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Foraging Behavior of Swainson's Thrushes (*Catharus ustulatus*) During Spring Migration Through Arkansas

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Running Title: Spring Foraging Behavior of Swainson's Thrushes in Arkansas

Abstract

Foraging behavior of Swainson's Thrushes on spring migration was studied in western Arkansas in the spring of 2013 and 2014. Observations were made in two forested field sites, one of them urban and the other suburban. The former had a significantly higher woody stem area (cm^2) than the latter. For each foraging observation, the following three parameters were noted: Foraging Stratum (Ground, Shrub, Sapling, Sub canopy, and Canopy); Foraging Substrate (Ground/Litter, Herb, Foliage, Bark, and Air); and Foraging Maneuver (Glean, Probe, Dive/Glean, Hover, Jump Hover, and Hawking). We tested the hypotheses that these foraging variables differed significantly between the urban and suburban sites, and between the two years. These hypotheses were rejected for all three parameters. The consolidated data from both the sites and years revealed that a significantly higher proportion (67%) of the observations were on the Ground stratum, compared to the Shrub (13.7%) and Sapling strata (13%). Similarly, a significantly higher proportion (66%) of the foraging substrate used was Ground/Litter, followed by Foliage (16.7%) and Bark (15.8%). Gleaning was the most common foraging maneuver used (71.5%), and was significantly higher than Probing (12.3%) and Dive Gleaning (8.4%).

Introduction

Stopover areas are important links in the annual cycle of migrants since a migrant's survival and ultimate reproductive success hinges on suitability of habitat in these areas (Moore et al. 1990). The energetic costs of stopover for thrushes in north-bound spring migration in the United States have been shown to be higher than their flight costs due to cold weather and efforts involved in foraging (Wikelski et al. 2003). Habitat structure in stopover areas may influence foraging strategies adopted by the migrants, which in turn may affect the rate at which they replenish their energy reserves. Urban parks and suburban woodlots serve as "convenience store" stopover sites, supporting migrants between short flights to higher-quality sites (Mehlman et al. 2005).

The Swainson's Thrush (*Catharus ustulatus*) breeds in the northern part of North America and migrates south in winter to Central and South America (Mack and Yong 2000). It is a common spring transient in Arkansas, observed in a variety of habitats, including yards in towns (James and Neal 1986). Although a common bird in much of North America, it has suffered widespread population declines (Mack and Yong 2000). Two factors may explain these declines: loss or fragmentation of breeding habitat (Wilcove 1988, Holmes and Sherry 1988), and also the possible anthropogenic landscape changes in its winter range in Central and South America (Robbins et al. 1989). Although several aspects of this species have been well-studied in its breeding grounds in North America (see review in Mack and Yong 2000), very little is known of its biology or habitat use while on migration. A thorough knowledge of the bird's ecology from its breeding, wintering, and migration range is needed to formulate sound management decisions pertaining to its conservation.

We studied the foraging behavior of Swainson's Thrushes during spring migration across western Arkansas in May 2013 and 2014. Our study had two objectives: 1) To quantify the foraging behavior of Swainson's Thrushes during their spring migration through Arkansas, and 2) to evaluate whether these foraging behaviors differ significantly between years and between sites with different vegetational structure.

Study Area and Methods

Foraging behavior was studied by modification of methods adopted by Holmes and Robinson (1988). Two forested sites were chosen for the study, an urban

(Ruth Armstrong Nature Area) and a suburban (Fianna Hills) woodlot, both in Fort Smith (Sebastian Co.), Arkansas. The former is managed by underbrush and fallen wood removal, and is a 2.6-ha track of woodland in the middle of Fort Smith, at the junction of two busy roads (Rogers Avenue and Old Greenwood Road). The latter is a less busy strip of forested hillside in the south part of the city, abutting Glen Flora Way, approximately 1 km long and 50 m wide.

Foraging tactics of Swainson's Thrushes were observed between May 1 and 15 of 2013 and 2014, coinciding with their spring migration through Arkansas (James and Neal 1986). Observations were made early mornings (0700-0900 hrs) and late afternoons till twilight (1600-2030 hrs). For each foraging activity (defined as a bird observed to capture prey), three variables were noted: Foraging Stratum (Ground - 0m; Shrub - 0.1-2m; Sapling - 2.1-8m; Sub canopy 8.1-14m; and Canopy - >14m), Foraging Substrate (Ground/Litter, Herb, Foliage, Bark, Air), and Foraging Maneuver (Glean, Probe, Hover, Dive/Glean, Jump-hover, Hawk). We defined each maneuver as follows, after Holmes and Robinson (1988): "Glean" was defined as a standing or walking bird picking up food; "Probe", when the bird creates a disturbance in the substrate to get its food; "Hover", when the bird momentarily flutters in the air to get food from vegetation or bark; "Dive/Glean", when the bird swoops down from an elevated perch and picks up food from the ground; "Jump-hover", when the bird on ground jumps and picks up food, usually from underside of a leaf; and "Hawk", when the bird flies and catches an insect in mid-air. Each bird was followed for a maximum of 5 observations (as opposed to Holmes and Robinson's [1988] method of following birds as long as possible) to minimize the dependency bias associated with sequential observations (Morrison 1984). Data were not normally distributed and hence analyzed by nonparametric Kruskal-Wallis (Siegel and Castellan 1988) and Wilcoxon-Mann-Whitney (Mann and Whitney 1947) tests. We tested for any significant difference between sites for the same year, and between years for the same site.

Habitat structure of the urban and suburban site was quantified in May 2014 using the protocol described by James and Shugart (1970). We measured 4 habitat variables within circular 0.04 ha plots (11m radius) in both sites. The centers of the plots were chosen at random along a trail. Five plots were sampled in the smaller urban site and 10 plots in the suburban site. The variables measured were woody stem area (cm^2), shrub understory density (/44 m^2), ground cover (%), and canopy cover (%). Woody stem area was measured by recording the diameter at breast height (DBH) of all stems >7.5 cm DBH within the plot by using a DBH tape. Shrub density was determined by counting the number of stems at breast height (1.2 m) along two 1-m wide orthogonal transects through the center of the plot, the direction of the transects chosen by the random twist of a compass dial; ground and canopy cover was quantified by taking 40 presence or absence readings of green vegetation in the two aforementioned transects sighted through an ocular tube at random points in each plot. Differences between urban and suburban plots were tested for significance using Wilcoxon-Mann-Whitney test (Mann and Whitney 1947).

Results

Vegetation structure.

The woody stem area (cm^2) was significantly higher (P = .0006) in the urban plot that in the suburban plot (Table 1). However, canopy cover, ground cover, and stem density were not significantly different between the sites (P > 0.08).

Foraging behavior.

We collected 226 foraging sequences of 1 to 5 observations as follows: 66 (29.2%) of the sequences yielded only one observation, 49 (21.7%) yielded 2, 31 (13.7%) yielded 3, 16 (7%) yielded 4, and 64 (28.3%) yielded the self-imposed maximum limit of 5 observations. The three foraging variables were not significantly different between the two years, and between the two sites (P > 0.6; Kruskal-Wallis Test; Figs.1-3).

Table 1. Analysis of 4 vegetational characteristics in the urban and suburban study sites. Underlined value represents significant difference between the two sites.

Vegetational characteristic	Urban plot (mean \pm SE)	Suburban plot (mean \pm SE)	P^*
Woody stem area (cm ²)	$263,822 \pm 27,120$	$77,634 \pm 14,839$	0.0006
Stem density $(/44m^2)$	13.4 ± 5.9	24.4 ± 7.4	0.337
Canopy cover (%)	88 ± 3.6	78.5 ± 3.1	0.089
Ground cover (%)	49 ± 6.5	37.7 ± 6.5	0.127

*Wilcoxon-Mann-Whitney test

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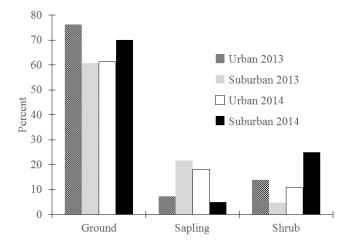


Fig. 1. Swainson's Thrush use (%) of main forest strata for foraging in 2013 and 2014 in the urban and suburban sites. Other strata were rarely used (see Table 2) and not included here.

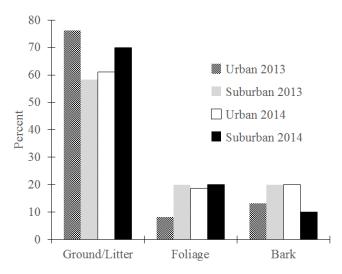


Fig. 2. Swainson's Thrush use (%) of three most common substrates for foraging in 2013 and 2014 in the urban and suburban sites. Other substrates were rarely used (see Table 3) and not included here.

Because the differences were not significant, we combined the data from both the years and from both the sites (Tables 2-4, n = 637 observations). Since the first observation in any foraging sequence tends to be biased toward conspicuous maneuvers like flying (Holmes and Robinson 1988), we tested for any significant difference between the 1st and the subsequent (2nd through 5th) observations (Tables 2-4) for all three foraging variables. The differences were not significant (P > 0.83, Wilcoxon-Mann-Whitney test, W = 12, 14, and 18 for stratum, substrate and maneuver, respectively). Hence, we combined the 1st observation data (n = 226) with the subsequent observations (n = 411) for all the analyses and

interpretations (based therefore on a total of 637 observations; Tables 2-4).

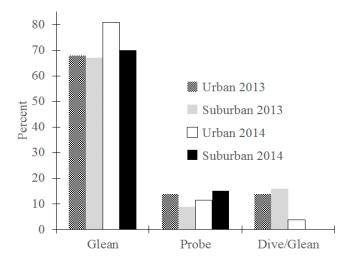


Fig. 3. Three most common foraging maneuvers used (%) by Swainson's Thrush in 2013 and 2014 in the urban and suburban sites. Other maneuvers were rarely used (see Table 4) and not included here.

A significantly higher proportion (67%) of the pooled observations were on the Ground stratum, compared to the Shrub (13.7%) and Sapling (13%) strata (n = 637 observations, Table 2). Similarly, a significantly higher proportion (66%) of the foraging substrate used was Ground/Litter, followed by Foliage (16.7%) and Bark (15.8%) (n = 637 observations, Table 3). Gleaning was the most common foraging maneuver used (71.5%), and was significantly higher than Probing (12.3%) and Dive Gleaning (8.4%) (n = 637 observations, Table 4).

Discussion

The Swainson's Thrush has generally been considered a "ground" (Holmes et al. 1979) or "nearground" (Mack and Yong 2000) forager, and this is supported by our data, with 67% of observations on the ground. However, it is noteworthy that more than a quarter (26.7%) of our observations were 0.1-8m above ground, with some (6.2%) observations extending even higher, into the sub canopy and canopy. We occasionally found the birds in mixed hunting parties far above the ground, hopping along boughs to pick prey off bark, or hopping along horizontally and then flying to vertical boles to glean prey off bark or adjoining foliage. Ten per cent of all prey attacks were in the forest canopy in Holmes and Robinson's (1988) study (hereafter referred as Hubbard Brook study or

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Stratum	1^{st} (n = 226 observations)	Subsequent $(n = 411 \text{ observations})$	All ($n = 637$ observations)
Ground	57.5	68.6	67
Sapling	22.6	12.2	13
Shrub	11.1	11.2	13.7
Sub canopy	6.2	4.6	4.4
Canopy	2.7	3.4	1.8

Table 2. Vertical distribution (% prey attacks in each stratum) of Swainson's Thrush foraging: data shown as 1st, subsequent (2nd through 5th), and ALL (combined) prey attacks on observed foraging sequences.

Table 3. Foraging substrate (% prey attacks in each substrate) used by the Swainson's Thrush: data shown as 1^{st} , subsequent (2^{nd} through 5^{th}), and ALL (combined) prey attacks on observed foraging sequences.

Substrate	1^{st} (n = 226 observations)	Subsequent ($n = 411$	All $(n = 637 \text{ observations})$
		observations)	
Ground/litter	57.5	67.6	66
Foliage	18.1	16.3	16.7
Bark	23.5	15.1	15.8
Herb	0	0.5	0.3
Air	0.9	0.5	0.8

Table 4. Prey-attack maneuver (% prey attacks by maneuver type) of the Swainson's Thrush: data shown as 1^{st} , subsequent (2^{nd} through 5^{th}), and ALL (combined) prey attacks on observed foraging sequences.

Maneuver	1^{st} (n = 226 observations)	Subsequent ($n = 411$	All $(n = 637 \text{ observations})$
		observations)	
Glean	74.8	75.2	71.5
Dive/Glean	12.4	15.1	8.4
Probe	5.3	5.4	12.3
Hover	4.4	2.9	4.7
Jump-Hover	2.2	1.0	2.3
Ĥawk	0.9	0.5	0.8

site), a much higher proportion than ours (1.8%) ostensibly because of the more vertical complexity of vegetation in that more mature New Hampshire site. This species is more arboreal than other *Catharus* thrushes (Mack and Yong 2000), and our data compared with other studies suggest that the bird increases its arboreal activity in forests with more vertical heterogeneity (foliage height diversity). The fact that the birds in the Hubbard Brook study foraged on the ground less (<50%) and attacked prey more often on tree foliage than our study (32 vs. 16.7%, respectively) may also be a reflection of more foraging opportunities available in the higher strata of more complex vertical environments.

The frequency of gleaning was strikingly different between our results (71.5%) and from that of the Hubbard Brook study (25%). This could be because both our sites had straight trails that gave us unimpeded views across a wide area, allowing us to see ground-foraging Swainson's Thrushes even far away. That may not have been the case in the more mature Hubbard Brook site. The preponderance of foliage cover in the Hubbard Brook site may also account for the high proportion of hovering (37.9%) in that study compared to ours (4.7%).

Holmes and Robinson (1988) argued that longer sequence data are necessary to record rare foraging maneuvers like jump-hover or hawking. However, longer sequences are likely to skew results with unusually common observations and pseudoreplication. There were occasions when we could have obtained dozens (if not more) of observations from small flocks of Swainson's Thrushes gorging on ripe Mulberry (*Morus* spp.) fruits from one particular tree in the suburban site for both years. This would have skewed the results to reflect an unusually high proportion of foliage gleaning (albeit of fruits and not insects) at strata higher than the shrub level. Besides, as indicated earlier, longer sequence data in general can be biased because the observations tend to be dependent on one another (Morrison 1984). Nevertheless, it is possible that behaviors recorded very rarely in our study, like hawking (0.8%) and hovering (4.7%) were less frequent than in the Hubbard Brook study (4.5% and 37.9%, respectively) partly because we did not follow the birds for more than 5 observations. The much more complex and mature nature of the Hubbard Brook site may also be responsible for the discrepancy, as discussed earlier.

Although four observers (RK, SW, and two field assistants) carried out the observations, RK did 72% of the observations in 2013, and SW did 86% in 2014. Since there was no significant difference between the years, we can state with confidence that any bias due to inter-observer variability was minimal.

Yong and Moore (1990) reported "foot-quivering" as a foraging maneuver in *Catharus* thrushes including Swainson's during migratory stopover in Louisiana, and suggested that it functions in flushing prey. We did not observe this behavior, nor was it observed in the Hubbard Brook study. It is possible that this behavior is exhibited only after a long migratory flight (like trans-Gulf) when energy reserves are severely depleted, and when any extra energy obtained by such behaviors is invaluable and may make a difference in survival.

Mack and Yong (2000) reported that the Swainson's Thrush inhabits a wider variety of habitats in migration than during the breeding season. We have seen the birds foraging in shrub-free grassy meadows with a scattering of mature planted oak *Quercus spp*. and other trees at the University of Arkansas - Fort Smith campus and in Tillis Park in the city. James and Neal (1986) observed the birds foraging in lawns, cemeteries, and urban woodlots in Arkansas. wide habitat use during spring migration seems in contrast to the relatively more restricted usage in their breeding (mainly coniferous forests) and wintering (mainly primary rain- or semideciduous forest) grounds (Unitt 1984, Ramos and Warner 1980, Howell and Webb 1995). It also suggests that dense undergrowth may be an important but not a "main determinant" (Mack and Yong 2000) of habitat during migration.

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