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USE OF EARLY-SUCCESSIONAL MANAGED NORTHERN FOREST BY MATURE-FOREST SPECIES DURING THE POST-FLEDGING PERIOD

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Abstract. In eastern North America, after the young fledge, both adult and juvenile mature-forest birds may use regenerating clearcuts, although which species frequent early-successional forest and during which life stages is not well documented. To assess whether birds nesting in mature forest in north-central Minnesota use regenerating clearcuts 2–10 years old, we netted after birds fledged (2006–2009) and during the breeding season (2009). In addition, we monitored Ovenbird (*Seiurus aurocapilla*) nests and banded nestlings in adjacent mature forest and estimated the age at which juveniles used regenerating clearcuts. While banding, we also recorded nests of any species encountered opportunistically in regenerating clearcuts as evidence of breeding in this cover type. During July and August, we captured 4556 birds of 62 species, of which 1746 (38%) were of 28 mature-forest species. As reported elsewhere, most (76%) mature-forest birds we captured were of only a few species: Ovenbird, American Redstart (*Setophaga ruticilla*), Least Flycatcher (*Empidonax minimus*), and Black-and-white Warbler (*Mniotilta varia*). In 2009, 21% of captures during the nesting period were of mature-forest birds. Comparing dates of fledging from monitored nests to dates of capture in clearcuts implies that nearly all (95%) hatch-year Ovenbirds using clearcuts were independent of adult care. Capture dates of juveniles of other mature-forest species were similar. Although we captured 340 hatch-year Ovenbirds in regenerating clearcuts, we captured only one of 424 Ovenbirds we had banded as nestlings in adjacent mature forest. Within the clearcuts, we encountered nests of five species that typically nest in mature forest.

Key words: *clearcut, forest management, habitat use, Minnesota, mist net, songbirds.*

Uso de Bosques Boreales Manejados y en Sucesión Temprana por Aves Jóvenes de Especies de Bosques Maduros

Resumen. En el este de América del Norte, después de que los pichones empluman, tanto los adultos como los jóvenes de especies de aves de bosques maduros utilizan áreas taladas en regeneración. Sin embargo, no está bien documentado cuáles especies frecuentan los bosques en sucesión temprana y durante qué estadios de sus historias de vida. Para evaluar si las aves que anidan en bosques maduros del norte-centro de Minnesota usan áreas de tala rasa de 2–10 años de antigüedad, capturamos aves con redes después del emplumamiento (2006–2009) y durante la época reproductiva (2009). Además, monitoreamos nidos de *Seiurus aurocapilla* y anillamos pichones en bosques maduros adyacentes, y estimamos la edad a la que las aves jóvenes usan las áreas de tala rasa en regeneración. Mientras anillábamos, también registramos los nidos de cualquier especie encontrados de forma oportunista en claros talados en regeneración como evidencia de reproducción en este hábitat. Durante julio y agosto capturamos 4456 aves de 62 especies, de las cuales 1746 (38%) correspondían a 28 especies de bosques maduros. Como se había documentado en otros trabajos, la mayoría (76%) de las aves de bosques maduros capturadas pertenecían a unas pocas especies: *S. aurocapilla*, *Setophaga ruticilla*, *Empidonax minimus* y *Mniotilta varia*. En 2009 el 21% de las capturas durante el período de anidación fueron de aves de bosques maduros. La comparación de las fechas de salida de los volantones de los nidos monitoreados con las fechas de captura en los claros talados impica que casi todos (95%) los individuos de *S. aurocapilla* que estaban usando los claros en su año de eclosión eran independientes de sus padres. Las fechas de captura de las aves jóvenes de otras especies de bosques maduros fueron similares. Aunque capturamos 340 individuos de *S. aurocapilla* en claros talados en regeneración, sólo capturamos uno de los 424 individuos que habíamos anillado como pichones en los bosques maduros adyacentes. Dentro de los claros encontramos nidos de cinco especies que anidan típicamente en bosques maduros.

INTRODUCTION

Forest harvest (clearcutting) in predominantly forested landscapes creates temporary heterogeneity of cover types, which is accompanied by increased diversity of breeding birds (Conner and Adkisson 1975). However, debate continues about the effects of clearcuts on bird communities of adjacent mature forest. In addition to the obvious temporary

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loss of nesting habitat, negative effects of clearcuts on nesting success in adjacent mature forest appear to be common (Manolis et al. 2000). However, many studies detecting increased predation near edges of clearcuts have used artificial nests, and the consistency of clearcut-edge effects on natural nests is unclear (Hanski et al. 1996, Vitz 2003, Streby 2010). In addition, when present in natural populations, edge effects on nesting success may sometimes be compensated for by increased brood size (Flaspohler et al. 2001). In contrast, the effects of edges and forest-patch size on nesting success in predominantly agricultural landscapes are relatively pervasive and often strong (Robinson et al. 1995, Hoover et al. 1995). Further confounding the issue, studies using mist nets, point counts, and radio telemetry have found that after young leave nests, but before migration, adult and hatch-year birds of many mature-forest species use regenerating clearcuts during the post-fledging period (Anders et al. 1998, Pagen et al. 2000, Marshall et al. 2003, Vega Rivera et al. 2003, Fink 2003, Vitz and Rodewald 2006). After young fledge, songbirds' habitat use can differ substantially from that during nesting (Anders et al. 1998, King et al. 2006), birds can be exposed to additional predator species (e.g., Streby et al. 2008), and mortality of young birds can be high (Ricklefs 1973, Anders et al. 1998, King et al. 2006), especially during the first few days after they leave the nest. Therefore, songbird survival and habitat associations during the post-fledging period may be as important to managers and conservationists as parameters associated solely with nest productivity (Anders et al. 1998, King et al. 2006).

An important first step in understanding the potential influence of clearcuts on mature-forest birds during the post-fledging period is to determine which species use clearcuts after nesting, and to what degree. Studies using mist nets to sample bird use of clearcuts in Missouri (Pagen et al. 2000), Virginia and West Virginia (Marshall et al. 2003), and Ohio (Vitz and Rodewald 2006) have each reported that adult and hatch-year mature-forest birds use regenerating clearcuts during the post-fledging period. In each of those studies, most captures of mature-forest birds were of only a few species, suggesting that clearcuts are not used similarly by all mature-forest birds. However, differences among species in capture rates may also reflect differences in population abundance or productivity. Of mature-forest species commonly captured in Missouri clearcuts, few were captured during the nesting period, but capture rates of some species, such as the Ovenbird (see Table 1 for scientific names of species included in our study) and Red-eyed Vireo, increased significantly during the post-fledging period (Pagen et al. 2000). In Virginia and West Virginia, adult Worm-eating Warblers (*Helmitheros vermivorum*) banded in entirely mature forest were later captured in clearcuts, some with dependent fledglings (Marshall et al. 2003). During the post-fledging period in Ohio, mature-forest birds used the interior of clearcuts more than their edges (Vitz and Rodewald 2006), and that use was generally associated more with vegetation structure than with fruit availability (Vitz and Rodewald 2007).

Previous studies of the use of clearcuts by mature-forest birds have focused on spatial variables, such as differences in capture rates between mature forest and clearcuts, among areas within clearcuts, or among clearcuts differing in total area. An overlooked and potentially important component of post-fledging use of clearcuts by mature-forest birds is time. For example, when does use of a clearcut begin relative to completion of nesting, and how does such use vary during the post-fledging period? Although each of the aforementioned mist-netting studies reported capture rates during a period that the authors defined as the post-fledging period, none directly compared the timing of captures to the nesting phenology of local populations. Differences in capture rates between studies may reflect differences in periods sampled, relative to breeding phenology. For example, 71% of mature-forest birds captured by Vitz and Rodewald (2006) in clearcuts in southeast Ohio were hatch-year birds, compared to only 29% of birds captured by Marshall et al. (2003) in clearcuts in neighboring West Virginia and Virginia. It is possible that there were large differences between those studies in productivity or habitat selection of forest birds. However, Vitz and Rodewald (2006) sampled regenerating clearcuts through 16 August, whereas Marshall et al. (2003) ceased sampling on 31 July. If use of clearcuts by hatch-year mature-forest birds increases through the post-fledging period—a reasonable hypothesis considering that the abundance and movement capabilities of hatch-year birds both increase through the post-fledging period—the difference between those studies may be an artifact of timing of sampling. However, neither Vitz and Rodewald (2006) nor Marshall et al. (2003) reported temporal variation in capture rates during sampling. Furthermore, relatively dense vegetation cover and abundance of food resources have been hypothesized to increase survival of birds that use regenerating clearcuts during the post-fledging period. Because of recently fledged birds' relatively high risk of predation (Ricklefs 1973, Anders et al. 1997, King et al. 2006), it is important to make a distinction between use of clearcuts by dependent (under adult care) and independent juveniles of species nesting in mature forest.

We studied use of regenerating clearcuts by birds in the managed Chippewa National Forest of north-central Minnesota. The mixed northern hardwood–conifer forests of northern Minnesota, Wisconsin, Michigan, and south-central Canada host some of the highest densities of forest-nesting songbirds in North America. However, to our knowledge, there are no published studies of songbirds' use of clearcuts during the post-fledging period in this region. Our first objective was to determine if mature-forest birds in this region follow the commonly reported pattern of use of clearcuts during the time between nesting and the onset of fall migration. We hypothesized that adult and hatch-year birds of many mature-forest species use clearcuts during the post-fledging

TABLE 1. Numbers of birds captured during the post-fledging period, 2006–2009, in regenerating clearcuts 2–10 years after harvest, and during the nesting season of 2009 in regenerating clearcuts 4–10 years after harvest, in the Chippewa National Forest, Minnesota. Species are categorized by association with nesting in mature forest, early-successional forest, or both. AHY, after hatch year; HY, hatch year.

Species	Post-fledging periods 2006–2009			Nesting season 2009
	Total	AHY	HY	
Mature-forest species				
Ruby-throated Hummingbird (*Archilochus colubris*)	73	52	21	14
Eastern Wood-Pewee (*Contopus virens*)	12	10	2	0
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	31	6	25	4
Least Flycatcher (*Empidonax minimus*)	226	73	153	4
Blue Jay (*Cyanocitta cristata*)	13	12	1	2
Black-capped Chickadee (*Poecile atricapillus*)	67	42	25	1
Hermit Thrush (*Catharus guttatus*)	52	18	32	4
Wood Thrush (*Hylocichla mustelina*)	12	10	2	0
Black-throated Green Warbler (*Dendroica virens*)	19	14	5	0
Blackburnian Warbler (*Dendroica fusca*)	16	7	9	0
Black-and-white Warbler (*Mniotilta varia*)	118	61	57	6
American Redstart (*Setophaga ruticilla*)	315	184	131	11
Ovenbird (*Seiurus aurocapilla*)	660	320	340	12
Northern Waterthrush (*Parkesia noveboracensis*)	18	5	13	0
Canada Warbler (*Wilsonia canadensis*)	59	43	16	1
Total[a]	1746	885	861	74
Early-successional species				
Gray Catbird (*Dumetella carolinensis*)	72	36	36	1
Golden-winged Warbler (*Vermivora chrysoptera*)	161	108	53	30
Nashville Warbler (*Oreothlypis ruficapilla*)	328	96	232	20
Chestnut-sided Warbler (*Dendroica pensylvanica*)	608	440	168	89
Mourning Warbler (*Oporornis philadelphia*)	141	92	49	25
Common Yellowthroat (*Geothlypis trichas*)	29	18	11	2
Wilson's Warbler (*Wilsonia pusilla*)	30	7	23	1
Song Sparrow (*Melospiza melodia*)	74	37	37	3
White-throated Sparrow (*Zonotrichia albicollis*)	168	81	87	6
Indigo Bunting (*Passerina cyanea*)	22	18	4	4
American Goldfinch (*Spinus tristis*)	15	15	0	0
Total[b]	1659	956	703	181
Forest generalist species				
Black-billed Cuckoo (*Coccyzus erythropthalmus*)	11	8	3	1
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	17	7	10	8
Red-eyed Vireo (*Vireo olivaceus*)	424	378	46	5
Traill's Flycatcher (*Empidonax traillii/alnorum*)	39	20	19	15
Veery (*Catharus fuscescens*)	311	216	95	23
Swainson's Thrush (*Catharus ustulatus*)	32	31	1	1
American Robin (*Turdus migratorius*)	18	9	9	1
Cedar Waxwing (*Bombycilla cedrorum*)	53	37	16	0
Tennessee Warbler (*Oreothlypis peregrina*)	58	36	22	0
Purple Finch (*Carpodacus purpureus*)	13	9	4	1
Scarlet Tanager (*Piranga olivacea*)	30	17	13	3
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	118	96	22	32
Total[c]	1150	879	271	90

[a]Total includes these species with fewer than 10 captures: Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*Picoides villosus*), Northern Flicker (*Colaptes auratus*), Yellow-throated Vireo (*Vireo flavifrons*), Blue-headed Vireo (*Vireo solitarius*), Brown Creeper (*Certhia americana*), Red-breasted Nuthatch (*Sitta canadensis*), White-breasted Nuthatch (*Sitta carolinensis*), Winter Wren (*Troglodytes hiemalis*), Golden-crowned Kinglet (*Regulus satrapa*), Ruby-crowned Kinglet (*R. calendula*), Orange-crowned Warbler (*Oreothlypis celata*), Northern Parula (*Parula americana*), Yellow-rumped Warbler (*Dendroica coronata*), Pine Warbler (*D. pinus*).

[b]Total includes these species with fewer than 10 captures: Olive-sided Flycatcher (*Contopus cooperi*), Yellow Warbler (*Dendroica petechia*), Chipping Sparrow (*Spizella passerina*), Clay-colored Sparrow (*S. pallida*), Savannah Sparrow (*Passerculus sandwichensis*), White-crowned Sparrow (*Zonotrichia leucophrys*).

[c]Total includes these species with fewer than 10 captures: Philadelphia Vireo (*Vireo philadelphicus*), Magnolia Warbler (*Dendroica magnolia*), Connecticut Warbler (*Oporornis agilis*), Swamp Sparrow (*Melospiza georgiana*), Baltimore Oriole (*Icterus galbula*).

period. In addition, we were specifically interested in when hatch-year Ovenbirds banded as nestlings in adjacent mature forest used clearcuts. We hypothesized that we would capture those and other hatch-year birds early in the post-fledging period and at a constant or increasing rate through the post-fledging period.

METHODS

MIST NETTING

We used mist nets and sampled bird use of six early-successional regenerating clearcuts ranging from 2 to 10 years after harvest and from 9 to 15 ha in area. Clearcutting is the most common (~85% of harvest in Minnesota) method of forest harvest in our study area (Puettman et al. 1998), and 9–15 ha is fairly representative of the 5- to 19-ha range of harvested stands in the area surrounding our study sites (U.S. Forest Service Chippewa National Forest 2007 GIS cover layer). Sampled stands were located within primarily mature forest (which we defined as stands >50 years since harvest) of the Chippewa National Forest in north-central Minnesota, and sampled stands were surrounded mostly by mature forest and adjacent to other regenerating clearcut stands in some cases. Mature forest at our sites ranged from primarily coniferous to primarily deciduous, and common tree species included 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*). The regenerating clearcuts we sampled ranged in vegetation composition from primarily red raspberry (*Rubus strigosus*) shrubs and aspen (*Populus* spp.) saplings of 1–2 m in the youngest stands to primarily aspen saplings of 4–6 m interspersed with red maple, hazel (*Corylus* spp.), pussy willow (*Salix discolor*), and other less abundant trees and shrubs in the 10-year-old stands. Mean canopy height in the stands we sampled, measured during 2008, ranged from 1.8 to 5.1 m.

Between 28 June and 4 July each year, we cleared (during 2006) and recleared (during 2007, 2008, and 2009) vegetation to create net lanes approximately 1.5 m wide and 15 m long, and set pairs (two nets on three poles) of 12-m, 4-shelf mist nets (32-mm mesh) at three locations within each clearcut: (1) ≤25 m from mature-forest edge, (2) 26–50 m from mature-forest edge, and (3) >50 m from mature-forest edge (all nets were >50 m from any other edge of the sampled stand). We generally oriented each pair of nets so that one net per pair was approximately perpendicular to the edge and one was approximately parallel to it. Each year, we sampled clearcuts for 8 weeks between 4 July and 28 August and opened nets 15–30 min before sunrise and closed them between 08:30 and 10:00 or when conditions such as rain, high winds, or extreme high or low temperatures may have placed undue stress on captured birds.

We sampled two clearcuts each day and sampled each clearcut twice per week for a total of 16 days of netting in each clearcut each year. We monitored nets at intervals of ≤30 min and removed entangled birds. We carried birds in soft cloth bags to a bird-banding station located between the two concurrently sampled clearcuts (<200 m from nets). We identified the species, sex, and age of each bird (weighing and measuring when necessary) according to Pyle (1997) and banded all birds except the Ruby-throated Hummingbird with standard aluminum U.S. Geological Survey bands. We released adult birds from the banding station immediately after banding and carried hatch-year birds and females in breeding condition (with a brood patch) for release <25 m from the point of capture. We returned hatch-year birds to near the point of capture in case they were dependent on adult care and might otherwise not have been found by the adults. We returned females in breeding condition to near the point of capture to minimize time away from the nest in case they were incubating a late clutch. During all netting, when we captured a bird more than once during one day, we included only the first capture in analyses to optimize the utility of our captures as a measure of abundance by reducing the influence of localized individual activity. We standardized capture rates by captures per 100 net-hours for temporal comparisons.

CLASSIFICATION OF NEST-COVER TYPE

We classified species on the basis of nest-cover type as mature-forest birds (those that nest nearly exclusively in mature forest), early-successional birds (those that nest nearly exclusively in early-successional forest or shrubby areas) and forest-generalist birds (those that nest commonly in both mature forest and early-successional forest or nest predominantly in edge vegetation or lowland forested wetland; Table 1). We initially classified birds on the basis of associations used in previous, similar studies (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2006). However, our observations suggested that multiple species categorized in those studies as mature-forest species nested in the clearcuts we sampled (Table 2). While clearing net lanes and erecting mist nets during late June of each year, we opportunistically searched the surrounding vegetation for nests of early-successional species of management concern (e.g., Golden-winged Warbler). During those searches, we observed nests of birds considered by Pagen et al. (2000), Marshall et al. (2003), and/or Vitz and Rodewald (2006) to be mature-forest species, including the Rose-breasted Grosbeak, Veery, Red-eyed Vireo, Scarlet Tanager, and American Robin, each within 20 m of our nets. Each of those species is described as sometimes or commonly nesting in early-successional forest (Poole 2010), and we observed nests of all of those species, except the Veery, in mature forest during a concurrent nest-monitoring study (Streby 2010). We therefore classified all five of those species as forest generalists.

Because we observed nests of species often categorized as mature-forest birds in the clearcuts we sampled, in 2009 we expanded our study and used mist nets to sample four of the original six clearcuts during the nesting season, 22 May–3 July. We used the same methods for mist netting during that period, except that we returned all female birds to <25 m from

TABLE 2. Numbers of nests observed opportunistically during mist-netting and radio-telemetry monitoring of fledgling songbirds in regenerating clearcuts in the Chippewa National Forest, north-central Minnesota. One or more previous studies[a] of birds' use of regenerating clearcuts during the post-fledging period had identified these species as nesting only in mature forest.

Species	Number of nests	Age of youngest clearcut (years)
Red-eyed Vireo	2	3
Veery	2	7
Hermit Thrush[b]	2	15
Wood Thrush[b]	3	15
American Robin	1	7
Ovenbird[b]	7	17
Scarlet Tanager	2	7
Rose-breasted Grosbeak	7	7

[a]Pagen et al. (2000), Marshall et al. (2003), and Vitz and Rodewald (2006).
[b]Classified as a mature-forest species in our study.

their location of capture to minimize time they spent away from nests.

NESTLING BANDING

From 2006 to 2008 we searched for and monitored Ovenbird nests in sixteen 10-ha plots randomly established in mature forest adjacent to the clearcuts we sampled. We monitored nests by procedures modified from Martin and Geupel (1993) and used in previous studies of forest-nesting birds in north-central Minnesota (e.g., Manolis 1996). We banded nestlings with standard aluminum U.S. Geological Survey bands 1 or 2 days prior to the date on which they fledged.

RESULTS

Over 4 years and 9376 net-hours during the post-fledging period, we captured 4556 birds, of which 1746 (38%) were of 28 mature-forest species, 1659 (37%) were of 18 early-successional species, and 1151 (25%) were of 18 forest-generalist species. Of mature-forest birds captured, 76% were of four species, the Ovenbird (n = 660), American Redstart (n = 315), Least Flycatcher (n = 226), and Black-and-white Warbler (n = 118). The remaining 25% of mature-forest birds captured were of 24 species of which number of captures ranged from 2 to 67 ($\bar{x} \approx 18$; Table 1).

During 2006, 2007, and 2008, we banded 424 nestling Ovenbirds that subsequently fledged from nests located 5–920 m from the nearest regenerating clearcut we sampled with mist nets. Their mean date of fledging was 21 June ± 7 days (SD), and in this population juvenile Ovenbirds are last attended by adults ~24 days after fledging (Streby 2010). Therefore, we estimated that a majority of hatch-year Ovenbirds was independent of adult care by ~14 July of each year. Of the 226 hatch-year Ovenbirds we captured in clearcuts from 2006 to 2008, only one was a bird we banded as a nestling 30 days earlier in a nest 565 m from the net of capture. Of the 340 hatch-year Ovenbirds we captured in clearcuts over all 4 years, we captured two (<1%) during the first week (4–10 July) and 16 (<5%) during the second week (11–17 July) of mist-netting. The remaining 95% of hatch-year Ovenbirds we captured in clearcuts were likely independent of adult care because they were captured after mid July.

Rates of capture of adult Ovenbirds were highest during the first week of mist-netting, whereas the rates of capture of hatch-year Ovenbirds were highest during weeks 6–8 (Fig. 1a). Similarly, rates of capture of adult Least Flycatchers were highest during the second and third weeks of mist-netting, whereas the rates for hatch-year Least Flycatchers were highest during weeks 5–8 (Fig. 1b). We captured adult American Redstarts at a relatively constant rate throughout the post-fledging period. However, we captured very few hatch-year American Redstarts before August, when capture rates peaked during the last 3 weeks of mist-netting (Fig. 1c).

Over 432 net-hours in four clearcuts during the nesting season of 2009, we captured 345 birds of 33 species, of which 74 (21%) were of 13 mature-forest species, 181 (53%) were of 10 early-successional species, and 90 (26%) were of 10 generalist species. During that period, we did not capture any hatch-year mature-forest birds. Of the mature-forest birds we captured during the nesting season, 60% were apparently in breeding condition, by the presence of a brood patch or cloacal protuberance. Of the early-successional birds and generalist birds we captured, 77% and 68%, respectively, were apparently in breeding condition.

DISCUSSION

Our finding that mature-forest birds constituted a considerable portion (37%) of birds using regenerating clearcuts during the post-fledging period is consistent with previous studies of forested regions in eastern North America (Pagen et al. 2000, Marshall et al. 2003, Vitz and Rodewald 2006). Of the 28 mature-forest species we captured, four species accounted for 76% of those individuals. Those four species (the Ovenbird, American Redstart, Least Flycatcher, and Black-and-white Warbler) are among the most common mature-forest birds in this region (Danz et al. 2008), which suggests that the differences in captures among species may reflect differences in local abundances. However, point counts of breeding birds in the Chippewa National Forest suggest that those four species constitute considerably less than 76% of mature-forest birds (Danz et al. 2008). In fact, the Hermit Thrush and Pine Warbler were the ninth and tenth most common of 103 species recorded during those surveys in 2007, whereas we captured only 52 Hermit Thrushes and seven Pine Warblers in our entire 4-year study. Therefore, it is likely that differences

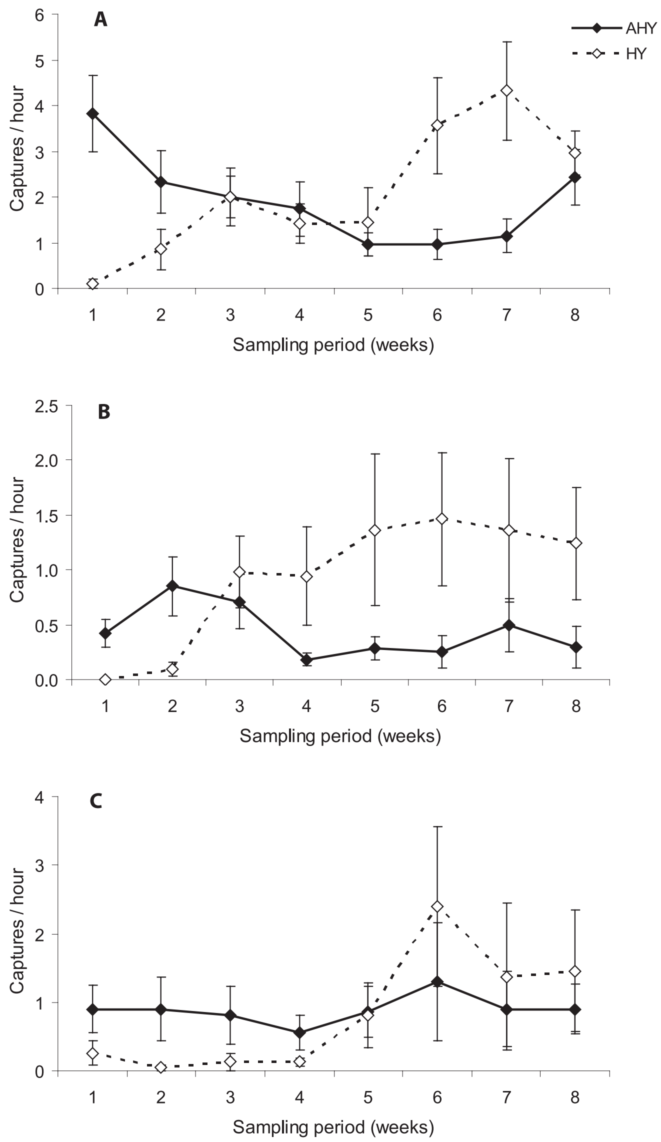

FIGURE 1. Rates of capture through the 8-week post-fledging period, 4 July–28 August, 2006–2009 of adult (AHY) and hatch-year (HY) birds of three species of mature forest, the (A) Ovenbird, (B) Least Flycatcher, and (C) American Redstart, in regenerating clearcuts in the Chippewa National Forest, Minnesota. Error bars represent SE.

in our captures of forest-nesting species reflect differences in the species' abundance and selection of cover type.

Vitz and Rodewald (2006) suggested that the use of clearcuts by hatch-year mature-forest birds may increase survival because cover and food are relatively abundant in clearcuts, and in our study area that seems to be true for hatch-year Ovenbirds in clearcuts 7–20 years after harvest (Streby 2010). We agree that those habitat characteristics probably attract adult birds and independent hatch-year birds with well-developed capabilities for flight and foraging. However, the temporal pattern of our rates of capture of hatch-year mature-forest birds, in the context of local nesting phenology, suggests that hatch-year birds rarely use clearcuts during the first weeks after fledging, when they are most vulnerable to predation. We estimated that nearly all (95%) hatch-year Ovenbirds we captured in clearcuts were independent of adult care. In addition, only one of the 226 hatch-year Ovenbirds we captured in clearcuts was one of the 424 nestlings we banded in adjacent mature forest, suggesting that hatch-year Ovenbirds rarely use early-successional stands until after they leave their natal area. This finding was supported by our concurrent radio-telemetry study of fledgling Ovenbirds at the same sites, in which the use of cover types other than mature forest increased after fledglings were independent of adult care and they moved a few kilometers from their natal area (Streby 2010). In combination, these results suggest that many of the hatch-year mature-forest birds we captured in clearcuts likely fledged from nests >1 km from our study sites. In Missouri, Anders et al. (1998) reported juvenile Wood Thrushes following a similar pattern, using mid- to early-successional forest only after dispersal from family groups. Because hatch-year mature-forest birds seem to use clearcuts primarily after independence from adult care, we caution that the simultaneous capture of juveniles and adults of a mature-forest species in a clearcut (common during our study) is likely not reliable evidence of family groups using clearcuts, as suggested by Marshall et al. (2003).

It would be difficult to compare our results for use of clearcuts by mature-forest birds with those of previous studies even if we followed identical protocols, because of regional differences in forest structure, regeneration patterns, and bird communities. But, in addition to inconsistencies between our study and previous work with respect to nest observations and classifications of nest-cover type, those previous studies' classifications were also inconsistent. For example, in southeast Ohio Vitz and Rodewald (2006) identified the American Redstart and Hooded Warbler (*Wilsonia citrina*) as mature-forest species. However, in West Virginia Marshall et al. (2003) considered the American Redstart and Hooded Warbler forest generalists, whereas Baker and Lacki (1997) considered them mature-forest species. Unless species are classified consistently, or regional differences in classification are justified, we caution that it is inappropriate to compare numbers of mature-forest species using clearcuts in different study areas (Vitz and Rodewald 2006), especially when most species are captured rarely and sampling periods are considerably different. It is also important to acknowledge that the transition from the post-fledging period to migration is gradual, both within and among species, as exemplified by our late-August captures of Wilson's Warbler, a species that does not nest at our study sites (Ammon et al. 1999).

It is also possible that our high capture rates during the nesting season and observations of mature-forest birds nesting in clearcuts reflect regional differences in the cover type in which species nest. Vitz and Rodewald (2006) reported little activity by mature-forest birds in regenerating clearcuts during the nesting season in southeast Ohio and concluded that their post-fledging captures were therefore not a consequence of birds nesting in clearcuts. However, territoriality and differences in activity rates between the nesting period and the post-fledging period likely limit the efficacy of surveys to compare abundance in these two periods. Pagen et al. (2000) concluded from point counts and mist netting during both the nesting and post-fledging periods that some mature-forest birds likely nested in the 9- to 10-year-old clearcuts they sampled in the Missouri Ozarks. With mist nets, they detected mature-forest birds in regenerating clearcuts during the nesting season but detected them infrequently or not at all in those stands during point counts. We suggest that a possible explanation is that males of some species sing from high perches at edges of mature forest—perches that are not available in many regenerating clearcuts—but females may choose nest locations in the relatively dense vegetation of adjacent regenerating clearcuts. During our concurrent nest-monitoring study, Veeries sang almost exclusively from mature-forest edge and the forest interior (H. Streby, pers. obs.). However, we found no Veery nests during intensive searching of that mature forest but found two nests opportunistically in clearcuts.

Not knowing which species are nesting in clearcuts emphasizes one major limitation of using mist nets alone to assess space use by birds. Although sample size per unit effort with mist nets is considerably superior to that with nest monitoring and radio telemetry, deciphering results requires substantially more speculation. During the nesting season of 2009, 21% of our captures in clearcuts were of mature-forest birds. It is possible that some of those birds were nonbreeding individuals that were avoiding competition from territorial birds in mature forest. Indeed, 40% of those mature-forest birds did not have either a brood patch or a cloacal protuberance, whereas only 23% of early-successional-forest birds captured during the same period lacked these characteristics. It is also possible that the mature-forest birds in breeding condition were nesting in adjacent mature forest and using clearcut stands as a portion of their home range to avoid predators or for foraging. However, we cannot rule out the possibility that many of the mature-forest birds we captured were nesting in regenerating clearcuts; certainly some were. Regardless, regenerating clearcuts were at least a portion of the home ranges of many breeding birds of several mature-forest species, some of which are commonly described as forest-interior or edge-sensitive species, including the Ovenbird, Scarlet Tanager, and Wood Thrush.

Our nest observations and nesting-season captures suggest that the age, or seral stage, at which regenerating clearcuts are first recolonized for nesting by many mature-forest species is earlier than generally assumed. As further evidence, we also observed Hermit Thrush, Wood Thrush, and Ovenbird nests in 16- to 19-year-old clearcuts during our concurrent nest-monitoring study (Table 2). That mature-forest birds nest in regenerating clearcuts does not diminish the potential importance of clearcuts to those species during the post-fledging period. Rather, it suggests that the utility of regenerating clearcuts to at least some mature-forest species also extends to the nesting period.

In summary, we found that mature-forest birds use regenerating clearcuts during the post-fledging period in managed mixed northern hardwood-conifer forests of north-central Minnesota, although that use was predominantly by only a few species. The percent of our mist-net captures mature-forest birds represented was as high as, or higher than, that reported in studies elsewhere in the eastern U.S., even after we removed five species from that group that nested in our clearcuts. We caution that the cover types in which many migratory songbirds nest may not be as clear cut as previous studies have suggested. Although mature forest is often defined by a minimum age or canopy height, "mature forest" birds colonize regenerating stands as they mature, not after they mature, and such colonization may occur earlier than is commonly assumed. Important considerations for the management of forest birds in clearcuts may be the rapidity with which species of concern recolonize regenerating stands and how well they reproduce within those stands. Intensive nest-monitoring studies in clearcuts of various stages of regeneration may improve the current understanding of the cover types in which birds nest and productivity within those cover types.

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