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STEREOTYPED FORAGING BEHAVIOR OF THE SWAINSON'S WARBLER

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Abstract.—I studied the foraging behavior of 399 individuals of Swainson's Warbler (*Limnothlypis swainsonii*) during the breeding season at more than 70 localities in the southeastern United States. Swainson's Warbler is a terrestrial dead-leaf specialist and "leaf-lifting" was the principal search/attack maneuver of all observed individuals. Pattering or vibration of feet is an important but previously unrecognized behavior associated with foraging in leaf litter. Observations indicate that leaf litter is a critical component of Swainson's Warbler habitat on breeding and winter territories and at migratory stopovers.

COMPORTAMIENTO ESTEREOTIPADO DE FORRAJEO EN *LIMNOTHLYPIS SWAINSONII*

Sinopsis.—Estudié el comportamiento de forrajeo de 399 individuos de *Limnothlypis swainsonii* durante la temporada reproductiva en mas de 70 localidades en el sudeste de los Estados Unidos de Norte America. Esta especies es especialista en hojarasca muerta en suelos y "levantando hojas" fué la maniobra principal de búsqueda/ataque de todos los individuos observados. Patear o vibración de patas es un comportamiento importante pero previamente desconocido asociado con el forrajeo en la hojarasca. Las observaciones indican que la hojarasca es un componente crítico del habitat de *Limnothlypis swainsonii* tanto en los territorios reproductivos e invernales como en las paradas migratorias.

The biology of the Swainson's Warbler (*Limnothlypis swainsonii*) has been of special interest since Brewster (1885), owing to the species' rarity, secretive demeanor, and the inhospitable character of its habitat (e.g., Meanley 1945, 1966, 1971). Despite the concern among conservationists about the habitat requirements and population status of this species (e.g., Terborgh 1989, Hunter et al. 1993, Thompson et al. 1993), little is known about its foraging ecology.

Meanley (1970) stressed the terrestrial nature of the Swainson's Warbler's foraging behavior. Barrow (1990) reported that the species in Louisiana (n = 17 observations) foraged primarily in the ground stratum (71%, <0.5 m) with less use of shrubs (29%, 0.5–2.0 m), yielding an average foraging height of 0.4 ± 0.5 m (Moser et al. 1990). This account and the anecdotes of aerial foraging in Brown and Dickson's (1994) review suggest that arboreal modes of foraging may be important components of its behavioral repertoire.

The purpose of this paper is to examine the generality of Meanley's (1970) observations and to report that Swainson's Warbler is a terrestrial dead-leaf specialist with a stereotyped foraging behavior. I also describe a "pattering" or foot-vibrating behavior that has not been previously reported in the Tribe Parulini (taxonomy of Sibley and Monroe 1990). Descriptions of habitat and nesting behavior for this poorly known species are found in Brewster (1885), Meanley (1945, 1966, 1971), Sims and

DeGarmo (1948), Eddleman et al. (1980), Graves (1992), Thomas (1994), and Brown and Dickson (1994).

METHODS

I observed the foraging behavior of Swainson's Warblers during the breeding season (25 April–26 June) at more than 70 localities in the southeastern United States (1986–1997), in conjunction with studies of habitat selection and breeding biology (Table 1; Graves 1992, unpubl.). Foraging observations were made on 202 field days during which my principal focus was Swainson's Warbler biology.

Observations reported here are of territorial adults, including 114 colored-banded males in the Great Dismal Swamp, southeastern Virginia. Foraging observations were made from 0700–1830 h. Lengthy observations were uncommon because of mosquitos and other factors that affect vision, such as deep shadows and dense understory vegetation. The sample reported here represents individuals (n = 399) observed for 30 s or more. Some individuals were observed for longer periods (>1 h) and 31 males were observed during two or more breeding seasons. Non-singing adults consorting with territorial males were assumed to be female. Sexual differences in foraging behavior were not observed, so all data are pooled.

Early in the study I recorded patterns of foraging behavior and substrate use (n = 25 individuals) with a micro-cassette recorder for later transcription, but this proved ineffectual. Foraging movements of Swainson's Warbler, particularly of its head, bill, and feet, were frequently too rapid to describe in real time even though motions were repetitive. Also, attacks directed at prey in leaf litter were often difficult to detect and quantify, and I was unable to document with certainty the capture or consumption of small prey items. As a consequence, I abandoned real-time narration of "leaf-lifting" foraging bouts for the remainder of the study and instead concentrated on categorizing the search and attack behaviors exhibited by each warbler.

RESULTS

Meanley's (1970:228) brief but excellent account constitutes the kernel of the published information on the foraging behavior of Swainson's Warbler:

> "Insects, the Swainson's principal food, are located as the bird pokes its bill under a leaf, pushing it upwards, searching the ground beneath it, or examining its underside. A leaf may be held up momentarily and tilted at an angle as the bird inspects the underside; and if a leaf is curled, it is opened as the bird inserts and spreads apart its mandibles. Sometimes, as the bird moves rapidly forward, lifting or shoving leaves upward, most of its body disappears beneath a pile of leaves."

My observations confirm those of Meanley and indicate that Swainson's Warbler is a terrestrial dead-leaf specialist with a remarkably limited repertoire of foraging behaviors. The "leaf-lifting" technique was the pri-

TABLE 1. Foraging maneuvers of the Swainson's Warbler (n = 399[a]).

State	County or parish	Terrestrial leaf-lift (n[b])	Flush-pursue (n[b])
Alabama	Covington	1	0
	Escambia	19	0
Arkansas	Arkansas	11	0
	Grant	4	0
	Lee	4	0
	Monroe	1	0
	Phillips	9	0
	Poinsett	2	0
Florida	Gulf	1	0
	Jefferson	1	0
	Leon	1	0
	Liberty	24	0
Georgia	Appling	1	0
	Bibb	13	0
	Houston	2	0
	Jeff Davis	2	0
	Montgomery	1	0
	Tattnell	3	0
	Telfair	2	0
	Toombs	1	0
	Twiggs	2	1
Louisiana	Madison	6	0
	Pointe Coupee	4	0
	St. Martin	63	1
	St. Tammany	11	0
	West Feliciana	1	0
Mississippi	Adams	6	0
	Amite	1	0
	Franklin	3	0
	George	2	0
	Hancock	2	0
	Sharkey	18	0
	Wilkinson	18	0
North Carolina	Camden	1	0
	Clay	1	0
	Jones	2	0
South Carolina	Berkeley	8	0
	Georgetown	2	0
	Oconee	1	0
Virginia	Dickensen	1	0
	Suffolk	140	0
West Virginia	Nicholas	2	0
	Webster	1	0

[a] Undisturbed individuals observed foraging for 30 s or more.
[b] Number of individuals performing foraging maneuver.

mary search/attack maneuver of each of the 399 individuals observed in this study (Table 1). In fact, 99% of those performed only leaf-lifting maneuvers and subsidiary gleaning, probing, and gaping motions directed toward insect prey. The leaf-lifting behavior is so universal and preeminent that long series of seemingly identical "lift-look-drop" motions, punctuated by prey capture, should not be considered as strings of independent events. Rather, leaf-lifting seems the most noticeable component of a fixed or obligate foraging syndrome peculiar to this species.

Undisturbed warblers searching leaf litter may meander 40 m or more across the forest floor before taking flight. Although the density of small stems is high in optimal habitat (e.g., 0–50,000 cane stems/ha and 13,500–54,300 woody stems [diameter <5 cm]/ha in Great Dismal Swamp; Graves, unpubl.), warblers preferred to forage in litter beneath vine "tents" and in small, well-shaded glades (1–40 m^2) nearly devoid of cane or shrub stems. During periods of high water they frequently foraged at drifts of flotsam deposited along exposed ridges in flood plain forest. Warblers occasionally searched leaf litter on semi-exposed or buttressed roots of trees and rarely foraged atop fallen logs, which are usually sparse in successional bottomland forest. In one case, a warbler ascended (<1 m) the base of a wind-thrown tree (<45°) to reach fallen leaves. Foraging maneuvers at dead leaves on wood substrates appeared to be identical to those performed over soil, and were pooled in Table 1. The Swainson's Warbler is adept at foraging in litter composed of a variety of leaf sizes, shapes, and degree of curling. Soils underlying leaf litter were moist or wet, and the feet and bill of mist-netted birds were often smeared with mud.

On one remarkable occasion, a territorial male disturbed by playback landed on the leaning trunk (15°, diameter = 13 cm) of a dead box elder (*Acer negundo*). After moving up the trunk (height = 1.3 m), which was partially devoid of bark, the male approached a clasping slab of bark (10 × 20 cm). The male inserted its bill under the edge and "dead lifted" the slab with a noticeable flexure of the hind limbs, peered underneath, and then lowered it.

Insects were also opportunistically *gleaned* (italicized foraging nomenclature from Remsen and Robinson 1990) from exposed surfaces of leaf litter, but gleaning maneuvers appeared to be incidental and of secondary importance to leaf-lifting. Warblers disturbed by humans or tape playback perched in trees and shrubs and occasionally gleaned insects from adjacent leaf and bark surfaces. However, once these disturbing stimuli ceased, warblers returned within seconds to minutes to the leaf litter. Based on my studies, I believe that reports of arboreal gleaning (e.g., Barrow 1990, Brown and Dickson 1994) may be based upon observations of disturbed or agitated birds.

Pattering or vibration of the feet is an important but unrecognized behavior of Swainson's Warbler associated with foraging in leaf litter. Meanley (1970:228) noted, "During 40 hours of observations of the ground locomotion of this species, I prefer to describe it as hopping some

of the time, though mostly it moves in a rather rapid step that is sort of a cross between a walk and a hop, suggesting a canter." As suggested by Meanley's description, the warbler's ambulatory movements are difficult to describe. Upon inspection, however, the erratic gait appears to result from a delicate, intermittent, rapid pattering, which I believe functions to flush insects from the leaf litter. Pattering was observed most frequently when these warblers foraged in relatively loose and unconsolidated litter. In one instance I observed a male attacking a prey item hidden in a large curled leaf. The warbler *probed* unsuccessfully in one end of the curled leaf and then circled to the other end while pattering the leaf litter with both feet. It finally extracted a smooth-skinned, gray caterpillar (ca. 40 mm), flew to a horizontal perch where it dismembered and consumed the prey, wiped its bill several times on the perch, and then returned to the ground. As noted by Meanley, *gaping* is employed to "uncurl" dead leaves, although this motion is very difficult to see under field conditions. Both *probing* and *gaping* were used only at curled dead leaves. I observed furtive and sporadic gleaning, probing, or gaping motions during all prolonged observations (>5 min) of warblers foraging in leaf litter. Swainson's Warblers were twice observed to *flush-pursue* moths flushed from the leaf litter. Otherwise, aerial attack maneuvers were not observed in undisturbed birds.

DISCUSSION

Pattering or foot vibrating has been reported only a few times for passerine birds (Hobbs 1954, Brackbill 1960, Porter and Davis 1974, Yong and Moore 1990, Davis 1996). This movement in Swainson's Warbler is performed intermittently and perhaps too rapidly to be described adequately without the aid of high-speed photography or videography.

The foraging behavior of Swainson's Warbler in terrestrial dead-leaf litter appears to be unique among the Parulini. Leaf-lifting, which is not listed by Remsen and Robinson (1990), is used exclusively throughout the annual cycle. Foraging behavior on the wintering grounds in Jamaica and during migration stopovers in Gulf coast cheniers appears to be remarkably similar to that observed during the breeding season (Graves 1996, unpubl.). As such, Swainson's Warbler has a most specialized foraging behavior—on par with those of Neotropical suboscines that forage exclusively at suspended dead leaves (e.g., Gradwohl and Greenberg 1982, Remsen and Parker 1984, Rosenberg 1990). These observations strongly indicate that leaf litter is a critical element in determining the local distribution of Swainson's Warbler. Indeed, the presence of extensive carpets of leaf litter overlying moist soil is a common denominator of every documented breeding locality (Graves, unpubl.).

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