The Condor 112(3):605–614

PREY SELECTION BY SWAINSON'S WARBLERS ON THE BREEDING GROUNDS

Amelia L. Savage[1,4], Christopher E. Moorman[1], John A. Gerwin[2], and Clyde Sorenson[3]

[1]*Fisheries and Wildlife Sciences Program, Department of Forestry and Environmental Resources, North Carolina State University, Campus Box 7646, Raleigh, NC 27695*
[2]*North Carolina Museum of Natural Sciences, 11 W. Jones St., Raleigh, NC 27601*
[3]*Department of Entomology, North Carolina State University, Campus Box 7613, Raleigh, NC 27695-8003*

Abstract. Swainson's Warbler (*Limnothlypis swainsonii*) breeds in bottomland hardwood forests across the southeastern United States, where it is believed to be one of the rarest breeding songbirds. Although information on its nest-site habitat is considerable, little is known about its foraging habitat except that the species is insectivorous, with a large bill used to flip fallen leaves on the forest floor. We captured Swainson's Warblers and flushed their crops to determine their diet and sampled leaf-litter arthropods and vegetation at each location of capture. We compared the proportion of arthropod orders in the crop samples to the proportion of arthropods collected in the leaf litter to determine the warbler's prey in proportion to its availability. Although Acari (mites and ticks) and Chilopoda (centipedes) were the most abundant arthropods in the leaf-litter samples (51% and 18%, respectively), these orders rarely occurred in the warblers' crops. Conversely, Araneae (spiders) and Coleoptera (beetles) were uncommon in leaf-litter samples (2% and 5%, respectively) but were the most abundant arthropod orders in the warblers' crops. Binary logistic regression with presence or absence of Araneae as the response variable and habitat measures as the predictor variables revealed that the probability of spiders occurring in the leaf litter increased as leaf-litter depth increased. To promote foraging habitat for Swainson's Warbler, deep leaf litter should be maintained by maintaining patches of closed-canopy forests and restoring natural regimes of flooding.

Key words: *arthropods, bottomland hardwoods, breeding,* Limnothlypis swainsonii, *prey selection, Swainson's Warbler.*

Selección de Presas por *Limnothlypis swainsonii* en las Áreas de Anidación

Resumen. *Limnothlypis swainsonii* se reproduce en bosques de bajura de madera dura a través del sudeste de Estados Unidos, donde se cree que es una de las aves canoras más raras. Aunque la información sobre el hábitat de anidación es considerable, se sabe poco sobre su hábitat de forrajeo excepto que la especie es insectívora, con un pico largo usado para dar vuelta hojas caídas en el piso del bosque. Capturamos individuos de *L. swainsonii* y enjuagamos sus buches para determinar sus dietas y muestreamos los artrópodos de la hojarasca y la vegetación en cada localidad de captura. Comparamos la proporción de órdenes de artrópodos en las muestras de los buches con la proporción de artrópodos colectados en la hojarasca para determinar las presas de *L. swainsonii* en proporción con su disponibilidad. Aunque Acari (ácaros y garrapatas) y Chilopoda (ciempiés) fueron los artrópodos más abundantes en las muestras de la hojarasca (51% y 18%, respectivamente), estos órdenes rara vez estuvieron presentes en los buches de *L. swainsonii*. Por el contrario, Araneae (arañas) y Coleoptera (escarabajos) fueron poco comunes en las muestras de la hojarasca (2% y 5%, respectivamente) pero fueron los órdenes de artrópodos más abundantes en los buches de *L. swainsonii*. Análisis de regresión logística binaria con presencia o ausencia de Araneae como la variable de respuesta y las medidas de hábitat como las variables predictivas revelaron que la probabilidad de que las arañas aparecieran en la hojarasca incrementó a medida que aumentó la profundidad de la hojarasca. Para promover el hábitat de forrajeo de *L. swainsonii*, la profundidad de la hojarasca debería ser mantenida mediante el mantenimiento de parches de bosques de dosel cerrado y la restauración de los regímenes natural de inundación.

INTRODUCTION

Swainson's Warbler, *Limnothlypis swainsonii*, winters in the Caribbean basin and breeds primarily in bottomland hardwood forests of the southeastern United States (Hunter et al. 1993). It is thought to be one of the rarest breeding songbirds in the southeastern United States (Hunter et al. 1993, 1994, Smith et al. 1993) and has disappeared from much of its historical range in Maryland, Delaware, Missouri, and Illinois (Graves 2001). Because of evidence for recent population declines, Swainson's Warbler has been designated as a high priority for conservation (Morton 1992, Hunter et al. 1993, 1999, Ruth 2004).

Manuscript received 31 March 2009; accepted 1 May 2010.
[4]Current address 7075 W. Gowan Rd., #2117, Las Vegas, NV 89129. E-mail: amlee001@aol.com

The Condor, Vol. 112, Number 3, pages 605–614. ISSN 0010-5422, electronic ISSN 1938-5422. DOI: 10.1525/cond.2010.090055

Typically, forests inhabited by Swainson's Warbler are situated on or near a floodplain and have a high canopy cover, dense undergrowth with little or no herbaceous ground cover, and relatively deep leaf litter (Meanley 1966, Eddleman et al. 1980, Thomas et al. 1996). Additionally, the species often breeds in association with patches of switchcane (*Arundinaria gigantea*) or vine tangles (Graves 2001, 2002, Thompson 2005). Most efforts to manage or create breeding habitat for Swainson's Warblers have emphasized restoration of switchcane and creation of gaps in mature bottomland hardwood forests (Hunter et al. 1993, 1999). Graves (2001, 2002) reported that a heterogeneous understory may be the principal consideration in the warbler's selection of breeding habitat.

Although researchers have investigated Swainson's Warbler's selection of nesting habitat (Graves 2002, Peters et al. 2005), limited information is available on the species' diet or foraging habitat. Swainson's Warbler is an insectivore, foraging almost solely in leaf litter by lifting dead leaves with its large bill (Graves 1998, Strong 2000). The bird forages in the top layer of leaf litter, so arthropods in the lower decaying leaf litter are unlikely available (Meanley 1971).

The species' reclusive nature and formidable breeding habitat composed of dense vegetation make direct observations of Swainson's Warbler difficult. Therefore, we flushed the crops of birds captured in mist nets to retrieve information about the species' diet (Major 1990, Moorman et al. 2007). We captured and crop-flushed Swainson's Warblers during the breeding seasons of 2007 and 2008 and compared the proportions of arthropod orders in crop flushes to the proportions of arthropod orders available in the leaf litter. We also modeled the habitat characteristics that best predicted the presence of leaf-litter arthropods the birds selected.

METHODS

STUDY SITE

We studied the diet of Swainson's Warbler on the 8000-ha Woodbury Wildlife Management Area (33° 52′ N, 79° 22′ W), which is owned and managed by the South Carolina Department of Natural Resources and located at the confluence of the Great and Little Pee Dee rivers near Britton's Neck, South Carolina. Elevation ranges from 0 to 25 m above sea level. The area floods irregularly during the spring and summer months and includes isolated wetlands, bottomland hardwood forests, and stands of planted loblolly (*Pinus taeda*) and longleaf (*P. palustris*) pines (Peters et al. 2005).

Much of the hardwood forest at Woodbury regenerated naturally following clear-cutting with a shearing blade between 5 and 30 years prior to our study. During shearing, all trees, saplings, and stumps were removed, but most drainage areas and other water-filled, low-lying areas were not harvested (Peters et al. 2005). The mix of uncut mature hardwood forest, regenerated forest, and sparsely vegetated areas where the soil was heavily compacted (e.g., logging roads and decks) during logging created a heterogeneous vegetation structure, which is correlated with Swainson's Warbler's occurrence (Thompson 2005).

DIET IDENTIFICATION

From 15 April to 31 July in 2007 and 2008, we passively captured Swainson's Warblers in four arrays of 12 mist nets each, set in areas of high population density. We operated each array for 6 hr, 1 out of every 10 days, checking the nets every 45 min. We estimate the average time from when birds were captured to when their crop was flushed as 30 min. We captured additional Swainson's Warblers by target-netting individuals that responded to broadcast songs and chip notes. We targeted the species by systematically broadcasting recorded songs and chip notes along all roads that intersected potential habitat. For portions of the property far from roads, we broadcast Swainson's Warbler songs as we walked through the woods. We attempted to capture all individuals that responded to broadcast calls by luring the birds into mist nets placed near low vegetation where the bird was heard or sighted. The time from when we started the playback to when the bird's crop was flushed averaged an estimated 30 min. Some birds responded immediately after the start of playbacks, but others took approximately 30–45 min to be caught and processed. We compared crop samples collected by the two capture techniques.

To assess the Swainson's Warbler's diet, we banded (if the bird was not already banded), weighed, and flushed the crop of each individual newly captured or recaptured. We flushed the crop as soon as we removed each bird from the net because of the high rate of digestion of prey. To avoid excessive stress, we did not flush the crop of any bird recaptured within 1 week of a previous flush (Major 1990). We flushed crops by inserting a plastic catheter, diameter 2 mm, down the throat into the crop, through which we gently squirted warm water while slowly removing the catheter (Moorman et al. 2007). We collected crop contents into a clean plastic bowl. We preserved crop contents in 75% ethanol in plastic vials for later identification (Major 1990). When handling Swainson's Warblers, we followed all protocols set by North Carolina State University's Institutional Animal Care and Use Committee (protocol 07-036-O).

A dissecting microscope was used to count and identify to order arthropod fragments found in the crop contents. We measured the length (mm) of whole arthropods found in the crop samples. We did not identify arthropods beyond order because the small fragments made it difficult to be more specific. The fragmentary nature of most of the crop contents made it difficult to count the exact number of individual arthropods in each crop sample; therefore, we estimated conservatively, and multiple individuals of the same order were counted only if we observed more fragments of the same kind (e.g., legs, antennae, and eyes) than are normally found on an individual arthropod

(Moorman et al. 2007). For example, if we found four spider legs of the same color, we counted one spider. If we found nine spider legs of the same color, we counted two spiders.

MICROHABITAT

For each Swainson's Warbler captured, we established one area for microhabitat sampling near the capture site. Vegetation and leaf litter were removed from the immediate vicinity during set-up of mist nets. Therefore, we moved approximately 20 m away from each capture location and established two concentric circular plots, radii 5 and 11.3 m. When we captured a Swainson's Warbler responding to a broadcast, we located the plot in the direction the bird was initially heard before its capture. For Swainson's Warblers captured during passive netting, we used a random direction. If the plot's center fell in an area where the birds were known not to forage (e.g., in a body of water or light gap), we relocated the plot to the nearest edge of the body of water or light gap.

Within the 5-m-radius plot, we visually estimated percentages of ground covered by switchcane, other grass, other herbaceous plants, vines, woody debris, bare ground, standing water, and herb-free litter. We used a convex densiometer to estimate the open canopy at the center of the plot. Within the 11.3-m-radius plot, we counted and measured the diameter at breast height (dbh) of all trees, counting them by five categories based on dbh: saplings (dbh <2.5 cm, height >30 cm), poles (dbh 2.5–8 cm), small trees (dbh 8–23 cm), medium trees (dbh 23–38 cm), and large trees (dbh >38 cm). Additionally, we assessed the density of understory vegetation by standing in the center of the plot and reading a density board positioned at 11.3 m in the four cardinal directions. Immediately adjacent to the point where we took each of the four subsamples of leaf litter (described below), we took one measurement each of percent soil moisture, soil pH (Kelway soil pH and moisture meter), and leaf litter depth (mm).

ARTHROPOD-COMMUNITY IDENTIFICATION

To quantify the arthropods available to Swainson's Warblers, we hand-collected leaf litter and associated litter-dwelling arthropods within a square frame, 0.25 m on side and 0.106 m deep, placed in a random location within each of the four quadrants of the 5-m plot. Therefore, we collected four subsamples of leaf litter per Swainson's Warbler captured. The sides on the frame prevented arthropods from escaping. Arthropods from the four subsamples within each plot were combined for analysis. We collected all leaf litter from the top surface of the leaf litter to the mineral soil layer and stored each sample in a plastic bag until placing it in a Berlese funnel for 24 hr to extract the arthropods (Barberena-Arias and Aide 2003). If the leaf litter was not completely dry after 24 hr, we left it in the funnel until it was dry. We used hand-collected leaf litter and Berlese funnels because the combination allowed us to capture both sedentary and active arthropods, whereas pitfall traps generally capture only arthropods that cruise the substrate actively. Arthropods were preserved in 75% ethanol, later identified to order and life stage (e.g., larva or adult) if possible, and counted. We measured the length (mm) of all whole arthropods collected in the leaf litter samples and assigned them to the following categories: 0–2 mm, 2.1–5.0 mm, 5.1–10.0 mm, 10.1–15.0 mm, or >15 mm (Brown et al. 2009).

In 2007, we checked for seasonal changes in the community of litter-dwelling arthropods by collecting 48 leaf-litter samples after 15 June 2007 from locations immediately adjacent to the 48 leaf-litter samples previously collected before 15 June 2007. Swainson's Warblers flip leaves on the surface of the leaf-litter layer, so only the insects in the upper dry layer of leaf litter are available as prey. Therefore, to assess the portion of the arthropod community actually available to the birds, we looked at a subsample of 28 of the 400 leaf-litter samples collected in 2008. We separated the 28 samples into the upper, dry portion of leaf litter and the lower leaf litter near the soil, distinguishing the latter by the presence of decaying leaves. The samples of dry and decaying leaf litter were processed in the manner detailed above.

STATISTICAL ANALYSES

We analyzed data from 2007 and 2008 separately because patterns of flooding in the drier 2007 season differed dramatically from those in the wetter 2008 season. Using two-tailed t-tests, we compared the proportion of arthropods of each order found in the crop samples from Swainson's Warblers captured during targeted and passive netting. We used two-tailed t-tests to compare each arthropod order found in samples from adult males and adult females and to compare arthropod availability early and late in the breeding season of 2007. Because the number of whole arthropods recovered in crop samples was small ($n = 24$ in 2007 and $n = 43$ in 2008), we were able to compare the lengths of whole arthropods in crop samples to those in leaf-litter samples only qualitatively. We arcsine-transformed all proportional data before making the t-tests.

We summarized the number of arthropods of each order within the upper dry and lower decaying leaf-litter layer samples as the proportion of the total number of arthropods in the 28 samples analyzed in 2008. Then, we multiplied the proportion of the arthropods of each order found in the upper dry portion of the 28 samples by the total number of individuals of each order for all samples in 2007 and in 2008. This gave us a corrected number of arthropods of each order that was available to the warblers. Using these corrected numbers, we then recalculated the proportion of the arthropods of each order (i.e., corrected number of arthropods in the order divided by the corrected total number of arthropods). Although this correction changed the proportional distribution of the leaf-litter arthropods available to the birds only slightly, we believe that it yielded more accurate assessments of Swainson's Warbler's diet selection.

We used Jacobs' (1974) index to determine if arthropods were consumed in proportion to their availability: $D_{hb} = (r - p)/(r + p - 2rp)$, where D_{hb} was the index of arthropod use, r was the fraction of an arthropod order in the crop-flush sample, and p was the fraction of a particular arthropod order in the total arthropod sample. Values of D_{hb} ranged from –1.00 to 1.00. We determined the warblers' selection and avoidance of arthropods with Morrison's (1982) categorization of D_{hb}, where –1.00 to –0.81 = strong avoidance, –0.80 to –0.40 = moderate avoidance, –0.40 to –0.16 = slight avoidance, –0.15 to 0.15 = no selection, 0.16 to 0.40 = slight selection, 0.41 to 0.80 = moderate selection, and 0.81 to 1.00 = strong selection. We calculated the Jacobs' (1974) index separately for the adult and larval life stages of recovered arthropods.

To identify microhabitat variables related to the presence of the warbler's important arthropod prey, we used a model-selection approach (Burnham and Anderson 2002). We used SAS JMP to run a Pearson's correlation matrix to identify highly correlated microhabitat variables ($r > 0.6$), and we removed the correlated variable we considered less biologically relevant (SAS Institute 2003). We used 13 microhabitat variables in subsequent analyses. Our study (see Results) and previous studies (Eaton 1953, Meanley 1971, Strong 2000) suggest that spiders are Swainson's Warbler's most important prey. Therefore, we conducted binary logistic regressions (Proc Logistic) with the presence or absence of spiders as the response variable and microhabitat measures as the predictor variables (SAS Institute 2003). Few leaf litter samples contained no spiders, but many had one or more. Therefore, we categorized spiders as rare if 0 or 1 individual was recorded and as present if more than one individual was recorded in a plot. All combinations of all habitat variables were run in binary logistic-regression models. We then used Akaike's information criterion for small sample sizes (AIC_c; Cody and Smith 1997, Burnham and Anderson 2002) to compare regression models and calculated an AIC_c weight for each model. We considered only models with $\Delta AIC_c < 2$.

RESULTS

DIET INFORMATION

Forty percent of crop samples did not contain any arthropod fragments. In 2007, we obtained 96 crop samples from 74 individuals (58 adult males, 9 adult females, and 7 hatch-year birds) and recaptured 22 individuals within the same season. The crop samples that contained arthropod fragments in 2007 represented 27 adult males, 4 adult females, and 5 hatch-year birds. In 2007, we captured 50 birds by targeted netting and 46 by passive netting. In 2008, we obtained 100 crop samples from 78 individuals (64 adult males and 14 adult females) and recaptured 22 individuals within the same season. We did not capture any hatch-year birds in 2008. The crop samples that contained arthropod fragments in 2008 represented 31 adult males and 6 adult females. Notably, 12 of the individuals flushed in 2008 were originally captured in 2007. In 2008, we caught 40 Swainson's Warblers by targeted netting and 60 by passive netting. Crop samples collected in 2007 contained 155 individual prey items representing 11 arthropod orders, and those collected in 2008 contained 227 individual prey items representing 12 arthropod orders (Table 1).

TABLE 1. Orders of invertebrates detected in samples from Swainson's Warbler crop and leaf litter at Woodbury Wildlife Management Area, South Carolina, 2007 and 2008.

	2007		2008	
Order	Crop sample	Leaf-litter Sample	Crop sample	Leaf-litter sample
Mollusca	—	+	—	+
Worm	—	+	+	+
Isopoda	—	+	—	+
Diplopoda	+	+	+	+
Chilopoda	+	+	+	+
Acari	+	+	+	+
Araneae	+	+	+	+
Pseudoscorpiones	—	+	—	+
Collembola	—	+	+	+
Archeognatha	—	+	—	—
Odonata	—	+	—	—
Orthoptera	—	+	—	+
Dictyoptera	—	+	—	—
Dermaptera	—	+	—	—
Miscellaneous others	+	—	—	—
Psocoptera	—	+	+	+
Hemiptera	+	+	+	+
Thysanoptera	+	+	—	+
Neuroptera	—	+	—	—
Coleoptera	+	+	+	+
Lepidoptera	+	+	+	+
Trichoptera	—	+	—	—
Diptera	+	+	+	+
Hymenoptera	+	+	+	+

In 2007, the arthropod orders detected in the highest proportion were Araneae (35%) and Coleoptera (25%) (Table 2), the others being Lepidoptera, Chilopoda, Acari, Hymenoptera, Hemiptera, Diptera, Diplopoda, and Thysanoptera (Table 1). Araneae (57%) and Coleoptera (16%) were also present in the highest proportions in 2008 (Table 3). There was also one worm in the 2008 crop samples. Collembola and Thysanoptera were recorded only once in the crop samples. In the 2007 crop samples, 82% of Coleoptera, 98% of Araneae, 9% of Lepidoptera, 87% of the Hemiptera, and 67% of Hymenoptera were adult. In the 2008 crop samples, 97% of Coleoptera, 56% of Araneae, 7% of Lepidoptera, and 47% of Hymenoptera were adult.

There were no differences between crop samples from passive and targeted netting in 2007 or 2008. Within each year, we therefore pooled crop samples collected by the two techniques. Because so few females were captured, we combined samples for 2007 and 2008 to compare the composition of the diet by sex. The proportion of each arthropod order in crop samples

TABLE 2. Proportion of total arthropods of each order for adult and larval life stages and the Jacobs' index for prey selection by breeding Swainson's Warblers at Woodbury Wildlife Management Area, South Carolina, 2007.

	Adult				Larva/immature/pupa			
Order	Arthropod in crop (proportion)	Arthropod in litter (proportion)	Jacobs' index	Selection[a]	Arthropod in crop (proportion)	Arthropod in litter (proportion)	Jacobs' index	Selection
Acari	0.05	0.52	–0.90	Strong avoidance	0.00	<0.01	–1.00	Strong avoidance
Araneae	0.32	0.01	0.94	Strong selection	0.03	<0.01	0.90	Strong selection
Diplopoda[b]	0.02	<0.01	0.58	Moderate selection	—	—	—	—
Chilopoda	0.01	<0.01	0.53	Moderate selection	—	—	—	—
Hemiptera	<0.01	<0.01	–0.31	Moderate avoidance	<0.01	<0.01	0.75	Moderate selection
Thysanoptera	0.01	0.02	–0.15	Slight avoidance	—	—	—	—
Coleoptera	0.20	0.03	0.79	Moderate selection	0.06	0.04	0.23	Moderate selection
Hymenoptera	0.05	0.09	–0.31	Moderate avoidance	0.03	<0.01	0.96	Strong selection
Lepidoptera	<0.01	<0.01	0.32	Moderate selection	0.08	<0.01	0.97	Strong selection
Diptera	0.02	0.02	–0.15	Slight avoidance	0.00	0.04	–1.00	Strong avoidance

[a]Morrison's (1982) categorization of D_{hb}, where –1 to –0.81 = strong avoidance, –0.80 to –0.40 = moderate avoidance, –0.40 to –0.16 = slight avoidance, –0.15 to 0.15 = no selection, 0.16 to 0.40 = slight selection, 0.41 to 0.80 = moderate selection, and 0.81 to 1= strong selection.
[b]Adult and larva/immature of Diplopoda, Chilopoda, and Thysanoptera were not distinguished.

TABLE 3. Proportion of total arthropods of each order for adult and larval life stages and Jacobs' index for prey selection by breeding Swainson's Warblers at Woodbury Wildlife Management Area, South Carolina, 2008.

	Adult				Larva/immature/pupa			
Order	Arthropod in crop (proportion)	Arthropod in litter (proportion)	Jacobs' index	Selection[a]	Arthropod in crop (proportion)	Arthropod in litter (proportion)	Jacobs' index	Selection
Acari	0.04	0.61	–0.95	Strong avoidance	0.00	<0.01	–1.00	Strong avoidance
Araneae	0.35	0.04	0.86	Strong selection	0.19	<0.01	1.00	Strong selection
Collembola[b]	0.01	0.08	–0.83	Strong avoidance	—	—	—	—
Diplopoda	0.01	<0.01	0.04	No selection	—	—	—	—
Hemiptera	0.03	<0.01	0.77	Moderate selection	0.00	<0.01	–1.00	Strong avoidance
Thysanoptera	0.01	0.04	–0.65	Moderate avoidance	—	—	—	—
Coleoptera	0.15	0.02	0.76	Moderate selection	<0.01	0.04	–0.81	Strong avoidance
Hymenoptera	0.05	0.06	–0.07	No selection	0.05	<0.01	0.98	Strong selection
Lepidoptera	<0.01	<0.01	0.03	No selection	0.06	0.01	0.76	Moderate selection
Diptera	0.03	0.02	0.33	Slight avoidance	0.00	0.02	–1.00	Strong avoidance

[a]Morrison's (1982) categorization of D_{hb}, where –1 to –0.81 = strong avoidance, –0.80 to –0.40 = moderate avoidance, –0.40 to –0.16 = slight avoidance, –0.15 to 0.15 = no selection, 0.16 to 0.40 = slight selection, 0.41 to 0.80 = moderate selection, and 0.81 to 1= strong selection.
[b]Adult and larva/immature of Diplopoda, Chilopoda, and Thysanoptera were not distinguished.

TABLE 4. Length (mm) of intact arthropods in samples from Swainson's Warbler crops and leaf litter, Woodbury Wildlife Management Area, South Carolina, 2007 and 2008.

	2007				2008			
	Crop samples		Leaf litter		Crop samples		Leaf litter	
Size (mm)	Number of individuals	Proportion	Number of individuals	Proportion	Number of individuals	Proportion	Number of individuals	Proportion
0.00–2.00	18	0.75	23 620	0.76	27	0.63	29 600	0.77
2.01–5.00	0	0.00	6123	0.20	5	0.12	7590	0.20
5.01–10.00	5	0.21	954	0.03	10	0.23	790	0.02
10.01–15.00	1	0.04	187	<0.01	1	0.02	116	<0.01
15.01+	0	0.00	210	<0.01	0	0.00	85	<0.01

from adult males and adult females did not differ ($P > 0.05$ for all arthropod orders, $n_{female} = 10$, $n_{male} = 58$). Of intact arthropods in the crop samples, we detected 24 in 2007 (orders Acari, Thysanoptera, Paraphyletic, Hemiptera, and Hymenoptera) and 43 in 2008 (orders Acari, Diptera, Hymenoptera, Araneae, and Collembola). In both years the majority of intact arthropods in the crop samples were 0–2 mm long, but 21% and 23% were 5.01–10 mm long in 2007 and 2008, respectively (Table 4). The majority of the arthropods from leaf-litter samples in 2007 and 2008 were 0–2 mm long and ≤3% were 5.01–10 mm long (Table 4). The percentage of intact arthropods between 2.01 and 5.00 mm in the crop samples was smaller than in the leaf-litter samples (Table 4).

ARTHROPOD-COMMUNITY IDENTIFICATION

In the leaf litter, we detected 23 arthropod orders and 31 040 individual arthropods in 384 samples collected in 2007 and 17 orders and 36 753 individual arthropods in 400 samples collected in 2008 (Table 1). Approximately 37% of leaf-litter arthropods were likely not available to Swainson's Warblers because they were in the decaying leaf litter (Table 5). In the comparison of leaf-litter samples taken between 11 May and 11 June 2007 to those taken between 15 June and 21 July 2007, the proportions of only Diplopoda ($t_{96} = -1.99$, $P = 0.04$) and Orthoptera ($t_{96} = 1.66$, $P = 0.05$) differed. The proportion of Diplopoda increased as the breeding season progressed, whereas that of Orthoptera decreased.

TABLE 5. Proportion of arthropods in each order recorded in the dry and decaying layers of leaf litter ($n = 28$) in 2008 and the uncorrected and corrected proportions of the total arthropods of each order recorded in leaf-litter samples collected at Woodbury Wildlife Management Area, South Carolina, 2007 and 2008.

Order	Proportion in dry litter	Proportion in decaying litter	Uncorrected[a] proportion 2007	Corrected[b] proportion 2007	Uncorrected proportion 2008	Corrected proportion 2008
Mollusca	0.68	0.32	<0.01	<0.01	0.03	0.04
Isopoda	0.32	0.68	<0.01	<0.01	<0.01	<0.01
Diplopoda	0.63	0.37	<0.01	<0.01	<0.01	<0.01
Chilopoda	0.88	0.12	<0.01	<0.01	0.26	0.32
Acari	0.67	0.33	0.54	0.53	0.38	0.36
Araneae	0.73	0.27	0.02	0.02	0.02	0.02
Collembola	0.75	0.25	0.18	0.20	0.08	0.09
Orthoptera	0.70	0.30	<0.01	<0.01	<0.01	<0.01
Psocoptera	0.95	0.05	<0.01	<0.01	<0.01	<0.01
Hemiptera	0.58	0.42	<0.01	<0.01	<0.01	<0.01
Thysanoptera	0.72	0.28	0.02	0.02	0.04	0.04
Coleoptera	0.50	0.50	0.07	0.05	0.06	0.04
Lepidoptera	0.63	0.38	<0.01	<0.01	0.01	0.01
Hymenoptera	0.72	0.28	0.09	0.10	0.03	0.03
Diptera	0.54	0.46	0.06	0.05	0.03	0.02

[a]The uncorrected proportion is overall proportion for that order in that year.
[b]We calculated the corrected proportion by multiplying the proportion of available arthropods in the dry leaf litter by the number of individuals of the order. Then, we recalculated the proportion of arthropods of each order by dividing the corrected number of arthropods in the order by the corrected total number of arthropods.

TABLE 6. Logistic-regression models used to predict the presence of Araneae at Woodbury Wildlife Management Area, South Carolina, 2007. The sign in parentheses indicates the direction of relationship.[a]

Model	n	K	ΔAIC_c	w_i	Concordance (%)	P-value
LLD[b](+)	93	2	0.00	0.50	72	<0.01
LLD(+), % grass[c] (+)	93	3	0.96	0.31	74	<0.01
LLD(+), % grass(+), % wood[d](+)	93	4	2.86	0.12	74	<0.01
LLD(+), % grass(+), % wood(+), % other[e](–)	93	5	5.02	0.04	74	<0.01
LLD(+), % grass(+), % wood(+), % other(–), % vine[f](+)	93	6	7.30	0.01	75	<0.01
LLD(+), % grass(+), % wood(+), % other(–), % vine(–), % leaf[g](–), med[h](+), poles[i](+), sap[j](+), sm[k](+), canopy[l](+)	93	12	8.83	<0.01	81	<0.01
LLD(+), % grass(+), % wood(+), % other(–), % vine(–), % leaf (–), med (+)	93	8	9.32	<0.01	76	0.01
LLD(+), % grass(+), % wood(+), % other(–), % vine(–), % leaf (–)	93	7	9.36	<0.01	74	0.01
Null (intercept only)	93	1	12.09	<0.01		

[a]Lowest AIC_c = 109.68.
[b]Leaf-litter depth in mm from surface to earth.
[c]Percent other grass cover.
[d]Percent woody debris.
[e]Percent other herbaceous ground cover.
[f]Percent vine ground cover.
[g]Percent leaf litter ground cover.
[h]Number of medium trees 23–38 cm dbh.
[i]Number of pole trees 2.5–8 cm dbh.
[j]Number of saplings trees >30cm tall, and <2.5 cm dbh.
[k]Number of small trees 8 cm–23 cm dbh.
[l]Percent open canopy cover, measured with a convex densitometer.

ARTHROPOD USE VS. AVAILABILITY

The Acari were the most abundant arthropod order recorded in the leaf litter but were one of the least detected in crop samples (Tables 2 and 3). Araneae, the most abundant order of arthropods found in the crop samples in 2007 and 2008, were one of the least abundant in the leaf litter. In both years, proportions of Diplopoda, Chilopoda, Hemiptera, Thysanoptera, adult Lepidoptera, and Diptera in both crop and leaf-litter samples were low (Tables 2 and 3). The arthropod orders selected by Swainson's Warblers in 2007 and 2008 were similar. In both years, the birds selected adult and larval Araneae, larval Hymenoptera, larval Lepidoptera, and adult Coleoptera (Tables 2 and 3). Adult Acari were strongly avoided in both years (Tables 2 and 3). Larval Coleoptera were selected in 2007 but avoided in 2008, adult Hymenoptera were avoided in 2007 but not in 2008, and Collembola were not recorded in crop samples in 2007 and avoided in 2008 (Tables 2 and 3).

HABITAT MODELS

The two models that best predicted the presence of Araneae for 2007 included (1) leaf-litter depth (positive relationship), and (2) leaf-litter depth (positive relationship) and percent other grass cover (positive relationship) (Table 6). The model that best predicted the presence of Araneae in 2008 included five variables: leaf-litter depth (positive relationship), percent other grass cover (positive relationship), percent woody debris cover (positive relationship), percent other herbaceous plant cover (negative relationship), and percent soil moisture (positive relationship) (Table 7). The top 10 habitat models for both 2007 and 2008 had ΔAIC_c lower than the intercept-only model.

DISCUSSION

At Woodbury, Swainson's Warblers selected larval and adult Araneae, larval Lepidoptera, adult Coleoptera, and larval Hymenoptera in proportions greater than their availability in the leaf litter. In Georgia, four stomach samples from breeding Swainson's Warblers contained primarily Orthoptera, Hymenoptera, Araneae, and larval Lepidoptera (Meanley 1971). Strong (2000) and Eaton (1953), using emetics and stomach sampling, respectively, found that on their wintering grounds Swainson's Warblers selected Araneae, Coleoptera, Lepidoptera, and Hemiptera. In all cases, Araneae composed the preponderance of the Swainson's Warbler's diet.

There are several possible explanations why the Araneae occur commonly in the Swainson's Warbler's diet. First, they may offer some unique nutritional value. Schowalter et al. (1981) determined that the sodium content of predatory arthropods such as the Araneae is higher than that of other arthropods. Second, Swainson's Warbler may have evolved prey-selection behaviors and physical characteristics uniquely adapted to

TABLE 7. Logistic regression models used to predict the presence of Araneae at Woodbury Wildlife Management Area, South Carolina, 2008. The sign in parentheses indicates the direction of relationship.[a]

Model	n	K	ΔAIC_c	w_i	Concordance (%)	P-value
LLD[b](+), % grass[c](+), % wood[d](+), % other[e](–), % moist[f](+)	99	6	0	0.50	71	0.07
LLD(+), % grass(+), % wood(+), % other(–), % moist(+), % vine[g](–)	99	7	2.31	0.16	71	0.11
LLD(+), % grass(+), % wood(+), % other(–), % moist(+), % vine(–), % leaf[h](–)	99	8	3.30	0.10	72	0.14
LLD(+), % grass(+)	99	3	4.42	0.05	66	0.09
% moist(+)	99	2	4.30	0.06	54	0.40
% other(–), % moist(+)	99	3	5.19	0.04	58	0.40
LLD(+), % grass(+), % wood(+)	99	4	5.48	0.03	67	0.06
LLD(+), % grass(+), % wood(+), % other(–), % moist(+), % vine(–), % leaf(–), med[i](+)	99	9	5.71	0.03	72	0.20
% Wood(+), % other(–), % moist(+)	99	4	6.04	0.02	60	0.37
LLD(+), % grass(+), % wood(+), % other(–), % moist(+), % vine(–), % leaf(–), med(–), % Pol[j](–)	99	10	8.01	<0.01	71	0.26
Null (intercept only)	99	1	8.59	<0.01		

[a]Lowest AIC_c =128.41.
[b]Leaf-litter depth in mm from surface to earth.
[c]Percent other grass cover.
[d]Percent woody debris.
[e]Percent other herbaceous ground cover.
[f]Percent soil moisture measured with moisture meter.
[g]Percent vine ground cover.
[h]Percent leaf litter ground cover.
[i]Number of medium trees 23–38 cm dbh.
[j]Number of pole trees 2.5–8 cm dbh.

the size or movements of spiders. Swainson's Warblers may select spiders because they are easily seen because of their high activity. Third, Swainson's Warblers may select soft-bodied arthropods because they may require less energy to digest than hard-bodied arthropods (Major 1990).

Life stage of the arthropod seemed to affect prey selection. Swainson's Warblers selected the larval forms of several arthropod orders, possibly because the limited mobility of some arthropods in the pupal and larval stages makes them easier prey. Larval forms also tend to be less sclerotized (softer bodied) than adult forms. However, the main portion of the warbler's diet, the Araneae, was strongly selected for in both the adult and immature stages, and the birds also selected adult Coleoptera.

Although the order Araneae was present in crop samples in proportions greater than its availability, it still could be underrepresented in crop samples because spiders are digested so rapidly. Soft-bodied arthropods, such as larval Lepidoptera and Araneae, are digested more rapidly than hard-bodied arthropods like adult Coleoptera (Wheelwright 1986, Major 1990). We generally flushed the birds' crops immediately after capture, which presumably helped to reduce bias associated with differences in digestion rates of hard- and soft-bodied arthropods.

Swainson's Warblers might not consume all potentially available arthropods because an arthropod's life stage, size, location, and activity patterns could limit its availability to foraging birds (Cooper and Whitmore 1990). Several arthropod orders rare or not found in the birds' crops included Collembola, Acari, Thysanoptera, Mollusca, Isopoda, Orthoptera, and Psocoptera. Isopoda live primarily in damp, decaying leaf litter, in which Swainson's Warblers likely do not forage. Acari, although common in the leaf litter, were not selected by Swainson's Warblers, possibly because they are small hard-bodied arthropods that possess little nutritional value, the nutrition is difficult to extract, or because being small they are not seen. Also, arthropod orders apparently not selected could be missed because they consist of animals digested too quickly (Major 1990).

Arthropod size may influence Swainson's Warbler's prey selection. Intact arthropods in the crop samples typically were small. Smaller arthropods likely did not require processing and therefore remained intact, whereas larger prey items would be processed (i.e., fragmented) before consumption. Intact spiders were rare in crop samples, and we detected no intact adult spiders. Because we were unable to determine the size of consumed Araneae, the order Swainson's Warblers selected most, we cannot adequately address the effect of prey size on the warbler's prey selection. However, the higher proportion of larger (5–10 mm) arthropods in crop samples may suggest that the birds selected larger arthropod prey or that the orders they selected tended to be larger bodied.

Araneae occurred most commonly in areas with deeper leaf litter. Swainson's Warbler's nesting habitat usually is associated with a dense understory, but its foraging habitat typically has a closed canopy and open understory with little or no herbaceous ground cover (Eddleman et al. 1980), where leaf litter should be deep. Few studies have identified leaf-litter depth as an important determinant of Swainson's Warbler's habitat, although in Arkansas its presence is correlated with depth and percent ground cover of leaf litter (Bednarz et al. 2005, Brown et al. 2009). Arthropod diversity and abundance increases as leaf-litter depth increases (Uetz 1976). Because arthropod abundance increases with leaf-litter depth, it is likely that the availability of prey for both Swainson's Warbler and spiders also increases as litter depth increases. The best predictive models for 2007 and 2008 suggest that spiders were more frequent where grass cover was greater. Swainson's Warblers typically forage in areas of exposed leaf litter free of grass and other herbaceous cover (Eddleman et al. 1980). Although percent grass was positively correlated with spider presence, the average values for grass cover were relatively small (3.7%). Also, in 2008, percent cover of other herbaceous plants was negatively correlated with spider presence.

Although the arthropod community changed relatively little within the 2007 season, it changed more significantly from 2007 to 2008, especially for some orders such as Chilopoda. The variation within the season for Diplopoda and Orthoptera probably do not affect Swainson's Warbler because these orders constituted such a small proportion of the warbler's diet. The changes in leaf-litter arthropods from 2007 to 2008 could have been dictated by differences in flooding patterns. In the summer of 2007 (May–August), average discharge of water from the Big Pee Dee River was 584.5 m^3 sec^{-1}, whereas in 2008 (May–August) it was 677.7 m^3 sec^{-1} (U.S. Geological Survey 2007, 2008). In Illinois, Uetz (1976) reported flooding and differences in leaf-litter depth to explain 99.3% of variation in the abundance and diversity of spiders. Because upstream efforts to control flooding can alter downstream habitat conditions such as leaf-litter depth and arthropod diversity and abundance, such management should be monitored closely where Swainson's Warbler is a priority species.

Forest management such as timber harvest and prescribed burning can reduce leaf-litter depth, often for several decades (e.g., Crawford and Semlitsch 2008). Because leaf-litter depth is an important predictor of the presence of Araneae, a prominent prey of Swainson's Warbler, special considerations for maintaining leaf litter might be incorporated into forest management. For example, uncut buffer zones could be maintained adjacent to streams or alternative silvicultural practices such as group-selection timber harvest might be considered to maintain leaf litter in all or some portions of forest stands (Crawford and Semlitsch 2008).

Graves (2001) suggested that during times of prolonged flooding Swainson's Warblers will abandon inundated areas because of the loss of their critical foraging habitat. Flooding can scour, concentrate, disperse, and cover with silt much of the food-bearing leaf litter (Bell and Sipp 1975, Uetz et al. 1979). Furthermore, flooding may delay the start of the breeding season (Thompson 2005). Also, the timing, depth, and duration of flooding affect plant and arthropod species (Wharton et al. 1982). Arthropod diversity and abundance may be higher at higher elevations that do not experience long-term flooding (Uetz et al. 1979). Because the natural flooding regime of most rivers has changed with floodplain alteration, construction of levees, and dam construction (Askins 2000, Benson and Bednarz 2010), Swainson's Warbler likely would benefit from restoration of water levels consistent with a more natural flooding regime.

ACKNOWLEDGMENTS

Financial support for this project came from the South Carolina Department of Natural Resources, North Carolina Museum of Natural Sciences, and North Carolina State University. We thank International Paper and the South Carolina Department of Natural Resources for allowing access to the study site. We are grateful for all the field support provided by S. Green, S. Tollfree, B. Desjardins, L. Fuller, G. Savage, R. Savage, S. Jaquith, C. Shake, C. Matthews, K. Jensen, and E. Corliss. Statistical advice was provided by C. Arelleno. We extend a special thanks to R. Lancia for reviewing an earlier version of the manuscript.

LITERATURE CITED

Askins, R.A. 2000. Restoring North American birds: lessons from landscape ecology. Yale University Press, New Haven.

Barberena-Arias, M. F., and T. M. Aide. 2003. Species diversity and trophic composition of litter insects during plant secondary succession. Caribbean Journal of Science 39:161–169.

Bednarz, J. C., P. Stiller-Krehel, and B. Cannon. 2005. Distribution and habitat use of Swainson's Warblers in eastern and northern Arkansas. USDA Forest Service General Techincal Report PSW-GTR-191.

Bell, D. T., and S. K. Sipp. 1975. The litter stratum in the streamside forest ecosystem. Oakes 26:391–397.

Benson, T. J., and J. C. Bednarz. 2010. Short-term effects of flooding on understory habitat and presence of Swainson's Warblers. Wetlands 30:29–37.

Brown, J. D, T. J. Benson, and J. C Bednarz. 2009. Vegetation characteristics of Swainson's Warbler habitat at the White River National Wildlife Refuge, Arkansas. Society of Wetland Scientists 29:586–597.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer-Verlag, New York.

Cody, R. P., and J. K. Smith. 1997. Applied statistics and the SAS programming language, 4th edition. Prentice Hall, Upper Saddle River, NJ.

Cooper, R. J., and R. C. Whitmore. 1990. Arthropod sampling methods in ornithology. Studies in Avian Biology 13:29–37.

Crawford, J. A., and R. D. Semlitsch. 2008. Post-disturbance effects of even-aged timber harvest on stream salamanders in southern Appalachian forests. Animal Conservation 11:369–376.

Eaton, S. W. 1953. Wood-warblers wintering in Cuba. Wilson Bulletin 65:169–174.

Eddleman, W. R., K. E. Evans and W. H. Elder. 1980. Habitat characteristics and management of Swainson's Warbler in southern Illinois. Wildlife Society Bulletin 8:228–233.

Graves, G. R. 2002. Habitat characteristics in the core breeding range of the Swainson's Warbler. Wilson Bulletin 114:210–220.

Graves, G. R. 2001. Factors governing the distribution of Swainson's Warbler along a hydrological gradient in Great Dismal Swamp. Auk 118:650–664.

Graves, G. R. 1998. Stereotyped foraging behavior of the Swainson's Warbler. Journal of Field Ornithology 69:121–127.

Hunter, W. C., R. Katz, D. Pashley, and B. Ford. 1999. Partners in Flight bird conservation plan for the southern Blue Ridge. American Bird Conservancy, The Plains, VA.

Hunter, W. C., A. J. Mueller, and C. L. Hardy. 1994. Managing for Red-cockaded Woodpeckers and neotropical migrants: is there a conflict? Proceedings from the Annual Conference Southeast Association of Fish and Wildlife Agencies 48:383–394.

Hunter, W. C., D. N. Pashley, and R. E. F. Escano. 1993. Neotropical migratory landbird species and their habitats of special concern within the southeast region, p. 159–171. *In* M. Finch and P. W. Stangel [eds.], Status and management of neotropical migratory birds. U.S. Forest Service General Technical Report RM-229, Fort Collins, CO.

Jacobs, J. 1974. Quantitative measurement of food selection: modification of the forage ratio and Ivlev's electivity index. Oecologia 14:413–417.

Major, R. E. 1990. Stomach flushing of an insectivorous bird: an assessment of differential digestibility of prey and the risk to birds. Australian Wildlife Research 17:647–657.

Meanley, B. 1971. Natural history of the Swainson's Warbler. North American Fauna 69:1–90.

Meanley, B. 1966. Some observations on habitats of the Swainson's Warbler. Living Bird 5:151–165.

Morrison, M. L. 1982. The structure of western warbler assemblages: ecomorphological analysis of Black-throated Gray and Hermit warblers. Auk 99:503–513.

Moorman, C. E., L. T. Bowen, J. C. Kilgo, C. E. Sorenson, J. L. Hanula, S. Horn, and M. D. Ulyshen. 2007. Seasonal diets of insectivorous birds using canopy gaps in a bottomland forest. Journal of Field Ornithology 78:1–10.

Morton, E. S. 1992. What do we know about the future of migrant landbirds, p. 579–589. *In* M. Hagan and D. W. Johnson [eds.], Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, DC.

Peters, K. A., R. A. Lancia, and J. A. Gerwin. 2005. Swainson's Warbler habitat selection in a managed bottomland hardwood forest. Journal of Wildlife Management 69:409–417.

Ruth, J. M. [online]. 2004. Partners in Flight. Patuxent Wildlife Research Center, Laurel, MD. <http://www.partnersinflight.org> (27 March 2009).

SAS Institute. 2003. Version 9.1. SAS Institute, Cary, NC.

Schowalter, T. D., J. W. Webb, and D. A. Crossley, Jr. 1981. Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. Ecology 62:1010–1019.

Smith, C. R., D. M. Pence, and R. J. O'Conner. 1993. Status of neotropical migratory birds in the northeast: a preliminary assessment, p. 172–188. *In* D. M. Finch and P. W. Stangel [eds.], Status and management of neotropical migratory birds. U.S. Forest Service General Technical Report RM-229, Fort Collins, CO.

Strong, A. M. 2000. Divergent foraging strategies of two neotropical migrant warblers: implications for winter habitat use. Auk 117:381–392.

Thomas, B. G., E. P. Wiggers, and R. L. Clawson. 1996. Habitat selection and breeding status of Swainson's Warblers in southern Missouri. Journal of Wildlife Management 60:611–616.

Thompson, J. L. 2005. Breeding biology of Swainson's Warblers in a managed South Carolina bottomland forest. Ph.D. Dissertation, North Carolina State University, Raleigh, NC.

Uetz, G. W., K. L. Van Der Laan, G. F. Summers, P. A. K. Gibson, and L. L. Getz. 1979. The effects of flooding on floodplain arthropod distribution, abundance, and community structure. American Midland Naturalist 101:286–299.

Uetz, G. W. 1976. Gradient analysis of spider communities in a streamside forest. Oceologica 22:273–385.

U.S. Geological Survey [online]. 2007. Water-resources data for the United States, water year 2007: U.S. Geological Survey Water-Data Report WDR-US-2007. <http://pubs.water.usgs.gov/wdr2007> (3 October 2009).

U.S. Geological Survey [online]. 2008. Water-resources data for the United States, water year 2008: U.S. Geological Survey Water-Data Report WDR-US-2008. <http://pubs.water.usgs.gov/wdr2008> (3 October 2009).

Wharton, C. H., W. M. Kitchen, E. C. Pendleton, and T. W. Sipe. 1982. The ecology of bottomland hardwood swamps of the Southeast: a community profile. U.S. Fish and Wildlife Service, FWS/OBS- 81/37.

Wheelwright, N. T. 1986. The diet of American Robins: an analysis of U.S. Biological Survey records. Auk 103:710–725.