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Dietary opportunism, resource partitioning, and consumption of coffee berry borers by five species of migratory wood warblers (Parulidae) wintering in Jamaican shade coffee plantations

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ABSTRACT. Diets reflect important ecological interactions, but are challenging to quantify for foliage-gleaning birds. We used regurgitated stomach samples from five primarily insectivorous species of long-distance migrant warblers (Parulidae) wintering in two moderate-elevation shade coffee farms in Jamaica to assess both foraging opportunism and prey resource partitioning. Our results, based primarily on 6120 prey items in 80 stomach samples collected during a one-week period in March 2000, confirm opportunism. The diets of all five warblers, including American Redstarts (*Setophaga ruticilla*), Black-and-White Warblers (*Mniotilta varia*), Black-throated Blue Warblers (*S. caerulescens*), Northern Parulas (*S. americana*), and Prairie Warblers (*S. discolor*), overlapped strongly based on consumption of the same prey types, even many of the same prey species (4 of 10 interspecific overlaps >0.9, range = 0.74–0.97). Moreover, all five species fed on similarly small, often patchily distributed prey, including coffee berry borers (*Hypothenemus hampei*; Coleoptera, Curculionidae). Nonetheless, permutational multivariate analysis of variance also revealed that the diets of these species differed significantly, primarily with respect to prey mobility (winged vs. sessile); American Redstarts fed on the most mobile prey, and Northern Parulas on the least mobile prey and a relatively restricted set of prey taxa compared to the other four species of warblers. Overall, our results suggest both dietary opportunism consistent with a migratory life-history, and interspecific resource partitioning consistent with differences in morphology and foraging behavior during a food-limited season. Having provided evidence of the three necessary conditions, namely intraspecific competition, resource limitation, and interspecific overlap in resource use, the results of our study, in combination with those of other studies, also provide evidence of interspecific competition among wintering migrant insectivores. We thus argue that diffuse interspecific exploitative food competition may be more important than previously recognized.

RESUMEN. **La dieta oportunista, la repartición de recursos, y el consumo de perforadores de la baya del café por cinco especies de mosquitero silbadores migratorias (Parulidae), invernantes en las plantaciones de café de sombra en Jamaica.**

Las dietas reflejan importantes interacciones ecológicas, pero son difíciles de cuantificar para las aves que depredan los artrópodos en el follaje. Para evaluar el forraje oportunista y la repartición de recursos, se utilizaron muestras regurgitadas del estómago de cinco especies, los cuales fueron reinitas (Parulidae) principalmente insectívoros y migrantes de larga distancia invernados en dos fincas de café de sombra en elevación moderada en Jamaica. Nuestros resultados, basados principalmente en 6120 presas de 80 muestras regurgitadas durante un período de una semana en marzo de 2000, confirman el comportamiento de forraje oportunista. Las dietas de las cinco reinitas (incluyendo *Setophaga ruticilla*, *Mniotilta varia*, S. *caerulescens*, *S. americana*, y *S. discolor*) se solapaban especialmente basada en el consumo de los mismos tipos de presas, además, consumieron muchas de las mismas especies de presa (4 de 10 interespecífica se superpone >0.9, rango = 0.74–0.97). Por otra parte, las cinco especies se alimentaban de presas igualmente pequeña, a menudo distribuidos irregularmente, incluyendo los perforadores de la baya del café (*Hypothenemus hampei*, Coleoptera, Curculionidae). Sin embargo, el análisis de varianza multivariado con permutaciones también reveló que la dieta de estas especies difieren significativamente, sobre todo en relación con la movilidad de la presa (alada contra sésiles); *S. ruticilla* se alimentaron de las presas más móviles, y *S. americana* se alimentaron de la presas menos móviles y un conjunto relativamente limitado de taxones de presas en relación con las otras

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cuatro especies de reinitas. En general, nuestros resultados sugieren tanto que la dieta oportunista es consistente con un ciclo vital migratorio, y la repartición de recursos interespecífica es consistente con las diferencias en la morfología y el comportamiento de forrajeo durante una temporada limitada de alimentos. Haber proporcionado pruebas de las tres condiciones necesarias, a saber, la competencia intraespecífica, la limitación de los recursos, y la superposición interespecífica en el uso de los recursos, los resultados de nuestro estudio, en combinación con las pruebas de otros estudios, también proporcionan evidencia de la competencia interespecífica entre migrantes invernantes insectívoros. Por tanto, argumentamos que la competencia interespecífica por explotación de presa puede ser más importante que se había reconocido.

Key words: diet, ecosystem service, *Hypothenemus*, interspecific competition, intraspecific competition, *Mniotilta*, *Setophaga*

Animal diets inform us about many ecological relationships, from competitive and predator-prey interactions to community structure and ecosystem services. The ecological relationships of migratory birds are particularly challenging to study because of their opportunistic life-histories, characterized by seasonally variable habitats, prey types, feeding substrates and microhabitats, predators, and other ecological constraints. Breeding, migration stopover, and wintering locations have different competitive communities, raising the question of how diets vary among species, particularly during wintering periods when foods are likely to be most limiting. The Greater Antilles Islands, for example, are a major wintering region for many species of migratory and resident wood warblers (Parulidae) that are largely insectivores (Toms 2011), all of which potentially compete for food. However, studies of diffuse competition among multiple species are almost non-existent.

Considerable evidence supports the potential for interspecific competition and niche partitioning among non-breeding migrant birds. First, intraspecific competition for food implies interspecific competition among species consuming similar prey (Dhondt 2011), and evidence supporting intraspecific competition for limiting resources is abundant, including indirect and inferential evidence (Baillie and Peach 1992, Katti and Price 1996, Sillett et al. 2000, Strong and Sherry 2000, Sherry et al. 2005, Norman and Peach 2013) and experimentation (Studds and Marra 2005, Brown and Sherry 2006, Smith et al. 2010, Cooper et al. 2015). Sexual habitat segregation, often involving social dominance hierarchies, is also widespread and interpreted as a consequence of intraspecific competition for food and/or habitat (Greenberg 1986, Marra and Holberton 1998, Marra 2000). Second, overt aggression involving apparent interspecific competition for food is well documented among wintering migrants (Willis 1966, Greenberg 1986, Greenberg et al. 1993, 2000, Greenberg and Salgado Ortiz 1994). However, in the Afrotropical system, and probably throughout tropical regions, interspecific territoriality and aggression are relatively rare among migrant species and between migrants and residents (Salewski and Jones 2006), so the extent to which there might be diffuse interspecific competition involving non-breeding migrant birds that do not interact via direct aggression is unclear. Third, some evidence supports resource partitioning by wintering migrant birds (MacArthur 1958, Strong 2000), and Lack (1976) argued that migratory birds wintering in Jamaica partitioned resources as a result of interspecific competition, but lacking information about diets, inferred ecological relationships from species-characteristic foraging behaviors and habitat, both indirect indicators (Sherry et al. 2005).

Alternatively, consideration of potential interspecific competition of migrants with year-round resident tropical species leads to the expectation of similarity in the diets of wintering migrants. Specifically, the Breeding Currency Hypothesis proposes that year-round residents should predominate in habitats with large prey suitable for reproduction (breeding currency), outcompeting and relegating migrants to habitats with less profitable subsistence prey (Greenberg 1995, Johnson et al. 2005; see also Poulin and Lefebvre 1996). Accordingly, migrants should feed opportunistically on such prey, which should in turn increase the extent of overlap in their diets and the potential for interspecific competition. Bell (2011:93) argued more directly that migration is inherently opportunistic, and migrants should thus tend to rely on "non-buffered" prey types, defined as "active insects, particularly when volant or in swarms, and fruiting or flowering trees and shrubs." Thus, the evolution of character displacement may be constrained in migrants because of their need to maintain foraging plasticity year-round (Toms 2011). Given these arguments, the diets of migrants should not diverge during the winter, but, rather, should converge, especially when co-occurring and sharing similar available prey. Wiens (1993) argued that whether species diverge or converge in their feeding niches should depend on the degree of food limitation, i.e., the extent of interspecific competition.

Shaded coffee farms facilitate the study of resource use by multiple species because of their habitat simplicity and productivity. The simplicity arises from the presence of just two layers (coffee plants and shade trees of typically one or a few species; Wunderle and Latta 2000) that should restrict the range of resources and microhabitats available to foragers. These farms are also likely productive for birds, as suggested by the abundance of resident and migrant birds and other wildlife (Sherry 2000, Donald 2004, Philpott et al. 2008). Moderate-elevation plantations in central Jamaica host abundant wintering populations of five species of migratory, foliage-gleaning wood warblers (Parulidae, Johnson and Sherry 2001), including American Redstarts (*Setophaga ruticilla*), Black-and-white Warblers (*Mniotilta varia*), Black-throated Blue Warblers (*S. caerulescens*), Northern Parulas (*S. americana*), and Prairie Warblers (*S. discolor*) (Table 1). These migrants show functional responses to winter arthropod abundance, with local populations increasing in response to greater concentrations of prey at multiple spatial scales, from different shade tree species in coffee plantations (Johnson 2000a) to diverse habitats across Jamaica (Johnson and Sherry 2001).

We hypothesized that wintering migratory warblers should thus both feed opportunistically, consistent with a migratory life-history and particularly in structurally simple winter habitats like shaded coffee plantations, and also partition resources that are often limiting in non-breeding habitats. Specifically, we tested four predictions using diets of five sympatric species of migratory warblers in shaded coffee plantations in Jamaica by largely controlling for habitat and food availability: (1) overlap of prey taxa should be considerable due to foraging opportunism, (2) different migrant species should have different diets

Table 1. Migratory bird species foraging in Jamaican shade coffee plantations, dates of samples, and sample sizes (number of stomach samples in parentheses). Italicized numbers refer to March 2000 subsample used in quantitative analyses of species similarities and differences.

Species	Year and month sampled (*N*)	Number of stomachs sampled	Total animal prey items	Average number of. items/sample
American Redstart	1997: January (2), February (4), April (1), November (2); 1998: March (5)	14	558	39.9
	2000: March	*22*	*1353*	*61.5*
Black-and-white Warbler	2000: March	*13*	*1264*	*97.2*
Black-throated Blue Warbler	2000: March	*23*	*1809*	*78.7*
Northern Parula	1997: January (1), February (6)	7	495	70.7
	2000: March	*11*	*886*	*80.5*
Prairie Warbler	1996: November (2); 1997: February (6)	8	460	57.5
	2000: March	*11*	*808*	*73.5*
Totals (all species)	Non March 2000	29	1513	52.2
	March 2000 samples	*80*	*6120*	*76.5*
	All samples and all years	109	7633	70.0

(i.e., partition resources) due to foraging behavioral and morphological differences, such that the most distinctive foragers, that is, American Redstarts that tend to feed relatively aerially, and Black-and-white Warblers that often forage like tree-creepers on branches and boles (Lack 1976, Morse 1989, Keast et al. 1995, Kricher 1995), should also have the most distinctive diets, (3) diets of males and females should, as a corollary of (2), differ in species where the two sexes forage differently, i.e., American Redstarts and Black-throated Blue Warblers in coffee plantation types and strata (Wunderle and Latta 1996, MD Johnson, pers. obs.) and, (4) as a corollary of first prediction, all five species should feed opportunistically on coffee berry borers (*Hypothenemus hampei*: Coleoptera, Curculionidae), small, but patchily abundant prey and an economically important pest in coffee plantations (Vega et al. 2003, 2009, Jaramillo et al. 2011).

METHODS

Study sites. Field work took place at two moderate-elevation, shaded coffee plantations in Clarendon Parish, central Jamaica, West Indies: Baronhall (18°13′N, 77°22′W; 550 m elevation) and Coleyville Farm (18°11′N, 77°22′W; 880 m elevation). Both plantations were located on hilly terrain, and surrounded by native lower montane vegetation (wet limestone forest).

Baronhall, in the Cave River Valley, was a 90-ha plantation during our study from 1996 to 2000. Coffee plants (*Coffee arabica* var. *typica*) were in rows and pruned lightly every year during the dry season (January–March), although a more severe pruning occurred in 1998. Two insecticides (Basudin and Thiodan) and a fungicide (Bayleton) were applied to affected coffee plants during April and May and again during June and July. Shade trees (*Inga vera*) provided 20–70% cover depending on their size and height (4–9 m; greater cover with greater height). *Leucaena* sp. and *Cupania* sp. occurred along roadsides. We sampled birds on a 5-ha plot centered in the plantation (typically >100 m from the nearest edge) near a small (<5 ha) pond within 500 m of where birds were captured. Surrounding habitats included mixed pastures and second growth wet forest.

Coleyville Farm was a 22-ha, relatively young (10 years old) plantation, shaded by banana (*Musa* sp.) and *Inga vera*, most of which were <8 m in height and heavily pruned to provide light (20–60%) canopy cover. The site also contained a few other shade trees such as *Psidium guajava* and *Persea americana*, and one large (>30 m) *Terminalia latifolia*. Coffee plants on this farm were pruned to remain short and encourage lateral growth, so the coffee layer was denser than at Baronhall. The farm was irregularly shaped along the lower slopes of surrounding hills dominated by second growth wet forest and thickets, so sampling locations were typically not far from a farm edge (often <100 m). We did not follow individual birds at either farm to determine the extent of foraging outside the coffee habitat, but radio-telemetry results suggest that most warblers in Jamaican coffee farms, even large farms, spend at least some time along farm edges and in adjacent habitats (Campos 2012).

Diet sampling. Our five focal species are all long-distance migrants that coexist during the non-breeding season throughout much of Jamaica, particularly at lower to mid-elevations (A. Sliwa and TW Sherry, unpubl. data), and are widespread throughout the Greater Antilles (Wunderle and Waide 1993, Toms 2011). Individuals of the five warbler species (Table 1) were captured in the coffee farms by passive mist-netting. We used ten 12-m, 30-mm-mesh mist-nets near the ground between coffee rows and run for 6 h per day, primarily during the dry season (January–March). Neither lures nor net placement were used to target particular birds or their territories. Most birds were captured in the morning when foraging actively and likely to have full stomachs, but ~25% of birds were captured between 12:00 and 18:00. Although samples were collected in four different years (1996, 1997, 1998, and 2000) and in every month from November–April (except December), most (80 of 109, 73%) were collected during a 1-week period from 11–17 March 2000 (Table 1), during peak dry season. To compare and contrast diets, we used only the March 2000 samples to control for potential temporal variation in available food, except where otherwise noted by reference to data from all time periods.

Most samples were obtained using the emetic antimony potassium tartrate to induce regurgitation; four entire stomach samples were collected from individuals that died ($N = 1$ Black-and-white Warbler, 2 Black-throated Blue Warblers, and 1 Prairie Warbler) after being given the emetic (Johnson et al. 2002). Dosage was dependent on body mass, i.e., 0.008 ml emetic per gram body mass. Distilled water was added to the emetic to make a 0.1 ml dose. The solution was administered through a vaseline-lubricated catheter tube attached to a syringe. After emetic administration, birds were placed in a small, dark cardboard box lined with waxed paper for 15 min, after which they were released and regurgitated samples transferred by scalpel to individual vials with 70% ethanol.

Identification of prey items in samples. Samples were examined in alcohol in 10-ml plastic petri dishes using a binocular dissecting microscope (Olympic SZH, Olympus Corp., Tokyo, Japan) at magnifications of 75–640×. Samples were inspected for occasional intact arthropods, and diagnostic prey fragments, such as whole or partial heads, beetle elytra, mandibles and other mouthparts, legs, and wings. For most arthropods, at least some part of the body is sclerotized or otherwise hard enough to persist in the stomach, so many arthropods could be identified using these fragments. However, most Dipterans (flies) and adult Lepidopterans (moths) are largely soft-bodied and are potentially poorly represented in stomach samples compared to diets, leading to biased samples (Rosenberg and Cooper 1990). Nonetheless, soft-bodied arthropods are preserved well enough to distinguish the diets of some species (e.g., Sherry 1984) so we assumed that we were able to, but also tested our ability to, detect real dietary differences.

Counts of prey eaten were based on diagnostic arthropod parts identified as precisely as possible, usually to order, but occasionally to morphospecies. We determined the fewest possible individual arthropods that could account for all body parts present per morphospecies (e.g., half the number of elytra or mandibles). We learned over time how to distinguish and identify particular parts (e.g., mandibles of larval Neuroptera or Psocoptera, and heads of Thysanoptera) by finding an occasional largely intact specimen or by dissecting the few voucher insects available, for example, a particular yellowish psyllid (Hemiptera) or coffee berry borer, and we examined every stomach sample at least three times to ensure consistency. Only samples with ≥ 10 prey were included in our analyses based on the assumption that smaller samples indicated inactive foragers that could potentially introduce bias.

Data analysis. We categorized arthropods both taxonomically and functionally for analyses. Every arthropod order was considered a distinct category, but we recognized sub-categories for some orders either because of diagnosability in our samples or because of distinctive prey behaviors that might affect foraging birds. We placed Hemipterans into three categories, including Hemiptera *sensu strictu* (true bugs), the one species of yellow Psyllidae (old order Homoptera, a common species particularly in the *Inga* shade trees), and other Hemiptera (Stenorhyncha). Two categories of Coleopterans included coffee berry borers (easily diagnosable, important economically, and probably occurring just in coffee plants) and all others. Hymenoptera included ants (Formicidae; almost certainly all workers, based on the absence of ant wings from the samples) and all others, mostly winged parasitoids (including Braconidae and Chalcidoidea). Lepidoptera were categorized as either larvae (caterpillars) or adults (all moths). Diptera included Chironomidae (multiple species, based on wing venation), muscoid flies (strong fliers, including calyptrate and acalyptrate muscoids), and all others. Those few prey not identified to order, but still recognizable as arthropods ($N = 137$ prey items, or 1.8% of the total; 0.6–5.1% depending on bird species), were included in our total sample size and in analyses involving all samples, but not in determination of diet overlap or other statistical analyses.

We calculated diet overlap using stomach samples collected in March 2000 (both farms combined) using Pianka's Index (1981) and, for comparison, we also calculated diet overlap using all samples. We tested dissimilarity in diets using just the March 2000 data, using the package "vegan" (Oksanen et al. 2012) in R (R Development Core Team 2010). We compared the performance of

Jaccard (Ružička), Bray-Curtis (Steinhaus), Chao, and Kulczyński dissimilarities. All were found to perform similarly. However, because Jaccard (Ružička) dissimilarity has the same rank order as Bray-Curtis, but better metric properties that more effectively preserve the relationships among the points in multidimensional space (Oksanen 2011, Oksanen et al. 2012), we selected it for use in subsequent analyses:

$$\text{Jaccard Index} = 2B/(1 + B),$$

where B = Bray-Curtis dissimilarity, d;

$$d[jk] = (\Sigma_i \text{abs}(x[ij] - x[ik]))/(\Sigma_i(x[ij] + x[ik])),$$

where j and k represent bird species j and k, abs = absolute value, and x_{ij} and x_{ik} = relative proportion of prey taxon i for bird species j and k, respectively. Ordination was performed using non-metric multidimensional scaling (NMDS) with a square-root transformation to better normalize count data and Wisconsin double standardization (insect taxa divided by maxima and bird species standardized to equal total). The best solution had three dimensions with a stress of 18.5%.

To assist in visualization and interpretation of species and sex relationships in diet space, we plotted both (1) the 95% confidence ellipses based on the standard deviation of the weighted averages from the centroid (ordiellipse; Oksanen et al. 2012), and (2) the convex polygons (ordihull) of each species to circumscribe total diet space. We interpret non-overlapping confidence ellipses of particular species pairs to indicate statistically significant differences in their centroids. We used function "adonis" (Oksanen 2011), a permutational Multivariate Analysis of Variance (PERMANOVA, the term used henceforth), to test for dietary differences among bird species and between sites (testing the hypothesis of no difference among centroids within multivariate diet space; Anderson and Walsh 2013). For this analysis, we ran 5000 permutations with bird species, site, and the interaction of bird species-by-site as predictor variables. We then used homogeneity of variances (function "betadisper"), a multivariate analog of Levene's test of equality of variances, using median distances to the centroid to assess species differences in the variability of the diet niche. Finally, we repeated these analyses separately for American Redstarts and Black-throated Blue Warblers, the two species with adequate and reasonably balanced sex-specific samples to determine if diet space differed by sex.

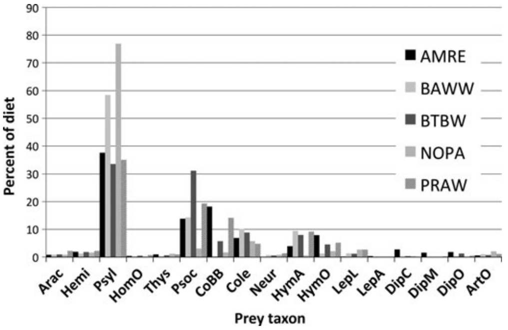

Fig. 1. Percent use of 17 prey categories by five species of wood warblers wintering in Jamaican shade coffee farms based on samples from March 2000. AMRE, American Redstart; BAWW, Black-and-white Warbler; BTBW, Black-throated Blue Warbler; NOPA, Northern Parula; and PRAW, Prairie Warbler. Codes for arthropod taxa: Arac = Arachnida (spiders), ArtO = other arthropods than all the other listed categories, HymA = Hymenoptera family Formicidae (ants), Cole = Coleoptera (beetles except coffee berry borer), CoBB (coffee berry borer beetle), DipC = Diptera family Chironomidae (flies, specifically midges), DipO =Diptera (flies) other than midges or muscoid flies, DipM = Diptera Muscoid (house flies and other robust-bodied flies), Hemi = Hemiptera *sensu stricto*, Homo = Homoptera other than psyllids, HymO = Hymenoptera except ants (mostly small parasitoid wasps from a variety of families), LepA = Lepidoptera (moth) adults, LepL = Lepidoptera (moth) larvae or caterpillars, Neur = Neuroptera (larval green lacewings = Chrysopidae), Psoc = Psocoptera (bark lice), Psyl = Homoptera family Psyllidae (psyllids), and Thys = Thysanoptera (thrips).

RESULTS

For all time periods combined, we obtained 109 samples from the stomachs of five species of warblers (range = 13–36 samples) that included 7633 identifiable arthropods, or an average of 70.0 items per sample (range = 53.1–97.2; Table 1). The March 2000 sample contained 6120 identifiable prey in 80 samples, with an average of 76.5 items per sample (range = 11 samples for Northern Parulas and Prairie Warblers to 23 for Black-throated Blue Warblers).

Data from all time periods included arthropods representing 13 orders. In addition to the nine orders in Fig. 1, we identified arthropods in the orders Pseudoscorpionida, Collembola, Orthoptera, and Isoptera. The number of stomach samples needed to reach an asymptote for number of prey taxa was ~10–15, similar to our actual sample sizes (Table 1; KA Williams, unpubl. rarefaction curves; Chao et al. 2009).

Samples from March 2000 contained the same prey morphospecies for all five warbler species. The most frequent recognizable morphospecies were a pale, yellow-bodied psyllid (Hemiptera), a small blackish Thysanopteran, adult and nymph Psocopterans (probably representing more than one species based on morphological variation), a blue-black iridescent chrysomelid Coleopteran, coffee berry borers, larvae of a green chrysopid Neuropteran, two species of similar-sized worker caste ants with distinctive reddish head capsules (0.4–0.5 mm wide), and chironomid Dipterans. Psyllid Hemipterans were the most frequent prey in samples from all five warbler species, and Psocopterans were the second most abundant prey for three of the five warbler species (Fig. 1). Three warbler species (American Redstart, Black-throated Blue Warbler, and Prairie Warbler) also had coffee berry borers as 5–10% of their prey, all five had >6% other beetles, all except American Redstarts had close to 10% ants, and three of the species had >5% other Hymenopterans. Arthropod taxa that represented <2% of the prey in the diets of all five warbler species included Arachnida, Hemiptera, Thysanoptera, and Neuroptera (Fig. 1), and Lepidoptera larvae were consistently <3% of prey items in stomach samples.

Diet overlap. Interspecific diet overlap, which can vary from 0 to 1, was uniformly high in March 2000 (Table 2), with half the possible pair-wise overlaps ≥0.895. The least overlap was between Northern Parulas and Black-throated Blue Warblers (0.74). Inclusion of the unidentified arthropods category (ArthOth) in the overlap calculations had little effect. Using data from all time periods, including the March 2000 samples (Table 2), the extent of overlap changed little. Overlap between Northern Parulas and Prairie Warblers changed the most, increasing from 0.830 to 0.927. Overlap between American Redstarts and the other four species of warblers decreased slightly using this larger sample, but for most of the other species, the amount of overlap tended to increase. Overall, our data do not support the idea that overlap increased (was biased high) because the birds were consuming one or a few abundant prey types during this particular 1-week sampling period.

Species differences. Our March 2000 samples also revealed some significant differences in the diets of the five species of warblers (PERMANOVA $F_{4,79} = 2.7$, $P = 0.0002$; Table 3A). Prey consumed at the two coffee farms also differed (PERMANOVA

Table 2. Half matrix of interspecific diet overlaps based on pooled prey contents by species for the March 2000 samples (coffee farms pooled), the same samples as used in the analyses of species dietary differences. Parenthetical overlap values are based on data from all time periods (Table 1), including the March 2000 samples.

	American Redstart	Black-and-white Warbler	Black-throated Blue Warbler	Northern Parula
Black-and-white Warbler	0.895 (0.854)			
Black-throated Blue Warbler	0.884 (0.854)	0.872 (0.872)		
Northern Parula	0.860 (0.820)	0.965 (0.973)	0.744 (0.771)	
Prairie Warbler	0.972 (0.929)	0.907 (0.966)	0.948 (0.924)	0. 830 (0.927)

Table 3. Results of PERMANOVA testing for differences among species in diet niche space, and tests for homogeneity of multivariate variances (dispersion in diet space) based on data from March 2000.

A. Analysis of variance (PERMANOVA) in diet space for all birds based on 5000 permutations

	df	Sum of squares	Mean sum of squares	*F*-statistic	R^2	*P*
Bird species	4	2.91	0.73	2.7	0.12	0.0002
Site (farm)	1	0.54	0.54	2.0	0.02	0.02
Bird species × site	4	1.23	0.31	1.1	0.05	0.24
Residuals	70	19.14	0.27		0.80	
Totals	79	23.81			1	

B. Analysis of variance (PERMANOVA) in diet space for just males based on 5000 permutations

	df	Sum of squares	Mean sum of squares	*F*-statistic	R^2	*P*
Bird species	4	2.58	0.64	2.4	0.17	0.0002
Site (farm)	1	0.33	0.33	1.2	0.02	0.23
Bird species × site	4	1.11	0.28	1.0	0.07	0.39
Residuals	41	10.99	0.27		0.73	
Totals	50	15.01			1.0	

C. Analysis of bird species homogeneity of variances in diet space for all birds

	df	Sum of squares	Mean sum of squares	*F*-statistic	*P*
Groups (bird species)	4	0.39	0.1	5.2	0.0009
Residuals	75	1.42	0.02		

D. Analysis of bird species homogeneity of variances in diet space for just males

	df	Sum of squares	Mean sum of squares	*F*-statistic	*P*
Groups (bird species)	4	0.38	0.1	4.4	0.0004
Residuals	46	1.0	0.02		

$F_{1,79} = 2.0$, $P = 0.02$), although the interaction between bird species and sites was not significant. Differences among species in diet space are also illustrated by the 95% confidence ellipses for the species centroids (Fig. 2). The diet of American Redstarts differed significantly (non-overlapping 95% confidence ellipse for the species centroids) from those of all other species except Prairie Warblers, and the diets of Prairie Warblers and Black-throated Blue Warblers differed significantly from that of Northern Parulas. Prairie Warblers and Black-throated Blue Warblers occupied similar diet space, as did Black-and-white Warblers and Northern Parulas.

Because our March 2000 samples were unbalanced by sex, particularly for Northern Parulas (10 male, 1 female) and Prairie Warblers (9 male, 2 female), we re-analyzed the data using only male samples (range = 6–14 samples per species). Differences among species remained significant (PERMANOVA $F_{4,46} = 4.4$, $P = 0.004$), but the site (farm) difference was no longer significant (Table 3B).

Ordination of arthropod prey taxa in the space defined by the diets of the five species of warblers (Fig. 2) allowed us to infer dietary differences. Diets differed primarily along a gradient from Dipterans (Muscoid flies, Chironomid flies, and other flies), Hymenopterans (other than ants), and coffee berry borers (in the upper left portion of the graph corresponding with high NMDS2 and low NMDS1 scores) to Lepidoptera larvae, Neuropterans (green lacewing larvae = Chrysopidae), and, to a lesser extent, Psocopterans and Psyllidae in the lower right (Fig. 2). Differences among species corresponded (see

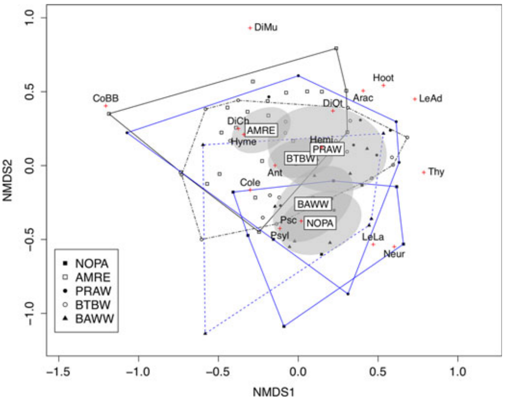

Fig. 2. Nonmetric Multi-Dimensional Scaling with 95% confidence ellipses for species centroids (based on weighted averages), and hulls (convex polygons for all observations per species), based just on March 2000 data. NOPA, Northern Parula; AMRE, American Redstart; PRAW, Prairie Warbler; BTBW, Black-throated Blue Warbler; and BAWW, Black-and-white Warbler. See Fig. 1 legend for arthropod taxa codes.

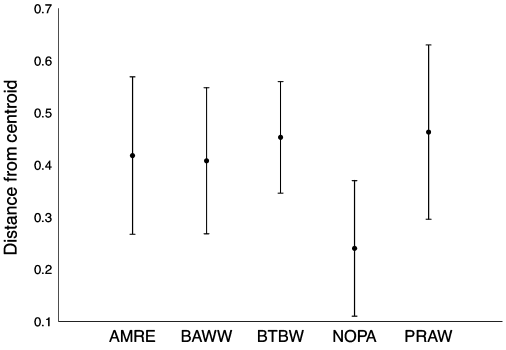

Fig. 3. Species comparisons in diet niche variability (mean ± SD) based just on March 2000 data. AMRE, American Redstart; BAWW, Black-and-white Warbler; BTBW, Black-throated Blue Warbler; NOPA, Northern Parula; and PRAW, Prairie Warbler.

Discussion) with a gradient from strong flying insects (especially Dipterans and non-ant Hymenopterans, i.e., parasitoid adult wasps) requiring predators adapted to attack and pursuit, to weaker flying (or sessile, possibly cryptic) prey requiring more searching behavior by the predators (including Lepidoptera larvae, i.e., moth caterpillars, and Neuroptera larvae).

Based on the March 2000 samples, the five warbler species differed in diet heterogeneity (homogeneity of multivariate dispersions test; $F_{4,75} = 5.2$, $P = 0.001$; Table 3C). Pairwise differences between species (Tukey's HSD test) showed significantly smaller variance in diet for Northern Parulas than for American Redstarts (adjusted $P = 0.007$), Black-and-white Warblers ($P = 0.03$), Black-throated Blue Warblers ($P = 0.0006$), and Prairie Warblers ($P = 0.003$) (Fig. 3). We re-ran this analysis with just males, and obtained nearly the same result (overall PERMANOVA $F_{4,46} = 4.4$, $P = 0.004$, Table 3C). The exception was that the difference in the dispersion in diet between Northern Parulas and Black-and-white Warblers was no longer significant (Tukey's HSD adjusted $P = 0.55$).

Heterogeneity in multivariate dispersion—of species' diets in our case (Northern Parulas the odd one, Fig. 3)—can weaken conclusions about PERMANOVA test results (Anderson and Walsh 2013). To assess the robustness of our result indicating that our five focal species differed in prey types consumed, we re-ran statistical tests without Northern Parulas. The four other species remained significantly divergent in diet (PERMANOVA: $F = 1.8$, $P = 0.003$), retained almost identical patterns of overlap and dispersion as shown by the original NMDS in Fig. 2, and did not differ in diet variability (homogeneity of multivariate dispersions test; $F_{3,65} = 0.6$, $P = 0.63$).

Sex differences. We had sufficient sample sizes from March 2000 for American Redstarts ($N = 14$ male, 7 female) and Black-throated Blue Warblers ($N = 11$ male, 12 female) to test for sex differences in diet. For American Redstarts, we found no difference in either prey types (PERMANOVA $F_{1,20} = 0.4$, $P = 0.9$) or prey variance (test for homogeneity of multivariate dispersions, $F_{1,20} = 0.4$, $P = 0.5$). However, for Black-throated Blue Warblers, we found a difference between the sexes in prey types (PERMANOVA $F_{1,19} = 1.8$, $P = 0.04$) and a difference by site that approached significance (farm PERMANOVA $F_{1,19} = 1.6$, $P = 0.08$; Fig. 4A and B). The difference in diets of warblers at the two farms (Fig. 4A) corresponded with a tendency for birds at the Baronhall farm (lower right hand part of Fig. 4A) to consume more chironomid Diptera, likely due to a nearby pond that could

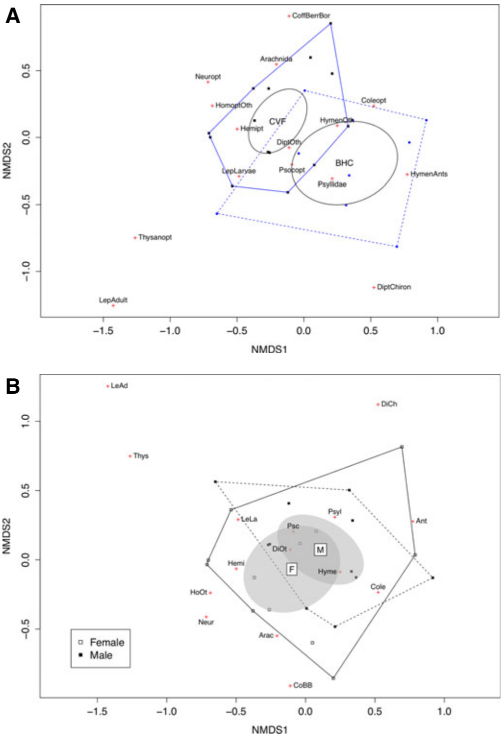

Fig. 4. Nonmetric Multi-Dimensional Scaling with 95% confidence ellipses for Black-throated Blue Warblers, using data just from March 2000 indicating (A) a difference between the two coffee farms (CVF = Coleyville Farm, BHC = Baron Hall Coffee), and (B) a difference between the sexes. See Fig. 1 legend for arthropod taxa codes.

serve as a breeding site for these insects with aquatic larvae. We found no difference in the diet variance of male and female Black-throated Blue Warblers.

DISCUSSION

We argued above that opportunistic foragers should converge behaviorally on the same relatively available, patchily distributed, and small prey. We found substantial diet overlap and evidence for several other components of opportunism among all five migratory warbler species wintering in Jamaican shade coffee plantations, but also found subtle diet differences consistent with resource partitioning, both interspecific and intraspecific. We discuss below the implications of these findings for migratory behavior, intra- and interspecific competition in winter, potential ecological services, and methods to study diets.

Species similarities and feeding opportunism. Multi-species stomach content data are rich with information relevant to feeding opportunism. In support of our first prediction of overall dietary similarity among the warbler species, all five species consumed similar prey down to the level of prey morphospecies, explaining the high interspecific diet overlaps. By far the most parsimonious explanation is that these prey were in fact most available when our stomach samples were obtained, the birds fed opportunistically. This overlap is all the more impressive considering that these birds may also forage outside the farms (Campos 2012). The farm effect on diets overall (Table 3A), consistent with aquatic insects (midges) in one of the farms, supports this opportunism. Such opportunism is also consistent with rapid (within days to weeks) numerical responses to changing or variable arthropod abundances by these insectivorous birds at both regional and local (between tree species) scales in Jamaica (Johnson 2000a, Johnson and Sherry 2001). The overall diet similarity is also consistent with both the close phylogenetic relationships of many of these warblers (four of the five are in the genus *Setophaga*; Lovette et al. 2010) and the morphologically similar paruline forelimbs, hindlimbs, and body axes that facilitate rapid hopping search movements through vegetation (Keast et al. 1995). High foraging niche overlap by American Redstarts with other Caribbean species (Bennett 1980, Toms 2011, 2013) reinforces the likelihood of high interspecific resource overlap involving multiple species. Poulin and LeFebvre (1996) compared the diets of insectivorous migrants (*Catharus* thrushes, multiple Parulidae genera, and *Empidonax* flycatchers) in Panama, and also found high overlap among species (based on diets including small ants, beetles, non-flying termites, millipedes, and centipedes), but diets were not considered opportunistic insofar as they differed from those of resident insectivorous species feeding in the same habitat on larger and nutritionally higher value prey.

Although we lack data on prey availability simultaneous with our stomach samples, qualitative information for two of the three most frequent prey in our stomach samples reinforces the conclusion that prey that were abundant in diets were also abundant in the coffee farms when we sampled. For example, Johnson (2000b) found the same yellowish psyllid species found in the stomach samples in our study to be consistently (1995–1997) abundant in the same coffee farms where our study was conducted (average 55%). In addition, this percentage tended to increase in *Inga vera* (the dominant shade tree in the farms and areas we sampled) and this psyllid species became the dominant insect available in February-March, consistent with our finding that this psyllid was the most frequent prey in our March stomach samples of all five warbler species (Fig. 1). The coffee berry borer was also abundant enough in Jamaican farms to be considered a persistent and well-documented pest, even by 1980 (Buddlall 1986, Martin-Wilkins 2012, MD Johnson and TW Sherry, pers. obs.). The coffee berry borer was also abundant enough to motivate multiple successful experimental tests of the capacity of birds to limit its abundance (Kellerman et al. 2008, Johnson et al. 2010), and thus it was likely abundant in the coffee farms at the time of our study.

Another component of feeding opportunism frequently neglected in diet studies is patchily distributed prey, including insect swarms (Sherry 1984, Bell 2011). All five warbler species in our study fed on patchily distributed prey, a conclusion based on three lines of evidence. First, all five species consumed coffee berry borers, whose numbers per stomach sample were sometimes high, e.g., 159, 71, 34, 29, 19, and 18 per sample in American Redstarts, 61, 10, 11, and six per sample in Black-throated Blue Warblers, and 113 in a Prairie Warbler sample. Coffee berry borers are also dispersed heterogeneously within and among farms, particularly when heavily infesting farms, such as in Jamaica, with densities up to 80 borers per branch, and the borers are conspicuous and available for hours at a time when dark-colored females bore into the contrastingly red coffee berries (Kellermann et al. 2008, Morris et al. 2015). Other abundant prey in our samples were also patchily distributed based on their ecology, including bark lice (Psocoptera) that tend to aggregate on plant stems (e.g., http://texasinsects.tamu.edu/aimg34.html, TW Sherry, pers. obs.) and ambrosia beetles (Curculionidae: Platypodinae; 41 individuals of the same species in an American Redstart stomach) that tend to aggregate around dead or dying plant stems (Sherry 1984, Beaver 1989), species of which are found in both coffee and *Inga vera* in Puerto Rico (Torres 1994) and likely Jamaica. Third, alternative hypotheses to explain such large numbers of a particular species of prey in some, but not all, stomachs we sampled are implausible. One alternative is that particular prey types were not patchy, but simply abundant, but only some stomach samples in our study contained large numbers of a particular prey type, which is unlikely given this alternative. Another alternative is that individual birds might develop a specific search image for a prey type, eating it out of proportion to its actual abundance, but this phenomenon is associated with cryptic prey benefitting from camouflage (Dukas and Kamil 2001), unlike the conspicuous prey in our study including dark-brown coffee berry borers emerging from green or red coffee berries (Damon 2000) as well as adult black thrips and swarming ambrosia beetles. Our diet data certainly suggest that individual birds of all five species experienced the environment as heterogeneous. Besides its relevance to foraging opportunism, patchiness of prey types is important to emphasize here and in future studies because it can increase predator foraging efficiency by reducing search time once a patch is discovered, can reduce search times in optimal foraging models (e.g., Ornes 2013), and it creates distinctively non-normal prey type frequency distributions, precluding many statistical procedures as well as complicating the sampling of available prey meaningfully.

A final component of foraging opportunism assessable with our stomach samples is small prey size, typical of non-buffered prey (Bell 2011). Multiple studies have considered prey <5 mm long as small (Johnson et al. 1995, Poulin and Lefebvre 1996). Modal arthropod body length in our study was 2–3 mm (TW Sherry and AM Hallauer, unpubl. data; Medori 1998), as estimated by occasional intact specimens from stomach samples measured directly, alcohol-preserved voucher specimens of known prey, and the sum of body part lengths of prey morphospecies (e.g., disarticulated, dorsoventrally projected head + pronotum + elytron length of Coleoptera, sometimes found together in stomach samples). The frequently consumed psyllids in our study averaged 2.4 mm long, coffee berry borers 1.7 mm, one species of bark lice 1.3 mm, chrysomelid beetles 1.6–1.8 mm, the most frequent ant species just under 2 mm, and Collembola <1 mm. Ants, and small insects generally, may represent relatively poor quality prey compared to what resident birds consume (Poulin and Lefebvre 1996). Our results, with all five species of migratory warblers feeding on similar small, relatively available, sometimes aggregated foliage arthropods in winter, prey that are likely to be relatively unbuffered by vegetation substrate, support the "resource buffering" hypothesis for the evolution of migratory life-histories (Bell 2011). Other investigators have found relatively opportunistic foraging by wintering migrants compared to residents (e.g., Salewski et al. 2003), but consistent diet and foraging differences between migrants and residents in winter are controversial (e.g., Salewski and Jones 2006).

Species differences. Our second prediction, that the diets of different species of migratory birds differ (i.e., partition resources), was also supported, even though most species pairs did not differ significantly based on 95% confidence ellipses (Fig. 2). This result is robust, and was supported by comparison of the diets of both sexes of all five species of warblers in our March 2000 samples, the diets of males in the same samples, and re-analysis with Northern Parulas excluded from the sample. Although we expected the most distinctive foragers, American Redstarts and Black-and-white Warblers, to be the most diagnosable dietarily, only American Redstarts were distinctive, with more Diptera and fewer caterpillars in their diet than in the diets of the other species of warblers (Figs. 1 and 2), which is consistent with redstarts' flycatching and prey-pursuit adaptations relative to most other species of warblers (Bennett 1980, Keast et al. 1995, Sherry and Holmes 1997, Wunderle and Latta 1998). The tendency for American Redstarts to eat more non-ant Hymenopterans (parasitic wasps, including chalcidoids and braconids) than the other four warblers may be due to their relatively frequent use of aerobatic foraging maneuvers during the winter (Lovette and Holmes 1995, Sherry and Holmes 1997). Such foraging specialization in winter is not unique to redstarts. For example, Worm-eating Warblers (*Helmitheros vermivora*) specialize on feeding from dead-leaf clusters in Caribbean wintering habitats (Greenberg 1987).

Despite their unique tree creeper-like foraging behavior, the diet of Black-and-white Warblers was similar to those of the other species, and differed only from the diet of American Redstarts in terms of non-overlapping centroids (Fig. 2). However, both Morse (1989) and Lack (1976) emphasized that, although spending most of their time foraging along tree trunks and branches, Black-and-white Warblers should nevertheless be considered generalist foragers due to their occasional foraging among leaves and twigs, including foliage-gleaning behavior typical of other parulid warblers. Our results from shade coffee habitat reinforce this notion of Black-and-white Warblers being opportunistic generalist foragers in winter, able to feed effectively on similar substrates (Wunderle and Latta 1998) and on the same prey as the other four warbler species.

The simplest hypothesis to explain interspecific differences in diet, based on prey taxa in stomach samples (Fig. 2), is that the warbler species in our study represent a spectrum from active search and pursuit of prey (especially American Redstarts) to more systematic searching for relatively sessile prey such as caterpillars (especially Northern Parulas; Moldenhauer and Regelski 2012). American Redstarts ate the most Dipterans and parasitic Hymenopterans, both of which tend to be strong fliers that probably require relatively adept aerobatic pursuit behavior, for which this bird species is well adapted morphologically (Bennett 1980, Keast et al. 1995, Sherry and Holmes 1997). Northern Parulas, on the other hand, tend to forage in winter by relatively stereotyped gleaning from inner branches (Moldenhauer and Regelski 2012), which is consistent with our result that this species had a narrower diet niche than the other four species. MacArthur (1958:617; see also Wunderle and Latta 1998) noted similar resource partitioning among five different, but congeneric (*Setophaga*), wood warblers, based largely on breeding season data, noting that "...there is every reason to believe that the birds behave in such a way as to be exposed to different kinds of food. They feed in different positions, indulge in hawking and hovering to different extents, move in different directions through the trees, vary from active to sluggish..." Such subtle resource consumption differences despite broad diet overlap is not unusual in birds (e.g., Buckton and Ormerod 2008, Wilson 2010, Dhondt 2011, Collins 2015).

Intraspecific and interspecific food competition? Our third prediction, that differences in the diets of males and females should correspond with differences in foraging behavior, was supported for Black-throated Blue Warblers, but not American Redstarts. The difference in diets of male and female Black-throated Blue Warblers is consistent with use of sex-specific foraging heights and behaviors in Jamaican coffee farms (i.e., intraspecific niche partitioning, with males disproportionately in the canopy; Smith et al. 2012), and with stronger aggression to simulated intruders in the food-rich canopy, particularly by larger males and males in general (Smith et al. 2012). Although we detected no difference in their diets, male and female American Redstarts are also ecologically segregated in coffee farms, with females tending to forage more in the coffee shrub layer and males in shaded coffee farms and in the shade trees forming the canopy in these farms (Wunderle and Latta 1996, MD Johnson, pers. obs.). More intensive sampling will be needed to determine if the diets of males and females of our other focal species, including American Redstarts, differ in coffee farms or other habitats.

The sex difference in diets and foraging behavior by Black-throated Blue Warblers is consistent with intraspecific competition in winter as an ongoing cause of such ecological segregation in this species (Wunderle 1995, see Dhondt 2011 for general discussion of competition as a historical versus ongoing ecological process). More direct evidence that these warblers compete intraspecifically in wintering areas comes from inferential and experimental evidence for food limitation (Sherry et al. 2005, Brown and Sherry 2006, Johnson et al. 2006, Wilson et al. 2011) and the demographic consequences thereof (Sherry and Holmes 1996, Marra et al. 1998, Sillett et al. 2000, Norris et al. 2004, Johnson et al. 2006, Smith et al. 2010), as documented in a variety of both migratory and non-migratory species of birds (Dhondt 2011, Norman and Peach 2013). Additional evidence comes from removal experiments with wintering birds (Marra et al. 1993, Studds and Marra 2005), sex-related competition for limited habitats (Greenberg 1986, Marra and Holmes 2001, Smith et al. 2010), and food-reduction experiments (Brown and Sherry 2006, Cooper et al. 2015). These studies involved a variety of wintering parulids and other birds in diverse habitats in Jamaica and elsewhere.

Dhondt (2011) listed three conditions necessary, but not sufficient, for interspecific competition, including intraspecific competition (as just discussed above), limited resources, and interspecific resource overlap, all of which appear to have been met by the warblers in our study. Although we did not test specifically for food limitation in all five species of warblers in our study, we argue that it can be inferred based on several lines of evidence. First, multiple exclosure experiments in Jamaican coffee farms have demonstrated that birds, and migrant insectivores including those we studied, significantly reduce the abundance of coffee berry borers and other insects (Kellerman et al. 1998, Johnson et al. 2010; see below for details), providing evidence for food limitation (Dhondt 2011). Additional evidence for food limitation involving multiple populations of migrant species wintering on Caribbean Islands, and indeed more generally (reviewed by Sherry et al. 2005), comes from the effects of food on body condition and annual survival (Sherry and Holmes 1996, Sillett et al. 2000, Strong and Sherry 2000, Johnson et al. 2006, Smith et al. 2010, Cooper et al. 2015), and evidence for density-dependence or food limitation in two Jamaican habitats (Marra et al. 2015). Evidence for food limitation, and for resource limitation generally (e.g., Winker 1998, Dhondt 2011), also comes from the presence of numerous floater individuals in wintering areas (e.g., Peele et al. 2015). Moreover, the multiple lines of evidence for feeding opportunism reviewed above, and involving all five warbler species in our study, should increase the likelihood of interspecific competition in winter by concentrating feeding efforts by these birds, both among and within habitats (Johnson 2000a, Johnson and Sherry 2001), on any small arthropods available on the foliage of coffee plants and on plants in other wintering habitats (e.g., Greenberg 1995, Bell 2011) that these warbler species share widely across the Caribbean islands (Wunderle and Waide 1993). For example, in less than two weeks in February 1996, numbers of small cicadellid Hemipterans increased more than five-fold in a thorn-scrub habitat in Jamaica and insectivorous birds, especially American Redstarts, Northern Parulas, and Prairie Warblers, increased in abundance (numerical response) as predicted (Johnson and Sherry 2001), consistent with prey limitation for these birds in winter and their ability to respond rapidly and opportunistically to changing food abundance. Feeding opportunistically on similar prey by the five species of warblers in our study may seem contradictory to diet specialization among species, but evidence for food limitation during the winter, coupled with a high degree of feeding opportunism associated with a migratory life-style, may be driving the evolution of winter feeding specialization as a way to partly mitigate the interspecific competition. Dhondt (2011) describes other examples of species that simultaneously compete interspecifically and overlap substantially in foraging behavior and diet. Moreover, because interspecific territoriality (aggression) is infrequent or absent among the five species we studied, and among wintering migrants generally (Salewski and Jones 2006), any interspecific food competition that occurs probably involves diffuse scramble competition among multiple species rather than contest competition. Toms (2011, 2013) also described exploitative food competition involving wintering American Redstarts and resident Adelaide's Warblers (*Setophata adelaidae*) in Puerto Rico, although redstarts were also locally constrained in where they foraged by the socially dominant Adelaide's Warblers.

Our results thus suggest the existence of interspecific competition among five species of warblers wintering in Jamaica, and diffuse exploitative competition as a likely mechanism. Direct experimental tests of interspecific competition are important for future studies, for example, to establish population and demographic impacts (Dhondt 2011). Addressing the question of possibly pervasive, diffuse interspecific competition among these abundant wintering migrants in the Caribbean region is particularly important given its implications for the wintering ranges of migrants, population limitation, community structure, life-histories, and conservation. However, interspecific competition via diffuse exploitation as suggested by our diet data will be difficult to detect in the field, and has not been either tested experimentally or documented previously to our knowledge, and was not mentioned in a recent review (Jankowski et al. 2012).

Ecosystem services. All five warbler species in our study ate coffee berry borers, supporting our fourth prediction, and the three species (American Redstarts, Black-throated Blue Warblers, and Prairie Warblers) that ate the most may consume enough of these insects, the most important pest of coffee plants globally (Vega et al. 2003, 2009, Jaramillo et al. 2011), to help control their numbers. For example, stomach contents of individual American Redstarts in our study included from 18 to 159 coffee berry borer remains. When multiplied by ~8 birds/ha in nearby Jamaican coffee farms (Peele 2015) and by the several months these birds reside in coffee farms during the dry season when coffee is ripening and under attack by these beetles (Kellermann et al. 2008), this translates into considerable consumption. Evidence that birds help control coffee berry borers in Jamaican coffee farms is also based on coffee plant exclosure experiments in the Blue Mountains, where American Redstarts, Black-throated Blue Warblers, and Prairie Warblers are the most abundant insectivores in the experimental areas (Kellermann et al. 2008), as well as in a shaded coffee farm at a similar elevation as the farms in our study where American Redstarts and Black-throated Blue Warblers are abundant (Johnson et al. 2010). By examining stomach contents, we identified some of the species of birds that contribute to the effects of these exclosure experiments on coffee berry borers. Our results are thus consistent with the suggestion that migratory birds help control populations of coffee berry borers in Costa Rica (Karp et al. 2013, Karp and Daily 2014), and to arguments that birds generally are important in controlling pests of coffee and other crops globally (Maas et al., 2016).

Table 4. Annual and monthly variability in percentage of three most frequent prey taxa overall in guts of five warbler species. Number of total stomach samples in parentheses. November 1997 samples were from calendar year 1997. Homoptera refers to the former order Homoptera (now Hemiptera) that included primarily family Psyllidae, but also occasional Ciccadellidae, Membracidae, Cercopidae, Aphididae, and superfamily Fulgoroidea.

	Amercan Redstart			Black-and-white Warbler	Black-throated Blue Warbler	Northern Parula		Prairie Warbler	
Year(s)	1997	1998	2000	2000	2000	1997	2000	1997	2000
A. Homoptera (incl. Psyllidae)									
Jan	5.1 (2)					30.3 (1)			
Feb	11.2 (4)					72.5 (6)		59.5 (6)	
Mar		27.5 (5)	38.1 (22)	58.6 (13)	34.0 (23)		78.0 (11)		35.8 (11)
Apr	0.0 (1)								
Nov	0.00 (2)							8.9 (2)	
B. Psocoptera									
Jan	0.0 (2)					6.06 (1)			
Feb	5.6 (4)					12.6 (6)		10.1 (6)	
Mar		3.0 (5)	13.8 (22)	14.3 (13)	31.1 (23)		2.9(11)		19.3 (11)
Apr	0.0 (1)								
Nov	6.8 (2)							6.7 (2)	
C. Coffee Berry Borer									
Jan	1.7 (2)					0.0 (1)			
Feb	33.5 (4)					0.0 (6)		0.0 (6)	
Mar		9.8 (5)	18.2 (22)	0.2 (13)	5.7 (23)		0.49 (11)		14.1(11)
Apr	2.8 (1)								
Nov	0.0 (2)							4.4 (2)	

Methodological considerations. A potential weakness of studying bird diets by examining stomach samples is digestion rate bias (Rosenberg and Cooper 1990). For example, Dipterans have few sclerotized body parts that could persist in stomachs, and would likely disappear relatively rapidly during digestion, possibly explaining why they were not one of the most frequent prey identified in our samples. Nonetheless, we detected enough Dipterans in our samples, primarily based on wing fragments, to help establish species-typical diets, particularly for American Redstarts. Psocopterans also have soft body parts, except for tiny mandibles that we learned to identify during our study, leading to the surprising recognition that Psocopterans were the second most frequent prey taxon overall, and >30% of all prey detected in stomach samples of Black-throated Blue Warblers (Fig. 1). Thus, digestion bias did not obscure differences among the five species of warblers in our study, probably because essentially all prey taxa have digestion-resistant body parts and, in fact, a surprising result of our study was how many prey we were able to identify per emetic sample (Table 1).

Another potential weakness of our study was the small sample sizes, specifically the concentration of samples from a single week in March 2000. However, we believe that this is a minor limitation for several reasons. First, we compared bird diets at two coffee farms with these samples. Second, we compared diets of several species of birds during multiple seasons and years to show some consistency in prey types (Table 4), and found consistency in the abundance of both coffee berry borers and a psyllid species in Jamaican coffee farms. Third, an important benefit of our concentrated sampling in March 2000 is that it controlled for prey availability in space and time, and allowed us to test for species-specific dietary differences when our focal bird species were exposed to the same resources/habitat. The large number of arthropods identified per stomach sample, coupled with many samples per species, allowed robust statistical tests for species differences, despite considerable variability in the diets of different individuals (Fig. 2, Table 3) and overlap in diet among species, a hypothesis we tested using just stomach samples of males and of all species except Northern Parulas, and again using pooled samples (all dates). The fact that our diet data revealed a significant difference between the two farms that was consistent with known habitat differences (a pond present in one farm), and between the sexes in Black-throated Blue Warblers, attests to the sensitivity of our diet samples and methods to detect subtle, but ecologically meaningful, variation. Nonetheless, we recognize that both prey—and predator—types and abundances almost certainly vary considerably within and among years, and among habitats, in ways that likely affect dietary relationships among different species of birds, as do the wintering strategies of migrants (Salewski and Jones 2006). Determining how overlap and variability in diets change with resource abundance is important for understanding mechanisms involved in, as well as the strength of, interspecific competition (Wiens 1993, Dhondt 2011).

Our results help identify research questions requiring further study, including how these birds forage in winter (e.g., what microhabitats, including possible sex differences), how and where they detect prey items and aggregations, what prey and predators are available and in what abundances, and how long different prey types persist in stomachs. Annual variation in food abundance in coffee farms (e.g., in El Niño versus La Niña years) may alter the degree of food limitation, and in turn the degree of diet specialization and overlap (Wiens 1993, Dhondt 2011). Our five focal species and other species of migrant warblers may show greater foraging and dietary niche differentiation in habitats more structurally complex than coffee, and their diets may differ from those of resident insectivorous birds. Testing hypotheses about interspecific competition experimentally will remain important, as will assessing its impacts on the demography of both migratory and resident insectivores.

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