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Do mature forest birds prefer early-successional habitat during the post-fledging period?

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ABSTRACT

Recent studies have highlighted the importance of the post-fledging period to bird populations, suggesting that the importance of this portion of the life cycle is equal to or greater than the nesting period. Nevertheless, few studies have compared abundance of forest nesting species between mature forest and early-successional habitats while controlling for differences in detectibility and for biases associated with comparing low stature shrubby vegetation and tall stature forests. We investigated habitat use by forest-nesting birds during the post-fledging period in 2004 using both point counts and mist-netting in regenerating clearcuts, maintained wildlife openings, and mature forest in the White Mountain National Forest of New Hampshire, USA. We captured 1151 individuals of 50 species with mist-nets and detected 1267 individuals of 50 species with point counts during the course of the study. Of the nine mature forest-nesting species for which we had sufficient samples, seven were more abundant in early-successional habitats than mature forest. Additionally, these species highest densities were in large clearcuts with tall, complex vegetation structure and large wildlife openings with tall vegetation and standing dead vegetation. Our findings provide the first comparison of mature forest bird abundance between mature forest and early-successional habitat during the post-fledging period using estimates corrected for detectibility and for habitat stature. These results suggest that mature forest birds might actually prefer early-successional habitat to mature forest during the post-fledging period, which has important implications for managers and conservationists weighing the effects of management on early-successional versus mature forest birds.

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1. Introduction

Declines of many Neotropical songbirds have prompted an increase in research and conservation efforts to identify the factors affecting these populations. These efforts have largely focused on understanding nesting habitat requirements (Hagan and Johnston, 1992; Martin and Finch, 1995). Recently attention has shifted to the post-fledging portion of the breeding season, which describes the period of time after young fledge from the nest and before they commence southward migration (Vega Rivera et al., 1998, 1999, 2003; Pagen et al., 2000; Suthers et al., 2000; Marshall et al., 2003; Vitz and Rodewald, 2006; King et al., 2006). During this period, which can last as long as two months for some species, birds are provisioning young as they develop mobility and foraging skills, and adult birds are also undergoing a pre-basic molt. Hazards throughout the post-fledging period are especially pronounced for dependent broods or newly independent young, which are particularly susceptible to both starvation and predation (Sullivan, 1989; Anders et al., 1998; King et al., 2006). It is suggested by some researchers that high mortality of young directly after fledging might be as important as nesting success in limiting recruitment in migrant populations (Anders et al., 1998; Sillett and Holmes, 2002; King et al., 2006). Survival of hatch-year birds during the post-fledging period should be of comparable concern to managers and conservationists as nest success.

Another characteristic of the post-fledgling period is the shift from the mature forest habitats in which they nest to early-successional habitats by some mature forest-nesting birds (Anders et al., 1997; Vega Rivera et al., 1998; King et al., 2006). For example, juvenile wood thrushes (*Hylocichla mustelina*) move from nesting sites in mature hardwood forests to areas of early and mid-successional forests (Anders et al., 1998; Vega Rivera et al., 1998). Similarly, fledgling ovenbirds (*Seiurus aurocapilla*) move from nesting sites in mature forests to mixed-aged forests characterized by denser under-story than nesting sites (King et al., 2006). The reasons for this shift are unclear, though there is evidence that these birds are in search of habitat that offers more protection from predators,

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provided by dense vegetation, and/or abundant food sources that are not found at the nesting site (Donovan and Thompson, 2001).

The use of early-successional habitat by mature forest birds and evidence of their importance to their populations has important conservation implications. Mature forest birds have historically been considered to be threatened by timber harvest, which creates shrubland conditions (King and DeGraaf, 2000), removes nesting habitat (Hagan et al., 1996) and might induce edge effects on individuals nesting near harvested areas (King et al., 1996). The negative effects on nesting mature forest birds hinder management for shrubland birds, a group that includes species of concern that require early-successional habitats and are unable to breed in mature forest (Schlossberg and King, 2007). Although numerous studies have shown that mature forest birds use these habitats during the post-fledging season, only one study has actually compared their abundance between mature forest and early-successional habitat (Pagen et al., 2000). Furthermore, no previous studies have controlled for differences in detectibility associated with point counts conducted on the ground when sampling early-successional habitat with relatively short vegetation, and mature forests with high canopies. Therefore, it is possible that higher numbers of birds in early-successional habitats could reflect greater detectibility, and not actual differences in abundance.

In order to advance our understanding of habitat use by mature forest-nesting bird species during the post-fledging period, we compared densities of mature forest birds among mature forest and two types of managed early-successional habitat, maintained wildlife openings and clearcuts. Though these habitat types are both in early-succession, their vegetative structure and composition is quite different due to the method of maintenance. In a clearcut, trees are uniformly removed and then the site is left to regenerate. In contrast wildlife openings are areas specifically designated to be maintained in an early-successional state, by either periodic mowing or burning, for the purpose of creating wildlife habitat. The wildlife openings that we studied had been treated with fire or mowing within 3–6 years prior to the initiation of the study and were dominated by spirea (*Spirea* spp.), goldenrod (*Solidago* spp.), and other herbaceous plants. The clearcuts were between 6 and 8 years post-harvest and were dominated by American beech (*Fagus grandifolia*), pin cherry (*Prunus pensylvanica*), sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and raspberries (*Rubus* spp.).

In addition to the central question of differences I abundance among habitats, we analyzed the abundance of mature forest birds in early-successional habitats in relation to habitat structure, fruit abundance, and patch size. We had three central *a priori* hypotheses about what characteristics of early-successional habitats influence abundance of mature forest breeding birds during the post-fledging period: (1) that the composition and structure of vegetation would influence the presence of forest breeding birds because more structurally complex vegetation, such as woody shrubs compared to grasses and forbs, would provide greater cover from predators, (2) that the presence of abundant food resources, in this case fruit, would attract birds that may be shifting from an insectivore diet to include fruit while preparing for migration, and (3) that the size of the early-successional habitat would influence presence and abundance of forest nesting birds because large patches would be easier for birds to detect and large patches may have a greater variation of micro-habitats suitable to these species. We were also interested in how habitat structure would affect the detectability of birds during the post-fledging period, and so it was our goal to evaluate any differences that could occur from conducting point counts from the forest floor and the forest canopy.

These results will inform managers and conservationists about the value of creating and maintaining early-successional habitats for mature forest birds during the post-fledging period and which practices produce the habitat characteristics that most benefit migratory passerines.

2. Methods

2.1. Study areas

This study was conducted during 2004 within the White Mountain National Forest in Carroll and Coos counties, New Hampshire, USA (44°03′N, 71°15′W). The White Mountain National Forest is nearly 800,000 acres, of which 97% is forested. Of this forested area, less than 3% was early-successional habitat ($\leqslant$15 yrs since disturbance). The 10 early-successional sites included in this study ranged from 3.5 to 16 ha in size, and were shaped such that a 150 × 150 m grid of eight mist-nets could be placed in the site with no net being closer than 25 m from any habitat edge. From each early-successional site we randomly chose a direction into the surrounding forest and established a forest site 100 m from the edge of the opening. The 10 mature forest sites had not been subject to silvicultural or natural disturbances in the recent past ($\geqslant$50 yrs), and were within continuous tracks of forest. The forests were dominated by American beech, yellow birch, sugar maple and Eastern hemlock (*Tsuga canadensis*).

2.2. Survey methods

Birds were surveyed from mid-July through August 2004, which was within the post-fledging period, as indicated by the presence of molt and absence of migratory fattening in birds we captured during this period. We used a combination of standardized mist-netting and point counts because we were concerned that the biases associated with these methods (heterogeneous detection probabilities and under sampling of habitat >3 m tall, respectively) could affect our results. We reasoned that both of these methods would give a more valid representation of actual species abundance then either method used individually (Verner, 1985; Pagen et al., 2002).

We captured birds using mist-nets in five clearcuts, five wildlife openings, and 10 mature forest sites with 12 m long, 3 m high, 32 mm denier mist-nets. Each site was visited twice with approximately 10 days between visits, and no site was revisited until all sites had been visited once. Eight nets were arranged in a grid with a distance of 50 m between each net and the grid was placed at least 25 m from the edge of the habitat type. Nets were opened just before dawn for 5 h, when weather conditions permitted. Birds were removed from nets identified to species and fitted with a US fish and wildlife metal band.

We assessed bird density at these same sites using 10-min unlimited radius point counts, during which all birds heard or seen, along with the detection cue (visual or song or call) were recorded. Point counts were located in each site at the four corners of a 150 × 150 m grid which were also used for mist-net locations. It is possible that birds may have moved from one point to another during a visit to a given site; however strict independence is not a requirement for point counts with detection functions based on distance (Buckland et al., 2001). Furthermore, our analyses indicated that average effective detection distances were smaller than for territorial, singing males during the breeding season (<30 m; Chandler, 2007), so it is unlikely individual birds were detected at multiple points within each site. Three trained observers used laser range finders to aid in determining distance and exact distances of observed birds were recorded. Point counts in clear cuts, wildlife openings, and mature forest were conducted between 17 July and 31 August, 2004. Clear cuts and wildlife openings were visited twice, and mature forest plots were visited once, for a simultaneous ground and canopy count.

The problems associated with reduced detectibility during the post-fledging period were compounded in this study by the potential effects of habitat stature on detectibility. Point counts conducted from the ground do not necessarily reflect bird abundance in the forest canopy, (DeSante, 1986; Remsen and Good, 1996), and so we were concerned about the potential biases in bird abundance in a comparison of wildlife openings and clearcuts, with canopy heights 2–3 m high, and forest habitats with canopy heights $\geqslant$20 m. In order to evaluate potential biases associated with canopy height, we conducted point counts from within the canopy at mist-net locations within the mature forest. Using tree climbing stands designed for deer hunting, an observer ascended a 12–15 m into the canopy and simultaneously performed a point count above the ground observer using the methodology described above.

We used a point intercept method to measure habitat variables at each net within each site. Using randomly chosen compass bearing and distances, we established ten points within a 10-m radius area around each net. At each point we measured the height of the plant closest to the point and categorized plants as herbaceous, woody, or dead. In mature forests sites, height of vegetation was limited to under-story plants that had a dbh 3 in. or smaller. Also, vertical structure was measured by counting the number of stems and branches that came into contact with a 3 m pole divided into segments of 0–0.25 m, 0.25–0.5 m, 0.5–1.0 m, 1.0–2.0 m and >2.0 m. One meter diameter circles were centered on each of the 10 random points at each net and the number of unripe, ripe, and desiccated fruit was counted and pooled for a measurement of total fruit.

2.3. Statistical analyses

We used analysis of variance (ANOVA) to test if capture rates of mature forest species differed among clearcuts, wildlife openings, and forests. Analyses were restricted to our nine focal species, which comprised of forest nesting species that were detected at point counts and captured in mist-nets at $\geqslant$30% of sites. We used a cutoff of 30% because it provided a sufficient number of species for heuristic purposes, and in practice eliminated species for which we had insufficient numbers for analyses. We included 'site' as a random effect in order to account for variability within treatments, therefore testing for the differences among treatments, which was the factor of primary interest (Zar, 1996). A Poisson distribution was used and significant differences in a species' abundance among treatments were evaluated using Markov Chain Monte Carlo sampling to determine 95% confidence intervals of the estimate.

In order to correct point count data for habitat specific differences in detectibility (Rosenstock et al., 2002), we compared the density of the nine forest nesting bird species among habitats using distance sampling. The program DISTANCE (Buckland et al., 2001) was used to evaluate and rank plausible detectibility models and estimate densities for the focal species from the point count data. All analyses were confined to species that occurred at $\geqslant$30% of sites as determined by both point count and mist-net data. Detections of individuals for each species were pooled within treatment and density estimates were determined for each treatment. Forest nesting species within our focal group that had low detection rates ($n \leqslant 20$) were pooled based upon similar traits that would influence detection such as song frequency, song volume, body size, and flight behavior, which were obtained from the literature (Robinson and Holmes 1982). Pooling resulted in three groups: (1) Black-throated Blue Warbler (scientific names in Table 1), Black-throated Green Warbler and Blackburnian Warbler, (2) Blue-headed Vireo, Red-eyed Vireo, Ovenbird, Swainson's Thrush, and Hermit Thrush, and (3) Yellow-rumped Warbler.

Detectibility was modeled for each group and density estimates for each species were generated using the group detection curves (Buckland et al., 2001). Birds both visually and audibly detected were included in the analysis, although the distance at which a bird is detected may be a function of the method in which the bird is observed. For example, there is a greater chance of detecting a singing bird at a far distance than seeing a bird at that same distance. To overcome this bias, a covariate of detection method was included in the model selection process. The models were selected based on the lowest Akaike's Information Criterion values adjusted for small sample sizes (AIC_c). Within the forest habitat, density estimates were calculated for both the forest floor and canopy.

Differences in habitat variables among treatments were analyzed using an ANOVA with site included as a random effect. Habitat variables were inspected for distribution assumptions and a square-root transformation was used for the variable 'average height of vegetation'. A Binomial distribution was used for percent cover, and a Poisson distribution was assumed for all other habitat variables. As before, significant differences in habitat variables among treatments were evaluated using Markov Chain Monte Carlo sampling of 1000 iterations to determine 95% confidence intervals of the estimate.

We analyzed bird–habitat relationships of forest nesting species within clearcuts and wildlife openings using mist-net captures rather than the point count data because densities calculated with DISTANCE were estimated at the treatment level, and thus did not permit the analysis of bird habitat use in relation to within site habitat variability. In any case, the point count and mist-net data showed similar trends among habitats (Chandler, 2007), so this choice likely did not affect the results of our analyses.

Models of abundance of individual species as a function of habitat characteristics did not converge; thus, these analyses were carried out on all mature forest bird species combined. Our expectation was that the variation within treatment and micro-habitats surrounding nets would reveal patterns of selection by forest nesting species. Therefore, models were limited to within each treatment type so that the large variation between treatments did not mask the fine scale variation of interest.

Generalized estimating equations (GEEs) were used to analyze the relationship of habitat variables and mature forest bird abundances within clearcuts and wildlife openings. GEEs are an extension of generalized linear models that adjust variance, standard error, and parameter estimates based upon the amount of correlation within the covariance matrix, allowing for correlated data to be used without violating the assumption of independence (Liang and Zeger, 1986). AIC cannot be used for model selection because AIC is based on maximum likelihood estimation while GEE is non-likelihood based. Therefore, model selection was based on the smallest quasi-likelihood criterion (QIC) value (Pan, 2001) and models with lower QIC values than the null model were considered supported (Burnham and Anderson, 2002). All analyses were performed using the statistical software *R* (R Development Core Team, 2008).

3. Results

We captured 1151 individuals of 50 species during the study. Of these, 33% of the species and 29% of individuals were forest nesting birds that do not nest in clearcuts (King and DeGraaf, 2000) or wildlife openings (Chandler et al., 2009). We detected 1267 individuals of 50 species during point count. Of these, 43% of the species and 27% of individuals were forest nesting birds that are not known to nest in clearcuts (King and DeGraaf, 2000) or wildlife openings (Chandler et al., 2009) in the White Mountains. Species that occurred in $\geqslant$30% of both point counts and mist-netting data were considered our focal species and used in the analyses (Table

Table 1
Birds captured in mist-nets and detected during point count surveys on the White Mountain National Forest, New Hampshire, 2004. Focal forest-nesting species are indicated in bold.

Species	Mist-net captures[a]			Point counts			Habitat[b,c]
	C	W	F	C	W	F	
Broad-winged hawk (*Buteo platypterus*)	0	0	0	1	0	1	MF
Pileated woodpecker (*Dryocopus pileatus*)	4	0	1	0	0	1	MF
Hairy woodpecker (*Picoides villosus*)	0	0	0	3	2	6	MF
Yellow-bellied sapsucker (*Sphyrapicus varius*)	0	0	0	2	0	8	MF
Eastern wood-pewee (*Contopus virens*)	1	0	0	0	0	0	MF
Common raven (*Corvus corax*)	0	0	0	0	4	7	MF
White-breasted nuthatch (*Sitta carolinensis*)	1	0	0	4	3	1	MF
Red-breasted nuthatch (*Sitta canadensis*)	0	0	1	8	0	17	MF
Brown creeper (*Certhia americana*)	0	0	0	0	1	4	MF
Winter wren (*Troglodytes troglodytes*)	1	2	0	0	0	4	MF
Swainson's thrush (*Catharus ustulatus*)	13	1	7	9	1	4	MF
Hermit thrush (*Catharus guttatus*)	3	1	10	1	1	9	MF
Golden-crowned kinglet (*Regulus satrapa*)	0	0	0	0	0	31	MF
Blue-headed vireo (*Vireo solitarius*)	1	3	0	2	9	4	MF
Red-eyed vireo (*Vireo olivaceus*)	54	0	2	20	5	15	MF
Ovenbird (*Seiurus aurocapillus*)	7	1	19	3	2	5	MF
Blackburnian warbler (*Setophaga fusca*)	15	13	0	2	6	0	MF
Black-throated blue warbler (*Setophaga caerulescens*)	28	6	8	18	5	9	MF
Black-throated green warbler (*Setophaga virens*)	25	20	8	8	2	10	MF
Yellow-rumped warbler (*Setophaga coronata*)	2	31	2	0	21	6	MF
Northern parula (*Parula americana*)	0	2	0	0	1	0	MF
Pine warbler (*Setophaga pinus*)	0	1	0	0	3	0	MF
Evening grosbeak (*Coccothraustes vespertinus*)	0	0	0	4	5	0	MF
Purple finch (*Carpodacus purpureus*)	4	2	0	1	1	1	MF
Scarlet tanager (*Piranga olivacea*)	3	4	0	1	0	0	MF
Ruby-throated hummingbird (*Archilochus colubris*)	0	0	0	6	2	0	ES
Northern flicker (*Colaptes auratus*)	0	0	0	4	1	2	ES
Alder flycatcher (*Empidonax alnorum*)	2	14	0	0	9	0	ES
Least flycatcher (*Empidonax minimus*)	7	6	0	1	8	0	ES
Tree Swallow (*Tachycineta bicolor*)	0	0	0	0	3	0	ES
House wren (*Troglodytes aedon*)	0	2	0	0	0	0	ES
Gray catbird (*Dumetella carolinensis*)	7	0	0	5	2	0	ES
Cedar waxwing (*Bombycilla cedrorum*)	20	3	0	40	24	11	ES
Black-and-white warbler (*Mniotilta varia*)	5	2	6	8	5	0	ES
American redstart (*Setophaga ruticilla*)	30	11	0	20	0	2	ES
Common yellowthroat (*Geothlypis trichas*)	31	124	1	41	71	0	ES
Chestnut-sided warbler (*Setophaga pensylvanica*)	132	23	0	35	11	0	ES
Mourning warbler (*Oporornis philadelphia*)	9	2	0	5	3	0	ES
Nashville warbler (*Vermivora ruficapilla*)	5	82	1	2	15	0	ES
Song sparrow (*Melospiza melodia*)	7	78	0	0	76	0	ES
Eastern towhee (*Pipilo erythrophthalmus*)	0	0	0	0	1	0	ES
Field sparrow (*Spizella pusilla*)	0	3	0	0	0	0	ES
White-throated sparrow (*Zonotrichia albicollis*)	28	25	5	9	16	2	ES
Chipping sparrow (*Spizella passerina*)	0	7	0	10	1	0	ES
Indigo bunting (*Passerina cyanea*)	4	12	0	9	12	0	ES
American goldfinch (*Spinus tristis*)	2	0	0	16	12	13	ES
Mourning dove (*Zenaida macroura*)	0	0	0	0	3	0	MF/ES
Downy woodpecker (*Picoides pubescens*)	0	0	0	3	1	0	MF/ES
Eastern pheobe (*Sayornis phoebe*)	0	2	0	1	2	1	MF/ES
American crow (*Corvus brachyrhynchos*)	0	0	0	0	0	4	MF/ES
Blue Jay (*Cyanocitta cristata*)	0	0	0	21	8	22	MF/ES
Black-capped chickadee (*Poecile atricapillus*)	28	4	29	16	31	50	MF/ES
American robin (*Turdus migratorius*)	0	0	0	5	9	6	MF/ES
Veery (*Catharus fuscescens*)	6	0	0	4	1	0	MF/ES
Canada warbler (*Wilsonia canadensis*)	18	11	3	2	4	0	MF/ES
Magnolia warbler (*Setophaga magnolia*)	10	10	22	1	6	0	MF/ES
Rose-breasted grosbeak (*Pheucticus ludovicianus*)	4	2	0	5	4	2	MF/ES

[a] C, clearcut; W, wildlife opening; F, forest.

[b] Assignment of habitat associations based on King and DeGraaf (2000) and Schlossberg and King (2007).

[c] MF, birds that nest exclusively (or nearly so) in mature forest at our sites; ES, birds that nest exclusively (or nearly so) in early-successional forest at our sites; MF/ES, birds that nest in both mature and early-successional forest at out sites.

1). Twenty-eight percent of all captures within early-successional habitats were of forest-nesting birds and 80% of captures of forest-nesting birds were in early-successional habitat.

3.1. Differences among habitats

Mist-net captures indicated that all of the nine focal species were detected in early-successional habitat during the post-fledging period, and none of the focal species were detected at significantly higher densities in forests than either early-successional habitat (Fig. 1a). Capture rates of black-throated blue warblers, red-eyed vireos and Swainson's thrushes were all significantly higher in clearcuts than either forest sites or wildlife openings. Capture rates of yellow-rumped warblers and blue-headed vireos were significantly higher in wildlife openings than either forest sites or clearcuts. Capture rates of black-throated green warblers

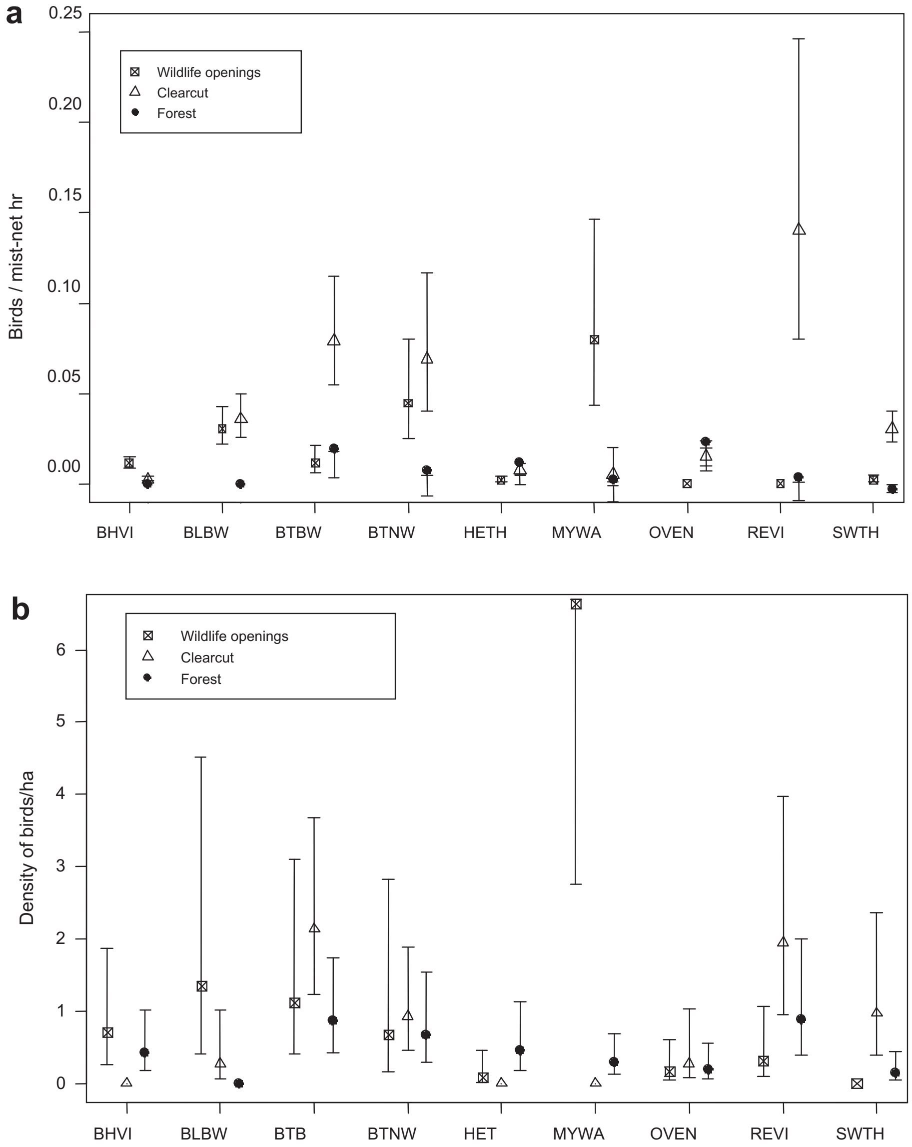

Fig. 1. Capture rates (a) and density (number of birds per hectare) calculated from point counts (b) of forest birds compared among wildlife openings, clearcuts and mature forests during the post-fledging period in northern New Hampshire. Means and 95% confidence intervals are presented. Species codes are BHVI, blue-headed vireo; BLBW, blackburnian warbler; BTBW, black-throated blue warbler; BTNW, black-throated green warbler; HETH, hermit thrush, MYWA, yellow-rumped warbler; OVEN, ovenbird, REVI, red-eyed vireo; SWTH, Swainson's thrush.

and blackburnian warblers were significantly higher in both early-successional habitat types compared to forest sites. Both ovenbirds and hermit thrushes were found in significantly higher numbers in clearcuts and forest sites than in wildlife openings.

Density estimates calculated from point count data also indicated that all of the nine focal species were detected in early-successional habitat during the post-fledging period, and none of the focal species were detected at significantly higher densities in forest sites than both early-successional habitats (Fig. 1b). Blue-headed vireos were significantly more abundant in wildlife openings and forest sites than clearcuts, blackburnian warblers were more abundant in wildlife openings than forest sites, hermit thrushes were more abundant in forest sites than clearcuts but not wildlife openings, yellow-rumped warblers were more abundant in wildlife openings than either clearcuts or forest sites, and Swainson's thrushes were more abundant in clearcuts and forest sites than wildlife openings.

Overall, the results of the mist-netting and point count analyses were similar, indicating that most species were more abundant in one or the other of the early-successional habitats we studied, although more significant differences were evident in the mist-netting data as the result of increased precision (narrower 95% CIs). It is notable that both mist-nets and point counts exhibited the same general pattern, given previous analyses that indicate the results of mist-net surveys are strongly biased towards lower vegetation strata (DeSante, 1986; Remsen and Good, 1996).

Clearcuts were characterized by a significantly higher percentage of dense woody vegetation, indicated by a high number of contacts between 0.5 and 2.0 m (Table 2). Clearcuts also had high berry abundance in comparison to wildlife openings and forests; due to extremely high variation within sites, models would not converge and confidence intervals could not be calculated. Wildlife openings had a significantly higher number of vegetation contacts between 0 and 0.25 m and were dominated by herbaceous cover with the presence of standing dead vegetation. Forest sites had relatively open under-story, with standing dead vegetation and a significantly higher percentage of bare ground than clearcuts or wildlife openings (Table 3).

Table 2
Habitat characteristics compared between clearcuts (C), forest (F), and wildlife openings (W) sampled during the post-fledging period on the White Mountain National Forest, New Hampshire, 2004.

Habitat variable	Habitat	Mean	Stand error	Lower CI	Upper CI
Number of berries	C	396.08		396.08	396.08
	F	0.00			
	W	0.00			
Average height of vegetation (m)	C	1.85	0.38	1.11	2.60
	F	1.56	0.47	0.65	2.48
	W	0.73	0.54	−0.33	1.79
Contacts 0–0.25 m	C	14.80	2.54	9.83	19.77
	F	2.20	3.11	−3.89	8.29
	W	20.18	3.59	13.14	27.21
Contacts 0.25–0.5 m	C	27.15	1.98	23.27	31.03
	F	4.80	2.42	0.05	9.55
	W	2.23	2.80	−3.26	7.71
Contacts 0.5–1.0 m	C	35.60	1.47	32.72	38.48
	F	5.88	1.80	2.34	9.41
	W	15.35	2.08	11.27	19.43
Contacts 1.0–2.0 m	C	29.30	2.37	24.65	33.95
	F	7.23	2.90	1.53	12.92
	W	2.45	3.35	−4.12	9.02
Contacts 2.0–3.0 m	C	9.75	2.60	4.66	14.84
	F	8.48	3.18	2.24	14.71
	W	1.30	3.67	−5.89	8.49
Total contacts	C	116.60	5.99	104.86	128.34
	F	28.58	7.34	14.20	42.95
	W	83.45	8.47	66.85	100.05
% of Woody vegetation	C	0.96	0.07	0.82	1.10
	F	0.66	0.09	0.49	0.83
	W	0.54	0.10	0.34	0.73
% Herbaceous vegetation	C	0.03	0.02	−0.01	0.07
	F	0.01	0.02	−0.04	0.05
	W	0.36	0.03	0.30	0.42
% Bare ground	C	0.02	0.06	−0.09	0.12
	F	0.21	0.07	0.07	0.34
	W	0.00	0.08	−0.15	0.15
% Dead vegetation	C	0.00			
	F	0.09	0.02	0.05	0.13
	W	0.06	0.02	0.01	0.11

Table 3
Generalized estimating equation (GEE) analysis of habitat variables and focal bird species captured in clearcuts and wildlife openings during the post-fledging period on the White Mountain National Forest, New Hampshire, 2004. Model selection was based on quasi-likelihood criterion values. Variable estimates (β) are presented with standard errors.

Treatment	Model	QIC	ΔQIC	$\beta 0$	(SE)	$\beta 1$	(SE)	$\beta 2$	(SE)	$\beta 3$	(SE)
Wildlife openings	Area + Avght.[a] + dead	−491.1	0	−5.6	(1.09)	0.29	(0.04)	2.75	(0.79)	−3.25	(1.52)
	Area	−20	471	−3.07	(0.37)	0.2	(0.02)				
	Null	61.2	552.3	−1.64	(0.54)						
	Contacts[c] 1.0–2.0 m	98.1	589.2	−1.99	(0.37)	0.1	(0.04)				
	Avght.	200.6	691.6	−2.56	(0.64)	1.22	(0.39)				
	% Dead vegetation	245.9	736.9	−1.78	(0.41)	1.86	(2.29)				
Clearcuts	Area + Avght + Tot.cnt.[b]	−1697.8	0	−4.56	(0.63)	0.243	(0.07)	0.47	(0.16)	0.01	(0.003)
	Total contacts	−917.4	780.4	−2.53	(0.37)	0.01	(0.004)				
	Contacts[c] 2.0–3.0 m	−644.6	1053.2	−1.28	(0.25)	0.03	(0.008)				
	% Woody vegetation	−617.9	1079.9	−2.86	(1.25)	2.04	(1.31)				
	Area	−375	1322.8	−1.71	(0.54)	0.17	(0.15)				
	Null	−342.6	1355.2	−0.9	(0.34)						
	Total berries	−340	1357.8	−0.86	(0.39)	−0.001	(0.002)				

[a] Average height of vegetation.
[b] Total number of stems that come into contact with a 3.0 m pole.
[c] Number of stems that come into contact with a pole at a certain height segment.

Five of the nine focal species detected on point counts in the forest were abundant enough for comparison between ground and canopy point counts (Fig. 2). Distance-corrected point counts indicated that estimates of bird density from point count locations on the ground and in the canopy did not differ.

3.2. Abundance in relation to habitat variables

GEE analyses of total focal species captures within both clearcuts and wildlife openings produced one model that explained more variation than the null model. In wildlife openings plot area,

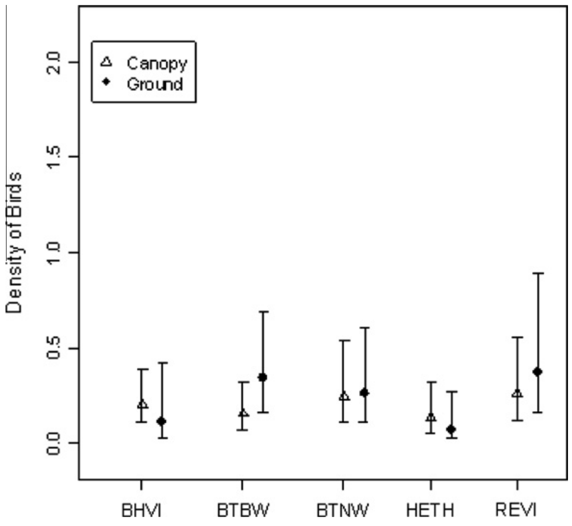

Fig. 2. Density (number of birds per hectare) estimates with 95% confidence intervals from DISTANCE analyses of point counts by observers positioned on the forest floor (ground) and observers positioned ~15 m above the forest floor (canopy). Species codes as in Fig 1. Point counts were conducted in the White Mountain National Forest, New Hampshire during the post-fledging period of 2004.

average height of vegetation, and percent of dead vegetation were positively correlated with captures of focal species. Similarly, in clearcuts plot area, average height of vegetation and the total number of stems (that came into contact with a 3 m pole) were positively correlated with captures of focal species (Table 3).

4. Discussion

Our finding that many forest nesting songbirds were more abundant in early-successional habitats than in mature forest during the post-fledging period constitutes an important advance in our understanding of the ecology of these species. Other studies have reported that juveniles of forest-nesting songbirds commonly use early-successional forests, such as abandoned farms, roadsides, and forest openings such as clearcuts during the post-fledging period (Anders et al., 1998; Vega Rivera et al., 1998; Pagen et al., 2000; Marshall et al., 2003; Vitz and Rodewald, 2006; Mcdermott and Wood, 2010). However the absence of comparisons of abundance of mature forest species between early-successional habitats and mature forest has represented a fundamental gap in our understanding of the ecology of these species during the post-fledging period. Although Pagen et al. (2000) compared the abundance of mature forest birds between early-successional habitats and mature forest our study also accounts for habitat specific differences in detectibility and for biases associated with vegetation stature in early-successional versus mature forest patches. Without these corrections we could not reject the possibility that higher numbers in openings reported in these earlier studies could actually reflect greater detectibility in these habitats, and not actual differences in abundance.

This study also shows quantitatively that some mature forest songbirds discriminate between different types of early-successional habitats during the post-fledging period: regenerating clearcuts versus maintained wildlife openings. Presumably these are responses by birds to differences in habitat conditions between wildlife openings and clearcuts. Although we were unable to analyze habitat associations for individual species due to small sample sizes, habitat characteristics of preferred opening type provide some indication of habitat associations: black-throated blue warblers, Swainson's thrushes and red-eyed vireos were associated with clearcuts, habitats typified by more fruit and taller, structurally complex vegetation. Yellow-rumped warblers and blue-headed vireos were associated with wildlife openings, characterized by more herbaceous and dead vegetation. We also considered the possibility that differences in species composition between wildlife openings and clearcuts during post-fledging were due to differences in surrounding forest type, which would have influenced the species composition of nesting species available to colonize openings. However, statistical comparisons of forest structure and composition indicated there were no significant differences in habitat characteristics among forest sites abutting early-successional sites (Chandler, 2007).

Mature forest birds could be selecting early-successional habitats during the post-fledging period because structurally complex habitats might mitigate the risks of predation. For example, Watts (1990) reported that wintering savannah sparrows (*Passerculus sandwichensis*) were subject to higher predation from raptors in areas where vegetative cover had been experimentally reduced by mowing. Similarly, Suhonen (1993) found that both crested (*Parus cristatus*) and willow tits (*P. montanus*) shifted their habitat use to areas of denser cover in response to increased predation risk from pygmy owls (*Glaucidium passerinum*). Newly hatched birds that are inexperienced at avoiding predators and adult birds undergoing molt may seek out the protective habitats offered by early-successional habitats and not found at nesting sites in mature forests (Anders et al., 1998; Vega Rivera et al., 1998; Pagen et al., 2000). Our observation that structural variables were strongly associated with abundance of forest nesting species, suggesting that birds undergo a habitat shift from mature forests to early-successional habitats with dense vegetative structure, is consistent with the theory that they are seeking protection from predators (King et al., 2006; Vitz and Rodewald, 2007).

Increased food abundance could also explain why mature forest birds occupy early-successional habitats during the post-fledging period. Early-successional habitats are characterized by fruit bearing species (Oliver and Larson, 1996) and plants in open habitat tend to have larger fruit crops (Salisbury, 1973; McDiarmid et al., 1977). Many of these species such as raspberry (*Rubus* spp.) and pin cherry (*Prunus pensylvanicus*) bear fruits that ripen, perhaps not coincidentally, during the post-fledging and migratory periods. Numbers of fruits are typically higher in early-successional forests because plants of open habitat tend to have larger fruit crops, and successional species divert more energy to growth and fruit production (Salisbury, 1973; McDiarmid et al., 1977). Some Neotropical migrant insectivores consume fruits throughout migration (Morton, 1971; Levey and Stiles, 1992; Parrish, 1997; Suthers et al., 2000), and for species such as wood thrush and Swainson's thrush (*Catharus ustulatus*) fruit is thought to be an important driver of habitat selection by juveniles during the post-fledging period (Anders et al., 1998; Vega Rivera et al., 1998; White et al., 2005). Our results, in accordance with those from Vitz and Rodewald (2006) and McDermott and Wood (2010), do not support this view. We found no evidence that mature forest birds were associated with fruit. It should be mentioned that mature forest birds were analyzed as a group, so it is possible that habitat use was related to fruit for some species but that these patterns were overshadowed by more abundant species whose habitat use was associated with structural characteristics.

Insects are another potentially important food resource that is known to be correlated with vegetation density (Schowalter et al., 1981; Blake and Hoppes, 1986; Van Horne and Bader, 1990), and might be more abundant in structurally complex habitats. Abundant herbaceous plant material and a favorable micro-climate may make early-successional habitats ideal for a number of insect species (Carpenter, 1936, Healy, 1985; Hollifield and Dimmick, 1995). For example Lepidoptera larvae, a preferred food choice of small passerines, have been found at significantly higher number in clearcuts compared to undisturbed mature forests (Van Horne and Bader, 1990; Keller et al., 2003)). Also, energetic studies of migrating birds have shown that fruit is typically lower in lipid and protein nutrients and provides smaller caloric rewards than comparable quantities of insects (Moermond and Denslow, 1985), making them a more preferable resource (Berthold, 1976). If a relationship between insect abundance and vegetation height does exist, it is an interesting explanation for why height of vegetation is an important microhabitat variable in both clearcuts and wildlife openings.

The presence of dead vegetation in wildlife openings, due to the use of fire as a treatment method, was also an important variable associated with the abundance of mature forest birds in this habitat. Dead vegetation does not likely provide protective cover for songbirds, but may support insect species that are associated with dead vegetation, or whose populations have a positive response to periodic burnings. For example, Anderson et al. (1989) found that 1 year after the burning of a sand prairie, the abundance of all insects combined was significantly lower than on unburned sites, but in subsequent years post-burning, insect populations were significantly higher on burned sites. Alternatively the relationship of mature birds to dead vegetation could indicate some other condition present in burned stands that we did not sample.

The issue of area-sensitivity is a fundamental concept of conservation biology, and is widely reported to occur in forest fauna; although the majority of research has been conducted during the nesting stage (Whitcomb et al., 1981; Askins et al., 1990; Robbins et al., 1989). Our finding that the abundance of mature forest birds is positively related to area of early-successional patches suggests that these species are area-sensitive outside of the nesting period. These results are consistent with other studies of early-successional birds during the nesting season (Annand and Thompson, 1997). Increased nest predation in small forest patches is thought to be responsible for area-sensitivity in some species such as the wood thrush (Hoover and Brittingham, 1995). Perhaps predators of fledglings are more abundant or more effective in smaller patches of early-successional habitat. Alternatively, smaller patches might support lower abundance and diversity of insects, as reported from mature forest fragments (Whitcomb et al., 1981; Burke and Nol, 1998). The greater abundance of mature forest species in larger patches of early-successional habitat could also result from the ease of finding a larger target (Pfenning et al., 2004). If birds depart their nesting sites in forests to search the landscape for discrete, early-successional habitats, a larger site may be more likely to be located. A final explanation is that larger sites have more area that is exposed to early morning sun which raises temperatures and increased insect activity (Murphy and King, 1992; Vitz and Rodewald, 2006).

Our findings contrast with the other studies examining area-sensitivity of mature forest birds in early-successional habitats during the post-fledging period, which reported that mist-net captures were lower in larger openings (Vitz and Rodewald, 2006). In addition, we did not find any relationship between forest breeding bird abundance and distances to the edge of the patch, as did McDermott and Wood, 2010, however; our findings are in contrasts with Vitz and Rodewald (2006), who reported that forest breeding birds avoid edges in early-successional habitats. The issue of area-sensitivity is obviously complicated among species groups, habitat types, seasons, and geographical locations, and needs more attention, particularly during stages other than the nesting period.

Quality habitat for songbirds must be available as they prepare for migration since populations are susceptible to limitations outside of the breeding period, and events during one period may influence survival in subsequent stages (Baille and Peach, 1992; Sherry and Holmes, 1995; Latta and Baltz, 1997; Marra et al., 1998; Newton, 1998; Sillett et al., 2000). Our results indicate that some birds appear to discriminate among different types of early-successional habitat, yet the height of vegetation within these sites and patch area are important characteristics of both clearcuts and wildlife openings for forest nesting birds. For managers this may translate into longer rotations between treatments of wildlife openings to allow vegetation to reach a height of at least one meter. Additionally, when it is practicable and does not conflict with other forest values, larger patches of early-successional habitat should be favored when outlining silvicultural and other wildlife management plans.

Studies that have investigated use of early-successional habitat by forest-breeding birds have acknowledged the dilemma of managing for quality nesting habitat, defined as undisturbed tracts of mature forest, and also for quality post-fledging habitat, such as early-successional forests that possibly provide food resources and protective cover (Anders et al., 1998; Vega Rivera et al., 1998; Vitz and Rodewald, 2006). Our results suggest that mature forest birds may prefer early-successional habitats to mature forest during the post-fledging period and provide the basis for developing a new paradigm for balancing the needs of early-successional and mature forest birds that takes into account the value of early-successional habitats for both of these groups.

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