

SPECIAL FEATURE: Advances in Avian Diet Methods and Applications

Extensions and limitations of MacArthur (1958): A review of ecological and evolutionary approaches to competition and diet in the New World wood warblers (Parulidae)

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Submission Date: January 14, 2021; Editorial Acceptance Date: January 28, 2022; Published March 15, 2022

ABSTRACT

The extent to which interspecific competition structures species interactions and coexistence within communities, and the relevant mechanisms, are still debated. We focus on New World wood warblers (Parulidae), beginning with Robert MacArthur's iconic 1958 paper in which he shows how subtle foraging behaviors, purportedly linked to dietary differences, within spruce trees contribute to the coexistence of 5 spruce-woods warbler species. MacArthur coined the phrase "resource partitioning", and profoundly impacted the field of Ecology for subsequent decades in diverse ways. To understand what MacArthur got right and what he missed, we reviewed both ecological and evolutionary approaches to questions of the origin and coexistence of competing species in the context of diet. We argue that an important, underappreciated, mechanism of competition among coexisting migratory warbler species, particularly in winter, is diffuse exploitation competition, based in part on our own studies of warbler diets in relation to foraging behavior, substrate use, bird morphology, and other traits. Our review and synthesis of interspecific competition and coexistence in warblers have important consequences, including our questioning of the importance and effectiveness of resource partitioning in birds. We also suggest a novel hypothesis for the success of warblers today in the Caribbean and other habitats, beginning with their relatively recent adaptive radiation and the ecological opportunity on Caribbean islands.

Keywords: adaptive radiation, coexistence, diffuse competition, evolutionary ecology, exploitation competition, interspecific competition, Parulidae, resource partitioning

LAY SUMMARY

- Robert MacArthur's pioneering study of New World wood warblers triggered immense interest in how competitor species partition resources to coexist.
- By reviewing resource competition and use among coexisting warbler species we address MacArthur's impressive legacy and consider what he missed.
- We integrate ecological and evolutionary information to argue that warblers coexist primarily by specializing on different foraging substrates (i.e., locations where food is sought) rather than partitioning resources themselves, which are diverse and substantially shared by demonstrably competing species.
- By comparing warbler diets, foraging behavior, and morphology we argue that diffuse exploitative interspecific competition favors substrate specialization; and we suggest a novel evolutionary hypothesis to explain the adaptive radiation of these warblers, particularly in the Greater Antilles islands.
- Diverse new data—especially diets—and approaches to warbler biology compel innovative perspectives on MacArthur's fundamental contributions to coexistence in competing species.

Extensiones y limitaciones de MacArthur (1958): Una revisión de los enfoques ecológicos y evolutivos de la competencia y la dieta de Parulidae

RESUMEN

Hasta qué punto la competencia interespecífica estructura las interacciones de las especies y la coexistencia dentro de las comunidades, y los mecanismos relevantes, todavía son temas de debate. Nos enfocamos en los parúlidos (Parulidae), comenzando con el 1958 artículo icónico de Robert MacArthur en el que muestra cómo comportamientos sutiles de forrajeo, supuestamente vinculados a las diferencias de la dieta dentro de los bosques de abeto, contribuyen a la

coexistencia de cinco especies de parúlidos de los abetos. MacArthur acuñó la frase "partición de recursos" e impactó profundamente en el campo de la Ecología durante las décadas siguientes de diversas maneras. Para comprender en qué acertó MacArthur y en qué se equivocó, revisamos los enfoques ecológico y evolutivo sobre las cuestiones del origen y la coexistencia de especies competidoras en el contexto de la dieta. Argumentamos que un mecanismo de competencia importante y subestimado entre las especies coexistentes de parúlidos migratorios, particularmente en invierno, es la competencia de explotación difusa, basados en parte en nuestros propios estudios de las dietas de los parúlidos en relación con el comportamiento de forrajeo, el uso de sustratos, la morfología de las aves y otros rasgos. Nuestra revisión y síntesis de la competencia interespecífica y la coexistencia en los parúlidos tiene consecuencias importantes, incluyendo el cuestionamiento de la importancia y la eficacia de la partición de recursos en las aves. También sugerimos una hipótesis novedosa del éxito actual de los parúlidos en el Caribe y otros hábitats, comenzando con su radiación adaptativa relativamente reciente y la oportunidad ecológica en las islas del Caribe.

Palabras clave: coexistencia, competencia de explotación, competencia difusa, competencia interespecífica, ecología evolutiva, partición de recursos, Parulidae, radiación adaptativa

INTRODUCTION

"In this study competition has been viewed in the light of the statement that species can coexist only if each inhibits its own population more than the others'. This is probably equivalent to saying that species divide up the resources of a community in such a way that each species is limited by a different factor. If this is taken as a statement of the Volterra-Gause principle, there can be no exceptions to it. Ecological investigations of closely-related species then are looked upon as enumerations of the divers [sic] ways in which the resources of a community can be partitioned." Robert MacArthur (1958, p. 617).

A major goal of Ecology is to explain the diversity and abundance of species. The New World wood warblers (Parulidae) have provided important insights due to their diversity, with 116 recognized species (Curson 2010), and up to 8–9 species coexisting locally; local species richness and abundance attest to New World wood warblers' evolutionary success. They comprise 90–95% of all Nearctic-Neotropical migratory bird individuals wintering in some Greater Antilles islands, and 50–60% of all birds—including migrants and year-round residents—breeding in north temperate zone forests (Sabo and Holmes 1983, Holmes 2011). These warblers also capture our imagination by their conspicuously bright plumages, insistently varied breeding-season songs, and active foraging. These birds represent one of the most dramatic avian adaptive radiations in North America (Lovette and Bermingham 1999) and understanding the resulting diversity of coexisting species remains both an ecological and evolutionary challenge.

The widespread coexistence of these closely related warblers prompted one of the most influential ecological studies ever, namely MacArthur's (1958) study of 5 coexisting warbler species breeding in the spruce forests of Maine. These 5 warbler species are congeneric (*Dendroica*, recently revised to *Setophaga*; Lovette et al. 2010), similar in body size and morphology, and largely insectivorous in summer,

prompting MacArthur's questioning of whether they violated the competitive-exclusion principle, in which identical competitors cannot coexist. Through this and more recent work, ecologically similar species like these warblers have contributed substantially to our understanding of species coexistence and thus community structure more generally.

Little consensus exists as to how these warblers, and competing species more generally, coexist. The purpose of the present paper was to critically review the ecology and evolution of New World wood warblers, to propose new ways to integrate ecological and evolutionary perspectives into a more comprehensive synthesis of how these birds came to occupy and coexist in the environments they now inhabit, and, in the process, to review which of MacArthur's (1958) findings and assumptions have endured. Key insights into these issues come from detailed diet studies using traditional, morphological methods (Hoenig et al. 2021, and Supplementary Materials Appendix A), coupled with studies of available foods, foraging behavior, and morphology, particularly in winter. Insights also come from long-term demographic studies of warblers, particularly those wintering in Jamaica. Such data lead us to question the appropriateness of "resource partitioning", and to propose an alternative coexistence mechanism, namely diffuse exploitative competition leading to the evolution of foraging substrate (i.e. structural features of the habitat where food is sought) specialization. Intense diffuse resource competition and poor dispersal abilities in mainland Neotropical insectivorous birds (Sherry et al. 2020b) suggest a novel hypothesis for the importance of the Caribbean Islands to the adaptive radiation of parulid warblers. Warbler diversity and local abundance are compelling in their own right but we argue that conclusions based on the wood warblers inform our understanding of biological communities more generally, just as MacArthur (1958) intended. We begin by reviewing the legacy of what MacArthur got right, emphasizing diet and foraging behavior, then delve into the evidence for intra- and interspecific competition in parulid warblers, including strong inferential evidence for diffuse exploitative competition, followed by evolutionary perspectives on competition and the origins and diversity of these birds. With this perspective we parlay

what little MacArthur missed, and why, into suggested future research directions concerning the origins and maintenance of species diversity.

MACARTHUR'S LEGACY

Although not a household name, Robert MacArthur is hard to miss in ecology texts (e.g., [Bowman and Hacker 2021](#)), and in multiple contexts. He coupled his considerable natural history experience with mathematical training to link empirical observations with theory, one important legacy ([Kaspari 2008](#)). His contributions provided a foundation for several fields of ecology today, including how organisms make optimal decisions such as what to eat, competition and community structure, island biogeography (and dispersal), geographical ecology, and the ecological niche (e.g., [Cody and Diamond 1975](#), [Chase and Leibold 2003](#), [Pianka and Horn 2005](#), [Kaspari 2008](#)).

MacArthur's (1958) Ph.D. dissertation research captured the imagination of ecologists for multiple reasons ([Kaspari 2008](#)), including its link to the theoretical conditions for ecological coexistence based on the Lotka-Volterra model of interspecific competition (Figure 1). He next provided evidence that the warbler population fluctuations were consistent with regulation, and thus with density-dependent competition for resources, a rarely cited but a critical building block for his arguments about interspecific competition. MacArthur interpreted this regulation as evidence for each species' resource limitation, via within-species competition, a prerequisite for resource competition among species.

MacArthur (1958) argued that the warblers do not violate Gause's principle, primarily because of subtle foraging behavioral differences leading to the consumption of different prey resources, providing a compelling case for ecological niche differentiation. The iconic figure of the 5 species coexisting by feeding in different parts of conifer trees (Figure 2) is what many textbooks tend to reproduce and thus emphasize, which misrepresents what MacArthur actually asserted by omitting all the other species differences he documented. MacArthur never claimed that the 5 warbler species fed on the same resources or that they partitioned space within trees. Rather, MacArthur provided evidence that the warblers' behavior exposed them to some of the same prey ("The actual food eaten does indicate that the species have certain foods in common", p. 617) and to many different insect prey taxa, which weakened but did not eliminate interspecific competition. The Bay-breasted Warbler (*Setophaga castanea*), for example, was the most deliberate searcher in MacArthur's study, probably discovering proportionately more caterpillars and other relatively cryptic or challenging-to-detect prey compared to a bird species moving more quickly through the foliage targeting more active and conspicuous prey. Based on

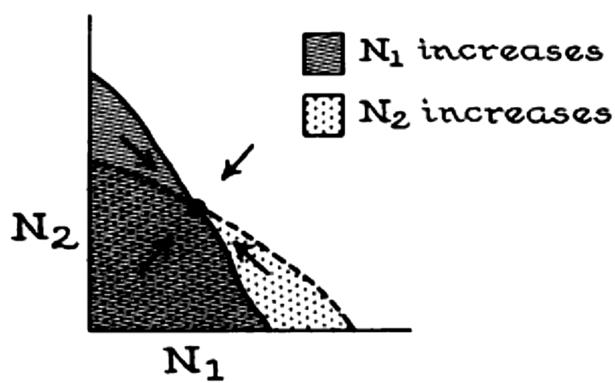


FIGURE 1. Equilibrium conditions for stable coexistence of two competing species, N_1 and N_2 , based on the Lotka-Volterra model and reproduced from [MacArthur \(1958\)](#). The lines have negative slope because each species reduces the abundance of the other via competition for population-limiting resources. Coexistence is favored by weak competitive effects (i.e. by each species being more strongly limited intraspecifically than interspecifically), implicit in the slopes of the lines describing conditions for population growth of each species. For example, the species 2 population can grow under conditions of greater abundance of species 1 than of species 2 because the competitive effect of an individual of species 1 damping population growth of species 2 is weaker than the effect of an individual of species 2 on itself. This is illustrated here by the line constraining species 2 growth intersecting the x-intercept at a greater abundance of species 1 (each individual having a relatively weaker effect) than it intersects the y-axis for abundance of species 2; and vice versa for species 1 population growth. MacArthur attributed this weakening of each competitor's impact to resource partitioning (i.e. each species' being limited by a different resource).

these more nuanced results than are often appreciated, including descriptions of each species' foraging movements through spruce trees, MacArthur proposed the metaphor of "resource partitioning" by the different species, as a result of interspecific competition (see epigraph). By feeding on different resources, he argued, each species' population was limited somewhat independently of the other species, thereby weakening the competition among species compared to competition within, consistent with theory (Figure 1). MacArthur also noted that, in addition to searching differently within spruce trees, the warblers differed in life-history responses to the superabundant food resource provided by spruce budworm (*Choristoneura fumiferana*) caterpillars, as well as in nesting traits that could contribute to coexistence, above and beyond food resource differences.

To summarize the enduring legacy of [MacArthur's 1958](#) paper, ecological coexistence is as important a problem today as ever. He also recognized that nesting behaviors and life-history characteristics—including degrees of opportunism in the face of competition—are all components of a species' niche and reflect evolutionary differences. He recognized that coexistence involves multiple spatial scales ([Lovette 2016](#)), and that both winter and summer are likely

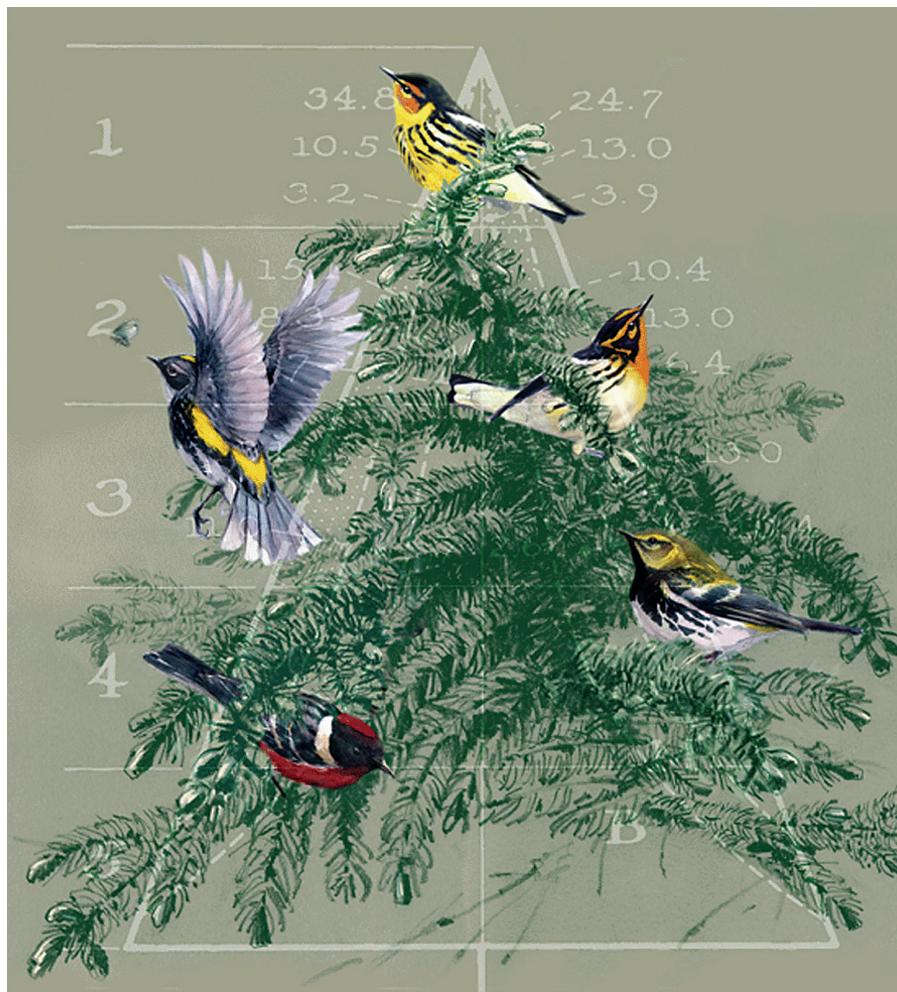


FIGURE 2. Composite illustration, based on multiple figures from MacArthur (1958) paper, showing different positions and substrates within conifer trees where the 5 warbler species under study tended to forage. Illustration by Debby Cotter Kaspari (Kaspari 2008) reprinted with permission. Species clockwise starting with top of tree: Cape May Warbler (*Setophaga tigrina*), Blackburnian Warbler (*Setophaga fusca*), Black-throated Green Warbler (*Setophaga virens*), Bay-breasted Warbler (*Setophaga castanea*), and Yellow-rumped Warbler (*Setophaga coronata*).

important to these warblers. He recognized that spruce trees influenced more than just where birds foraged, by documenting different tempos and patterns of movement through the trees, which he inferred (probably correctly) exposed each bird species to different prey. This was his strongest evidence for resource partitioning by these species. To appreciate what he missed necessitates reviewing what we now know about these warblers, some 60-plus years later, and particularly their diets.

One other contribution to MacArthur's legacy, well after his 1958 paper, warrants emphasis here because of its relevance to diets and competition for resources, namely "diffuse competition". MacArthur (1972) coined this term to describe how multiple overlapping, flanking species competitively exclude an intermediate one along a spectrum of resources. Pianka (1974) expanded this concept to include many species competing along diverse resource (niche)

axes for shared resources and linked the mean and total niche overlap in a community to the number of species. Elsewhere, Sherry et al. (2020b, p. 4) reviewed a variety of other definitions and applications of diffuse competition, arriving at the following definition, which we elaborate below: "the combined effects of 3 or more species depressing the abundance of a limiting resource sufficiently to affect the population dynamics and/or evolution of one or more coexisting species."

ECOLOGICAL PERSPECTIVES ON COMPETITION IN PARULID WARBLERS

Interspecific competition in birds is comprehensively reviewed (Dhondt 2012, Greenberg 2016), allowing focus here on evidence for interspecific competition and relevant coexistence mechanisms specific to

parulid warblers. The evidence is conflicting, thus paradoxical: why is there so much evidence for the ecological species differences documented among coexisting warbler species (e.g., MacArthur 1958, Lack and Lack 1972, Lack 1976, Morse 1989) despite a paucity of convincing evidence for ongoing interspecific competition in the majority of coexisting species? We argue, below, that interspecific competition in warblers is important, ongoing, and often overlooked for reasons that are revealing about how competition works, although we also consider a variety of alternative hypotheses. To appreciate this paradox better necessitates considering competition within species, a building block for competition among species, then addressing the evidence for interspecific competition involving warblers, in a full annual cycle context.

Competition in Summer

A classic experimental method to study competition for space or for food within species, a prerequisite for competition among species, is the removal of individuals, followed by monitoring recolonization of the “empty” territories or space. Hensley and Cope (1951) and Stewart and Aldrich (1951) did extensive removal experiments with breeding male spruce-woods parulid warblers, which resulted in more individuals re-colonizing the vacancies than were there originally; Morse (1989) interpreted these results as evidence for territoriality limiting some individuals from breeding. However, Marra and Holmes (1997) re-did this experiment with breeding Black-throated Blue Warblers (*Setophaga caerulescens*) and concluded that the earlier experiments said less about competition for space or food than for mates.

Nonetheless, Black-throated Blue Warblers provide compelling evidence for breeding season population regulation via intra-specific territoriality. “Site-dependent regulation” of populations, involving gradients of breeding territory quality (Rodenhouse et al. 1997, 2003; McPeek et al. 2001), generates competition for the best quality sites, and relegation of other individuals to poorer quality sites. Because proportionally more individuals are constrained to poor sites as the population grows, a greater population size leads to lower average demographic success, thus providing negative feedback on population growth. In other words, resources including food and safe breeding sites limit populations via contests for the best sites. Sillett et al. (2004) showed experimentally that a crowding mechanism contributes to population regulation in this species. Territoriality has also been proposed as evidence for breeding season competition among species, probably by way of securing limiting resources, and is widespread in parulid warblers (Loisin 2012, Loisin et al. 2016).

Competition During Migration

Stopover sites during migration are relatively little studied, and occupied for little time annually, but migrating individuals may nonetheless compete during migration, which should favor efficiency in food exploitation. For example, Moore and Yong (1991; see also Moore et al. 2005) studied migratory birds during spring stopover in Louisiana, following their crossing of the Gulf of Mexico, and showed with exclosure experiments that these birds in aggregate depressed insect resources including caterpillars; in most species studied, including a variety of parulid warblers, birds gained body mass faster when fewer migrants were present. Moreover, Wolfe et al. (2014) found that during stopover in Costa Rica, frugivorous migrants responded most to food (fruit) abundance, whereas insectivorous migrants responded most to structural habitat features, probably due to the ease of foraging in different kinds of vegetation and to the difficulty of predicting where food abundance would be greatest. These latter results are consistent with insectivorous warblers’ adaptations to specialize by foraging in particular substrates. Morse (1989) cites numerous other examples of warblers en route competing intraspecifically, a prerequisite for food resource competition among species, as discussed below.

Migrant-Resident Species Competition in Winter

Much of the research on warbler interspecific competition in winter has focused on potential competition between migratory species on their winter grounds with year-round resident birds. Interspecific competition in winter is probably best known from cases of interspecific territoriality, which can be as important during the nonbreeding period (e.g., Greenberg 1986, Greenberg et al. 1993, 1994, Greenberg and Ortiz 1994, Toms 2011, 2013, Powell et al. 2020) as in summer. However, few experiments have been conducted that controlled for multiple factors that could help explain the aggressive behaviors characterizing some species pairs. Such winter interspecific territoriality as has been documented almost invariably involved a single pair of species, missing possible interactions involving many species simultaneously. Nonetheless, interference competition involving aggressive species interactions certainly provides one mechanism of resolving competition, in at least some warbler species.

Migrants often winter in many Neotropical habitats at high densities, which would suggest they should impact food availability and thus compete with both resident and other migrant species. This logic has motivated comparisons of the behavior of residents before, during, and after the migrants were present in the same habitats, and even motivated a more theoretical treatment (Ricklefs 1992). Several studies have documented a variety of spatio-temporal patterns consistent with interspecific competition for food between residents and migrants (e.g.,

Morse 1989, Jedlicka et al. 2006). Jedlicka et al. (2006) showed that a resident tropical parulid, the Rufous-capped Warbler (*Basileuterus rufifrons*), shifted to foraging predominantly in the shaded coffee plants in the understory when migrants were abundant in the dry season, and disproportionately depressed arthropod resource abundance in the canopy shade trees; exploitation competition for arthropods mediated this interaction.

A special case of wintering migrant-resident competition is addressed by the Breeding Currency Hypothesis (BCH; Greenberg 1985). This idea was devised to explain how resident insectivorous bird species in the tropics coexist with the seasonal influx of migrant insectivores at a time of year when food supply tends to decline during the tropical dry season. Greenberg proposed that migratory bird populations tend to be limited by different ecological circumstances from the resident birds, mitigated by different habitats. The resident bird species, he argued, should tend to occupy habitats with relatively more large insects that comprised their tropical “breeding currency” necessary for reproductive success, whereas the migrants plus residents are supported in winter habitats by smaller insects sufficient for self-maintenance. Our own diet data support the small size of insects (median length = 2 mm) on which many of the migratory parulids depend while wintering in Jamaica, among other indications of opportunism (Sherry et al. 2016). Johnson et al. (2005, 2006) tested the BCH by quantifying both summer and winter insect abundances and sizes, along with abundances of migrant and resident birds, across a range of Jamaican habitats. These studies’ qualified support for the BCH provides several takeaways: food limits population size in these birds, competition for food has likely impacted habitat selection patterns, this competition is likely to be diffuse and exploitative at least insofar as direct, aggressive territoriality between migrants and residents is infrequent, and the migrants are likely better adapted than the resident bird species to exploit small insects for self-maintenance.

Competition Among Wintering Migrants

Dozens of parulid warbler species seasonally flood parts of the Neotropics, including Mexico, higher elevations in Central and South America, and virtually every habitat in the Caribbean Islands. Sliwa and Sherry (1992) found 100% of the Neotropical-Nearctic migratory birds encountered wintering across Jamaica to be parulid warblers, and more recent examination of Jamaican eBird data (observations made and reported online by bird-watchers) reinforce this view, showing that although these warblers are not the only wintering migrants, they are by far the most abundant and most predictably encountered species year-after-year (C. M. K., personal observation). Parulids are not necessarily as numerically dominant outside the Caribbean basin as

within but can comprise some of the commonest birds locally wherever they winter, often reaching densities much higher than documented for the same species while breeding (e.g., Keast and Morton 1980, Mills 2006).

The potential for competition among these wintering migrants, particularly where they are so abundant in the Greater Antilles, confronts us again with the paradox noted above: coexisting parulids exhibit numerous niche differences, and yet most of these species coexist locally in winter without any obvious interspecific territoriality or interference that would suggest strong ongoing interspecific competition. Moreover, Lack and Lack (1972, Lack 1976) argued for almost complete ecological isolation, i.e., niche differentiation, of wintering warblers and other species in Jamaica based on their foraging behavior. The maintenance of such niche differences among coexisting species suggests the potential for ongoing interspecific competition that could have favored evolutionary divergence, a topic we address below. However, if interspecific competition is pervasive among wintering parulid warblers, then why is there so little evidence to support it?

Reinforcing the paradox, migratory warblers, which experience different habitats throughout the year with changing available foods, are necessarily more opportunistic than some tropical residents (e.g., Sherry 1984). Diets overlap extensively in Jamaica (Sherry et al. 2016, Kent et al. 2021). This opportunism is consistent with extensive dry-season movements (Peele et al. 2015), presumably tracking seasonally variable foods—at least in Jamaica, where we have focused our long-term demographic and ecological research. Opportunism is thought to preclude competition more widely, because the fluctuations and unpredictability of food implicit in opportunistic feeding strategies should preclude depletion of population-limiting resources consistently enough for competition to become important, an argument emphasized for shrub steppe and grassland birds (e.g., Wiens 1977, Wiens and Rotenberry 1979, 1980, 1981; Rotenberry 1980), not to mention warblers (McMartin 2002). Assuming resource partitioning to be the outcome of interspecific competition, then high dietary overlap—the absence of resource partitioning—implies an absence of competition.

The absence of interspecific competition due to resource fluctuations is a viable alternative hypothesis to the competition-based resolution of the paradox. In fact, El Niño-La Niña climate fluctuations in winter drive variable annual adult survival in warblers, probably via fluctuations in food abundance (Sillett et al. 2000, Wilson et al. 2011). Another plausible alternative hypothesis to interspecific competition for food in warblers is competition for nesting sites safe from predators (e.g., Martin 1988, 1993, 1996). In support of this latter idea, migrant bird populations wintering in the Caribbean experience enough annual

variation in reproductive success, in part due to fluctuating nest predator populations, to trace cohorts of young birds migrating to the wintering areas and returning in spring to breed (Holmes 2007). Moreover, Ricklefs (2010) suggests that pathogens may also cause population declines, leaving food on the table for other species to exploit, thereby reducing competition for food. All of these sources of population fluctuations arguably reduce the potential for interspecific competition for food. Additionally, little evidence supports interspecific territoriality amongst wintering warbler species, with a few notable exceptions mentioned above; rather, many migrant species in winter forage in proximity, with little obvious behavioral interaction of any kind. Lack and Lack (1972) spent a year following birds, including parulids (which comprised 25% of all the birds they observed), without mentioning interspecific contests. Thus, one can argue plausibly both that migrants do compete for food and that they do not, contributing to the paradox about the importance of interspecific competition in warblers.

Resolving the Paradox Via Diffuse Exploitation Competition

Based partly on extensive diet studies, we propose that warbler species indeed compete for food resources, more or less continuously through the annual cycle, and largely via a mechanism that is both diffuse (defined in section "MacArthur's legacy") and exploitative. Exploitation competition is indirect and operates via species depleting resources that would otherwise be available to individuals of other species, contrasting with direct interference mechanisms that result from behavioral interactions associated with territoriality and dominance hierarchies. We argue that exploitation competition among coexisting warbler species has selected for evolutionary differences in diets and foraging behavior, consistent with the observations of foraging differences documented above, while not precluding high levels of niche overlap and associated competitive interactions altogether. The intensity of competition among years probably varies due to fluctuating bird population sizes and food resource availability in winter (e.g., Sillett et al. 2000, Jedlicka et al. 2006), but, unlike the shrub steppe and grassland birds studied in cold deserts and rainfall-limited continental environments (e.g., Wiens 1977), wintering warblers experience relatively more predictable arthropods and substrates annually in their subtropical and tropical environments.

The existence of interspecific competition in warblers, and perhaps many other birds, has remained largely invisible, we argue, for two reasons. First, cases of interspecific aggression have likely attracted disproportionate attention from ornithologists (e.g., Greenberg 1986; Greenberg et al. 1993, 1994), which may have distracted the search for

other evidence for competition. Second, testing for interspecific competition in complex communities is difficult because the effect of any experimental manipulation will be diminished by a large number of competitors (Cody 1974). However, accumulating diet data from communities of coexisting warblers has confronted us with results that are most parsimoniously explained by diffuse exploitative interspecific competition.

Meeting the Conditions for Interspecific Competition

Dhondt's (2012; see also Prins 2016) arguments about interspecific competition in birds suggest how to investigate it using intraspecific competition coupled with diet data. Along with colleagues, we have accumulated the data necessary to apply Dhondt's criteria to wintering communities of parulid warblers. Sherry et al. (2016) delineated arguments for diffuse exploitative competition among five species wintering in Jamaican shaded coffee plantations, and inferred such competition, but this study's location in a non-native plant habitat for birds arguably limits generalization to native, more complex habitats. We have since investigated available prey, diets, foraging behavior, and relevant morphological traits of five coexisting parulid warblers in native, wet-limestone forest at moderate elevation in Jamaica, showing similar results (Kent et al. 2019, Kent and Sherry 2020, Kent et al. 2021).

These essential conditions for interspecific competition (Dhondt 2012) are: (1) two or more species' populations are limited by a particular resource, (2) they compete intraspecifically for that resource, and (3) they overlap in the use of that resource. Additionally, Dhondt specified sufficient conditions for interspecific competition: (4) resource use by one species affects another, (5) fitness of one or more species is impacted by other species' use of that resource, and (6) a species' distribution or abundance is impacted by that of another species. We cannot yet demonstrate all six conditions in wintering parulid warblers, but we come close, anchored by our population-level studies in Jamaica since 1986. Sherry et al. (2016) enumerated the many studies addressing population-limitation within species (reviewed by Sherry et al. 2005), including winter rainfall impacts on both annual adult survival (e.g., Sillett et al. 2000 for Black-throated Blue Warblers) and carry-over effects into the breeding season influencing reproductive success of individuals (e.g., Norris et al. 2004, Norris and Marra 2007), as well as intraspecific competition for insect food by wintering warblers (e.g., Sherry et al. 2005, Cooper et al. 2015, Marra et al. 2015b). Winter food limitation, indicating the potential for intraspecific competition, has been shown in a variety of other parulid species (Strong and Sherry 2000, Johnson and Sherry 2001, Brown and Sherry 2006, Smith et al. 2010, Wunderle and Arendt 2017), suggesting generality. The third of Dhondt's necessary conditions has been

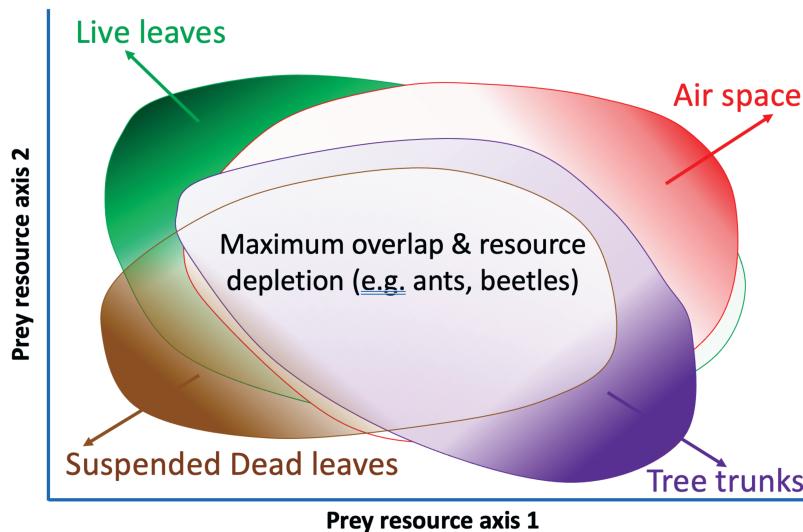


FIGURE 3. Conceptual model of diffuse exploitative interspecific competition and resource depression involving 4 hypothetical coexisting species of insectivorous foliage-gleaning birds. High overlap on common, relatively easy-to-catch insects (e.g., small ants and beetles in Caribbean Islands in winter) corresponds with greater depletion of arthropod abundance compared to more difficult-to-access prey and/or substrates. The relatively greater abundance of difficult-to-access prey is indicated here by color intensity. Arrows indicate evolutionary selection pressures for behavioral or morphological traits to specialize on less easily exploited substrates or prey types. Individuals within a species would be favored that could augment their diet, and thus survive better, by exploiting the additional prey accessible with a particular specialization, such as aerobatic capacity to capture flying insects in the airspace.

shown by our recent diet studies (Sherry et al. 2016, Kent and Sherry 2020, Kent et al. 2021). The effects of winter food limitation on annual adult survival and carry-over effects into the breeding season, just cited, establish fitness consequences of food resource competition and, in the case of the largely insectivorous parulid warblers, this means insect and spider abundance. Moreover, exclosure experiments have shown the potential for these insectivorous birds in aggregate to deplete resources in winter (Jedlicka et al. 2006, Kellermann et al. 2008, Johnson et al. 2009, 2010) as well as summer (Holmes et al. 1979).

Diffuse Exploitative Interspecific Competition

High dietary overlap in coexisting parulid warbler species, particularly in winter, coupled with demonstrable intra-specific competition, strongly implicates ongoing inter-specific competition for food across multiple habitats. The need to invoke competition during some hypothetical past era to explain the niche differences of coexisting species observed today, an idea caricaturized by the “ghost of competition past” (Connell 1980), disappears. Sporadic competition can select for morphological feeding differences among species (e.g., Grant and Grant 2006), but may not be the most parsimonious explanation for such differences in species-rich communities. An ongoing interspecific competition involving diverse warbler species prompts the question of mechanism. Because we are unaware of much interspecific territoriality or other strife in winter among most parulid warbler species, as reviewed above, we argue

here for diffuse exploitation competition as the mechanism. Accordingly, ecologically opportunistic species like migratory warblers eat much of what they encounter, and they overlap substantially on the most conspicuous or easy-to-catch prey, depressing the abundance of such prey. This resource depression would then create resource-abundance gradients in which other prey that are harder to find, catch, and/or handle become relatively more available, and thus beneficial to whichever species are adapted to exploit them (Figure 3). This, we argue, favors individuals that supplement their diet with more elusive prey, especially when resources are generally in short supply, leading to better survival, and thus higher fitness of these individuals. This process would intensify during an extended seasonal drought, such as an El Niño event in the Caribbean Islands. Theoretically, species that forage optimally should maintain their ability to feed on the easy prey while simultaneously specializing on elusive prey that are less well exploited by other species (Robinson and Wilson 1998), consistent with the conceptual model in Figure 3.

The concept of diffuse exploitative competition applies readily to parulid warblers. We know that the five warbler species that coexist in shaded coffee plantations overlap highly in their use of small, locally abundant insects, particularly psyllids (sucking insects related to aphids) in the trees shading the coffee plants, bark lice (Order Psocoptera feeding on trunks and branches), and coffee berry borer beetles (Sherry et al. 2016). All these insects are conspicuous, if small (~2 mm length), and relatively easy for

small-beaked, warbler-sized birds to catch and handle. We replicated this shaded coffee study in floristically and physiognomically complex wet limestone forest (Kent and Sherry 2020, Kent et al. 2021), and, again, found high diet overlaps, particularly on ants and beetles. These insects are also relatively conspicuous, by their often dark or bright colors (beetles) and movement while foraging (ants), small size (~2 mm length), and relatively high abundance (Kent et al. 2019). These arguments supporting the Figure 3 concept depend on accurate diet data, warranting elaboration on our methods (Supplemental Material A).

In addition to these high diet overlaps among coexisting warbler species in both Jamaican coffee and wet limestone habitats, among others (Kent et al. 2021), ordination analyses identify significant differences in diets (e.g., Sherry et al. 2016, Sherry et al. 2020b, Kent and Sherry 2020). American Redstarts forage aerobatically, flashing their wings and tails likely to flush potential prey from hiding and chasing arthropods in the airspace (Sherry et al. 2020a). Consistent with this active search-and-attack behavior, we found more mobile insects like flies and small, winged parasitic wasps in their stomach contents, compared to the other four warbler species, a pattern supported by a variety of other parulid warbler species (Rosamond et al. 2020). The Worm-eating Warbler (*Helmitheros vermivorum*) feeds largely on caterpillars in summer (Vitz et al. 2020), but on insects in suspended dead leaves (aerial litter) in winter (Greenberg 1987, Kent and Sherry 2020). The most distinctive insects in these dead leaves, corresponding with this species' stomach contents, were Orthoptera, including crickets and cockroaches, and spiders. The Worm-eating Warbler also ate proportionately more caterpillars than the other wintering warblers, just as in summer, but few were available in winter. The Black-and-white Warbler (*Mniotilla varia*) is well known for its tree-creeping behavior, foraging in winter along tree trunks and branches, and its winter diet was best distinguished by proportionately many bark lice and pseudoscorpions, as expected considering its foraging substrate. The Northern Parula (*Setophaga americana*) forages primarily from leaves and small twigs, in outer and higher parts of trees, and its diet was broad, but more than the other species (except for Worm-eating Warbler) the parula ate proportionately many spiders, Orthoptera, and caterpillars, all of which would be expected to occur where foliage is concentrated, in the tree canopy. The Black-throated Blue Warbler forages lower in vegetation than the other four coexisting species, and forages somewhat aerially like the redstart; correspondingly, its diet included a lot of flies and parasitic (winged) Hymenoptera. The Black-throated Blue Warbler also ate more fruit than the other four species, based on seeds found in most of the stomach samples we examined, and this is another potential resource niche difference for

ecological isolation in these birds. When we looked at foraging differences overall, including height above ground and position in the trees, the substrates where these five warblers fed best distinguished them (Kent and Sherry 2020).

MacArthur (1958), Keast et al. (1995), and Lovette (2016) have emphasized warblers' overall phenotypic similarity, especially compared to other bird assemblages such as Darwin's finch and Hawaiian honeycreeper adaptive radiations. Indeed, most warblers are small bodied (8–12 g body mass), with short and narrow beaks, and long legs for active hopping in foliage or on the ground, though a few species like the ground-foraging Ovenbird (*Seiurus aurocapilla*) are somewhat larger-bodied. Despite their overall morphological similarity, warbler species also differ morphologically in often subtle ways relevant to foraging (e.g., Keast 1995, Price et al. 2000, Curson 2010, Rosamond et al. 2020) and migratory behavior (Gray 2019). For example, Rosamond et al. (2020) predicted diets based on the external morphology of 13 warbler species finding that larger bird species tended to eat larger prey, and that species with flatter beak, longer rictal bristles, and relatively large wings and tail—adaptations for flycatching—tended to eat more flying prey like flies and small wasps. These results support our model for diffuse exploitative food (arthropod) competition (Figure 3), resulting in small, heritable phenotypic differences among species to allow for some level of resource differentiation, the result of the interspecific competition. However, this morphological specialization is constrained by the need to maintain efficient foraging on the most available prey items, resulting in a body plan that is generally conserved.

Whereas opportunism in many wintering populations of coexisting warblers has been presented as evidence that these birds rarely compete, we argue that environments do vary, but they also change predictably, especially seasonally. For example, based on our experiences in Jamaica, going back three decades, most of the same arthropods are available annually during the Caribbean dry season, even if abundances vary annually (e.g., Johnson and Sherry 2001). Opportunism of species like these warblers is precisely what drives them to converge behaviorally on the same resources in the same places and times, which exacerbates their interspecific competition for food (Sherry et al. 2016). These warbler species' inherited morphological similarities (Keast et al. 1995)—evolutionary conservatism—biases many of them to find and eat similar, relatively accessible, and easy to catch prey (Figure 3).

This tendency towards substantial dietary overlap in coexisting species which exacerbates competition may be more general in nature than appreciated. Besides the warbler studies reviewed above, Root (1967) documents this in describing the ecological guild concept, Sherry

et al. (2020b) document high overlap on particular prey species for many Neotropical flycatcher species, Rosenberg (1990, 1993, 1997) describes Amazonian rainforest species feeding from suspended dead leaves overlapping substantially on the same insects, and Poulin and Lefebvre (1996) show high overlap in migrant birds wintering in Panama regardless of foraging guild. Darwin's finches are "imperfect generalists" overlapping in exploitation of many of their seed resources, and simultaneously adapted to exploit "private resources" important to survival and coexistence (De León et al. 2014). Darwin's finches relied increasingly on their private resources during a drought that reduced the shared food resources, especially insects. Wilson (2010) describes three pygoscelid penguin species all eating essentially the same prey species, krill (*Euphausia superba*), noting that their different foraging depths likely fail to prevent competition because krill move readily among these depths. Other animals likely exacerbate diffuse food exploitation, strengthening the ecological pressure for evolutionary specialization (Figure 3), including hummingbirds (Spence et al. 2021), bats (Gordon et al. 2019) studied using molecular methods (see Hoenig et al. 2021, Forsman et al. 2021), frogs (Wunderle and Arendt 2011), and lizards, many of which eat ants (e.g., Wright 1981, Lister 1976, Floyd and Jenssen 1983, Waide and Reagan 1983) much like the warblers in Jamaica. Most of these studies indicate that the potentially competing species within a community or guild can be simultaneously dietary opportunists and foraging specialists (Kent et al. 2021). Taken together, these studies suggest that interspecific competition via diffuse exploitative competition for many of the same resources may be widespread, and likely contributes to selection for diversification of diets on harder-to-access foods or substrates.

While we argue that diffuse exploitative competition may be a prevalent, if largely overlooked, mechanism of food competition in migratory parulids, and is the most parsimonious interpretation of our diet and foraging data, we acknowledge other mechanisms of competition described above. Contest competition, defined as direct behavioral competition, typically via aggression as in defense of a territory, can vary in degree of symmetry. When asymmetric, with one species socially dominant to another, the subordinate species either tends to avoid the dominant competitor, or expands the range of habitats, substrates, and prey exploited, i.e., broadens its ecological niche. Two socially dominant resident warblers—Adelaide's Warbler (*Setophaga adelaiae*) in Puerto Rico (Toms 2011, 2013) and the Yellow Warbler (*S. petechial petechial*) in Jamaica (Powell et al. 2020), are illustrative, both cases involving American Redstart as the subordinate species.

Multiple mechanisms of interspecific competition require different tests. The diffuse exploitation hypothesis is particularly challenging to test experimentally—considered by some authors to be *de riguer* in competition studies—because the traditional addition or removal of individuals of any one species, or manipulation of food, if indeed possible (challenging, considering how mobile these birds are in winter; Peele et al. 2015), is likely to have little measurable effect in field experiments, when many species coexist locally (Cody 1974).

Since MacArthur's (1958) publication, other mechanisms of coexistence have been suggested that do not assume niche differences or resource shortages. One of the most prominent is Hubbell's Unified Neutral Theory, envisioning plant species coexisting not through niche differentiation, but rather stochastic colonization processes and local extinctions. This theory assumes species to be functionally equivalent, or at least to have equal fitness (Hubbell 2005), and is poorly supported in complex, vertebrate communities, such as birds (McGill 2003, Jankowski et al. 2012), which regularly show non-random species assembly (Gotelli and McCabe 2002, Lovette and Hochachka 2006). Another theoretical possibility, "modern coexistence theory", also attempts to explain cases in which species do not coexist through evolved resource differences alone. This theory explains coexistence jointly through a mix of equalizing (e.g., similar fitness) and stabilizing (e.g., resource partitioning) mechanisms (Chesson 2018), thus in some ways linking the concepts of neutral theory with more classical concepts like diffuse competition. However, unlike neutral theory, these recent models demonstrate that some minimum level of niche differentiation is necessary for coexistence (Song et al. 2019) because equalizing mechanisms alone only delay competitive exclusion (Chesson 2000). These ideas are still sufficiently recent and theoretical that we cannot yet address their possible applicability to warblers. However, this is an exciting path for further exploration through newly proposed empirical studies (Godwin et al. 2020, Ellner et al. 2019).

EVOLUTIONARY PERSPECTIVES ON COMPETITION IN PARULID WARBLERS

In addition to the evolutionary selection pressures that we argued above contributed to the behavioral and morphological—and ultimately diet—differences documented in coexisting parulid species, we provide here three additional evolutionary insights into parulid diets and coexistence, insights that strengthen our recommendation for more studies that integrate evolutionary and ecological perspectives. These insights illustrate how evolutionary approaches to understanding interspecific competition for

food resources ask different questions, use different tools, and may produce different answers.

Caribbean Ecological Opportunity for Parulid Adaptive Radiation?

Parulid warbler individuals and species numerically dominate wintering Neotropical-Nearctic migrant birds on Caribbean islands, adding to the resident warblers on all the Greater Antilles and some Lesser Antilles islands (Lack 1976). This diversity of Caribbean parulid warblers is part of an extraordinary adaptive radiation (Lovette and Bermingham 1999, Oliveros et al. 2019), which likely necessitated an ecological opportunity (Schluter 2000). Because the parulids are largely insectivorous—some species nearly exclusively so, others adding fruit or nectar to their winter diet (Greenberg 1981, Morton and Greenberg 1989)—the ecological opportunity implicates a paucity of other insectivorous competitors among Caribbean birds. If so, then why would the diversity hot spots for insectivorous birds of Central and South America (e.g., Harvey et al. 2020, Sherry et al. 2020b) not have spilled into the Caribbean Islands long before parulids began to radiate 5–6 million years ago? Many mainland families of Neotropical insectivorous birds are completely absent from the Caribbean Islands. An equally important question: why did more migratory bird taxa not evolve to exploit Caribbean habitats seasonally alongside the warblers?

Many insectivorous birds other than warblers indeed colonized the Caribbean islands, likely many times independently given the variety of different endemic genera, especially diverse tyrannid flycatchers (Lack 1976). However, what was striking about the stomach content data and feeding substrates of the Jamaican warblers we reviewed above is not just which bird taxa colonized the Caribbean Islands, but how many bird taxa never did so—taxa that the warblers appear to replace ecologically. The American Redstart feeds remarkably like *Myioborus* warblers, a genus containing 12 parulid flush-and-chase species in Central and South America (Sherry et al. 2020b) that never colonized the Caribbean Islands. Coexisting warblers appear to replace several other avian clades that failed to colonize Caribbean islands: The Black-and-white Warbler feeds much like diverse Neotropical woodcreepers (Furnariidae). The Worm-eating Warbler forages largely on insects in suspended dead leaves, a distinctive feeding substrate of the 12 *Epinecrophylla* antwren species of South and Central America. The Northern Parula feeds restlessly amongst the leaves and small twigs of the canopy, much like *Phylloscartes* and *Phylloscopus* flycatchers (S. Robinson, Pers. Comm.). The Black-throated Blue Warbler feeds from diverse substrates in the understory, much like a variety of small furnariid ovenbirds. The Ovenbird (*Seiurus aurocapilla*)—unrelated to the similarly named

Furnariidae—and Swainson's Warbler (*Limnothlypis swainsonii*) are migratory parulids occupying the same habitats as the other insectivorous warblers we studied in Jamaica, and that forage largely on the ground much as mainland antthrushes and antpittas. Thus, we infer that the parulid adaptive radiation in the Caribbean resulted at least partly from the relative dearth, and thus reduced potential competition, from diverse mainland Neotropical insectivores, and notably the absence of many of the diverse suboscine passerine adaptive radiations. Our list of feeding behaviors and microhabitats to which parulids have become adapted is incomplete—see Curson (2010) for a thorough review—we also acknowledge that parulids are not precise replacements for the mainland equivalents just described, insofar as parulids are all small birds, feeding on the relatively small prey available on Caribbean islands (Johnson et al. 2005, Sherry et al. 2016).

Sherry et al. (2020b) argue that evolutionary pressures in the most species-rich mainland Neotropics favored evolutionary specialization in the insectivores, especially in the species-rich suboscine passerines, which induced poor dispersal as a tradeoff, and could help explain the dearth of insectivore competitors on Caribbean islands contemporaneous with parulid adaptive radiations. Evolutionary tools such as the time-constrained phylogeny of perching birds (Passeriformes) can help pinpoint the timing of the parulid warbler adaptive radiation (Oliveros et al. 2019), a step in testing this hypothesis for the importance of the Caribbean islands in the parulid adaptive radiation.

Mechanism and Scales of Coexistence

Questions about species coexistence can be addressed both ecologically, the approach of MacArthur (1958; Figure 1), and evolutionarily. For example, locally co-occurring parulid warblers breeding in North America, which might be expected to compete most intensively for food resources, tend not to be each other's closest relatives phylogenetically (Lovette and Hochachka 2006, Lovette et al. 2010). This indicates that some minimal phylogenetic difference, presumably associated with ecological differences resulting at least in part from interspecific competition for food, are necessary for these birds to coexist. The coexisting warbler species we studied in the context of morphology and diets were also not each other's closest relatives (Rosamond et al. 2020), nor were MacArthur's (1958) warblers, except possibly Bay-breasted (*Setophaga castanea*) and Blackburnian warblers (*S. fusca*), which Lovette (2016) suggests may have “coexisted” locally in MacArthur's study only temporarily during a spruce budworm outbreak. Our hypothesis of coexistence resulting from feeding specializations in response to diffuse exploitation competition provides a potential explanation of these differences that Lovette and Hochachka (2006) and others documented for warbler

breeding assemblages, but the generality of this pattern and whether or not it arose via species differences arising *in situ* or from species-sorting upon secondary contact are issues requiring further research.

The analysis of Lovette and Hochachka (2006) examines very local coexistence mechanisms in warblers. These birds may also segregate ecologically at broader, geographic, and habitat scales. For example, many warblers are limited to breeding in eastern versus western North America, and yet others to different regions within western North and Middle America (Toews et al. 2016, Sanín 2017); by habitat in both winter and summer, based on high specificity of breeding and winter habitat; by breeding elevations in different seasons (e.g., Black-throated Blue Warbler winters at higher elevations in Jamaica than redstarts). All these scales and mechanisms of ecological isolation would satisfy MacArthur's criterion for coexistence (Figure 1) by weakening the potential interspecific competition compared to intraspecific, which brings us back to MacArthur's (1958) challenge encountered while trying to study the foraging ecology of spruce-woods warblers both in summer and winter. MacArthur tested and rejected the idea that warbler species sympatric in summer may be allopatric in winter—an idea still worth examining—but he acknowledged the possibility that species coexisting in summer (e.g., within spruce forests) may occupy different habitats in winter, a seasonal difference that could contribute to year-round coexistence.

Season of Selection for Foraging Traits?

Based on ecological findings, Sherry et al. (2015) argued that the American Redstart population is likely limited simultaneously in summer, winter, and migration, and that the ecological factors differ by season. An evolutionary approach to interspecific competition, by contrast, asks how parulid warbler foraging adaptations necessary for coexistence arose, and are maintained—i.e., about the targets of selection—and we suggest a different answer to this question than the target of population limitation. Specifically, we hypothesize that winter is more important than summer or migration in influencing morphological trait adaptations associated with feeding behavior and coexistence because winter directly impacts both annual adult survival (e.g., Sillett et al. 2000, Wilson et al. 2011) and reproductive success via carry-over effects (Marra et al. 1998, Norris et al. 2004). Efficiency exploiting winter foods should impact both survival and reproduction via winter foraging efficiency and body condition. Moreover, foraging behavior suggests food may be relatively scarce in winter, also favoring efficient foraging (Lovette and Holmes 1995) and substrate specialization (Greenberg 1987, Kent and Sherry 2020). The breeding season, by contrast, involves not just feeding, but also mating and

nesting success, and so may exert less leverage than winter on feeding trait evolution.

SYNTHESIS AND CONCLUSIONS

Starting with his Ph.D. dissertation, MacArthur (1958) compelled ecologists to link observations with theory, by looking more rigorously at how ecologically similar species diverge in response to competition so as to coexist. He argued that the major way species coexist is via resource partitioning—the outcome of contesting the resources that limit populations—a conclusion that stimulated decades of important research on how diverse organisms differ ecologically. With the benefit of hindsight, we update MacArthur's (1958) insights, emphasizing detailed warbler resource use and related traits, non-breeding ecology, diffuse exploitation competition, and phylogenies.

Perhaps the most consequential way in which we would amend MacArthur's (1958) conclusions concerning spruce woods warblers, is to question the generality and degree of resource *partitioning*. In the warbler communities we've studied, competing species appear to have become specialized in their adaptations to exploit particular resources, especially substrates, rather than diverging from each other by partitioning resources per se. It makes no sense to consider the use of different substrates as resource partitioning because substrates are not resources and cannot be consumed and thereby used up. Coexisting species certainly differ from each other ecologically and evolutionarily, but probably not generally by diverging in response to each other, for example as represented by character displacement. We also suggest amending the idea that interspecific competition is greatly *reduced* by resource partitioning or other coexistence mechanisms, an idea that has led to the generally untestable inference that past competition was responsible for ecological and evolutionary differences we see today among competing species, an idea caricaturized by the “ghost of competition past”. We argue for a parsimonious alternative to a reduction of interspecific competition via resource partitioning, namely substrate specializations among coexisting species in response to diffuse exploitation competition for extensively overlapping resources. Future comparisons of actual resources and diets with surrogates like foraging behavior will be invaluable, because the latter may overestimate or misrepresent species differences (e.g., Poulin and Lefebvre 1996, Gordon et al. 2019, Kent and Sherry 2020).

Views of interspecific competition described in this paper, particularly the diffuse exploitation mechanism, recognize competition to be as much an evolutionary as an ecological phenomenon, which paves the way to integrate

ecological and evolutionary approaches to the same question that has motivated many of us—both ecologists and evolutionary biologists—for generations, namely how and why do particular species coexist? In the case of MacArthur's (1958) iconic parulid warblers, this means recognizing them as the product of one of the most spectacular adaptative radiations in North America. To his credit, MacArthur (1958) recognized the importance of some morphological adaptations—interestingly the tongue of Cape May Warblers (*S. tigrina*) adapted to the consumption of nectar in winter—but discounted the importance of other subtle species differences in beaks, wings, and tails. Lack and Lack (1972) explicitly acknowledged the importance of morphological differences among coexisting warbler species in Jamaica, even within the genus *Setophaga* containing the warblers MacArthur studied; and Price et al. (2000) also explicitly linked ecological and evolutionary perspectives in a comparative study of parulid warblers in the Americas with the Old World *Phylloscopus* warblers.

Our suggestion of an ecological vacuum in the Caribbean region that may have contributed to the adaptive radiation of parulids emphasizes the non-breeding phase of the annual cycle, in contrast to MacArthur's emphasis on breeding populations. Important future research is needed to understand this adaptive radiation more comprehensively, including a better understanding of speciation mechanisms, communication-related traits (e.g., Simpson et al. 2021), and climate niches (e.g., Winger et al. 2011, Gómez et al. 2016). Genomic evolutionary methods down to the level of specific genetic loci, unknown in MacArthur's time, also promise considerable insights into parulid evolution, both intraspecifically (e.g., Ruegg et al. 2014) and interspecifically (Irwin et al. 2018, Simpson et al. 2021). Finally, some of the most novel insights into warbler coexistence that eluded MacArthur have come from diet studies such as we have emphasized in this paper. Additional insights will come from expanding the temporal and spatial scales of study. Full annual cycle studies (e.g., Hostetler et al. 2015, Marra et al. 2015a, Wilson et al. 2018, Faaborg et al. 2010) are critical to understanding not just population limitation, but also the target of selection for feeding adaptations. More long-term ecological research such as the Jamaican studies that facilitated the insights reviewed here are needed to address temporal variation in the nature and strength of competition and of diverse food resources year-round. For example, a fluctuating abundance of spruce budworms within and among summers (e.g., Patten and Burger 1998, McMartin et al. 2002, Lovette 2016) likely impacts the strength of interspecific competition. Although MacArthur (1958), and many subsequent authors citing his paper, emphasized local coexistence within spruce trees, additional spatial scales of divergence are likely equally important.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithology* online.

ACKNOWLEDGMENTS

We thank Sabrina Taylor and Allison Snider for inviting us to participate in the 2020 North American Ornithological Conference symposium on avian diets, which inspired this special feature. We thank Richard T. Holmes, Sabrina Taylor, Kate Huyvaert, and three anonymous reviewers for valuable feedback on drafts of this manuscript.

Funding statement: Writing of this paper was supported by the Department of Ecology and Evolutionary Biology, Tulane University. Research was supported by three National Science Foundation Long-term Research in Environmental Biology grants (#1242584, 1242588, 8008614). Tulane University Department of Ecology and Evolutionary Biology and its Gunning Fund supported work in wet limestone forest. Newcomb Foundation of Tulane University funded work in Louisiana bottomland hardwood forest.

Ethics statement: Research underlying this review was conducted with approval from the Bird Banding Laboratory of the USFWS (Permit Number: 22526). We carried out work in privately owned wet limestone habitat in Jamaica with approval from the National Environment & Planning Agency of Jamaica (Permit Numbers: 18/27 & 22/23) and approved by the Institutional Animal Care & Use Committee (IACUC) of Tulane University (Protocol Number: 0473). We conducted work in Southern Louisiana on public land with approval from the Louisiana Department of Wildlife and Fisheries (Permit Number: WL-Research-2009-3), USFWS (Permit Number: 43616-09-01), and Tulane University IACUC.

Author contributions: T.W.S. and C.M.K. conceived the idea, design, and experiment. T.W.S. wrote the paper. T.W.S. and C.M.K. contributed substantial materials, resources, or funding.

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