

## Invertebrate availability and vegetation characteristics explain use of nonnesting cover types by mature-forest songbirds during the postfledging period

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**ABSTRACT.** Some species of mature-forest-nesting songbirds use regenerating clearcuts and forested wetlands during the postfledging period (between nesting and migration). Relatively dense vegetation structure and abundant food resources in non-mature-forest cover types have been hypothesized to explain this phenomenon. We examined the relative importance of vegetation structure and invertebrate availability on use of nonnesting cover types by adult and hatch-year Ovenbirds (*Seiurus aurocapilla*) and American Redstarts (*Setophaga ruticilla*) during the postfledging period of 2009 in northern Minnesota. We used mist nets to sample bird use of forested wetlands and regenerating clearcuts of three age groups: 1–6, 7–12, and 16–19 yr after harvest. We modeled captures of birds using vegetation characteristics and invertebrate availability sampled around nets as explanatory variables. For all birds studied, captures were best explained by food availability and secondarily by vegetation characteristics including litter depth and woody debris for Ovenbirds and canopy height for American Redstarts. Shrub-level invertebrate availability received a cumulative weight of 0.74–0.99 in Akaike's information criterion corrected ranked models for adult and hatch-year birds of both species. Vegetation density and variation in vegetation density explained almost no variation in captures of either species. We conclude that both invertebrate availability and some vegetation characteristics influence use of nonnesting cover types by Ovenbirds and American Redstarts during the postfledging period, but that invertebrate availability is generally the stronger predictor of that use.

**RESUMEN.** La disponibilidad de invertebrados y las características de la vegetación explican el uso de hábitat de aves (Paseriformes) de bosque maduro durante el periodo post-volantón

Algunas especies de aves Paseriformes que anidan en bosque maduro usan áreas desmontadas en regeneración y humedales con bosque durante el periodo de volantón (entre la anidación y la migración). La presencia de vegetación con una estructura relativamente densa y los recursos de comida abundantes en los tipos de cobertura de bosque no maduro han sido propuestos para explicar este fenómeno. Examinamos la importancia relativa de la estructura de la vegetación y la disponibilidad de invertebrados en el uso de tipos de cobertura usadas por adultos e individuos en su primer año de las especies *Seiurus aurocapilla* y *Setophaga ruticilla* durante el periodo posterior a la anidación de 2009 en el norte de Minnesota. Para este análisis no se considera la anidación. Utilizamos redes de niebla para muestrear el uso de aves de humedales con bosque y áreas desmontadas en regeneración de tres grupos de edad: de 1 a 6, 7 a 12, y 16 a 19 años después de la cosecha. Modelamos la captura de aves usando las características de la vegetación y la disponibilidad de invertebrados muestreados alrededor de las redes como variables explicativas. Para todas las aves estudiadas, la mejor explicación para las capturas fue la disponibilidad de alimentos, seguido por las características de la vegetación, incluyendo la profundidad de la hojarasca y restos de madera (para *S. aurocapilla*), y la altura del dosel (para *S. ruticilla*). La disponibilidad de invertebrados a nivel arbustivo recibió un peso acumulado de 0.74 a 0.99 en modelos de AIC<sub>c</sub> para adultos e individuos en su primer año, de ambas especies. La densidad de la vegetación y la variación en la densidad de la vegetación explicó casi nada de la variación en las capturas de ambas especies. Concluimos que tanto la disponibilidad de invertebrados y algunas características de la vegetación influyen en el uso de tipos de cobertura (pero no para anidar) de *S. aurocapilla* y *S. ruticilla* durante el periodo posterior al periodo de volantón, pero que la disponibilidad de invertebrados en general es el pronosticador más fuerte de ese uso.

*Key words:* American Redstart, clearcut, forest songbirds, Ovenbird, postfledging, *Seiurus aurocapilla*, *Setophaga ruticilla*

Studies of Wood Thrushes (*Hylocichla mustelina*), Scarlet Tanagers (*Piranga olivacea*), Swainson's Thrushes (*Catharus ustulatus*), and

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Ovenbirds (*Seiurus aurocapilla*) indicate that these generally mature-forest species increase use of early- to mid-successional clearcuts, riparian areas, and forested wetlands during the post-fledging period (Anders et al. 1998, Vega Rivera et al. 2003, White et al. 2005, King et al. 2006). Hypothesized explanations for use of nonnesting cover types include predator avoidance and food acquisition (Marshall et al. 2003). Vitz and Rodewald (2007) tested these hypotheses by using vegetation parameters and fruit abundance to model capture rates of forest-nesting birds in non-mature-forest stands, and concluded that vegetation structure was generally more important than fruit abundance in explaining capture rates of forest birds in early-successional regenerating clearcuts. However, most species studied by Vitz and Rodewald (2007) were insectivores that may have selected areas based on availability of arthropods rather than fruit.

Although abundance of forest invertebrates generally declines immediately after forest harvest, abundance and species richness tend to increase linearly during the first 20 yr of succession (Niemela 1997). Therefore, use of areas with taller canopies within young clearcuts by mature-forest birds (e.g., Vitz and Rodewald 2007) could reflect use of areas with greater abundance of invertebrates. Further, harvest-induced reductions in forest invertebrate abundance are less pronounced in smaller harvested stands (e.g., Niemela et al. 1988), possibly explaining why capture rates of forest-nesting birds are higher in smaller early-successional stands (Vitz and Rodewald 2006). However, to our knowledge, the possible importance of invertebrate availability in explaining use of non-mature-forest cover types by mature-forest birds during the postfledging period has not been examined.

We investigated use of nonnesting cover types, including regenerating clearcut stands and forested wetlands, during the postfledging period by after-hatch-year (adult) and hatch-year Ovenbirds and American Redstarts (*Setophaga ruticilla*) in a managed, northern hardwood-conifer forest landscape in north-central Minnesota. Our first objective was to determine whether food resources (i.e., invertebrate availability) or vegetation characteristics were more important in explaining postfledging use of nonnesting cover types by Ovenbirds and American Redstarts. Because Vitz and Rodewald

(2006) found that mature-forest birds used areas of taller canopy within young clearcuts, we sampled clearcuts of a wider range of ages (and therefore structures) to include older, taller stands. Second, we compared invertebrate availability among the stands we sampled and the adjacent mature forest to determine if invertebrate availability was higher in non-mature-forest cover types during the postfledging period. Third, we examined the relationship between fruit abundance and invertebrate availability during the postfledging period in non-mature-forest stands. Because many invertebrates are attracted to fruits (Sallabanks and Courtney 1992), fruit abundance may be a useful index of invertebrate availability during the postfledging period.

## METHODS

At three study sites located across the Chippewa National Forest in north-central Minnesota (Fig. 1), we used mist nets to sample 10 non-mature-forest stands (four stands at each of two sites and two stands at the third site) for use by Ovenbirds and American Redstarts during the postfledging period in 2009. At each site, we sampled two regenerating clearcuts, one 1–6 yr after harvest and another 7–12 yr after harvest. At two of the three study sites, we also sampled one clearcut 16–19 yr after harvest and one forested wetland. Each stand sampled was surrounded by mature (>100 yr since harvest) northern-hardwood and conifer forest where both focal species were known to nest. Mature-forest stands were dominated by sugar maple (*Acer saccharum*), American basswood (*Tilia americana*), red pine (*Pinus resinosa*), paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), big-tooth aspen (*P. grandidentata*), and red maple (*A. rubrum*). All non-mature-forest stands sampled were 9–15 ha in area except one 2.5-ha forested wetland. Clearcuts 1–6 yr after harvest were dominated by shrubs (*Rubus* spp.), and aspen (*Populus* spp.) and pussy willow (*Salix discolor*) saplings 1–3 m tall. Clearcuts 7–12 yr after harvest were dominated by aspen saplings 5–8 m tall with fewer low shrubs. Clearcuts 16–19 yr after harvest were dominated by aspen saplings 8–15 m tall, with relatively open understories of maple (*Acer* spp.) and American basswood and little shrub-layer vegetation. Forested wetlands

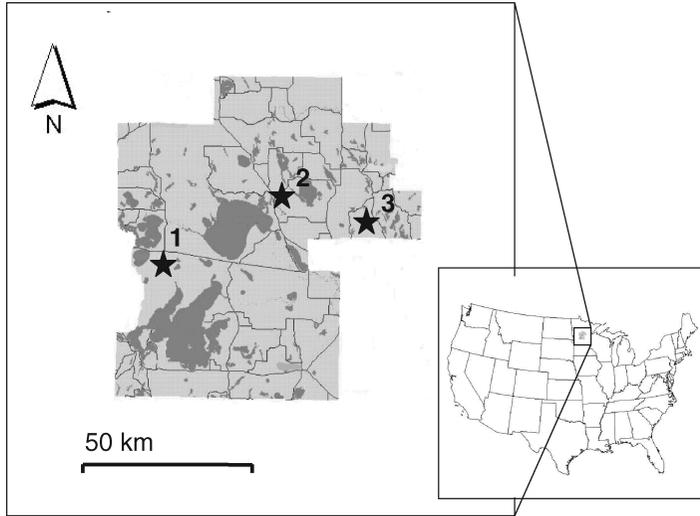


Fig. 1. Study sites included (1) Pike Bay, (2) Cutfoot Sioux, and (3) Suomi Hills in the Chippewa National Forest, north-central Minnesota, where we used mist nets to sample non-mature-forest cover types for use by mature-forest nesting Ovenbirds and American Redstarts during the postfledging period, July and August 2009.

we sampled were dominated by black spruce (*Picea mariana*), tamarack (*Larix laricina*), and alder (*Alnus* spp.) that ranged in height from 2 to 14 m, with ground cover of sedges, sphagnum (*Sphagnum* spp.) mats, and shallow open water.

In each stand, we erected three pairs of 12-m, four-shelf mist nets (36-mm mesh), with one pair placed at each of three locations:  $\leq 25$  m, 26–50 m, and 50–75 m from mature-forest edge. There was no area  $> 50$  m from mature-forest edge at one forested wetland so we placed the third pair of nets in the center of the stand, 30 m from mature-forest edge. Using mist nets to sample comparable areas within stands that differ in canopy height can be challenging because mist nets sample a vertical plane that may not reach the canopy of taller stands (Marshall et al. 2003). Therefore, we erected net-pairs end-to-end in stands with canopies  $\leq 5$  m, and stacked net-pairs vertically in stands with canopies  $> 5$  m (i.e., both clearcuts 16–19 yr after harvest, and one forested wetland) to reduce bias from differences in canopy height while sampling the same total area in each stand. We believe this successfully reduced potential bias in captures because we found no considerable difference ( $< 4\%$ ) in overall (all species) captures between the two forested wetlands where we

used different netting methods (H. M. Strebby and D. E. Andersen, unpubl. data).

We sampled each stand twice weekly (on 2 consecutive days) from 4 July to 27 August. We opened nets 15–30 min before sunrise and closed them either after 3 h or when weather conditions (i.e., high wind or rain) precluded safe netting and handling of birds. We opened nets late on one day and closed and reopened nets twice on second day resulting in a total of 2.5 h of delay in netting, but we still netted for 3 h each day.

We monitored nets at  $\leq 30$ -min intervals, removed entangled birds, and carried them in soft cloth bags to a banding station  $\leq 200$  m from capture locations. We identified species and age of each bird, referring to Pyle (1997) when necessary. All birds except Ruby-throated Hummingbirds (*Archilochus colubris*) were banded with an aluminum U.S. Geological Survey leg band.

**Vegetation sampling.** From 1 to 7 August, we sampled vegetation around each pair of mist nets in each stand. Although vegetation density and canopy height change considerably in May and June in early-successional stands in our study area, both remain relatively constant during July and August. Around each pair of nets, we established 16 0.75-m-radius circular

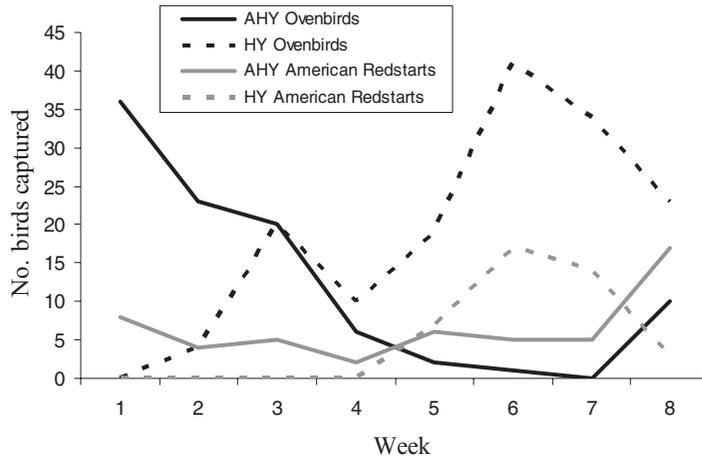


Fig. 2. Mist-net captures of hatch-year (HY) and after-hatch-year (AHY) Ovenbirds and American Redstarts in 10 non-mature-forest stands during the postfledging period, 4 July to 27 August 2009, in the Chippewa National Forest, Minnesota.

plots (Fig. 2). On each side of each pair of nets, we established four plots 2 m from nets, and four plots 5 m from nets. Within each plot, we visually estimated canopy height and percent ground cover (from ground to 0.25 m above ground) by vegetation and by woody debris. In addition, we measured leaf-litter depth at the center of each plot. We used the mean of the 16 values for each parameter as the value of that parameter for each pair of nets.

We estimated vegetation density around each pair of nets using a profile-board method modified from MacArthur and MacArthur (1961). We divided a 2 m  $\times$  0.25 m board into eight 0.25 m  $\times$  0.25 m squares, and painted the squares alternately orange and white. We stood the board vertically against nets at four locations, directly facing the vegetation plots. We viewed the board from each of the eight 5-m vegetation plots and estimated the percent (rounded to the nearest 10%) of each square obscured by vegetation. We used estimates from all squares from each sample and produced eight estimates of vegetation density around each pair of nets. We used the mean of those eight estimates to produce one estimate of mean vegetation density for each pair of nets. In addition, we used the standard deviation of those eight estimates as an estimate of variation in vegetation density around each pair of nets. Two researchers collected all vegetation data, and we calibrated all visual estimates by practicing each method

including the profile-board method prior to data collection until paired estimates differed by less than 10% between observers.

**Food sampling.** We used flytape and pitfall traps to sample invertebrates at each pair of nets during each week of netting. Sticky tape and other glue-trap methods have been used to quantify parasitic flies at songbird nests (Tomas et al. 2008) and to compare abundance of flying insects among habitats (Polis and Hurd 1995), and pitfall traps are commonly used to sample abundance of ground-dwelling arthropods (e.g., Yi and Moldenke 2005). Although traps may not directly sample invertebrate availability for songbirds, we considered captures of invertebrates to be an index to availability. Availability is a function of abundance and accessibility and, to be captured in a trap, invertebrates must be present (abundance) and active (accessible). On the first of 2 consecutive days of netting within a stand, we deployed two pitfall traps and two flytape traps at each pair of nets (Fig. 2). We used a 473-ml plastic cup with  $\sim$ 50 ml of 50% ethanol solution for each pitfall trap. We set one pitfall trap at the center of each net, such that the top of the cup was level with the ground. We used a 10 cm  $\times$  1 cm double-sided strip of attractant-free flytape for each flytape trap. We attached each flytape trap to a small branch that protruded into the net lane 1–2 m above ground. We collected and counted the contents of each pitfall trap and flytape trap

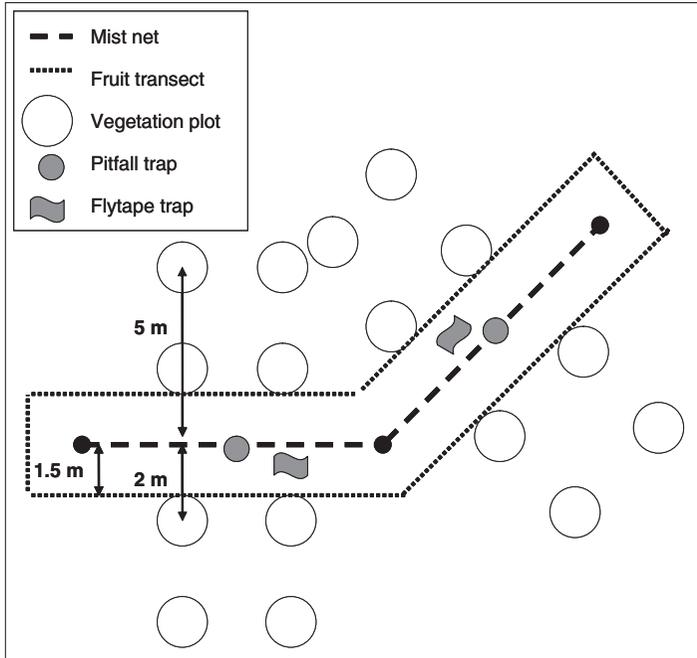


Fig. 3. Vegetation, invertebrate, and fruit sampling design around a pair of 12-m mist nets. Canopy height, leaf-litter depth, and percent ground cover by low vegetation and woody debris were recorded in each of 16 vegetation plots during the first week of August. Vegetation density was estimated using a profile board (not shown) placed against the net perpendicular to, and viewed from, each of the eight 5-m vegetation plots. Two pitfall traps and two flytape traps were deployed weekly for 24 h between 2 consecutive days of netting.

24 h after deployment (i.e., after the second of two consecutive mornings of netting). We used the number of invertebrates captured in pitfall traps as an index of ground invertebrate availability. We used the number of invertebrates captured on flytape traps as an index of shrub-level invertebrate availability. In addition, we counted all ripe fruit within 1.5 m of each pair of nets each week (Fig. 2). To compare our sampled stands and adjacent mature-forest stands, we established one 25 m  $\times$  3 m transect in a mature-forest stand at each site from 8 to 14 August. We counted fruit and deployed seven flytape traps (24 h) in each mature-forest transect.

**Statistical analysis.** Before analysis, we tested variables for normality and linearity. One variable (canopy height) had an apparent non-linear relationship with captures of adult Ovenbirds so we included an additional quadratic term for canopy height in models of adult Ovenbird captures. We modeled captures of adult Ovenbirds, hatch-year Ovenbirds, adult American Redstarts, and hatch-year American

Redstarts. Because use of nonnesting cover types by adult and hatch-year mature-forest birds is not necessarily temporally similar (Fig. 3; Streby 2010), we included in models only data from weeks when birds of the group in question were captured. For example, in models of hatch-year American Redstart captures, we included only data from weeks 5 to 8 (Fig. 3). No hatch-year American Redstarts were captured before August so including data from weeks 1 to 4 in our analysis intended to compare habitat use within nonnesting cover types would likely yield erroneous results for explanatory variables that increase or decrease throughout the 8-week sampling period. Using the same logic, we included only data from weeks 2 to 8 for hatch-year Ovenbirds, and all 8 weeks for adults of each species.

Because all sampling events were equal in duration (6 h; 3 h during each of 2 consecutive days), counts of birds captured were equivalent to capture rates. Therefore, we used counts of birds captured in each pair of nets per week as

the response variable in Poisson regression in PROC NLMIXED (SAS Institute 2008). For each species, we developed a set of a priori candidate models based on biologically relevant variables. Ovenbirds typically occupy ground litter and low vegetation, foraging primarily on the ground and secondarily in shrub-level and understory vegetation (Van Horn and Donovan 1994). Therefore, we included ground-level and shrub-level variables in models of Ovenbird captures. We developed 19 candidate models for Ovenbirds that included ground invertebrate availability (Pitfall), shrub-level invertebrate availability (Flytape), litter depth (Litdep), percent ground cover by woody debris (Wood), canopy height (Canopy), mean vegetation density (Vegden), and variation in vegetation density (Varden).

American Redstarts occupy all available vegetation from near ground to canopy, and forage primarily from foliage and secondarily from the air (Sherry and Holmes 1997). Because American Redstarts use the ground for brief prey attacks, but otherwise use the ground rarely, we included ground-level invertebrates, but not litter depth or woody debris in models of American Redstart captures. We developed 10 candidate models for American Redstarts that included the Pitfall, Flytape, Canopy, Vegden, and Varden variables. Because the 10 sampled stands were located at three sites separated by ~25 km, we included a random Site effect in all models.

We used Akaike's information criterion corrected for small sample size ( $AIC_c$ ; Burnham and Anderson 2002) to rank candidate models. The best-supported model and all models with  $\Delta AIC_c$  values  $< 2.0$  were considered competing models. We did not consider models with one additional parameter, but otherwise identical to the best-supported model, to be competing models regardless of  $\Delta AIC_c$  values because the additional parameter in such models is generally uninformative (Arnold 2010). We included each variable in the same number of candidate models, and we used the cumulative Akaike weights ( $w$ ; Burnham and Anderson 2002) of all models that included a given variable to identify the relative support for that variable for predicting bird captures.

To determine if food availability was greater in non-mature-forest cover types than mature forest, we used Student's  $t$ -tests and compared invertebrate counts from sampling in each stand

with invertebrate counts sampled simultaneously in adjacent mature-forest stands. We did not compare fruit abundance because we found no fruit in mature-forest transects. To test the reliability of fruit abundance as an index of invertebrate availability in non-mature-forest stands, we used linear regression and compared fruit counts with Pitfall and Flytape counts. We considered results of statistical tests significant at  $\alpha = 0.05$ .

## RESULTS

We captured 253 Ovenbirds (102 adult and 151 hatch-year) and 92 American Redstarts (51 adult and 41 hatch-year) during 1440 net-hours (pairs of nets). Around nets, we counted 5627 ripe fruits and captured 6200 and 5783 invertebrates in pitfall traps and flytape traps, respectively. Most fruits ( $> 90\%$ ) were *Rubus*, including American red raspberry (*R. idaeus*), dwarf red raspberry (*R. pubescens*), and common blackberry (*R. allegheniensis*). Pitfall samples included representatives of 23 invertebrate orders, with  $> 90\%$  of pitfall contents in the orders Hymenoptera, Coleoptera, Diptera, Araneida, and Orthoptera. Flytape traps sampled dipterans, hemipterans (leafhoppers), hymenopterans, and adult and larval lepidopterans. Flytape traps therefore captured both flying and flightless shrub-level invertebrates.

Adult Ovenbird captures were best explained by the model including ground and shrub-level invertebrate availability, woody debris, and canopy height vegetation structure variables (Canopy, Wood, and Litdep), and a second competing model that included ground and shrub-level invertebrate availability, woody debris, and litter depth (Table 1). Cumulative weights indicated that shrub-level invertebrate availability ( $w = 0.97$ ) and ground invertebrate availability ( $w = 0.96$ ) were the strongest predictors of adult Ovenbird captures, with canopy height ( $w = 0.49$ ) and woody debris ( $w = 0.49$ ) less important. Vegetation density ( $w < 0.01$ ) and variation in vegetation density ( $w < 0.01$ ) were unrelated to captures of adult Ovenbirds.

There were four competing models of hatch-year Ovenbird captures (Table 1), and all included shrub-level invertebrate availability. Cumulative weights indicated that shrub-level invertebrate availability ( $w = 0.78$ ) was the strongest predictor of hatch-year Ovenbird

Table 1. Best-supported and competing models ( $\Delta AIC_c \leq 2.0$ ) describing captures of adult (AHY) and hatch-year (HY) Ovenbirds (OVEN) and American Redstarts (AMRE) in forested wetlands and regenerating clearcuts during the postfledging period of 2009 in the Chippewa National Forest, Minnesota. All models include an additional variable (not shown) for a random site effect. Model variables included leaf-litter depth (Litdep), percent ground cover by woody debris (Wood), canopy height (Canopy), a quadratic canopy height term in adult Ovenbird models only (Canopy\*\*2), shrub-level invertebrate availability (Flytape), and ground invertebrate availability (Pitfall).

Bird group	Model	K	AIC <sub>c</sub>	$\Delta AIC_c$	$w_i$
OVEN AHY	C <sub>Flytape</sub> + Pitfall + wood + canopy + canopy**2	6	424.03	0.00	0.49
	C <sub>Flytape</sub> + pitfall + Litdep + wood	7	424.10	0.08	0.47
OVEN HY	C <sub>Flytape</sub> + litdep + Wood	5	477.71	0.00	0.23
	C <sub>Flytape</sub> + Pitfall	4	478.05	0.34	0.20
	C <sub>Flytape</sub>	3	478.40	0.69	0.16
	C <sub>Flytape</sub> + Litdep + canopy	5	479.57	1.86	0.09
AMRE AHY	C <sub>Flytape</sub> + canopy	4	230.16	0.00	0.74
AMRE HY	C <sub>Flytape</sub> + canopy	4	168.04	0.00	0.55

captures, with twice the cumulative weight as the second strongest predictor (leaf-litter depth;  $w = 0.39$ ). Vegetation density ( $w = 0.03$ ) and variation in vegetation density ( $w = 0.02$ ) explained little variation in captures of hatch-year Ovenbirds.

Captures of adult American Redstarts were best explained by the model including Flytape and Canopy (Table 1). Cumulative weights indicated that shrub-level invertebrate availability ( $w = 0.99$ ) was the strongest predictor of adult American Redstart captures, followed closely by canopy height ( $w = 0.98$ ). Vegetation density ( $w < 0.01$ ) and variation in vegetation density ( $w < 0.01$ ) were unrelated to captures of adult American Redstarts.

Captures of hatch-year American Redstarts were also best explained by the model including Flytape and Canopy. Cumulative weights indicated that shrub-level invertebrate availability ( $w = 0.74$ ) and canopy height ( $w = 0.74$ ) were the strongest predictors of hatch-year American Redstart captures. Vegetation density ( $w = 0.05$ ) and variation in vegetation density ( $w = 0.06$ ) explained little variation in captures of hatch-year Ovenbirds.

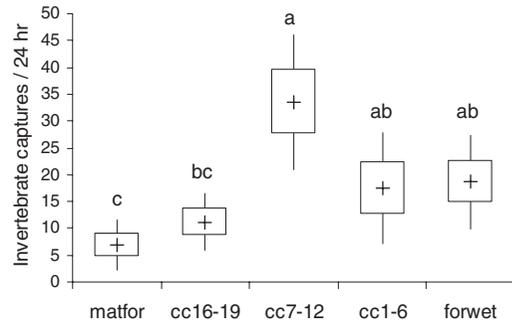


Fig. 4. Invertebrates captured on flytape traps deployed in the shrub layer of 13 stands representing five cover types in the Chippewa National Forest, Minnesota, including mature forest (matfor), clearcuts 16–19 yr after harvest (cc 16–19), clearcuts 7–12 yr after harvest (cc 7–12), clearcuts 1–6 yr after harvest (cc 1–6), and forested wetlands (forwet). Stands were sampled for 24 h from 8 to 14 August 2009. Plus signs, boxes, and whiskers represent means, SE, and 95% CI, respectively. Letters indicate statistically significantly different groups at  $\alpha = 0.05$ .

Shrub-level invertebrate availability was significantly higher in clearcuts 1–12 yr after harvest and in forested wetlands than in mature forest, but was similar between clearcuts 16–19 yr after harvest and mature forest (Fig. 4). Among non-mature-forest cover types, shrub-level invertebrate availability was highest in 7- to 12-yr-old clearcuts (Fig. 4). Fruit abundance explained little variation in estimates of either Pitfall ( $r^2 < 0.01$ ,  $F_{1,239} = 0.7$ ,  $P = 0.41$ ) or Flytape ( $r^2 < 0.1$ ,  $F_{1,239} < 0.1$ ,  $P = 0.96$ ) invertebrate availability.

## DISCUSSION

Our results support the hypothesis that both food availability and vegetation structure influence use of nonnesting cover types by Ovenbirds and American Redstarts during the postfledging period. However, our results also suggest that food availability is generally the stronger predictor of that habitat use. Although our inference is limited by having only a single year of vegetation and food availability data, capture rates and temporal patterns in captures were similar to those during the previous 3 years in the same study area (Streby et al. in press).

Although fledgling Ovenbirds experience higher survival in some nonnesting cover types during the first few days after fledging, 95%

of hatch-year Ovenbirds using nonnesting cover types are independent of adult care (i.e., >25 d after fledging), and therefore beyond the high-mortality early postfledging period (i.e., first 4 d after fledging; Streby 2010). If nonnesting cover types were used primarily for predator avoidance, we would expect to capture adult and hatch-year birds in these stands throughout the postfledging period, and captures would relate more strongly to vegetation parameters than food availability. However, many of our models that included vegetation density and variation in vegetation density performed worse than null models, suggesting that those parameters were generally uninformative. Predator avoidance may be more important when birds undergo prebasic molt (Rimmer 1988, Pagen et al. 2000). However, 94% of adult Ovenbirds and 56% of adult American Redstarts we captured in nonnesting cover types had not begun prebasic molt (H. M. Streby, unpubl. data). Thus, our results suggest that these stands were used primarily for food acquisition, possibly in preparation for the increased metabolic demands of molt (Lindstrom et al. 1993) and migration. Woody debris was a good predictor of adult and hatch-year Ovenbird captures. It is unclear whether woody debris is important for predator avoidance or food acquisition, although it could provide opportunities for both.

Ovenbirds are described as ground-foragers (Van Horn and Donovan 1994). However, we found that captures of adult and hatch-year Ovenbirds were more strongly related to shrub-level invertebrate availability, suggesting that they may forage more in the shrub layer in non-mature-forest stands than in mature forest. In mature forest, where shrub-layer vegetation is patchy and relatively uncommon, Holmes and Robinson (1988) reported that 29% of Ovenbird prey attacks occurred on foliage of shrubs and understory trees. If Ovenbirds forage in shrubs based on availability, they likely forage more in the relatively abundant shrubs in the stands we sampled. Indeed, during a radio-telemetry study, we observed hatch-year Ovenbirds perched in trees and shrubs during >50% of observations in non-mature-forest stands compared to <10% of observations in mature forest (H. M. Streby, unpubl. data).

Our results complement those of Vitz and Rodewald (2007), who concluded that vegetation structure rather than fruit abundance

explained use of clearcuts by Ovenbirds, American Redstarts, and other mature-forest songbirds. However, we demonstrated the importance of including species-appropriate food resources (i.e., insects for insectivores) in habitat-use models. Because invertebrates can be attracted to fruits (Sallabanks and Courtney 1992), assuming that fruit abundance is a reasonable index of invertebrate availability may seem valid. However, we found no relationship between fruit abundance and invertebrate availability in our study area.

Some non-mature-forest cover types (i.e., early successional clearcuts) have negative effects on mature-forest birds during the nesting season, including loss of nesting habitat and reduced nest success near edges (e.g., Manolis et al. 2000, 2002). However, our results support previous assertions that non-mature-forest cover types may provide important resources for forest-nesting birds during the postfledging period. Our results also emphasize the importance of considering the effects of regenerating clearcuts during all stages of succession. Survival of dependent fledgling Ovenbirds may be low near recent clearcuts (Streby 2010). However, our results suggest that midsuccessional clearcuts and forested wetlands provide mature-forest species of birds with more food resources than mature forest.

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