




Morphological traits influence prey selection by coexisting species of New World warblers (Parulidae)

Kristen M. Rosamond,^{1,3}  Cody M. Kent,¹  Sarah Chieko Hunter,^{1,2} and Thomas W. Sherry¹ 

¹Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, Louisiana 70118, USA

²Department of Biology, Delgado Community College, New Orleans, Louisiana 70119, USA

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ABSTRACT. New World wood warblers (Parulidae) represent one of the most dramatic adaptive radiations in North America. However, the ecological bases for the morphological differences among these species remain poorly understood, especially considering how many foraging and habitat studies the family has inspired. We hypothesized the existence of relationships between parulid morphology and diet. We combined a principal component analysis (PCA) of 18 external morphological traits of 11 species of warblers with stomach-content data from coexisting species in one breeding community in Louisiana and three wintering communities in Jamaica. The primary morphological differences, corresponding with the first three PCA axes, were **body size**, morphological adaptations for **aerial foraging versus gleaning**, and **arboreal versus ground-foraging** adaptations. Our analysis revealed little morphological overlap among the 11 species. Differences in diet among the warblers showed a significant relationship to the first two PCA axes of morphological traits. For five coexisting, foliage-gleaning species wintering in Jamaican wet limestone forest, larger warblers ate larger beetles and Orthopterans but not larger ants. In analyses including all four communities, species of warblers with aerial foraging morphologies consumed a greater proportion of winged insects than other warbler species. These findings document prey selection relevant to multiple subtle morphological differences among coexisting species. Overall, our results indicate that food and foraging have likely played an integral role in the morphological diversification and coexistence of species in the family Parulidae.

RESUMEN. **Características morfológicas influncian la selección de presas en chipes (Parulidae) que coexisten**

Los chipes (Parulidae) representan una de las más dramáticas radiaciones adaptativas en Norteamérica. Sin embargo, las bases ecológicas de dichas diferencias morfológicas entre especies siguen siendo pobremente comprendidas, especialmente considerando cuántos estudios de forrajeo y hábitat se han inspirado en esta familia. Hipotetizamos la existencia de relaciones entre la morfología de los parúlidos y su dieta. Combinamos un análisis de componentes principales (PCA) de 18 características morfológicas externas de 11 especies de chipes con datos de contenidos estomacales de especies que coexisten en una comunidad reproductiva en Luisiana y tres comunidades invernales en Jamaica. Las principales diferencias morfológicas, que corresponden a los primeros tres ejes del PCA, fueron tamaño corporal, adaptaciones morfológicas para forrajeo aéreo versus forrajeo en follaje y adaptaciones para el forrajeo arbóreo versus forrajeo en el suelo. Nuestros análisis revelaron un pequeño traslape morfológico entre las 11 especies. Las diferencias de dieta entre los chipes mostraron una relación significativa con los dos ejes de características morfológicas del PCA. Para cinco especies que forrajeaban en follaje y coexisten en el bosque húmedo sobre calizas de Jamaica, los chipes más grandes se alimentaron de los escarabajos más grandes y de ortópteros, más no de las hormigas más grandes. En los análisis que incluyen las cuatro comunidades, los chipes con morfologías para forrajeo aéreo consumieron una mayor proporción de insectos alados que otras especies de chipes. Estos hallazgos documentan la selección de presas y su relación con múltiples y sutiles diferencias morfológicas entre especies que coexisten. En general, nuestros resultados indican que la dieta y el forrajeo muy probablemente jugaron un papel central en la diversificación morfológica y la coexistencia de especies en la familia Parulidae.

Key words: adaptive radiation, community, diet, evolution, foraging morphology

Adaptive radiation has contributed significantly to global biological diversity and can be recognized by four criteria: common ancestry, phenotype–environment correlation, trait utility, and rapid speciation (Schluter

2000). The New World wood warblers (Parulidae) are an exemplary continental adaptive radiation (MacArthur 1958, Morse 1989, Lovette and Bermingham 1999, Oliveros et al. 2019). Lovette et al. (2010) established common ancestry in the parulids, and Oliveros et al. (2019) established rapid speciation for parulids generally. Price et al. (1998)

³Corresponding author. Email: kristenrosamond@gmail.com

and Lovette and Bermingham (1999) determined rapid speciation for the most species-rich parulid genus, *Dendroica* (now *Setophaga*; Lovette et al. 2010). These studies date the rapid speciation of parulids to the late Pliocene or early Pleistocene. Increased rates of passerine diversification generally do not correspond with increases in temperature or arrival in new continents (Oliveros et al. 2019), leaving the causes of passerine diversification, particularly for parulids, enigmatic.

Several lines of evidence point to the importance of efficient foraging for the coexistence of parulid warblers. Studies of food limitation have focused on parulids such as Black-throated Blue Warblers (*Setophaga caerulescens*; Rodenhouse and Holmes 1992, Nagy and Holmes 2005a, b, Salgado-Ortiz et al. 2008), Swainson's Warblers (*Limnothlypis swainsonii*; Pappas et al. 2010), American Redstarts (*Setophaga ruticilla*; Marra 2000, Cooper et al. 2015, Marra et al. 2015), Northern Parulas (*Setophaga americana*), and Prairie Warblers (*Setophaga discolor*; Johnson and Sherry 2001). Limited food supplies influence demographic characteristics, including body mass and body condition of American Redstarts (Sherry and Holmes 1996, Johnson et al. 2006) and Ovenbirds (*Seiurus aurocapilla*; Brown and Sherry 2006) in winter, as well as Black-throated Blue Warblers during both the breeding and non-breeding seasons (Sherry and Holmes 1996, Sillett et al. 2000, Rodenhouse et al. 2003). Enclosure experiments targeted at small foliage-gleaning birds support the inference that these birds can deplete arthropod resources, thus contributing to food limitation, in both summer (Holmes et al. 1979, Holmes 1990) and winter communities (Kellermann et al. 2008, Johnson et al. 2009), where parulids comprise most of the small insectivores.

Interspecific competition for food resources, via either direct selective pressures or species sorting, is widely considered the primary driver of ecological differences among these coexisting species (MacArthur 1958, Schluter 2000, terHorst et al. 2018). Despite these ecological differences and the potential partitioning thereof, evidence for interspecific competition for food resources among parulid warblers exists in both summer and winter (Greenberg and Ortiz 1994, Toms 2011, Sherry et al. 2016, Kent and

Sherry 2020), which further supports its potential importance in shaping morphological food-exploitation adaptations contributing to the clade's adaptive radiation. Sherry et al. (2016) found small interspecific dietary differences in warblers coexisting in shaded-coffee plantations, using Dhondt's (2012) criteria to infer diffuse exploitative interspecific competition based on species overlaps coupled with intraspecific competition for food resources. Additionally, interspecific aggression related to defense of food resources is well documented between American Redstarts and both Yellow Warblers (*Setophaga petechia*; Sherry et al. 2016) and Adelaide's Warblers (*Setophaga adelaidae*; Toms 2011, 2013), as well as between Yellow Warblers and several other parulid species (Greenberg and Ortiz 1994). Ecological release has been documented in Northern Parulas in both summer (Morse 1971, 1989) and winter (Lack and Lack 1972), as interspecific competition theory predicts.

Some authors have minimized the importance of morphological differentiation relative to differences in foraging behavior independent of morphology, particularly among species in the genus *Setophaga* (Lovette and Bermingham 1999), and in *Setophaga* compared to Old World *Phylloscopus* warblers (Price et al. 2000). In contrast to their relatively similar bill shapes and other foraging-related traits, species in the genus *Setophaga* exhibit striking variation in sexually selected traits such as plumage and song (Lovette and Bermingham 1999). Including parulid genera other than *Setophaga*, such as ground-foraging species, increases the amount of morphological variation in the family, but all parulids are relatively small-bodied and short-beaked, and most forage by either foliage-gleaning or fly-catching (Billerman et al. 2020).

Despite the overall morphological homogeneity of Parulidae, morphological adaptations to foraging niches are documented in tropical insectivorous species generally (Mansor et al. 2018) and birds globally (Pigot et al. 2020). In parulids specifically, Price et al. (2000) found a relationship between a multivariate measure of overall body size and prey length in parulids (see also Greenberg 1981, Vézina 1985). Some evidence exists that relatively long and flat bills, large wings and tails, and long rectal bristles

contribute to aerobic maneuvering by warblers to capture prey that jump or fly rapidly to evade predation (Ficken 1962, Robinson and Holmes 1982, Leisler and Winkler 1985, Keast et al. 1995, Sherry et al. 2020). Likewise, the long tarsi of wood warblers are related to clinging behaviors as well as rapid hopping through vegetation to capture prey (Keast et al. 1995). However, even these studies were based largely on foraging behavior with little information about actual prey, which is important because diet, not foraging behavior, provides the basis for resource competition (Kent and Sherry 2020). Few of these studies included species foraging at the same times and places, so variable prey availability could not be ruled out as a potential explanation for some of the species differences. Moreover, beak shape is not as strongly related to dietary differences among birds as generally thought (Navalón et al. 2019).

We used extensive diet datasets from both breeding and wintering seasons to examine possible relationships between diet and morphology (based on museum skins) among primarily insectivorous, coexisting species of migratory wood warblers. We hypothesized that differences in diet are a major cause of this morphological variation. We predicted that coexisting species differ in morphological traits, and specifically in traits that might predict dietary differences. Such species differences would indicate the importance of foraging in the diversification of Parulidae. Specifically, we hypothesized that (1) body size predicts prey sizes of coexisting species, (2) the presence of aerial foraging (flattened beaks and relatively large wings and tails) versus gleaning adaptations predicts the proportion of flying insects consumed, and (3) arboreal (deep and curved claws) versus ground-foraging (walking) morphologies predict consumption of insects found on branches and tree trunks. Establishing such relationships and tradeoffs would help link heritable, if subtle, parulid morphologies with the ecological basis for species differences. This would aid in identifying phenotype–environment correlations and trait utility in the Parulidae clade, which Schluter (2000) identified as criteria for adaptive radiation.

METHODS

Study species. We included 11 species for which we had detailed diet data, including American Redstart, Black-and-white Warbler (*Mniotilta varia*), Black-throated Blue Warbler, Hooded Warbler (*Setophaga citrina*), Kentucky Warbler (*Geothlypis formosa*), Northern Parula, Prairie Warbler, Prothonotary Warbler (*Protonotaria citrea*), Swainson's Warbler, Worm-eating Warbler (*Helmitheros vermivorum*), and the non-migratory, Caribbean subspecies of Yellow Warbler (*Setophaga petechia petechia*). Although primarily insectivorous, these species forage in different ways to obtain diverse prey (del Hoyo et al. 2010, Kent and Sherry 2020). All 11 species belong to a monophyletic clade of New World wood warblers (Parulidae; Lovette et al. 2010; Fig. S1) but are evolutionarily independent. Although Black-and-white Warblers, Swainson's Warblers, and Prothonotary Warblers are the most closely related species, all three are distinctive in both morphology and foraging behavior. Swainson's Warblers and Prothonotary Warblers are sister species in Lovette et al.'s (2010) phylogeny, but they diverged early and forage distinctively, the former largely on the ground and the latter mainly gleaning from branches and leaves.

Diet sampling. We obtained diet data at four different sites, allowing us to look at diverse species and check robustness of conclusions by replicating across both habitat and season. We accounted for differences in sites in our statistical methods. We collected stomach contents from breeding American Redstarts, Hooded Warblers, Kentucky Warblers, Prothonotary Warblers, and Swainson's Warblers coexisting in bottomland hardwood habitat in Bogue Chitto National Wildlife Refuge (30.45°N, 89.75°W; 6 m asl) and Honey Island Swamp (30.38°N, 89.72°W; 1 m asl) in Louisiana from 22 May to 6 July 2006. Bayous with slow streams and cypress-tupelo swamp characterize these locations. Slightly higher elevations with better-drained soils at both sites contain bottomland hardwood tree species including sweetgum (*Liquidambar styraciflua*), green ash (*Fraxinus pennsylvanica*), red maple (*Acer rubrum*), water hickory (*Carya aquatica*), and several oak (*Quercus*) species.

We collected stomach contents from American Redstarts, Black-and-white Warblers, Black-throated Blue Warblers, Northern Parulas, and Prairie Warblers at two shaded-coffee plantations, Baronhall Farms (18°12' N, 77°22' W, 555 m asl) and Coleyville Farm (18°11' N, 77°30' W, 880 m asl), located in Clarendon Parish, central Jamaica, West Indies. We obtained diet samples in these two coffee farms over four years (1996, 1997, 1998, and 2000) in every month from November to April except December. However, we collected most of the data in peak dry season during a one-week period from 11 to 17 March 2000 (Sherry et al. 2016). Both plantations are located on hilly terrain surrounded by wet limestone forest. The Baronhall plantation encompasses 90-ha and consists of rows of coffee plants (*Coffea arabica* var. *typica*) with shade trees providing 20–70% cover. Coleyville Farm is a 10-year-old, 22-ha plantation shaded primarily by banana (*Musa*) and *Inga vera*, and its coffee layer is denser than that at Baronhall.

Winter stomach contents from American Redstarts, Black-and-white Warblers, Black-throated Blue Warblers, Northern Parulas, and Worm-eating Warblers came from two replicate Jamaican wet limestone forest sites. We obtained data from the first site, located in a cattle ranch near Bethelton in Westmorland Parish (18.25°N, 77.94°W; 487 m asl), from 15 February to 15 March 2017. We collected data from a second site near the Windsor Research Station in Trelawney Parish (18.36°N, 77.65°W; 139 m asl) in Cockpit Country from 16 to 31 March 2017. Wet limestone habitat is native and widespread in Jamaica and has a wide array of diverse and structurally complex emergent and canopy trees, ground cover and shrubs, vines and vine tangles, and epiphytes. The first site is one of the largest and most intact native forest fragments in the region, although there is visible evidence of degradation due to cattle grazing along its edges. The second site is well within the largest area of intact wet limestone forest in Jamaica (Windsor Research Centre 2016).

We collected stomach contents from winter-resident American Redstarts and non-migratory Yellow Warblers in the Font Hill Nature Preserve, Luana Point (St. Elizabeth Parish), Jamaica (18.03°N, 77.95°W; < 5 m asl), from 13 January to 14 March 2014.

This habitat consists of nearly pure stands of black mangrove (*Avicennia germinans*) woodland.

Dietary methods. We captured warblers at all sites using ground-based mist-nets. We sampled most birds during morning hours to ensure full stomachs for the best possible prey samples. We collected diet samples at approximately the same time at each site to control for varying prey types in space and time. Sample collection occurred during a six-week period except when otherwise specified. This ensured that dietary differences would be largely attributable to differences in bird foraging behavior and morphology rather than changing prey availability. We used the emetic antimony potassium tartrate to induce regurgitation in warblers at all sites except Jamaican black mangrove by mixing 0.008 mL of emetic per gram body mass with distilled water for an overall total dosage of 0.1 mL (Sherry et al. 2016). We injected the emetic directly into the esophagus using a syringe attached to a vaseline-lubricated catheter tube. We placed individuals inside a small cardboard box lined with waxed paper for 15 min to allow for regurgitation. After we released birds, we immediately preserved their stomach contents in 70% ethanol. Jamaican black mangrove samples came from birds sacrificed using thoracic compression and dissected immediately in the field as part of another study, and the entire stomach was preserved in 70% ethanol.

In the laboratory, we washed samples into petri dishes with 70% ethanol for inspection with an Olympus SZH binocular dissecting microscope at 75–650× magnification. We sorted identifiable arthropods or arthropod parts into additional petri dishes, including heads or partial heads, elytra, mandibles, legs, and wings, the latter of which we spread to show venation. We identified insects to either order or family based on the distinguishability of body parts present and recorded the minimum number of individual arthropods that could account for all of the available insect fragments (Table S1). We only used stomach-content data from the Jamaican wet limestone sites to test relationships between bird size and prey size. We measured sufficiently intact and diagnostic body parts from this subset to the nearest 0.1 mm and used them as prey size surrogates. These measurements included

head width of ants (Hymenoptera) and elytron length of beetles (Coleoptera). We chose these taxa because they preserved well in stomach contents, were easy to measure, and were consumed in large numbers by all bird species. In addition, we included the width of the most distal part of the mandible of grasshoppers, crickets, tree crickets and relatives (Orthoptera), and cockroaches (Blattodea). These taxa were common prey of both Northern Parulas and Worm-eating Warblers in Jamaican wet limestone sites. We assumed that mandible size is proportional to prey body size. We treated the order Orthoptera, as well as cockroaches from Blattodea, as one group (hereafter, Orthoptera) because their mandibles are morphologically similar and difficult to distinguish in stomach contents. We similarly assumed that beetle elytron length and ant head width are proportional to insect body size. We excluded measurable Staphylinidae beetle elytra because they have truncated elytra compared to other beetle families, which would potentially bias our overall elytron-to-beetle size ratio. Thus, we assumed that any significant difference between species in ant head width, beetle elytron length, or Orthoptera mandible size corresponded with a difference in overall prey body size.

Morphological measurements. We obtained warbler morphological measurements from specimens of all 11 warbler species at the Louisiana State University Museum of Natural Science. We used museum specimens because they are more easily and accurately measured than live birds, especially for small or difficult-to-measure features, like claw or rictal bristle length. We measured five study skins of each sex for each species, except when constrained by available specimens (i.e., for both Swainson's Warblers and Yellow Warblers, we measured five male and four female skins). Specimens came primarily from individuals in the southeastern United States (Louisiana, Alabama, Texas, and Gulf of Mexico) during migration, but Yellow Warbler specimens came from the resident subspecies collected in Jamaica where we obtained our diet data. One outlier Black-throated Blue Warbler was from California. Although warbler morphology varies geographically in some species, and we could not confirm that the study skins we used

represented the same subspecies or population from which we took diet samples, intraspecific geographic trait variation is not evident in most of the species included here (Billerman et al. 2020). Of the species with geographic morphological variation, variation in Prairie Warblers is not relevant here because the documented difference involves the resident Florida subspecies (Nolan et al. 2020), and none of our morphological or diet data came from that subspecies. Some intraspecific geographic variation is present in Black-and-white Warblers, Northern Parulas, and Prothonotary Warblers (Billerman et al. 2020). We minimized this issue by restricting our morphological data to individuals from the southeastern United States that likely include Jamaica as a wintering site. Moreover, any variation in these three species is likely not as great as differences among species, which was the focus of our study. Any subspecific variation should make it less likely to detect morphological-diet relationships among species, making our analyses conservative.

We measured 15 external morphological traits per individual study skin to get 18 characters, including three ratios, as follows: beak length, width, and depth at the anterior margin of the nares (1-3), width and depth at half length of the beak to determine bill shape (4-5), rictal bristle number (per side of beak, 6) and length of longest bristle (7), unflattened wing chord (length from the leading edge of the specimen's wrist to the tip of its longest primary feather, 8), Kipp's distance, an index of wing pointedness (difference between length of the most distal primary and most distal secondary feather on the folded wing, 9), tarsus length (distance from the proximate notch near the heel of the specimen's tarsus distally to the point of articulation of the hind toe with the forward toes, 10), hind toe length (length of the hind toe from where it separates from the other toes distally to the start of the exposed hind claw, 11), hind claw length (longest distance of the exposed claw, measured from the point of the claw's insertion into the toe distally toward its tip, 12), claw depth (greatest distance from the outside curve of the claw perpendicularly to a line from the tip of the claw to the point of insertion of the exposed claw with the toe, 13), tail length (distance from the point of

tail feather insertion into the skin at the base of the tail outwards to the tip of the longest feather, 14), total body length (distance from the anterior-most projection of the bill to the tip of the longest tail feather, 15), claw curvature (flat vs. arched toes as the ratio of claw depth to length, 16), bill flatness (ratio of bill width to depth using lengths measured at the anterior margin of the nares, 17), and degree of bill area toward tip (ratio of beak width at half length to half the full beak width, 18). The intermediate value for the latter ratio (1.0) represents a triangular beak shape projected dorsoventrally. Ratio values distinguish spatulate bills that are wide toward the tip (ratio > 1.0) from tweezer-like bills (ratio < 1.0). Body mass values were not available for Yellow Warblers, so we did not include mass in our analyses.

Statistical analysis. We conducted all statistics in R version 1.3.1093 (R Core Team 2019, Appendix S1). Using the package *vegan* (Oksanen et al. 2018), we ran a principal component analysis (PCA) on all 11 warbler species to reduce dimensionality and identify the greatest morphological differences among the 11 species. We scaled all variables to a mean of 0 and standard deviation of 1 prior to analysis.

We used an ANOVA incorporating data from the five warbler species (American Redstart, Black-and-white Warbler, Black-throated Blue Warbler, Northern Parula, and Worm-eating Warbler) sampled in Jamaican wet limestone habitat to test for species differences in prey size. We ran independent analyses for ant head width and beetle elytron length. We ran a Tukey post-hoc test on significant results to determine which pairs of warbler species exhibited significant differences.

We used linear mixed-effects models (package *lme4*; Bates et al. 2015) to test for relationships between PC1, which was a measure of body size (see Results), and prey item size. We included data from only the five coexisting wet limestone species (American Redstarts, Black-and-white Warblers, Black-throated Blue Warblers, Northern Parulas, and Worm-eating Warblers) because we had the best prey size data for this community. Northern Parulas and Worm-eating Warblers were the only species that consumed enough Orthopterans for statistical comparison of this

prey type. We averaged all prey item sizes found in each individual stomach sample to make each bird's prey size independent. A random effect of bird species controlled for repeated measures. We ran independent analyses using beetle elytron length and ant head width, each as a function of PC1. We used a Student's *t*-test to compare the size of Orthoptera mandibles consumed by Northern Parulas and Worm-eating Warblers. We calculated pseudo- R^2 values here and for all regression analyses using the package *MuMIn* (Bartón 2020).

We tested the relationship between aerial foraging versus gleaning adaptations, or PC2 (see Results), and two different insect groups, namely winged insects and "strong flyers." Winged insects included all arthropods that have wings, namely adult individuals in the taxa Odonata, Orthoptera, winged Blattodea termites, Heteroptera, Psyllidae, Auchenorrhyncha, Thysanoptera, Psocoptera, Coleoptera, Neuroptera, winged Hymenoptera, adult Lepidoptera, Mecoptera, and Diptera. "Strong flyers" were a subset of the winged insects, including only arthropods that move primarily by flying (Diptera, winged Hymenoptera, Odonata, and Mecoptera). We ran analyses with the package *lme4* (Bates et al. 2015). We ran generalized linear mixed-effects models with a binomial distribution and logit link to test whether birds with more aerial foraging adaptations consumed a higher percentage of winged insects and strong flyers than birds with gleaning adaptations (PC2). The response variable was either the proportion of winged arthropods or strong flyers identified out of all consumed invertebrates. Predictor variables included PC2 and crossed random effects of species and site to control for repeated measures of bird species and differences in arthropod availability (or different methods of sampling stomach contents between sites), respectively. These analyses incorporated data from all 11 species of warblers and thus all sites, both breeding and wintering. We collected all diet data within sites at the same time to control for available prey. We tested hypotheses with the package *pbrtest* (Halekoh and Højsgaard 2014) to perform parametric bootstrapping, comparing the fitted model to a simplified null model not containing the principal component score. We used enough simulations (winged

insects and PC2: 10,000; strong flyers and PC3: 2000) so that P values did not change when the test was rerun.

We similarly used a generalized linear mixed-effects model to test the relationship between PC3, a measure of arboreal versus ground-foraging adaptations (see Results), and Psocoptera (barklice), the only abundant prey taxon found primarily on tree boles and branches (Kent et al. 2019). Similarly to above, the response variable was the proportion of Psocoptera out of all invertebrates in the diet and contained the fixed effect of PC3 and crossed random effects of bird species and site. We performed parametric bootstrapping using sufficient simulations (2000) to stabilize results.

RESULTS

We obtained prey size measurements from 850 identifiable insect remains from stomachs of the five warbler species coexisting in Jamaican wet limestone habitat. This sample included 556 ant heads from 54 stomachs of five warbler species, 126 beetle elytra from 43 stomachs of five warbler species, and 168 Orthoptera mandibles from 33 stomachs of two warbler species. We calculated the percentage of winged prey and Psocoptera from a sample of 12,390 arthropods in the stomach contents of all 11 species of warblers sampled in both winter and summer habitats (Table S2).

Morphological differences. The PCA revealed that the warblers in our study were morphologically distinct (Figs. 1 and 2). This analysis extracted three components that accounted for ~70% of the overall morphological differences (Table 1). The first axis (PC1, 41% of variance) is best described as a measure of overall body size, with characteristics such as beak depth, beak length, claw length, wing chord, and total body length loading positively and highly on PC1. The next morphological factor (PC2, 20% of variance) encompassed aerial foraging versus gleaning adaptations, with characteristics like bill flatness, tail length, bill area toward tip (i.e., spatulate versus tweezer-like), rictal bristle length, and rictal bristle count all loading positively. PC2 was negatively associated with claw curvature, which is consistent with the limited use of claws by aerial foragers while

foraging. The third and weakest principal component (PC3, 10% of variance) had the strongest (negative) loadings for claw curvature and depth, suggesting an interpretation of arboreal versus ground-foraging adaptations.

Morphology and diet. Warblers in wet limestone habitat did not differ with respect to width of ant heads consumed ($F_{4,49} = 0.8$, $P = 0.56$; Fig. S2). Consistent with this result, PC1 did not predict ant head width ($F_{1,3} = 0.4$, $P = 0.59$, $R^2 = 0.013$; Fig. S3). However, warblers differed with respect to the length of beetle elytra consumed ($F_{4,38} = 5.4$, $P = 0.001$). Linear regression showed a positive relationship between elytron length and PC1 ($F_{1,3} = 21.8$, $P = 0.019$, $R^2 = 0.33$; Fig. 3). Additionally, larger Worm-eating Warblers (based on PC1 score) consumed Orthopteran prey with significantly larger mandibles (0.38 mm average mandible width) than Northern Parulas (0.28 mm average) ($t_{19,0} = -2.4$, $P = 0.028$; Fig. S4).

Species that scored highly on morphological aerial foraging characteristics (higher PC2 values) ate more winged insects than other species ($\chi^2 = 5.0$, $P = 0.048$, $R^2 = 0.23$, 97.5% CI of slope = [0.09, 1.02]) (Fig. 4). When restricted to “strong flyers,” we found no significant trend with PC2 ($\chi^2 = 2.3$, $P = 0.17$, $R^2 = 0.44$, 97.5% CI = [-0.53, 3.62]; Fig. S5). Finally, there was no relationship between PC3 and percentage of Psocoptera in diets ($\chi^2 = 0.1$, $P = 0.56$, $R^2 = 0.58$, 97.5% CI = [-5.18, 4.13]; Fig. S6).

DISCUSSION

We used a variety of body measurements to identify three independent axes capturing much (~70%) of the external morphological variation among these species of warblers. Moreover, the most distinctive of these axes, the first two principal components associated with bird body, and especially bill, size, and aerial foraging versus gleaning adaptations, predicted multiple aspects of diet. Warbler size predicted prey size for two independent insect size proxies, namely beetle elytra length and Orthoptera mandible width, but not ant head width as a third proxy. Additionally, warblers adapted for aerial foraging consumed proportionately more winged insects than the

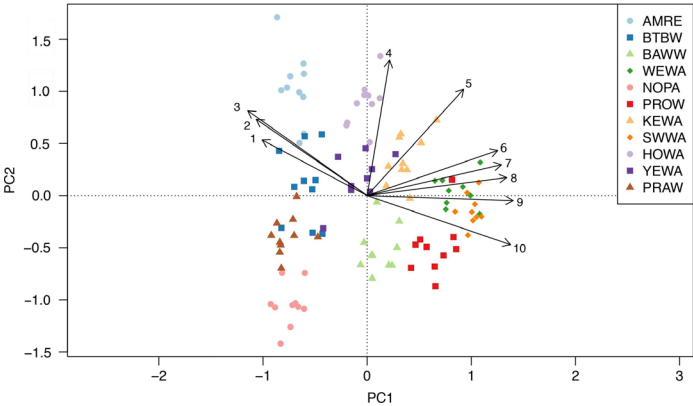


Fig. 1. Morphological characteristics loading highly on PC1 (41%) and PC2 (20%). Alpha codes denote warbler species including American Redstart (AMRE), Black-throated Blue Warbler (BTBW), Black-and-white Warbler (BAWW), Worm-eating Warbler (WEWA), Northern Parula (NOPA), Prothonotary Warbler (PROW), Kentucky Warbler (KEWA), Swainson's Warbler (SWWA), Hooded Warbler (HOWA), Yellow Warbler (YEWA), and Prairie Warbler (PRAW). Arrow length denotes magnitude of the loading for each variable. The 10 morphological variables with the highest averaged PC1 and PC2 loadings (absolute values) are included: (1) rictal bristle count, (2) bill flatness, (3) rictal bristle length, (4) beak width at half length, (5) full body length, (6) wing chord, (7) claw length, (8) beak depth at half length, (9) beak depth, and (10) beak length. [Colour figure can be viewed at wileyonlinelibrary.com]

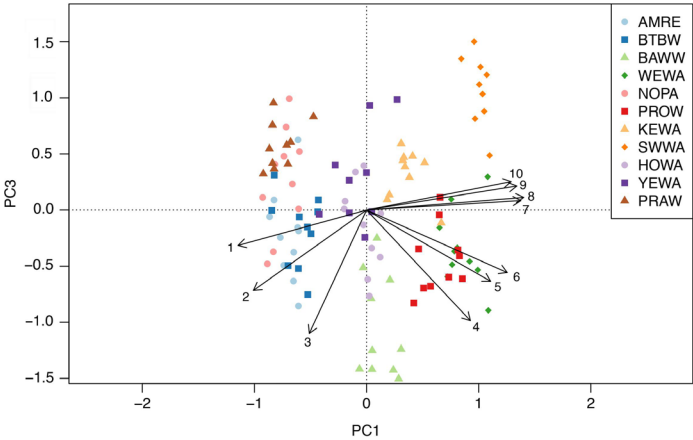


Fig. 2. Morphological characteristics loading highly on PC1 (41%) and PC3 (10%). Alpha codes denote warbler species, including American Redstart (AMRE), Black-throated Blue Warbler (BTBW), Black-and-white Warbler (BAWW), Worm-eating Warbler (WEWA), Northern Parula (NOPA), Prothonotary Warbler (PROW), Kentucky Warbler (KEWA), Swainson's Warbler (SWWA), Hooded Warbler (HOWA), Yellow Warbler (YEWA), and Prairie Warbler (PRAW). Arrow length denotes magnitude of the loading for each variable. The 10 morphological variables with the highest averaged PC1 and PC3 loadings (absolute values) are included: (1) rictal bristle length, (2) rictal bristle count, (3) claw curvature, (4) claw depth, (5) Kipp's distance, (6) wing chord, (7) beak length, (8) beak depth, (9) beak depth at half length, and (10) claw length. [Colour figure can be viewed at wileyonlinelibrary.com]

other species, as predicted. The third principal component and analysis of Psocoptera consumption revealed no significant

relationship involving arboreal versus ground-foraging adaptations, although this is likely due to limitations of our data.

Table 1. Loadings and cumulative amount of variation explained by each of the three principal components (PC's) obtained from a principal component analysis of the 18 morphological features measured from 11 warbler species.

	PC1	PC2	PC3
Proportion of variance explained	0.4087	0.1968	0.09841
Cumulative proportion explained	0.4087	0.6055	0.70392
Beak length	1.37657	-0.47120	0.08489
Beak width	0.64597	0.78347	-0.18100
Beak depth	1.40190	-0.04832	0.11235
Beak depth at half length	1.34029	0.17292	0.21419
Beak width at half length	0.21537	1.29950	0.25910
Bill flatness	-1.06522	0.73241	-0.22877
Bill area toward tip	-0.36087	0.93897	0.59340
Rictal bristle length	-1.14617	0.81429	-0.31550
Rictal bristle count	-1.00908	0.53375	-0.71653
Wing chord	1.25423	0.43319	-0.55726
Kipp's distance	1.10674	-0.03622	-0.63522
Tarsus length	0.53602	0.54310	0.12848
Hind toe length	1.21990	0.12230	-0.06364
Claw length	1.28950	0.29603	0.25313
Claw depth	0.92583	-0.17184	-0.98542
Claw curvature	-0.51068	-0.57648	-1.09942
Tail length	-0.08852	1.31293	-0.32686
Full body length	0.92653	1.02017	-0.22478

Although finding a relationship between form and function is not novel, four results of our study are notable: (1) major differences in the external morphology of coexisting parulid warbler species were directly related to differences in diet, supporting our hypothesis that diet specializations are a major cause of general morphological variation, (2) multiple morphological traits predicted species differences in diet, which is most often studied using foraging behavior or morphology alone as a diet surrogate, (3) morphology predicted differences between species in diets while largely controlling for prey availability, that is, when the birds are potentially competing directly, and thus making relationships more directly relevant to understanding the adaptive radiation of coexisting species, and (4) the relationships we found were surprising considering the subtle morphological differences among this restricted set of foliage-gleaning species. The 11 species in our study, a small subset of the 107 species in the family Parulidae, thus had sufficient morphological variation to explain significant dietary differences. The species included in our study also

come from a relatively morphologically homogenous clade of birds, with six of the 11 species congeneric *Setophaga*. Lovette and Bermingham (1999) recognized that up to eight species of *Setophaga* coexist when breeding. This high degree of sympatry is noteworthy because *Setophaga* species lack the dramatically variable morphologies of other coexisting groups, such as the Galapagos finches and Hawaiian honeycreepers, famous for their differences in bill morphology (Lovette and Bermingham 1999).

Morphology and diet. The PCA separated warbler species primarily by body size (PC1), aerial foraging versus gleaning adaptations (PC2), and arboreal versus ground-foraging adaptations (PC3). The first two principal components were readily interpretable. Warblers wintering in Jamaican wet limestone habitat appear to segregate ecologically at least in part by differences in prey size. We detected variation in the size of beetles consumed by different warbler species that was probably facilitated by the diversity of beetle taxa and sizes available to the birds in the floristically and physiognomically complex wet limestone study

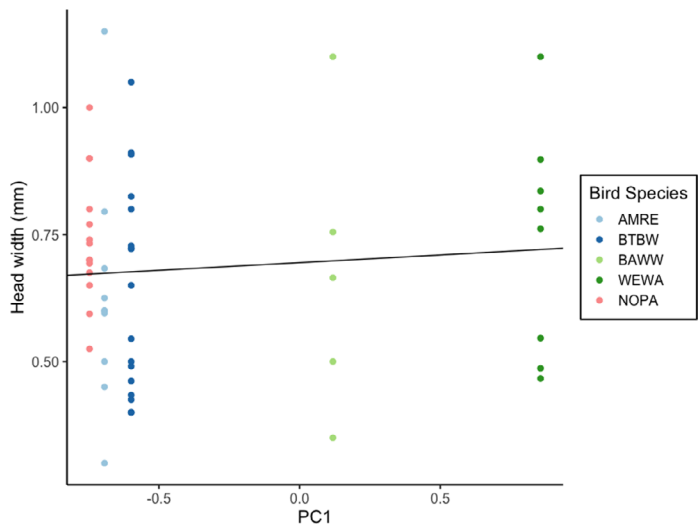


Fig. 3. Beetle elytron length as a function of PC1. The trend line shows a statistically positive relationship of PC1 to elytron length. [Colour figure can be viewed at wileyonlinelibrary.com]

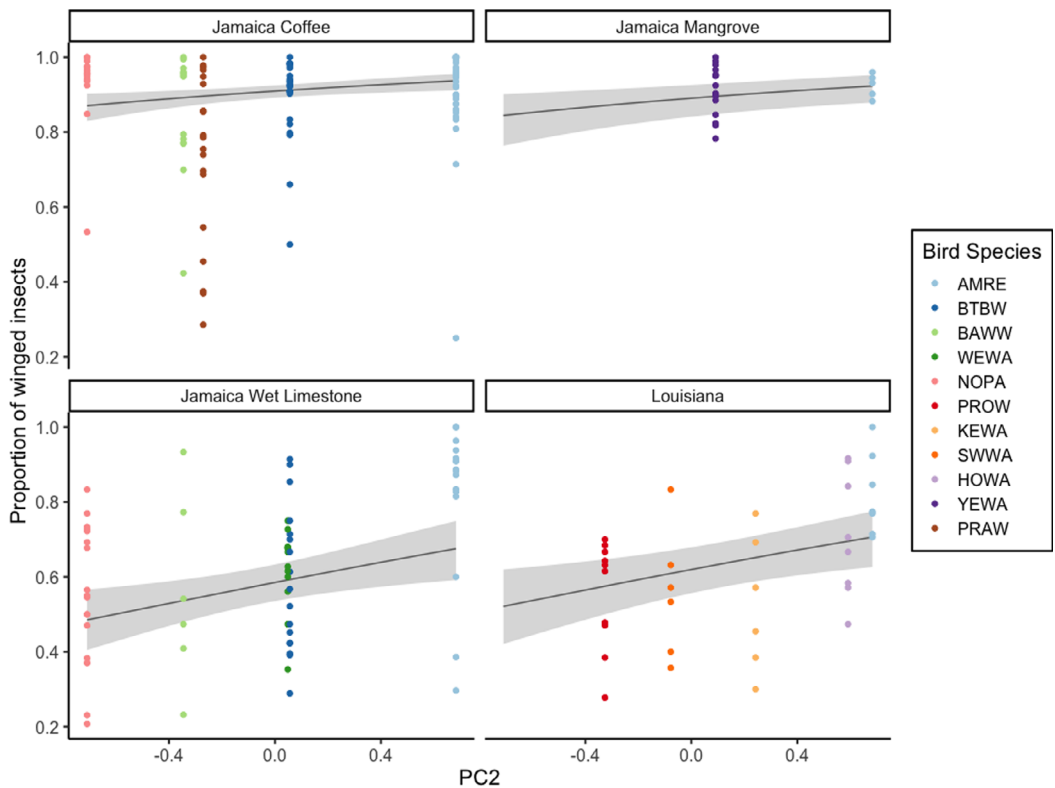


Fig. 4. PC2 and proportion of winged insects consumed by warblers, by site, with 97.5% confidence intervals. [Colour figure can be viewed at wileyonlinelibrary.com]

site. Additionally, the size of Orthoptera mandibles in the diets of Northern Parulas and Worm-eating Warblers differed as predicted, with larger-bodied Worm-eating Warblers eating larger Orthopterans. A variety of ecologically and phylogenetically similar, sympatric species of birds have been found to exhibit similar prey size partitioning (Martínez 2004, Garcia and Arroyo 2005, Kasahara and Katoh 2008, Borah et al. 2012). Both aquatic (Thierry et al. 2011) and terrestrial (Owen-Smith and Mills 2008) mammals also exhibit size structuring of predator–prey relationships and food webs, but the presence of a relationship between body mass and trophic level in terrestrial mammals has been questioned (Tucker and Rogers 2014). Differences in the head size of ants consumed were not significantly related to differences in warbler body size in our study. A possible explanation for this is that ants were the most commonly available and consumed food source for all five warbler species in the Jamaican wet limestone habitat (Kent et al. 2019) and came from few morphospecies (Kent, pers. observ.). Thus, these ants exhibited little size variation that could facilitate morphological differentiation by birds.

The strong relationship of PC2 with aerial foraging versus gleaning adaptations, along with relevant prey types, implies that such foraging characteristics are important for ecological segregation in these birds (Lack and Lack 1972, Lack 1976, Lovette and Hochachka 2006). The strength of these differences varied across sites, with little variation in the Jamaican coffee and mangrove sites, where all species consumed many flying insects (~ 90% of their diet). The consumption of a large number of presumably abundant flying psyllid pests in coffee plantations and reproductive termites in mangrove forests drives this pattern. This pattern was more pronounced at the other two sites, where the percent of winged prey increased from ~ 50% in the less aerial-adapted species to near 80% in the most. As such, the relative abundance of winged prey likely drives the difference in the strength of this pattern between sites. This finding is novel in that few studies have revealed direct empirical links between stomach contents and aerial morphological foraging adaptations. These results provide support for MacArthur's (1958) unsubstantiated supposition that breeding spruce-woods warbler

species, including *Setophaga* species not included in our study, can coexist due to subtle variations in foraging behavior that correspond with differences in prey taxa consumed. Sherry et al. (2016) also interpreted the dietary differences of five coexisting warblers wintering in Jamaican shaded-coffee plantations as primarily related to flycatching versus foliage-gleaning foraging behaviors.

The third principal component, interpreted as arboreal versus ground-foraging adaptations, provided a weaker description of morphologies relevant to foraging. Claw depth and claw curvature, features typically adapted for tree-creeping movements by facilitating the gripping of tree trunks and branches by birds, both had strong negative loadings with PC3. However, other relevant features such as tarsus (Osterhaus 1962, Morse 1989) and toe length were only weakly correlated with this principal component. Additionally, the only species that differentiated along PC3 were Black-and-white Warblers (deep, curved claws) with negative values and Swainson's Warblers (shallow, flat claws) with positive values. This difference is expected because Swainson's Warblers are adapted to forage primarily on the ground. The lack of a strong interpretation for the PC3 axis may have resulted because relevant prey taxa were not restricted to ground, foliage, or bark substrates, making it difficult to use such prey as a surrogate of foraging strategy. For example, psocopterans were not strictly limited to tree trunks in our study (Kent and Sherry 2020), allowing ground and aerial foragers to consume them using different foraging tactics than Black-and-white Warblers. Additionally, bark lice are common in the airspace, so American Redstarts and other aerial foragers may be able to catch them in flight (Kent et al. 2019, Kent and Sherry 2020).

Our results support the proposition that differences in bird size, selected evolutionarily in relation to prey sizes, may be important for ecological coexistence of these warbler species. However, available data cannot resolve whether the bird size–prey size relationship resulted because larger birds actively selected larger prey or because warblers are adapted to different substrates containing different-sized prey. Suspended dead leaves tend to contain relatively large prey such as Orthoptera and cockroaches (Greenberg 1987, Rosenberg 1990, 1993).

Worm-eating Warblers in Jamaica foraged consistently from hanging dead leaves and dead leaf clusters (aerial litter; Kent and Sherry 2020), encountering relatively large and hidden Orthoptera compared to Northern Parulas that foraged almost strictly from live leaves (Lack and Lack 1972, Kent and Sherry 2020). Thus, our results support the substrate hypothesis, and no additional prey size selection while foraging per se is necessary to account for our results. Divergence in species' traits supports coexistence (Pigot et al. 2018), whether it arose directly in response to interspecific competition or evolved independently and favored particular species assemblages locally. We suggest that the morphological differences among the warblers in our study may contribute to their successful sympatry, regardless of whether the species are selecting for prey traits or foraging substrates.

Our study is unique in that we focused on migratory species with different prey availability during winter and summer. We recognize that community structure varies between breeding and wintering areas and note that the foraging relationships of these warblers may differ in their breeding areas (Oksanen 1987). For example, Worm-eating Warblers forage more on suspended dead leaves during the non-breeding season than the breeding season (Greenberg 1986). Although some investigators have found that migratory species may show relatively little adaptation to their non-breeding range compared to sedentary relatives (O'Connell et al. 2019), we still find notable differences here. In fact, we may expect less dietary overlap and more competition between these birds than resident species because migrants do not defend the same territories year-round (Freeman et al. 2019).

Morphological divergence. We argue that selection for efficient foraging is the most important mechanism for the adaptive radiation of warblers, although the exact role of this selection in allowing coexistence remains an open question (Kent and Sherry 2020). Parulid warblers have played an outsized role in advancing interspecific competition and coexistence theory, but evidence for interspecific competition causing evolutionary diversification in coexisting parulids, such as those in our study, is mixed. MacArthur (1958) emphasized foraging differences as a mechanism for coexistence and downplayed the potential importance of morphology, but he largely lacked diet

data. Likewise, other authors have noted the relatively small differences in foraging morphology of parulid warblers, instead emphasizing variation in traits like song and plumage that are potentially related to sexual selection (Lovette and Bermingham 1999). However, we illustrate here that these warblers also differ morphologically in ways that can be directly linked to foraging.

Our results indicate that, in addition to these dramatic species differences potentially linked to sexual selection and other life-history traits (e.g., Mitchell et al. 2019), parulids also differ significantly in external morphological traits relevant to foraging behavior. The nature of these predictions, linked directly to foraging behavior (e.g., for larger insects and for flying versus non-flying insects), help explain the kinds of foraging differences among coexisting insectivorous birds that past authors interpreted as coexistence mechanisms (e.g., MacArthur 1958, Morse 1989, Mansor et al. 2018). Increasing evidence that these warblers compete intraspecifically for limited food resources (see Introduction and Sherry et al. 2016), coupled with evidence of extensive diet overlap among coexisting warblers (Kent and Sherry 2020), strongly implicates interspecific competition (Dhondt 2012). We thus argue that the morphological and corresponding dietary differences among species that we documented in coexisting parulid warblers are most parsimoniously interpreted as the evolutionary outcome of interspecific competition. We cannot yet determine if these differences have arisen from more or less continuous (within the lifetime of birds) stabilizing selection or episodically during possible ecological-crunch periods such as severe El Niño droughts in the Caribbean.

Interspecific competition can operate via different mechanisms, necessitating different tests and test criteria. For instance, these traits may have evolved separately as species followed different evolutionary trajectories arising from a common selection pressure (Langerhans and DeWitt 2004), that is, efficient foraging in a food-limited system. Here, interspecific competition may only act as a filtering mechanism, allowing species to coexist if they have limited niche overlap upon secondary contact (Pigot et al. 2018). Small-scale habitat heterogeneity, such as different foraging microhabitats or variation in prey size

that are present in this system, may further promote coexistence via this mechanism (Questad and Foster 2008).

Disentangling these possibilities and the importance of past ecological interactions on these evolutionary questions remains an important and fundamental goal. The spatial and phylogenetic scale of studies is important for detecting morphological–resource relationships such as those documented in our study. However, regardless of the underlying mechanism, our results provide strong evidence that foraging selection pressures have played an important role in the morphological divergence of these species. Because this is far easier to quantify across a wide range of taxa than diet or foraging behavior, we recommend studies comparing phylogenetic and morphological diversification rates in this clade to help shed light on their timing and potential ecological causes (e.g., Folk et al. 2019).

Methodological considerations. We acknowledge that the warblers in our study may digest different insect taxa at different rates, with soft-bodied prey disintegrating and becoming unrecognizable relatively rapidly (Rosenberg and Cooper 1990). This potential bias was minimal in our study because almost all insects had diagnostic parts that persist in the gut, including hard mouthparts of many taxa (Sherry et al. 2016) and wings of Diptera, which often persist intact even as far downstream in the digestive process as fecal matter (Kent, pers. observ.). Moreover, even though hard-bodied prey are more likely to preserve well, this potential bias should affect all warbler species similarly. Thus, we argue that differences in warbler diets, such as prey size and percentage of flying insects, are not attributable to digestion bias. Additionally, we only used prey parts in our prey size comparisons (ant heads, beetle elytra, and Orthoptera mandibles) that tend to remain intact in stomach contents even when other body parts of the same insects may have become unrecognizable from digestion.

Conclusions. Our results illustrate the importance of morphology in constraining the diets of coexisting species of parulid warblers. We suggest that morphological differences among species may have arisen and be maintained as a result of interspecific competition in ecological communities. We demonstrated that the most significant evolved morphologies in

these species are directly linked to differences in diet, and in predictable ways based on functional morphological considerations. Although diet data are scarce in most previous studies of these birds, we illustrate the potential value of such data. Morphology is valuable in understanding the relationship between diet and community structure because it reflects a wide range of an organism's ecological and evolutionary characteristics. Studying morphological specialization is key to developing a more complete understanding of the role that it plays, in coordination with diet, in shaping ecological interactions among species such as competition and community assembly.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Table S1. Order and common name of arthropod prey identified in diet samples.

Table S2. Sample size of bird stomachs and individual prey included in analyses by site.

Fig. S1. Phylogeny of 107 species of Parulidae (Lovette et al. 2010), with study species marked by points denoting which species were sampled from which study sites.

Fig. S2. Black-throated Blue Warbler (BTBW), American Redstart (AMRE), Black-and-white Warbler (BAWW), Northern Parula (NOPA), and Worm-eating Warbler (WEWA) did not differ in median ant head length consumed.

Fig. S3. Ant head width as a function of PC1.

Fig. S4. Worm-eating Warblers consumed Orthopteran prey with a larger median mandible width (solid horizontal bars) than Northern Parulas.

Fig. S5. PC2 and proportion of “strong flyers” consumed by warblers, by site, with 97.5% confidence intervals.

Fig. S6. PC3 and proportion of Psocoptera consumed by warblers, by site, with 97.5% confidence intervals.

Appendix S1. Warbler morphology code.