USING WOOD WARBLER FORAGING BEHAVIOR TO UNDERSTAND AVIAN RESPONSES TO FOREST MANAGEMENT

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ABSTRACT.—Although uneven-aged forest management often retains large numbers of canopy trees that can benefit mature forest birds, understory vegetation also may be removed. In a concurrent study, mature stands subjected to understory removal and canopy thinning had few forest understory birds relative to mature stands (Rodewald and Smith 1997). We hypothesized that this difference was related to foraging habitat requirements. We studied foraging behaviors of Black-and-white, Worm-eating, and Hooded Warblers in mature oak-hickory forests of northwest Arkansas during May-July 1993-94. Worm-eating and Hooded warblers were strongly associated with forest understory, with foraging heights averaging < 5 m and trees used for foraging averaging < 8 m. Black-and-white Warblers foraged at greater heights (mean = 8.5 m), and in taller trees (mean = 15.1 m), and this may explain their lower sensitivity to understory management. Foraging Worm-eating Warblers used aerial leaf litter and live foliage substrates (especially flowering dogwood) in equal amounts (39 percent), and Hooded Warblers used live foliage substrates heavily (88 percent); both substrates were heavily reduced by management. Black-and-white Warblers primarily used bark substrates (84 percent), which were less affected by management. Results suggest that foraging ecology of Worm-eating and Hooded Warblers may be incompatible with management practices that involve understory removal. Alternative practices that remove less understory vegetation could lessen negative effects on understory birds in hardwood forests.

With rising concern for conservation of forest birds over the last 25 years, forest management has become increasingly complicated as managers struggle to conduct silvicultural activities while minimizing negative impacts on mature forest birds and other wildlife. Uneven-aged management is a silvicultural approach suggested to strike a balance between these potentially conflicting goals. Certainly, retention of large numbers of overstory trees within stands will promote use by many forest bird species. However, avian ecologists have some concerns about uneven-aged management if widely used to replace more traditional even-aged methods. Use of uneven-aged management in oak-hickory forest presents a great challenge, as oak does not regenerate well in dense shady stands. Consequently, in 1992, the Southern Research Station, U.S. Forest Service, initiated research that examined effects of uneven-aged management on growth and regeneration of oak-hickory stands in the Ozark-St. Francis National Forest (Graney and Murphy 1993). Management practices used in that study included a heavy cutting of understory vegetation, either alone or in combination with both thinning and group-selection cutting of overstory trees. After treatment, forest stands had an open park-like understory with scattered small gaps in the canopy. An unintended result of these forest management practices was avoidance of treated stands by common understory nesting birds, including Worm-eating (*Helmitheros vermivorus*) and Hooded (*Wilsonia citrina*) warblers, Ovenbird (*Seiurus aurocapillus*), and Acadian Flycatcher (*Empidonax virescens*), but not for Black-and-white Warblers (*Mniotilta varia*) (Rodewald and Smith 1997). Because these species are known to frequently forage in the forest understory, foraging habits were suspected to have played a role in reduced abundances within treated stands.

We quantified foraging behavior of Worm-eating, Black-and-white, and Hooded warblers during the breeding season in mature oak-hickory forests of the Arkansas Ozarks. We discuss foraging behavior and habitat use in relation to uneven-aged forest management practices used in the Arkansas Ozarks. This information is useful in identifying habitat characteristics of importance to these species and to successfully design uneven-aged management practices that lessen their effects on forest understory birds.

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Study Area

Study sites were located in Ozark-St. Francis National Forest, Pope and Newton counties, northwest Arkansas. Forests in that area are oak-hickory with little pine and elevations ranged from 400-620 m. Common tree species included: white oak (*Quercus alba*), northern red oak (*Q. rubra*), black oak (*Q. velutina*), red maple (*Acer rubrum*), sugar maple (*A. saccharum*), black gum (*Nyssa sylvatica*), mockernut hickory (*Carya tomentosa*), black hickory (*C. texana*), black cherry (*Prunus serotina*), and flowering dogwood (*Cornus florida*).

Methods

From May-July 1993-94 we collected foraging data in mature, mesic secondary forests that were 80-100 years old and occurred on north- and east-facing slopes. Approximately 70 percent of foraging data were collected within 250 m of vegetation sampling plots (see below); the remaining 30 percent were more widely collected, but still within 10 km of study sites. Data were collected throughout the day, but mostly between 0700-1200 hours. After locating a foraging warbler, we waited at least ten seconds before recording data on the first foraging maneuver observed. We collected observations on as many individual birds as possible to minimize potential influence of individual differences in behavior. We alternated sites of data collection on a daily basis to try to avoid collecting data from the same individual on different days within a given year. Up to three observations were recorded from some individuals, but for most individuals, only a single observation was recorded. To increase statistical independence of observations, multiple observations from an individual bird were included in analyses only after at least two foraging maneuvers had occurred since the previous observation.

We collected data on type of foraging maneuver, foraging substrate, foraging height, tree height, and tree species in which maneuver took place. Foraging maneuvers were recorded as either gleans (near-perch attacks directed towards prey on a substrate) or sallies (wing-powered attacks used to capture aerial prey). We defined foraging substrates as the substrate towards which a foraging maneuver was directed and these included bark surface, foliage, foliage curls (leaf shelters of leaf-rolling caterpillars), aerial leaf litter (dead leaves suspended in vegetation), air, spider webs, and ground leaf litter. Foraging height and tree height were visually estimated.

In June-July 1993, woody vegetation was characterized at 12 point-count locations in mature secondary forest on north- and east-facing slopes (Rodewald and Smith 1997) using a modified James and Shugart (1970) approach. Four vegetation plots were completed at each point: one at the point-count center, and three located 35 m from the center in directions of 120°, 240°, and 360°. All shrubs and saplings (0-8 cm in diameter at 10 cm above the ground) were counted by species within a 5 m radius. Trees greater than 8 cm DBH were counted by species within an 11.3 m radius.

Chi-square tests were used to compare frequencies of substrate use, tree species use, and foraging maneuvers across bird species. To minimize numbers of cells with low values in contingency tables, only the six most commonly used tree taxa were included, black gum, dogwood, elms (*Ulmus* spp.), hickories, oaks, and maples. Likewise, rarely-used substrates (e.g. spider web) were not included in contingency tables. Chi-square was also used to test whether birds foraged in tree species in proportions different than the relative availability of tree species. This test used the same tree taxa mentioned above, but to minimize numbers of cells with low values, did not include elms. Low sample sizes for Hooded Warbler prevented an analysis of selectivity. Foraging height and tree height data were not normally distributed, so comparisons among species were made using Kruskal-Wallis test (SAS Institute 1990).

Results

Sample sizes for foraging observations were: Hooded Warbler 51, Black-and-white Warbler 89, and Worm-eating Warbler 274. The three warbler species differed in their foraging behavior in several respects. Warblers differed in use of the six most frequently used tree taxa ($\underline{X}^2 = 69.3$, df = 10, $\underline{P} < 0.001$; Fig. 1). Worm-eating Warblers foraged most often in dogwood (40.7 percent of observations),

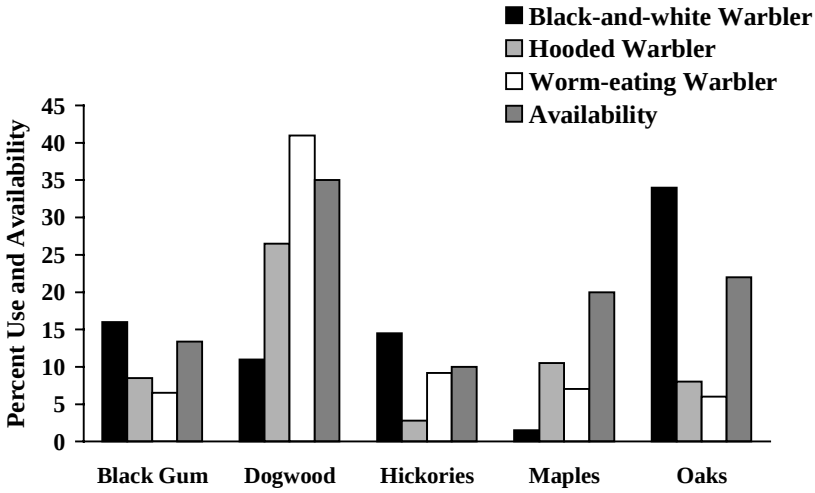

Figure 1.—Percent use of tree taxa by three wood warbler species in relation to percent availability in the Arkansas Ozarks, May-July 1993-94.

whereas other trees were used in much lower frequencies (hickories 9.7 percent, black gum 6.6 percent, and oaks 6.2 percent). Hooded Warblers also foraged in dogwood most frequently (26.1 percent), and used other plant taxa less frequently (black gum 8.7 percent and oaks 8.7 percent). Alternately, Black-and-white Warblers were most frequently observed foraging in oaks (34.2 percent), and less frequently in black gum, hickory, and dogwood (15.9 percent, 14.6 percent, and 11.0 percent, respectively). Hooded, Black-and-white, and Worm-eating warblers were observed foraging in 39 different species of trees and shrubs (19, 17, and 30 species, respectively).

Both Worm-eating and Black-and-white warblers utilized tree taxa in proportions different from relative availabilities (Fig. 1). Worm-eating Warblers used black gum (X^2 = 9.3, df = 1, P = 0.002), oaks (X^2 = 34.2, df = 1, P < 0.001), and maples (X^2 = 25.7, df = 1, P < 0.001) less frequently than relative availabilities, whereas hickories (X^2 = 0.1, df = 1, P = 0.738) were used in proportions similar to availability. For Worm-eating Warblers there was a trend towards greater use of dogwood relative to availability, but the difference was not significant (X^2 = 3.3, df = 1, P = 0.068). Black-and-white Warblers used oaks (X^2 = 7.4, df = 1, P = 0.006) more frequently than availability, whereas maples (X^2 = 17.8, df = 1, P < 0.001) and dogwood (X^2 = 20.3, df = 1, P < 0.001) were used less frequently. Black-and-white Warblers used black gum (X^2 = 0.5, df = 1, P = 0.492) and hickories (X^2 = 1.5, df = 1, P = 0.214) in proportions similar to availability.

Mean foraging heights were 8.5 m (± 4.9 SE) for Black-and-white, 4.6 m (± 3.9 SE) for Hooded, and 4.2 m (± 3.8 SE) for Worm-eating warblers. Black-and-white Warblers foraged at greater heights than either Hooded (Kruskal-Wallis X^2 = 22.4, df = 1, P < 0.001) or Worm-eating warblers (Kruskal-Wallis X^2 = 57.3, df = 1, P < 0.001). Hooded and Worm-eating warblers foraged at similar heights (Kruskal-Wallis X^2 = 0.7, df = 1, P = 0.415).

Mean tree heights used by foraging warblers were: 15.1 m (± 7.4 SE) for Black-and-white, 7.7 m (± 6.7 SE) for Hooded, and 7.1 m (± 6.0 SE) for Worm-eating warblers. Black-and-white Warblers foraged in taller trees than either Hooded (Kruskal-Wallis X^2 = 30.6, df = 1, P < 0.001) or Worm-eating warblers (Kruskal-Wallis X^2 = 71.6, df = 1, P < 0.001). Hooded and Worm-eating warblers foraged in trees of similar heights (Kruskal-Wallis X^2 = 0.2, df = 1, P = 0.731).

The three warbler species directed prey attacks toward different substrates (X^2 = 245.5, df = 6, P < 0.001). Substrates commonly used by Worm-eating Warblers included foliage (39 percent), aerial leaf

Table 1.—Mean (± SE) foraging height and tree height of three wood warbler species in Oak-hickory forests of the Arkansas Ozarks, May-July 1993-94.

Warbler species	Black-and-white Warbler	Hooded Warbler	Worm-eating Warbler
Foraging height a	8.5 (4.9) A	4.6 (3.9) B	4.2 (3.8) B
Tree height	15.1 (7.4) A	7.7 (6.7) B	7.1 (6.0) B

[a]Habitat means within a row that do not share a letter were significantly different (Kruskall-Wallis test; ± = 0.05).

litter (39 percent), and foliage curls (13 percent). Foraging maneuvers made by Worm-eating Warblers were 84 percent gleans, with nearly half of these being probes of aerial leaf litter and foliage curls; sallies accounted for 16 percent of maneuvers. Black-and-white Warblers primarily used bark (tree trunks, limbs, and twigs; 84 percent), and foliage (13 percent) substrates, and gleaned prey from these substrates for 74 percent of observations; sallies (18 percent) typically involved a downward chase of falling prey. Hooded Warblers used foliage substrates (88 percent) heavily while foraging, and frequently employed sally maneuvers to obtain prey from the underside of leaves; gleans were used less often (26 percent).

Discussion

Our results demonstrate heavy use of mature forest understory habitat by Worm-eating and Hooded warblers, and indirectly suggest that this habitat is a required component of their foraging ecology. In nearby areas, forest understory removal, whether or not it was done in combination with overstory cutting, was associated with low abundance of several forest understory bird species (Rodewald and Smith 1997). We believe that removal of understory vegetation likely precluded foraging of these and other understory species on managed plots. Included in the understory layer were many different species of trees and shrubs from which these birds would normally obtain their prey. Bird species may alter their foraging behavior in response to changes in vegetation structure associated with forest cutting (Szaro and Balda 1979, Maurer and Whitmore 1981, Franzreb 1983), or in response to differences in vegetation structure associated with particular tree species or forest strata (Robinson and Holmes 1982, Robinson and Holmes 1984). However, in our study the nearly complete removal of understory vegetation likely made behavioral modification impossible.

While the near absence of understory birds from plots receiving understory cutting could have been caused by loss of nesting habitat, the inability to forage in the understory of managed plots likely played an important role. For example, if understory birds avoided plots due solely to changes in nesting habitat, we expect that these birds would have foraged in midstory and canopy vegetation, but this happened very infrequently. Overstory tree removal could have been responsible for some of the differences in understory bird abundance. However, the three warblers and other understory birds (e.g. Acadian Flycatcher and Ovenbird) were common in nearby forest stands where the forest canopy had been selectively logged, but the understory was still largely intact (Rodewald and Smith 1997).

Tree Species Use and Availability

The three warblers foraged in a wide variety of plant species, but the greater diversity used by Worm-eating Warblers may have been a function of sample size. Warblers foraged at different frequencies in the different tree taxa, using some taxa at frequencies different from their relative availabilities. Most striking was the heavy use of dogwood by Worm-eating and Hooded warblers. Dogwood not only provided prey items on foliage and bark surfaces, but also in accumulated aerial leaf litter, which had fallen from overstory trees. However, nearly all dogwood trees were cut within stands receiving understory removal, making it the most heavily cut understory tree (pers. obs.). This alone may have been responsible for the near absence of Worm-eating and Hooded warblers from managed plots. Overall, 73 percent of Worm-eating Warbler foraging, 80 percent of Hooded Warbler foraging, and 38 percent of Black-and-white Warbler foraging within mature forests occurred in tree and shrub species that were extensively removed during forest management in nearby areas.

Black gum was regularly used by Hooded and Worm-eating Warblers and was the second most frequently utilized tree species by Black-and-white warblers. However, black gum was also heavily cut during understory removal (pers. obs.). Black-and-white Warblers used oaks and hickories more frequently than the other warblers, and used oaks more frequently than their availability. Because many oaks and hickories were retained during forest management, removal of those tree species from managed plots was less likely to have had a strong effect on Black-and-white Warbler abundance. The low use of maples by Black-and-white Warblers suggests a possible aversion to maples. This may have been because young and mid-aged sugar and red maples have smooth bark, providing little foraging substrate for a primarily bark-foraging species. Additionally, the long petiole of maple leaves should make foliage arthropods less accessible (Robinson and Holmes 1984) to a near-perch gleaning species. Although Black-and-white Warblers occasionally used sally maneuvers, which could allow access to more distant prey, nearly all sallying involved chasing prey that had flown or fallen from bark substrates. Interestingly, Hooded Warbler, a species that frequently used sallying to glean prey from foliage, used maples more than the other two warblers. This is consistent with Holmes and Schultz (1988) who suggested that bird species that use sally techniques to obtain prey might have greater foraging success in sugar maple.

Foraging and Tree Heights

Although all three species foraged in forest understory, Black-and-white Warblers also regularly foraged on tree trunks and limbs in the midstory and subcanopy within mature forests. This habit may have made that species less sensitive to understory removal on managed stands because many larger trees were not cut during forest treatment. Survey data are consistent with this idea because Black-and-white Warbler was the only understory-nesting species with similar abundance on both managed and mature plots (Rodewald and Smith 1997). Individual trees used by foraging Worm-eating and Hooded warblers averaged shorter in height than trees used by Black-and-white Warblers, indicating that Hooded and Worm-eating warblers are not simply foraging at low heights on tall trees. Thus, understory removal effectively eliminated foraging habitat for Hooded and Worm-eating warblers, and other understory species.

Substrate Use and Foraging Methods

Foraging substrates and maneuvers were used in different proportions by the three warbler species in mature forests. Bark substrates used heavily by Black-and-white Warblers were primarily those of larger trees, which may explain why this species was occasionally found on managed forest plots where other understory species were very infrequently recorded (Rodewald and Smith 1997). Hooded and Worm-eating warblers frequently used live foliage substrates while foraging in the understory. Worm-eating Warblers utilized aerial leaf litter heavily for foraging (39 percent) in mature forests. Aerial leaf litter provides shelter for a variety of different arthropods and accounted for 58 percent-84 percent of foraging maneuvers by Worm-eating Warblers in non-breeding areas in Central America and the Caribbean (Greenberg 1987). However, aerial leaf litter accounted for only 11 percent of foraging during breeding periods in Maryland (Greenberg 1987), suggesting a higher importance of this foraging substrate in the Ozark mountains. Understory foliage and aerial leaf litter were removed from managed plots and this significantly altered substrate availability for understory birds.

Management Implications

Forests in this area are primarily managed for oak-hickory, and understory removal is believed to be important in lowering competition for regenerating oak and hickory. In addition to strongly affecting nesting habitat, understory removal has, at least in the short-term, excluded these and other forest understory birds from foraging in managed plots. As a result, forest managers should consider reducing, eliminating, or altering the pattern of removal of understory vegetation (e.g. retaining patches of understory) in forest management plans as this could lessen negative effects on mature forest birds. Experiments that examine effects of removing varying amounts of understory on both birds and forest regeneration would be useful. Acceptable regeneration of oak and hickory might be obtained under uneven-aged systems by cutting smaller percentages of understory tree and shrub species important for forest birds. If this is possible, some understory bird species may then be able to utilize

these managed forests for foraging and possibly nesting. However, even if adequate regeneration of marketable tree species were achieved, additional research on the long-term effects of this uneven-aged management technique on bird abundance and reproductive success would be necessary.

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