorous birds (Johnsons et al. 2009), and supplementation experiments on Ovenbirds in Jamaica found ants to be limiting (Brown and Sherry 2006).

This finding of higher dietary overlaps than expected based on foraging substrates questions the importance of behavior-mediated dietary niche partitioning in this system, where it has long been assumed to be integral to coexistence by reducing competition for food. It is possible that although food resources are generally limiting, they may not be so severely so as to necessitate larger differences in diet. Thus, the small differences documented here, driven in part by differences in foraging behavior, may well be sufficient to allow for coexistence. We also find it likely that these species coexist in part

through some other mechanism, such as partitioning niches along an axis other than foraging behavior or some alternative coexistence mechanism entirely. It is also theoretically possible that the species under study do not compete, thus not needing to partition resources. However, the combination of known intraspecific competition and food limitation documented in some of these species supports ongoing interspecific competition (see Dhondt 2012, Prins 2016), as do past studies of competition in many of these warblers (e.g., Greenberg and Ortiz 1994, Sherry et al. 2016b), necessitating some coexistence mechanism. Additionally, despite selecting a field site and sampling period to maximize niche partitioning and finding few high-quality prey items in our samples of available prey, it is possible that in different years, under worse conditions, species could overlap less in diet. However, regardless of the current resource availability, we found very large, sometimes complete, separation in foraging behavior between species, indicating a limited ability to further partition the habitat.

These findings also leave unresolved how, if not for resource partitioning, these differences in foraging behavior evolved, since intermediate evolutionary stages in terms of foraging behavior would likely correspond with even less dietary separation than our study documented. Potentially, differences evolved separately and independently from one another as unique solutions to increase foraging efficiency (Robinson and Holmes 1982) in a food-limited system dominated by prey that are highly mobile, of low nutritional value, or otherwise difficult to consume (Johnson et al. 2005).

We acknowledge two potential shortcomings of the present study, but argue that they would not fundamentally alter our conclusions. First, several biases are inherent in generating our expected diets. All insect sampling methods have potential biases compared to the prey community available to the predator. Specifically, the collar sticky traps directed at bark-dwelling arthropods are likely biased toward Diptera and other flying insects (Kent et al. 2019), and both sticky trap methods may contain a nocturnal bias, since they were left exposed day and night. Additionally, we characterized foraging behavior of Black-and-white Warblers based on a relatively small number of individuals, although there were a large number of observations. However, our findings are consistent with past work involving this species (Lack 1976), and the low variation in foraging behaviors we observed for this species (126 attempts on bark, 2 on branch tips, 13 on dead leaves) allowed for confidence in the predictions, shown by small credibility intervals for this species (Fig. 1B). Moreover, in validating our expected diets, we found that they explained a large percentage of the variance in actual diet, and performed better than several alternative estimates (Appendix S4), indicating that neither insect sampling methodology, nor sample sizes inordinately bias results. That is, our methodology, acknowledging any potential flaws, performed well at explaining observed diets overall, but

performed less well at explaining dietary differences between species.

Second, we were unable to generate expected diets for Worm-eating Warbler, but past research on the prey available in dead leaf clusters allows us to make relevant inferences. Blattodea and Orthoptera were the most unique prey of Worm-eating Warblers in our observed diets. Dead leaf clusters in Peru were dominated by these two taxa (Rosenberg 1997), and work from Windsor, Jamaica found that Orthoptera were disproportionately common in dead leaf clusters (Greenberg 1987). Thus, we expect that Worm-eating Warblers would show similar patterns as the other species and species pairs in respect to their observed and predicted diets.

CONCLUSIONS

To the best of our knowledge, this study is the first to directly compare differences in foraging behavior, available prey, and observed diet, and our results raise important questions about the relationships among these variables. Specifically, it is unclear how, when, and if behavioral specializations correspond to resource partitioning, and under what circumstances behavior contributes to coexistence: a widely held assumption in the literature. Overall, we found mixed support for behavioral niche partitioning, since large differences in foraging behavior translated into only small differences in actual diets. Regardless of whether or by what mechanism our focal species coexist, this study illustrates the potential pitfalls of relying on resource proxies, such as foraging behavior, to study niche partitioning. Since species are almost certain to contrast in some way, biologists must be critical when testing niche partitioning and consider alternative explanations. Lastly, it is unclear if these smaller differences in foraging behavior are enough to fully explain coexistence or why these differences evolved. If we conclude that minor differences in diet generated by major differences in foraging behavior are evidence of niche partitioning, then further research is necessary to understand how these patterns evolved, since less substantial differences in foraging behavior would generate even smaller differences in resource use.

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