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Photo: Lillian Stokes

A review of wood warbler (Parulidae) predation of vertebrates and descriptions of three new observations

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Abstract Wood warblers (Parulidae) eat insects, spiders and other small arthropods, fruit, and nectar, but have also been documented preying on vertebrates. We conducted a literature review to determine which species of Parulidae have been observed capturing or consuming vertebrate species, such as small lizards, amphibians, and fish. We also include information and discussion of three previously unpublished observations: 1) a Black-and-white Warbler (*Mniotilta varia*) photographed with a bark anole (*Anolis distichus*) in its mouth on San Salvador Island, The Bahamas, 2) a Black-and-white Warbler that had small lizard bones (*Anolis* spp.) in its stomach contents in Jamaica, and 3) a Yellow-throated Warbler (*Setophaga dominica*) photographed preying on a brown anole (*Anolis sagrei*) in Florida, USA. The latter observation was particularly interesting as the brown anole shed its tail and briefly escaped before being recaptured by the warbler. Including these three unpublished events, our literature review found 24 separate records of 12 Parulidae species preying on vertebrates. The majority of predation records were of lizards (58%), with an additional 25% predation records of amphibians and 17% of fish. We hypothesize that vertebrate predation by wood warblers is opportunistic and potentially limited by the difficulty in capturing, handling, and consuming larger vertebrate prey. There is also non-mutually exclusive evidence to suggest birds exhibit plasticity in prey items, partially switching to larger, more difficult-to-handle vertebrate prey during taxing periods when invertebrate prey are less available. Our study synthesizes previous work and can assist future research in better understanding trophic interactions, foraging efficiency and prey size, evolution, and the natural history of both warblers and their vertebrate prey.

Keywords bird diet, caudal autotomy, foraging efficiency, non-breeding, predatory behavior, Squamata

Resumen Revisión de la depredación de vertebrados por parte de parúlidos (Parulidae) y descripción de tres nuevas observaciones • Los parúlidos (Parulidae) se alimentan de insectos, arañas y otros pequeños artrópodos, frutas y néctar; pero también se ha documentado que depredan vertebrados. Realizamos una revisión bibliográfica para determinar qué especies de Parulidae han sido observadas capturando o consumiendo especies de vertebrados, como pequeños lagartos, anfibios y peces. También incluimos información y discutimos tres observaciones inéditas: 1) un individuo de *Mniotilta varia* fotografiado con un lagarto de la especie *Anolis distichus* en el pico en la isla de San Salvador, Bahamas, 2) otro individuo de *Mniotilta varia* que tenía pequeños huesos de *Anolis* spp. en su contenido estomacal en Jamaica, y 3) un individuo de *Setophaga dominica* fotografiado mientras depredaba a otro de *Anolis sagrei* en Florida, Estados Unidos. Esta última observación fue especialmente interesante, ya que el lagarto soltó la cola y escapó brevemente antes de ser recapturado por el ave. Incluyendo estos tres eventos no publicados, en nuestra revisión de la literatura encontramos 24 registros separados de 12 especies de Parulidae que cazan vertebrados. La mayoría de los registros de depredación fueron de lagartos (58%), mientras que otro 25% se correspondió con anfibios y un 17% con peces. Nuestra hipótesis es que la depredación de vertebrados por parte de parúlidos es oportunista y potencialmente limitada por la dificultad de capturar, manipular y consumir presas vertebradas de mayor tamaño. También existen evidencias no excluyentes que sugieren que las aves muestran plasticidad en sus presas y pueden cambiar parcialmente a presas vertebradas de mayor tamaño y más difíciles de manejar durante los periodos más exigentes, en los que las presas invertebradas están menos disponibles. Nuestro estudio resume trabajos anteriores y puede ayudar en futuras investigaciones a comprender mejor las interacciones tróficas, la eficiencia de forrajeo y el tamaño de las presas, la evolución y la historia natural tanto de los parúlidos como de sus presas vertebradas.

Palabras clave autotomía caudal, conducta depredadora, dieta de las aves, eficiencia de forrajeo, no reproductivo, Squamata

Résumé Examen de la prédation des vertébrés par les parulines (Parulidae) et description de trois nouvelles observations • Les parulines (Parulidae) se nourrissent d'insectes, d'araignées et d'autres petits arthropodes ainsi que de fruits et de nectar, mais il a aussi été constaté qu'elles peuvent s'attaquer aux vertébrés. Nous avons réalisé une étude bibliographique pour déterminer quelles espèces de Parulidae ont été observées capturant ou consommant des vertébrés, tels que

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des lézards, des amphibiens et des poissons de petite taille. Nous incluons également des informations et une discussion sur trois observations inédites : 1) une Paruline noir et blanc (*Mniotilta varia*) photographiée avec dans le bec un anolis (*Anolis distichus*), sur l'île de San Salvador, aux Bahamas ; 2) une Paruline noir et blanc dont l'estomac contenait des os de petits anolis (*Anolis spp.*), en Jamaïque ; et 3) une Paruline à gorge jaune (*Setophaga dominica*) photographiée en train de capturer un anolis brun (*Anolis sagrei*) en Floride, aux États-Unis. Cette dernière observation était particulièrement intéressante, car l'anolis brun a perdu sa queue et s'est brièvement échappé avant d'être repris par la paruline. En incluant ces trois observations non publiées, notre étude bibliographique fait état de 24 enregistrements distincts de 12 espèces de Parulidae capturant des vertébrés. Les mentions de prédation concernaient majoritairement des lézards (58 %), mais aussi des amphibiens (25 %) et des poissons (17 %). Nous supposons que la prédation des vertébrés par les parulines est opportuniste et potentiellement limitée par la difficulté à capturer, manipuler et consommer des proies vertébrées plus grandes. Il existe également des éléments non mutuellement exclusifs qui indiquent que les oiseaux font preuve de plasticité dans le choix de leurs proies, se tournant partiellement vers des proies vertébrées plus grandes et plus difficiles à manipuler lors des périodes où les proies invertébrées sont moins disponibles. Notre étude synthétise les travaux antérieurs et pourra aider les recherches futures à mieux comprendre les interactions trophiques, l'efficacité de la recherche de nourriture et la taille des proies, l'évolution et le cycle de vie des parulines et de leurs proies vertébrées.

Mots clés autotomie caudale, comportement de prédation, efficacité de la recherche de nourriture, espèce non nicheuse, régime alimentaire des oiseaux, Squamata

Many larger passerine species regularly eat small lizards and other vertebrates in tropical and subtropical regions (Wunderle 1981, Hasegawa 1990, Kupriyanov et al. 2012). In the Caribbean and mainland North America, small vertebrates have been preyed upon by larger songbirds, including tanagers (Pérez-Rivera 1997, Delgado-V. and Brooks 2003), flycatchers (Wunderle 1981), thrushes (Rolle 1963, Sandoval et al. 2008), thrashers (Bent 1948, Arendt 2020), towhees (Hendricks and Hendricks 2002), and other families and species that have relatively larger bills (Lopes et al. 2005, Powell and Henderson 2008). One of the more common vertebrate taxa consumed by passerines in North America are *Anolis* lizards (Pérez-Rivera 1997, Poulin et al. 2001, van den Burg and Brisbane 2021). These lizards are abundant throughout a variety of habitats and can be readily consumed, as most are relatively small vertebrates (Schoener and Schoener 1978, 1980, McLaughlin and Roughgarden 1989).

In contrast to some larger passerines, small passerines (< 15 g) do not regularly prey on vertebrates (Lopes et al. 2005). The bill size of most small passerines likely prohibits capture and consumption of vertebrate prey (Wunderle 1981, Poulin et al. 2001). However, some small passerines, such as wrens (Storer 1920, Barquero and Hilje 2005, Ayers and Armacost 2010), sparrows (Pipher and Cox 2011, Howell and Clements 2019), and vireos (Sykes et al. 2007) have been recorded depredating vertebrates on rare occasions.

Despite their small size, wood warblers (Parulidae) have also been observed infrequently preying upon and consuming vertebrates (e.g., Eaton 1953), but to our knowledge, no study has previously synthesized literature on this topic. Wood warblers are a family of approximately 120 species that reside in North and South America and include many Nearctic–Neotropical migratory species that winter in the tropics and subtropics, as well as non-migratory resident species that live in the tropics year-round (Lovette et al. 2010, Billerman et al. 2020). Compiling records of wood warblers preying on vertebrates is valuable because much of the literature on the topic is scattered in historic, difficult-to-find references (e.g., Wetmore 1916), and some re-

searchers have incorrectly stated that Parulidae have not been previously observed consuming vertebrates (e.g., White and Cove 2016). Moreover, determining which species of parulids have been observed preying on vertebrates, along with the specific prey taken, is useful to better understand food webs, trophic links, and the natural history and evolution of both warblers and the vertebrate prey (Winemiller and Polis 1996, Blomberg and Shine 2000, Devenish-Nelson et al. 2019).

We conducted a literature search to create a compilation of all wood warblers that have been observed capturing or consuming vertebrates. We also provide new documentation of two Black-and-white Warblers (*Mniotilta varia*) and a Yellow-throated Warbler (*Setophaga dominica*) preying on anoles. Black-and-white Warblers and Yellow-throated Warblers are primarily insectivorous, although Black-and-white Warblers occasionally supplement their diet with fruit (Kricher 2020, McKay and Hall 2020).

Methods

We conducted a broad search of the published literature and internet records for articles or other unpublished documentation of wood warblers preying upon vertebrates. From April 2020 to March 2021, we searched Google, Google Scholar, YouTube, WorldCat, and the Searchable Ornithological Research Archive (SORA) with the following search terms: “warbler eating lizard”, “warbler preying on lizard”, “warbler eating anole”, “warbler eating salamander”, “warbler eating fish”, “warbler vertebrate prey”, “Parulidae comiendo anfibios”, “Parulidae comiendo lagartijas”, and “Parulidae comiendo pescado”. Additionally, we conducted a systematic search of all 120 Birds of the World Parulidae accounts, scanning the “Diet and Foraging” sections for any mention of vertebrate prey (Billerman et al. 2020). Further, we searched for any mention of vertebrate prey in field guides (Ehrlich et al. 1988, Stiles and Skutch 1989, Raffaele et al. 1998). Lastly, we used backward and forward ‘snowballing’ searches (Wohlin 2014, Akresh et al. 2021), in which we examined ‘Cited by’ lists in Google Scholar, as well as reference lists within published studies with vertebrate prey observations.

Although we conducted our search to the best of our ability, we note that we only searched for articles in English and Spanish (the latter with limited ability), and there could be more unpublished or published observations in the subtropics and tropics that we were unaware of (Konno *et al.* 2020).

For each publication or observation, we recorded the bird species, vertebrate prey, date, and location. Some references did not contain a date or the exact species of vertebrate prey, and we noted these omissions in our records. We included records from studies that examined bird stomach contents, as well as from observations of birds capturing or consuming vertebrates in the field. For three unpublished observations, we included detailed accounts of these records.

Results

Literature Review

Out of approximately 120 species in Parulidae, we found evidence of 12 species preying on vertebrates (Table 1), including both tropical residents and Nearctic–Neotropical migratory species. A large proportion of the species (75%) were migrants that winter in the Caribbean, Central America, or South America. The compiled list includes wood warbler species that forage on the ground (e.g., Ovenbird [*Seiurus aurocapilla*], Northern Waterthrush [*Parkesia noveboracensis*]) as well as species that usually prey on insects in shrubs or trees (e.g., Black-and-white Warbler).

Lizards, including anoles, were some of the most depredated taxa, but small amphibians and fish were also captured by warblers. Of the predation events with known dates, most were during the non-breeding season in either the fall, winter, or early spring. A few observations were during the breeding season, notably for Northern Waterthrush and Louisiana Waterthrush (*Parkesia motacilla*). Most records (83%) were in the southeastern United States and in the Caribbean. Over half (63%) were from records of prey found in stomach contents, while the remainder were from field observations. In addition to our Yellow-throated Warbler observation (see below), two other studies noted warblers beating their prey on branches, presumably to maim or kill their prey.

New Observations

Black-and-white Warbler, The Bahamas.—One of the new Black-and-white Warbler records was an observation on the grounds of the Gerace Research Centre (GRC; 24°07'03"N, 74°27'52"W), on San Salvador Island, The Bahamas (see Akresh and King 2015 for the GRC location and a map of the island). Black-and-white Warblers are an uncommon to common wintering migrant that use a variety of habitats on San Salvador (Sordahl 1996, Murphy *et al.* 2001, MEA unpubl. data). On the morning of 6 March 2020, MEA, SL, and JMCS were observing and photographing birds in primarily non-native vegetation at the GRC (see Jones *et al.* 2013, Akresh *et al.* 2019a for detailed vegetation composition and structure). While birding, JMCS photographed a female Black-and-white Warbler that had a bark anole (~4 cm total length) in its bill at 0808 (Fig. 1). We could not determine if the anole was alive. The bird was perched 5–6 m above ground in a non-native almond tree (*Terminalia catappa*). After photographing the bird, we unfortunately did not follow

the warbler to determine if the bird consumed its prey.

Black-and-white Warbler, Jamaica.—The second new record of a Black-and-white Warbler occurred at Copse Hill on the Kew Park Estate near Bethel Town in Westmoreland Parish, Jamaica (18°15'00"N, 77°56'24"W), as part of a study quantifying dietary overlap and specialization in wintering warbler communities (Kent and Sherry 2020). The study site was in wet limestone forest habitat, in one of the few old-growth wet limestone forest fragments in the region. Black-and-white Warblers are consistently present at this site in low numbers throughout the winter (CMK unpubl. data). During the Kent and Sherry (2020) study, CMK captured a Second Year (< 1 year old) female Black-and-white Warbler (Pyle 1997) in a mist net on 25 February 2017 at 0957 and administered an emetic to induce regurgitation (Johnson *et al.* 2002). Stomach contents were placed in 70% EtOH and were later examined in the lab using an Olympus SZH binocular dissecting microscope at 75–650× magnification.

Alongside typical arthropod fragments, the stomach contents of this Black-and-white Warbler contained the bones and parts of a small lizard (Fig. 2), including seven claws, several vertebrae, fragments of the pelvic and shoulder girdle, bones of the lower jaw, and teeth. The lizard was identified as an *Anolis* species based on a tricuspid tooth (J. Daza pers. comm.). In addition to the lizard, the individual had been foraging on ants ($n = 46$, including 11 *Camponotus capperi* and 34 *Pheidole jamaicensis*), bark-lice ($n = 7$), caterpillars ($n = 4$), spiders ($n = 3$), Orthoptera ($n = 1$), and Auchenorrhyncha ($n = 1$). During the entire Kent and Sherry (2020) study, 80 stomach content samples were collected across two sites (Copse Hill and the Windsor Research Center), from five warbler species (American Redstart [*Setophaga ruticilla*], $n = 18$; Black-throated Blue Warbler [*S. caeruleascens*], $n = 20$; Northern Parula [*S. americana*], $n = 20$; Worm-eating Warbler [*Helmitheros vermivorum*], $n = 16$; and Black-and-white Warbler, $n = 6$), and the sample from this female Black-and-white Warbler was the only one containing vertebrate remains.

Yellow-throated Warbler, Florida, USA.—At the J.N. Ding Darling National Wildlife Refuge, Sanibel Island, FL, USA, on Wildlife Drive (26°27'34"N, 82°07'44"W), LS observed a Yellow-throated Warbler vertebrate predation. On 8 February 2010, at 1328, LS was birding and noticed a Yellow-throated Warbler 1–1.5 m above the ground on horizontal branches, within mangrove and buttonwood (*Conocarpus erectus*) vegetation. Yellow-throated Warblers are uncommon in southwestern Florida, and LS proceeded to photograph the warbler between 1328 and 1330. LS took 40 photos in total, with the best photos of the predation sequence presented here (Fig. 3). The warbler appeared to be a Second Year individual (< 1 year old), and possibly a male, based on plumage characteristics and molt limits (Pyle 1997). The warbler was first seen without any prey, and then grabbed a small brown anole by the head. The warbler then switched its grip to holding the anole by the tail, and the anole was able to briefly escape. The warbler looked around and was able to recapture the anole, now holding it by the legs. In this latter photo and in subsequent photos, the anole's tail was shorter, and the end was clearly broken off (caudal autotomy), which occurred when the anole briefly escaped (Fig. 3).

The warbler then proceeded to process its prey by biting on the head of the anole, as well as holding onto the legs while bashing

Table 1. Literature records of Parulidae preying on vertebrates. For each bird species, vertebrate prey species, date and location of observation, record type (field observation or prey found in bird stomach contents), interesting additional information, and the reference is given.

Vertebrate Prey	Date	Location	Record Type	Additional Information	Reference
Ovenbird (<i>Seiurus aurocapilla</i>)					
"tree toad" (<i>Eleutherodactylus</i> sp.)	Dec–Apr	Puerto Rico	stomach content		Wetmore 1916
"bones of small lizard"	23 Dec 1948– 3 Jan 1949	Cienfuegos, Cuba	stomach content		Eaton 1953
Worm-eating Warbler (<i>Helminthos vermivorum</i>)					
"bones of small lizard"	23 Dec 1948– 3 Jan 1949	Cienfuegos, Cuba	stomach content		Eaton 1953
Northern Waterthrush (<i>Parkesia noveboracensis</i>)					
small minnows	20 Jan 1887	Charleston, SC, USA	stomach content		Wayne 1910
"bone from the head of a tiny fish"	Feb or Apr 1900– 1901	Puerto Rico	stomach content		Wetmore 1916
<i>Desmognathus</i> sp. salamander	Apr, May	Ashford, CT, USA	field observation		Craig 1987
Louisiana Waterthrush (<i>Parkesia motacilla</i>)					
fish ~0.2 inches long	prior to 1916	New York City, NY, USA	field observation	"picked off flesh with bill"	Hix 1916
"tree toad" (<i>Eleutherodactylus</i> sp.)	Jan	Puerto Rico	stomach content		Wetmore 1916
killifish (fish within Cyprinodontiformes)	unknown	FL, USA	stomach content		Howell 1932
"bones of small amphibians"	23 Dec 1948– 3 Jan 1949	Cienfuegos, Cuba	stomach content		Eaton 1953, Eaton 1958
"terrestrial salamanders"	1996–2005	Appalachian Highlands, PA, USA	field observation	adults feeding young at nests	Mulvihill et al. 2008
Black-and-white Warbler (<i>Mniotilta varia</i>)					
small lizard	1901–1905	TX, USA	stomach content		Oberholser 1974
brown anole (<i>Anolis sagrei</i>)	7 Nov 2015	Key West, FL, USA	field observation	"the warbler proceeded to beat the lizard against a tree trunk similarly to the expected handling of a large insect as prey."	White and Cove 2016
anole	21 Oct 2016	Palm Beach, FL, USA	field observation	head-first consumption	Karlapudi (macaulaylibrary.org/ asset/47723181)
anole	25 Feb 2017	Bethel Town, Jamaica	stomach content		this study
bark anole (<i>Anolis distichus</i>)	6 Mar 2020	San Salvador Island, The Bahamas	field observation		this study

Table 1. cont.

Vertebrate Prey	Date	Location	Record Type	Additional Information	Reference
Prothonotary Warbler (<i>Protonotaria citrea</i>)					
3-cm lizard	28 Sep 2002	New Orleans, LA, USA	field observation	pounded against branch; attempted to consume prey head-first, then pulled apart and ingested	Davis and Komar 2003
Swainson's Warbler (<i>Limnothlypis swainsonii</i>)					
"bones of small lizard"	23 Dec 1948– 3 Jan 1949	Cienfuegos, Cuba	stomach content		Eaton 1953
gecko (<i>Sphaerodactylus goniorhynchus</i>)	winters of 1993–1994 to 1996–1997	Clarendon, Jamaica	stomach content		Strong 2000
Kentucky Warbler (<i>Geothlypis formosa</i>)					
juvenile <i>Anolis</i> spp.	Oct 1993– Nov 1994	Soberania National Park, Panama	stomach content		Poulin <i>et al.</i> 2001
Bahama Yellowthroat (<i>Geothlypis rostrata</i>)					
<i>Anolis</i> lizards	unknown	The Bahamas	unknown		Curson 2020
Whistling Warbler (<i>Catharopeza bishopi</i>)					
"small newt" presumed lizard	unknown	St. Vincent (Lesser Antilles)	stomach content		Lister 1880
Yellow-throated Warbler (<i>Setophaga dominica</i>)					
brown anole (<i>Anolis sagrei</i>)	8 Feb 2010	FL, USA	field observation		this study
Adelaide's Warbler (<i>Setophaga adelaidae</i>)					
"tree toad" (<i>Eleutherodactylus</i> sp.)	Dec 1911– Aug 1912	Puerto Rico	stomach content		Wetmore 1916

the anole on the branch. The behavior appeared to be very similar to prey-handling behavior of Parulidae when processing large invertebrate prey, such as large caterpillars (e.g., Nolan 1978:491). The last photos were taken with the anole in the warbler's bill. We are unsure if the warbler consumed its prey or how this may have occurred, as the warbler proceeded to move out of view.

Discussion

Our study presents a comprehensive list of Parulidae species that have been observed preying upon or consuming vertebrates. We found both historic, obscure records (e.g., Wayne 1910) as well as more recent observations in journal articles (e.g., Davis and Komar 2003) and social media (e.g., Twitter). We also describe the first observation of a Yellow-throated Warbler preying on vertebrates, and the fourth and fifth vertebrate prey records for Black-and-white Warblers. Our compilation is important for better understanding the complexity of food webs, trophic interactions, and predator-prey dynamics (Polis 1991, Winemiller and Polis 1996). Simplistic food webs that leave out uncommon predation events, such as warblers consuming vertebrates, may not embody complete, community-wide relationships (Goldwas-

ser and Roughgarden 1993, Poulin *et al.* 2001). Additionally, acknowledging warbler predation on vertebrates may be important for studies using stable isotopes to determine dietary preferences (Kelly 2000).

Warblers consuming vertebrates may be opportunistic foraging events, including our observations in The Bahamas, Jamaica, and Florida. In The Bahamas, both Black-and-white Warblers and bark anoles often forage along tree trunks (Hillbrand *et al.* 2011, Kricher 2020), thus it is possible that the bird we observed had encountered the bark anole on the trunk of the almond tree while foraging for insects. Given the shared habitat, we suspect the anole in The Bahamas was alive and not found dead on the ground when captured. Yellow-throated Warblers similarly often forage along tree trunks in their non-breeding grounds (LS and MEA pers. obs.), and the observed Yellow-throated Warbler may also have opportunistically found the anole in Florida. We did not follow the photographed Black-and-white Warbler or Yellow-throated Warbler to determine if they consumed their respective anoles. It is possible the birds removed the anoles from the trees to reduce interspecific competition for prey (i.e., insects). However, this



Fig. 1. Black-and-white Warbler (*Mniotilta varia*) with a bark anole (*Anolis distichus*) on San Salvador Island, The Bahamas, on 6 March 2020. Photographed by Janet M. Clarke Storr.

hypothesis seems extremely unlikely, as the records of vertebrates found in stomach contents document the consumption of lizards, including our new record in Jamaica (Table 1, Fig. 2), and we observed the Yellow-throated Warbler exhibiting prey-handling behavior.

Opportunistic predation of vertebrates may rarely occur because of the difficulty for warblers to successfully find, capture, and consume vertebrate prey (Pérez-Rivera 1997). Small fish and amphibians may only be accessible prey for warblers residing in wetter habitats, including areas with small streams (Mulvihill et al. 2008). Furthermore, the most common lizard prey, anoles, are generally fast-moving and can elude avian predation by moving up, down, or to the opposite side of the trunk (Schneider et al. 2000, Hillbrand et al. 2011, Antley et al. 2016). However, anoles may be more active in the dry season while they search for invertebrate prey (Wunderle 1981), and thus may be more likely to be captured by predators during this season. Warblers may also have difficulty in handling and killing relatively large vertebrate prey, as we witnessed with the Yellow-throated Warbler. Indeed, other studies have also observed warblers having difficulty handling and swallowing their vertebrate prey (Davis and Komar 2003, Sykes et al. 2007). One apparent option is to swallow the entire vertebrate head-first (macaulaylibrary.org/asset/47723181), while another method involves tearing up the prey and ingesting it incrementally (Davis and Komar 2003).

An alternative, non-mutually exclusive hypothesis is that these predation events represent behavioral plasticity in warblers' normal foraging tactics and prey items in response to underlying environmental conditions (Aborn and Froehlich 1995). Both of our new Black-and-white Warbler observations occurred during the late winter dry season in the Caribbean (Sealey 2006, Akresh et al. 2019a). The observation in The Bahamas occurred during a winter that was especially dry, with very little precipitation in January and February (T. Dexter pers. comm.), and vegetation on the island appeared to be particularly water-stressed at the time of the observation, even in comparison to previous dry seasons. Likewise, during the period of the Black-and-white Warbler capture in Jamaica, an arthropod sampling study documented a scarcity of high-value arthropod prey at the field site

(Razeng and Watson 2015, Kent et al. 2019). Indeed, the Black-and-white Warbler's stomach sample was dominated by relatively low-value ants. Given the likely shortage of typical avian food resources, such as insects and fruit, during the time of our observations at both sites, the Black-and-white Warblers could have partially shifted to feeding on alternative prey items, such as lizards, to compensate (Poulin et al. 2001, Latta and Faaborg 2002, Wunderle et al. 2014). This latter hypothesis is consistent with previous studies that have shown wintering, migratory warblers to be especially stressed during late winter in very dry years and thus have difficulty maintaining overwinter body condition and adequately preparing fat and muscle stores for spring migration (Studds and Marra 2007, Akresh et al. 2019a). Additionally, events and processes on the wintering grounds can subsequently influence birds both during migration and on the breeding grounds (e.g., carry-over effects; Paxton and Moore 2015, Akresh et al. 2019b). The behavioral plasticity hypothesis is also consistent with these migratory warblers' life history and their capacity to exploit different food resources depending on availability (Bell 2011).

Observations of other small passerines preying on vertebrates have also occurred during stressful environmental conditions or taxing periods during the avian life cycle, further supporting the behavioral plasticity hypothesis. For instance, a Prothonotary Warbler (*Protonotaria citrea*) consumed a lizard 2 days after a tropical storm (Davis and Komar 2003), and Red-eyed and Yellow-throated Vireos (*Vireo olivaceus* and *V. flavifrons*) were observed eating green anoles (*Anolis carolinensis*) during migration (Sykes et al. 2007). Mulvihill et al. (2008) observed that salamanders were fed to Louisiana Waterthrush nestlings more often in acidified, poorer-quality streams compared to circumneutral streams on the breeding grounds. Optimal foraging theory predicts that predators should try to maximize food intake and energy gain per unit of foraging time (Krebs 1978). Therefore, larger, more difficult, time-consuming prey such as vertebrates may only be efficient prey items for warblers during taxing periods or in environments with a lack of available invertebrate prey (Hase-

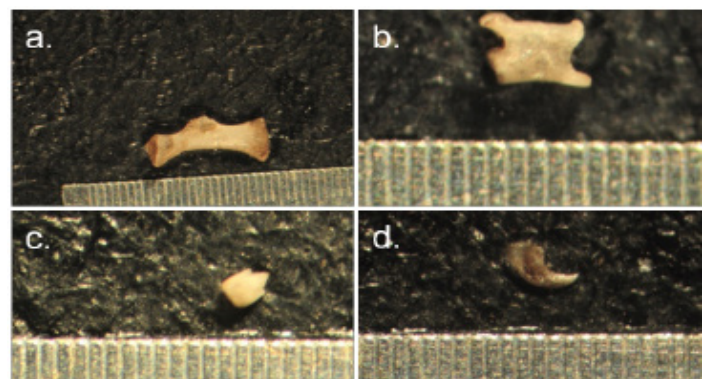


Fig. 2. Photographs of some of the parts and bones of an *Anolis* sp., found in a Black-and-white Warbler (*Mniotilta varia*) stomach contents sample that was collected in western Jamaica on 25 February 2017. (a) Scapulocoracoid, (b) vertebrae, (c) tricuspid tooth, (d) claw. Photographs were taken through an Olympus SZH binocular dissecting microscope using a TDI high-precision micro ruler with 0.1 mm divisions. Photograph by Cody M. Kent.



Fig. 3. Sequence of photographs of the Yellow-throated Warbler (*Setophaga dominica*) handling a brown anole (*Anolis sagrei*) in southwestern Florida, USA, on 8 February 2010. Times given as hr:min:sec. a) Bird is without prey, 13:28:13, b) catches anole, 13:28:38, c) still has anole, 13:29:05, d) has prey by leg and tail, but anole begins to escape, 13:29:06, e) without the anole, 13:29:13, f) begins to recapture anole, 13:29:15, g) recaptures anole, 13:29:18, h) anole is immobile on branch, 13:29:20, i–l) further handling of anole, including bashing on branch, 13:29:37–13:29:59. Photos by Lillian Stokes.

gawa 1990, Hirvonen and Ranta 1996, Tremblay *et al.* 2005). Although a single anole has more weight and calories than individual invertebrate prey, it may have similar caloric content per gram compared to certain insect taxa (Vitt 1978, Ramos-Elorduy *et al.* 1997).

Many of the prey items recorded in our literature review were lizards and amphibians, which are both abundant in the

non-breeding grounds of migratory Parulidae and small enough to be captured (Schoener and Schoener 1978, McLaughlin and Roughgarden 1989, Poulin *et al.* 2001, Rosamond *et al.* 2020). Moreover, lizard abundance may be increasing in these regions; regional and international trade has resulted in the human-mediated introduction of many new anole species in North America and the Caribbean (Losos 2009). For instance, the brown anole is

an introduced species now found throughout Florida, with population densities as high as 12,000 individuals/ha (Krysko et al. 2019). Interestingly, besides being a newly abundant potential prey item, introduced lizards could also impact and potentially reduce invertebrate prey density and availability for warblers (Schoener et al. 2002). Determining if warbler consumption of anoles increases in the future would improve our understanding of how trophic interactions are shifting in changing environments (David et al. 2017, Calizza et al. 2021).

Further research would help elucidate why only certain species of wood warblers have been observed preying on vertebrates, and if determinants such as bill size, foraging behavior, habitat type, and geographic range explain variation of vertebrate predation among warbler species (Poulin et al. 2001, Rosamond et al. 2020). Incidentally, wood warblers that have preyed on vertebrates appear to have relatively longer and larger bills (Davis and Komar 2003, Kricher 2020); based on the 80 stomach content samples of five species examined in Kent and Sherry (2020), only the longer-billed Black-and-white Warbler consumed a vertebrate. Further studies should also examine how avian predation, even from warblers, may influence herpetofauna's behavior and evolution (Wunderle 1981, McLaughlin and Roughgarden 1989, Poulin et al. 2001, Acosta and Morún 2014). The ability of anoles to lose their tails (caudal autotomy) can give them a chance to escape predation (Clause and Capaldi 2006, Bateman and Fleming 2009, Hoefler and Robinson 2020), as we observed in Florida. We recommend researchers and citizen scientists photograph and report on more foraging observations of warblers and other birds, especially in tropical and sub-tropical regions where less is known about predation behavior (Boal 2008, Devenish-Nelson et al. 2019, Naude et al. 2019, Berryman and Kirwan 2021).

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Title Page Illustration

Yellow-throated Warbler (*Setophaga dominica*) captured a brown anole (*Anolis sagrea*) in southwestern Florida on 8 February 2010. Photo by Lillian Stokes.

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