USE OF REGENERATING CLEARCUTS BY MATURE-FOREST BIRDS DURING THE POST-BREEDING PERIOD

A Thesis

Presented in Partial Fulfillment of the Requirements for

the Degree Master of Science in the

Graduate School of The Ohio State University

By

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2003

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ABSTRACT

Population declines of mature-forest birds have stimulated numerous studies of breeding and wintering ecology. However, until recently, little attention has been given to the post-breeding period, which spans from completion of nesting until commencement of migration (ca. 2-3 months). Several species of birds that breed in mature forest are known to move from their breeding territories into early successional forests during the post-breeding period. Reasons for these shifts are largely uninvestigated and remain unclear. Post-breeding birds must avoid predation and starvation while accumulating fat reserves to facilitate migration. Moreover, post-breeding birds are especially vulnerable because juveniles are inexperienced at foraging and evading predators, while adults undergo their pre-basic molt, which inhibits flight. Mortality rates can be extremely high for post-breeding birds and a lack of post-breeding habitat may increase mortality rates. I examined the extent to which post-breeding habitat use by mature-forest birds was associated with (1) microhabitat characteristics (structural and food resources), (2) patch area (i.e., small vs. large clearcuts), and (3) habitat edge.

I studied post-breeding birds at 12 regenerating hardwood clearcut sites (3-7 years post harvest). Sites were located within Athens, Vinton, Jackson, and Gallia counties in southeast Ohio, which is found within the Ohio Hills physiographic province. Sites were

equally divided between small (4-9 ha) and large (13-18 ha) clearcut stands. I used constant effort mist-netting to quantify relative abundance of mature-forest birds between 15 June and 16 August in 2002 and 2003. Nine nets were arranged systematically at each site, and each site was sampled approximately once per week with a total of 9 visits per year. Hatch-year (HY) individuals and after-hatch-year (AHY) birds showing a wrinkled brood patch, flight feather molt, or extensive body molt (>25% of body) were identified as post-breeding individuals. At each net, I sampled fruit (3x per season), arthropod (3x in 2002, 2x in 2003), and vegetation characteristics (once during study).

I captured 1648 post-breeding mature-forest birds of 31 species with 7331 net hours. The most common species captured in descending order were Ovenbird (*Seiurus aurocapillus*), Worm-eating Warbler (*Helmitheros vermivorous*), Red-eyed Vireo (*Vireo olivaceus*), Hooded Warbler (*Wilsonia citrina*), Scarlet Tanager (*Piranga olivacea*), and Wood Thrush (*Hylocichla mustelina*). The majority of captures consisted of hatch-year individuals (71%).

For analysis I selected the 6 most common species and 3 groups of interest (all mature-forest birds, hatch-year birds, after-hatch-year birds). Microhabitat features hypothesized to affect post-breeding habitat use were examined using an information theoretic approach. Seven *a priori* models were created and subsequently ranked using food (number of fruit) and cover (density of low vegetation and average canopy height) variables for each of the 3 groups and species of interest. Hierarchical linear models using Proc Mixed (SAS) were used to calculate Akaike's Information Criterion (AIC) values to rank models.

Capture rates of Scarlet Tanager were positively related to fruit abundance, and best explained by the model containing fruit abundance. In general, capture rates for other species and groups of interest, were best explained by models that incorporated vegetation structure variables. For all groups and the 6 species of interest (except Red-eyed Vireo and Scarlet Tanager), an inverse relationship existed between capture rates and density of low vegetation (stem and leaves < 1.5 m tall) and a positive relationship with average canopy height. Overall, habitat selection by post-breeding birds was influenced by both food and cover variables.

Capture rates of the 3 groups and 6 species of interest also were analyzed in relation to stand size and distance from the mature forest edge. I used a split-plot analysis of variance to evaluate all mature forest-breeders where the whole-plot (site) consisted of 3 split-plot units (20, 50, 80 m from edge). To examine responses of the 3 groups and 6 species of interest, I used a multivariate analysis of variance (MANOVA) to test for differences in capture rates between stand sizes and another to test for differences associated with distance from the edge. Using *posteriori* univariate analysis of variance, I identified which groups and species showed the strongest responses to both stand size and distance to the edge.

Mature-forest post-breeders were captured more frequently in small stands than in large stands. This relationship was strongest for hatch-year individuals, Scarlet Tanager, Wood Thrush, and Hooded Warbler. Interestingly, captures of mature-forest post-breeders increased with distance to the mature forest edge. Causes of apparent area and edge sensitivity are unclear. Microhabitat characteristics (i.e., fruit, arthropods, low vegetation structure, average canopy height) were not related to stand size or distance from the edge. Nevertheless, managers aiming to improve value of clearcutting to mature-forest birds during the post-breeding period may need to consider size and shape of clearcuts.

The post-breeding period may be an important phase in the avian life cycle because mortality rates can be extremely high, and this vulnerability may be partly ameliorated by habitat (e.g., dense cover). This study is the first to (1) evaluate the influence of microhabitat features on habitat use within regenerating clearcuts and (2) evaluate area and edge sensitivity of post-breeding birds. These results demonstrate that mature-forest post-breeding birds are a diverse and abundant component of bird communities in early successional forests, and that post-breeding habitat selection is a function of both vegetation structure and fruit resources. Consistent with breeding ecology of mature-forest birds, post-breeding birds appear to be sensitive to edge and area, and this may warrant special management consideration. My findings are important because they both elucidate the ecology of the poorly understood post-breeding period of migratory songbirds and identify habitat features that can be manipulated by wildlife biologists to improve the value of early successional forests to a wider bird community.

ACKNOWLEDGMENTS

I would like to thank my advisor, Amanda D. Rodewald, for her constant advice and steadfast support and encouragement throughout this research. This work has benefited substantially from her insightful input. I thank my committee members Robert J. Gates, Thomas C. Grubb, Jr., and David A. Swanson for their support and interest in my work. I would like to acknowledge my funding sources for their support including the Ohio Division of Wildlife, The Ohio State University's School of Natural Resources, and GradRoots (SNR). I would like to extend a special thanks to all who provided countless hours of field assistance: Marja H. Bakermans, Johanne Berthiaume, Katie Higgins, Amy Schwarzer, Anne L. Balogh, Aaron T. Boone, and Bob Baldesberger, Jr. I am grateful to Paul G. Rodewald III, Kathi L. Borgmann, and the Wildlife Lab for thought-provoking discussions and moral support throughout my graduate research. I thank David A. Swanson, Mike Reynolds, and Mike Tonkavich (Ohio Division of Wildlife), and Wayne Lashbrook (MeadWestvaco) for assistance in locating study sites and for making life a little easier for me and my crew with their humor and generosity. I am indebted to Bert L. Bishop, Robert J. Gates, and James E. Christensen for statistical guidance. Finally, I would like to extend a special thanks to Marja H. Bakermans for her perseverance in reading through and providing helpful suggestions with the thesis in its entirety.

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CHAPTER 1

Introduction

Many Neotropical migrant songbirds have declined precipitously over the last several decades (Robbins et al. 1989, Askins et al. 1990, Hagan and Johnston 1992). These declines are well documented for some mature-forest (Robbins et al. 1989, Terborgh 1989, Askins et al. 1990, Askins 2001) and early successional species (Wiltham and Hunter 1992, Askins 1993, Hagan 1993). More specifically, for the eastern United States Breeding Bird Survey data revealed significant population declines between 1980-2001 for several mature forest species including: Cerulean Warbler (*Dendroica cerulea*), Wood Thrush (*Hylocichla mustelina*), and Eastern Wood-Pewee (*Contopus virens*; Sauer et al. 2003). Consequently, Partners in Flight, a non-profit avian conservation organization, has named several mature forest birds as species of 'very high concern'. Declines of mature forest birds have largely been attributed to loss and fragmentation of breeding and wintering habitat (Terborgh 1989, Askins 1995, Rappole 1995, Robinson et al. 1995). As a result, biologists have examined the breeding and wintering grounds to explain population declines, but few studies have evaluated the post-breeding period. A lack of appropriate post-breeding habitat may increase mortality rates and contribute to these declines. Early successional forests may provide important habitat for mature-forest birds during the post-breeding period (Anders et al. 1998, Vega Rivera et al. 1999). I examined the mechanisms which may be responsible for the use of early successional forests by juvenile and post-breeding mature forest birds.

Ornithologists have only recently become interested in post-breeding ecology of Neotropical migratory birds (Askins et al. 1990). In fact, the post-breeding period is considered the least known and understood portion of the avian life cycle (Greenwood and Harvey 1982, Rappole and Ballard 1987, Morton 1991, Baker 1993, Vega Rivera et al. 1998b). I defined the post-breeding period as beginning with fledging of young and lasting until the onset of migration (ca. 2-3 months; Pagen et al. 2000). Once hatch-year passerines become independent, they must quickly learn to exploit their surroundings while meeting the dietary and metabolic requirements for molting, as well as depositing fat to fuel migration (Morton 1991). Birds may be more vulnerable to predation or starvation during this period than at other life cycle stages because (1) juveniles have little experience foraging and/or evading predators, and (2) adults molt their remiges and rectrices, potentially inhibiting flight. Indeed, mortality rates for juvenile birds can be extremely high (Sullivan 1989).

Although post-breeding and breeding habitat requirements have traditionally been assumed to be similar, recent work shows that they can be very different (Rappole and Ballard 1987, Anders et al. 1997, Vega Rivera et al. 1999, Pagen et al. 2000). Changing seasonal requirements may stimulate shifts in habitat use, which is common among birds (Morton 1980, Ramos 1983, Hutto 1985a, Rappole and Ballard 1987, Parrish and Sherry 1994, Rappole 1995, Pagen et al. 2000). Evidence suggests that mature-forest birds seek refuge in dense vegetation of early successional forests during the post-breeding period (Anders et al. 1998, Pagen et al. 2000). Limited research documented birds shifting habitats from the breeding to the post-breeding period, but no studies have explicitly addressed the underlying reasons. Several have suggested that food resources and dense cover increase survival and promote fat accumulation for migration (Morton et al. 1991, Vega Rivera et al. 1998b). Thus, availability of suitable habitat during the post-breeding period may be critical for avian conservation. Concern over fragmentation effects on forest interior species has lead to a reduction of timber harvest (at least on public lands). But loss of early successional habitat may adversely affect those species as well as early successional dependant forest birds.

Objectives and Hypotheses

The goal of my research was to gain a better understanding of the use of early successional forests by juveniles and post-breeding mature-forest birds. I examined potential ecological mechanisms accounting for this phenomenon. In chapter 2, I evaluate whether habitat use by mature-forest birds during the post-breeding period is better explained by fruit abundance or vegetation structure in order to elucidate possible mechanisms governing habitat use. In chapter 3, I investigate the extent to which mature-forest birds are sensitive to area or edge during the post-breeding season. Collectively, these chapters will inform management and conservation strategies for eastern North American mature-forest birds.

Based on published literature and personal observations, I hypothesized that mature-forest breeders select early successional forest habitat primarily based on vegetation structure (associated with reduced predation risk) and food resources. More specifically, I predicted that (1) use of early successional forests by birds is positively associated with stem density and vertical foliage diversity and (2) use by hatch-year birds is associated with fruit abundance and to a lesser degree by arthropod abundance. Because I propose that local resources (food and cover) are most important to juveniles and post-breeding adults I did not expect to find edge or area-sensitive patterns during the post-breeding period.

Literature Review

Post-breeding Movements

Ecologists often think of the post-breeding period as a subset of the breeding season, but it is a distinct phase of the avian life cycle. Whereas breeding birds concentrate their efforts on reproduction, birds during the post-breeding period are no longer restricted by breeding requirements and can focus on survival and self-maintenance. The post-breeding period for hatch-year birds and single-brooded adults begins at the time of fledging and extends until the onset of migration (Pagen et al. 2000). For adults with multiple broods, the post-breeding period begins with the fledging of their final brood. Extensive post-breeding movements are relatively well understood for several groups including waterfowl and herons (Salomonsen 1955, Palmer 1976, Johnson and Richardson 1982, Jehl 1990, Rappole 1995). For example, Lesser Scaup (*Aythya affinis*), that breed on ponds in the Canadian prairies, fly north after breeding to molt on taiga lakes (Palmer 1976). However, little is known about the post-breeding period for passerines. Fledglings of open-cup nesting passerines likely remain within 50 m of their nest during the first week (Morton et al. 1991). After approximately 2-4 weeks they become independent of their parents and can move several km from the nest (Morton et al. 1991). During this period, they often use habitats very different from typical breeding habitat (Pulich 1976, Anders et al. 1998).

There is increasing evidence that many mature-forest breeders move into early successional habitats during the post-breeding period, and this is especially true for juveniles (Rappole and Ballard 1987, Anders et al. 1998, Vega Rivera et al. 1998b, Pagen et al. 2000). These shifts are well documented for Ruffed Grouse (*Bonasa umbellus*) (Thompson and Dessecker 1997) and Wood Thrush (Anders et al. 1997, Vega Rivera et al. 1998b). For example, Rappole and Ballard (1987) exclusively caught Wood Thrush in a mature forest habitat before July 15, but Wood Thrush were solely caught in the adjacent old-field from July 30-September 17. Studies utilizing radio telemetry also have documented adult Scarlet Tanagers (Vega Rivera et al. 2003) and both adult (Vega Rivera et al. 1999, Powell et al. 2000) and hatch-year Wood Thrush (Anders et al. 1998, Vega Rivera et al. 1998b) leaving their mature oak-hickory (*Quercus*-*Carya*) breeding habitat in favor of early and mid-successional forests. Limited evidence also shows that Black-throated Blue Warblers (*Dendroica caerulescens*; Rimmer and McFarland 2000) and other mature-forest breeders (Anders et al. 1998, Pagen et al. 2000, Marshall et al. 2003) move into early successional habitat after breeding.

Shifts in habitat use during the post-breeding season also occur for early successional species, although movement generally occurs between different types of early successional habitats. For example, in a 10 year study Morton (1991) documented juvenile Green-tailed Towhees (*Pipilo chlorurus*), which nest in shrub-steppe habitat, moving into subalpine meadows. Of the 104 captured Green-tailed Towhees, all were juveniles and most were molting. Following completion of their post-juvenile molt, birds quickly gained mass and disappeared, presumably on migration. Interestingly, the majority of captures occurred during drought years, suggesting food resources as a stimulus (Morton 1991). Although subalpine meadows have a relatively depauperate breeding bird community, they were heavily used by birds during late summer when they contained abundant food resources compared to lower elevations (Pattie and Verbeek 1966, Martin and Ogle 1998). Similarly, post-breeding Yellow-breasted Chats (*Icteria virens*) and Gray Catbirds (*Dumetella carolinensis*) selected food-rich, vegetation dense early successional habitats that were structurally distinct from their breeding habitat (A. M. Maxted, unpublished data). Although data suggest both adult and young of a number of species disperse into non-breeding habitat following nesting, ornithologists lack a complete understanding about the cause and benefits of these movements (Rappole 1995).

Several hypotheses have been proposed to explain post-breeding movements, including a gradual southward drift, aggregation of conspecifics, and intraspecific competition. The limited evidence for southward drift is found in the disappearance of birds from the breeding grounds, as well as recoveries of banded birds south of breeding ranges (Hahn 1937, Bent 1953, Pulich 1976, Cherry 1985, Rappole and Ballard 1987). However, this theory lacks support from radio telemetry (Anders et al. 1998, Vega Rivera et al. 1998b) or intensive banding (Nolan 1978) studies. Some evidence suggests conspecific socialization as a stimulus for post-breeding movement (Morton et al. 1991), but it remains unclear whether birds select early successional sites for this or other reasons (Vega Rivera et al. 1998b). Also, Winker et al. (1995) suggested intraspecific competition with adults may force juvenile birds into marginal habitats spurring post-breeding movements, but both empirical and anecdotal evidence for this argument are absent.

Another potential explanation is a form of dispersal known as prospecting, which is a complex evolutionary strategy that aides breeding habitat selection (Cody 1985). Evidence suggests that breeding sites are selected in late summer by juvenile Field Sparrows (*Spizella pusilla*; Adams and Brewer 1981) and White-crowned Sparrows (*Zonotrichia leucophrys*; Morton 1992). Furthermore, young of many non-passerines are believed to prospect for breeding sites in late summer or autumn (Mead and Harrison 1979, Greenwood 1980, Reed and Oring 1992, Cadiou et al. 1994), which may expedite breeding activity in spring. Prospecting potentially allows late summer evaluations of conspecific reproductive success, although productivity may not reflect habitat quality (Reed et al. 1999). Additional information gathered by prospecting birds may include locations of breeding territories, vegetation structure, and food availability (Brewer and Harrison 1975, Morton 1992, Reed et al. 1999). Another function of prospecting may be to create a navigational map that facilitates return to the area in subsequent years (Morton 1992, Baker 1993). Although there are obvious advantages associated with prospecting, there also are potential costs. Prospecting requires extensive movements in unfamiliar areas, potentially increasing predation risk (Dufty and Belthoff 2001). This cost may outweigh the benefit of late summer prospecting especially since many juvenile birds will not survive to breed the following summer (Lack 1954). Although prospecting may influence some post-breeding movements (Reed et al. 1999), the extent to which it is a general phenomenon is unknown, and does not easily explain the use of non-breeding habitat.

Post-breeding habitat use may be largely governed by food availability. In fact, food resources have been suggested to determine avian community structure (Ramos 1983, Hutto 1985a, Martin 1985, Blake and Loiselle 1991, Strong and Johnson 2001), which often fluctuates over time and space (Karr et al. 1982, Levey 1988, Loiselle and Blake 1991). For example, both frugivores (Martin and Karr 1986, Rappole et al. 1989, Loiselle and Blake 1991) and insectivores (Johnson 2000) are known to track food resources. Indeed, numerous studies have found associations between avian habitat selection and food abundance, during the breeding (Burke and Nol 1998) and non-breeding seasons (Levey 1988, Johnson and Sherry 2001).

Although strictly frugivorous birds are largely absent in eastern North America, many species that are primarily insectivorous while breeding show dietary plasticity outside of the breeding season, when they consume both fruit and arthropods (Martin et al. 1951, Parrish 2000, McCarty et al. 2002). Some species, such as the Northern Mockingbird (*Mimus polyglottos*), even feed their nestlings fruit, which may provide needed carbohydrates and water (Breitwisch et al. 1984, Willson 1986). However, fruit lacks significant amounts of protein and a high protein diet composed of arthropods promotes chick development (Stiles 1980). Since juvenile passerines are essentially fully-grown at fledging, their protein requirements are greatly reduced while their lipid and carbohydrate requirements increase (Stiles 1980). Therefore, frugivory during the post-breeding period may be an important strategy for many North American species. Frugivory offers several advantages as a foraging strategy, including ease with which birds can find and obtain fruits, reduced search movements compared to insect foraging, and high-energy content (Parrish 2000, McCarty et al. 2002). These advantages may especially benefit hatch-year birds that lack foraging experience (Desrochers 1992, Suthers et al. 2000).

Numerous studies have documented decreased foraging proficiency by juveniles relative to adults in various species (Mueller and Berger 1970, Porter and Sealy 1982, Gochfeld and Burger 1984, Breitwisch et al. 1987, Jansen 1990, Wunderle 1991, Desrochers 1992, VanderWerf 1994). Part of this foraging inefficiency may be explained by the combination of learned and innate behaviors responsible for food recognition (Wunderle 1991). Juvenile birds may initially peck at both appropriate and inappropriate objects, however, with increased experience young birds focus their foraging maneuvers on edible objects (Mueller and Berger 1970), which may result from the development of a search image (Dawkins 1971, Desrochers 1992, VanderWerf 1994). Capture and handling abilities also may influence differences in age-related foraging. In fact, juveniles are least successful with complex techniques (flight-dependent foraging), which require greater skill and consequently develop relatively late (Davies and Green 1976, Moreno 1984, Breitwisch et al. 1987, Wunderle 1991, VanderWerf 1994). This lack of foraging proficiency may cause starvation to contribute to juvenile mortality (Sullivan 1988). Consequently, young birds may forage longer in order to maintain a positive energy budget (Wunderle 1991), but increased time spent foraging may increase predation risk (Lima 1985). Juveniles may adopt unique foraging techniques including using different habitats, or search patterns, consuming different types of prey, or stealing from more skilled foragers (Wunderle 1991). Furthermore, juveniles may compensate for their lack of foraging proficiency by concentrating on easily captured or located food items (Breitwisch et al. 1984, Stevens 1985). For example, juvenile European Starlings

(*Sturnus vulgaris*) foraged on fruit within orchards while adults continued to prey on large insects elsewhere (Stevens 1985).

Some birds may select habitat based on fruit abundance (Blake and Loiselle 1991) or foliage density of fruiting plants (Martin and Karr 1986, Malmborg and Willson 1988), thereby enhancing foraging efficiency. Because early successional forests begin producing ripe fruits in early July, before they are available in mature forests (Willson 1986), seasonal selection of the habitat may be promoted (Anders et al. 1998, Vega Rivera et al. 1998b, Krementz and Christie 1999, Pagen et al. 2000, Parrish 2000). Furthermore, fruits ripen in early successional habitat as the first broods fledge. Early successional plants may fruit during summer to reduce competition with mature-forest species while benefiting from the influx of juvenile birds. Whereas fall fruiting species are often thought to have co-evolved with migrating birds (Willson 1986), a similar evolutionary relationship may be present between early successional plants and birds during the post-breeding period (Stiles 1980).

Another factor that may promote the use of early successional forests during the post-breeding period is arthropod abundance. Arthropods are the primary food source for most breeding passerines and their nestlings. Selection of breeding territories (Smith and Shugart 1987, Petit and Petit 1996, Burke and Nol 1998, Bakermans 2003), reproductive success (Conner et al. 1986, Martin 1987, Simons and Martin 1990, Zanette et al. 2000, Bakermans 2003), and bird abundance (Hutto 1985b, Forsman et al. 1998) all have been found to be positively correlated with arthropod biomass or abundance. In fact, spring-to-fall changes in insect density have been correlated with seasonal variation in bird abundance (Hutto 1985b). Furthermore, Johnson and Sherry (2001) found that wintering warblers in Jamaica were not only positively correlated with arthropod abundance, but were significantly more dependent on arthropod biomass than vegetation variables. Early successional forests may have high invertebrate resources during late summer, because arthropods may be attracted to their abundant summer flowers and fruits. If arthropods have a strong positive correlation with saplings and shrubs, as was found by Jokimäki et al. (1998), then arthropods should be abundant in regenerating clearcuts. Overall arthropod abundance (Keller et al. 2003) or that of specific taxa (Helle and Muona 1985) were found to be higher in regenerating forests than the adjacent mature forest. Furthermore, evidence exists that arthropod abundance can be higher in regenerating clearcuts than mature forests in southern Ohio (Stoll et al. 1999). Conversely, Duguay et al. (2000) found greater arthropod biomass in mature forest, compared to clearcuts, although this may have been the result of a recent insecticide treatment.

Habitat Structure

If food availability is not limiting or birds do not track food resources, then food resources should not explain avian distribution (Wiens 1976, Rotenberry and Wiens 1980, Recer et al. 1987). Instead, predation risk may be a better explanatory factor (Rappole et al. 1989), and dense cover providing protection from predators may be the primary impetus for selecting early successional habitats during the post-breeding period. Both adult and juvenile birds may be more vulnerable to depredation during the post-breeding period. Adults undergo a complete pre-basic molt (Pyle et al. 1997), potentially inhibiting flight (Nolan 1978, Rimmer 1988, Jenni and Winkler 1994, Vega Rivera et al. 1998b). In fact, adult Wood Thrush are extremely reluctant to fly while molting (Vega Rivera et al. 1998a). Juveniles have little or no experience detecting and evading predators (Wunderle 1991), and depredation is frequently the primary cause of post-fledging mortality (Sullivan 1989, Anders et al. 1997). For example, during the first 8 weeks post-fledging A.M. Maxted (unpublished data) documented 61% mortality rates (primarily depredation) on Yellow-breasted Chats and Gray Catbirds (*Dumetella carolinensis*). Depredation is often high prior to (Anders et al. 1997) or during dispersal (Nilsson and Smith 1985), but dramatically declines following dispersal (Anders et al. 1997, Powell et al. 2000). For example, Anders et al. (1997) reported that 51% of hatch-year Wood Thrush were depredated during the first 4 weeks post-fledging. Mortality rates dropped to zero after dispersal when Wood Thrush selected habitats with dense cover, presumably decreasing predation risk (Anders et al. 1997). In fact, Vega Rivera et al. (1998b) found that post-breeding sites had more woody stems and saplings compared to natal sites.

The combination of dense cover and abundant food resources in early successional forests may provide ideal habitat for birds during the post-breeding period. Because juveniles experience high mortality rates (Dhondt 1979, Krementz et al. 1989, Sullivan 1989, Zann and Runciman 1994), providing suitable post-breeding habitat may be critical for bird conservation. Mounting evidence suggests that early successional forests provide important post-breeding habitat for birds, and consequences of changes in forest management that cause dramatic declines in this habitat may need to be reevaluated.

Early Successional Habitats

Early successional habitats were historically created by natural disturbances including fire (Lorimer 1977, Clark 1990, Lorimer 2001), windstorms (Canham and Loucks 1984), beavers, insects, disease, and giant herbivores (DeGraaf and Miller 1996, Askins 1998). Natural levels of early successional habitat were inflated as forests were cleared beginning in the mid 1700's and lasting almost two centuries (Askins 2001). However, today many of these forests have regenerated into later seral-stage forests, and the combination of fire suppression, local beaver extirpation, reductions in clearcutting and farm abandonment have made ephemeral, early successional habitats increasingly uncommon (Lorimer 2001, Trani et al. 2001). The result of reduced amounts of early successional habitats, especially in the Northeast, has been a simplified landscape dominated by mature forest (Keller et al. 2003).

The majority of eastern North America's remaining early successional forests result predominantly from timber harvest and farm abandonment (Hunter 1993, Askins 2000). Recent loss and fragmentation of old forests have lead to conservation efforts that emphasize forest preservation, accelerating declines in early successional forest habitat. In fact, several early successional habitats (grassland, savanna, shrubland) in North America have declined by >98% from historic levels (Noss et al. 1995, Askins 2001, Thompson and DeGraaf 2001). This has lead to a widespread recognition of the importance of disturbance in community ecology and bird conservation (Thompson and Willson 1978, Botkin 1990, Brawn et al. 2001, Hunter et al. 2001, Lorimer 2001).

Restoring natural disturbance regimes is impractical in many places (Brawn et al. 2001), so ecologists must identify alternative processes to create disturbance. Scrub-successional habitats created by clearcutting often structurally resemble and provide similar resources to those shaped by natural disturbance (Welsh and Healy 1993, Askins 2001). However, humans typically perceive clearcuts as aesthetically unappealing (Hunter 1990, Gobster 2001), even though they effectively create early successional habitat for wildlife including many species of songbirds (Hunter 1990, DeGraaf et al. 1992, Costello et al. 2000, King et al. 2001). In fact, 95 of the 187 breeding species in the Midwest use regenerating forests during the breeding season (Thompson and Dessecker 1997). Furthermore, species richness and abundance often equal (Thompson and Fritzell 1990, Krementz and Christie 1999) or exceed (Conner and Adkisson 1975, Conner et al. 1979) that found in mature-forest habitat. Early successional forests representing shrub-scrub habitats are important for both early- and late-seral breeders during the migratory (Moore and Simons 1992, Moore et al. 1995, Parrish 1997) and over-wintering periods (Terborgh 1980, Kricher and Davis 1992, Wunderle and Waide 1993, Petit et al. 1995), presumably because they provide abundant food resources (Karr 1976, Hutto 1980, Martin 1985, Levey 1988, Loiselle and Blake 1990, Levey and Stiles 1992, Krementz and Christie 1999).

Populations of many early successional specialists are declining concomitantly with their habitat (Askins 2001, Hunter et al. 2001, Thompson and DeGraaf 2001). For example, New England cottontail (*Sylvilagus transitionalis*), Appalachian cottontail (*Sylvilagus obscurus*), bobcat (*Lynx rufus*; Litvaitis 2001), and several early successional birds are experiencing population declines (Askins 1993). These declines may be explained, in part, by a return to more natural levels of early successional habitats (Lorimer 2001). However, historical population sizes are often difficult to assess, and it is important to manage for uncommon and potentially at-risk species (Thompson et al. 1993). In addition, management for early successional habitat can be implemented while conserving large tracts of mature forest (Litvaitis 1993).

Clearcutting does raise several concerns when managing for forest wildlife. For example, open areas may act as a movement barrier for wildlife (Hass 1995, Sieving et al. 1996, Desrochers and Hannon 1997, Rail et al. 1997, St. Claire et al. 1998, Grubb and Doherty 1999, Belisle et al. 2001, Belisle and Desrochers 2002). However, any barrier effect caused by clearcut openings disappears following a few years of forest regeneration (Harris and Reed 2001, Robichaud et al. 2002). For example, Harris and Reed (2001) documented Black-throated Blue Warblers readily moving into open habitat created by clearcutting. Forest edges created by clearcutting may alter the microclimate (Matlack and Litvaitis 1999), vegetation (Chen et al. 1992, Fraver 1994, Euskirchen et al. 2001), and rates of nest depredation and brood parasitism on forest birds (Gates and Gysel 1978, Brittingham and Temple 1983, Wilcove 1985, Paton 1994, Donovan et al. 1995, Hoover et al. 1995, Manolis et al. 2002).

Although forest edges created by clearcuts are often abrupt (Hunter 1990, Matlack and Litvaitis 1999) and may act as an ecological trap for some species (Flaspohler et al. 2001), they do not appear to produce the extensive negative effects associated with agricultural and urban edges (Andrén 1995, Wiens 1995, Marzluff and Restani 1999, DeSante and Willson 2001). For example, Brown-headed Cowbirds (*Molothrus ater*) are positively correlated with agricultural habitat (Andrén 1992), but do not necessarily increase with the presence of forest edges or clearcuts, which lack the feeding opportunities present in agricultural systems (Rudnicky and Hunter 1993, Welsh and

Healy 1993). Even if higher numbers of Brown-headed cowbirds were found in forested landscapes with clearcuts compared to those without them, it might be the result of the greater diversity and abundance of potential hosts within regenerating stands (Annand and Thompson 1997).

Another concern is the possible increase in nest depredation associated with clearcuts. Nest depredation is often high in shrub habitats (Martin 1992, 1993), yet it is notably low in regenerating clearcuts (Rudnicky and Hunter 1993, King et al. 2001). This is likely the combined result of increased nest concealment (Rudnicky and Hunter 1993) and low predator abundance (King et al. 2001) in regenerating clearcuts. In fact, nest predators (King and DeGraaf 2000) and depredation rates (Ratti and Reese 1988, Rudnicky and Hunter 1993, King et al. 1999) are often lower in regenerating clearcuts than in mature forests. This may be, at least partially, a result of the lack of perching sites for avian predators (Yahner and Wright 1985), or the slow rate at which predators are able to colonize regenerating forests (Hanski et al. 1996). Furthermore, dense ground vegetation may reduce predator foraging efficiency (Bowman and Harris 1980, Yahner 1988, Martin 1992). Although corvids, important nest predators, may increase with agricultural habitat fragmentation (Andrén 1992), they have not been found to increase in managed compared to unmanaged forests (Thompson et al. 1992, Welsh and Healy 1993). The relationship between nest predators and fragmentation is complex (Chalfoun et al. 2002), and recent work suggests that both predator and cowbird abundance may largely be driven by landscape variables (Hahn and Hatfield 1995, Donovan et al. 1997, DeSante and Willson 2001, Rodewald and Yahner 2001). Overall, there is little evidence within forested landscapes for increased nest depredation at the clearcut/forest edge (Ratti and Reese 1988, Rudnicky and Hunter 1993, Andrén 1995, King et al. 1996, Marzluff and Restani 1999, Heske et al. 2001, Rodewald 2002; but see King et al 1996).

Rationale and Significance

Despite widespread concern for conservation of eastern forest birds over recent decades, most studies continue to overlook major components of their annual life cycle. Most notably habitat requirements during the post-breeding period remain poorly understood for most species. Anecdotal evidence suggests that adults and juveniles of many mature-forest species select early successional forests, perhaps due to increased food resources or protection from depredation. In fact, creating early successional forest habitat in a managed forest landscape may benefit Neotropical migrants by providing breeding habitat for early successional species, and post-breeding habitat for mature-forest species. Understanding the extent and causes of selection of early successional habitat is important because early successional habitat is declining throughout eastern North America. With a better understanding of post-breeding habitat requirements and use, biologists will be able to augment conservation plans.

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CHAPTER 2

Vegetation and fruit resources as reasons for use of regenerating clearcuts by mature-forest birds during the post-breeding period

ABSTRACT.–Recent studies have demonstrated that many birds of mature forests heavily use early successional habitat during the post-breeding period. The two most frequently invoked hypotheses to explain these shifts are that post-breeding birds select (1) dense cover to reduce risk of predation, and (2) abundant fruit resources that are easily obtained. However, no studies have explicitly examined evidence for these 2 hypotheses. I captured juveniles and adult post-breeding mature-forest birds in 12 regenerating hardwood clearcuts (3-7 years old) in southeast Ohio, using 9 mist-nets (12 m) per site. Each site was visited 9 days per season from 15 June – 16 August in 2002 and 2003, and 1648 mature-forest birds were captured during the post-breeding period. Vegetation structure and fruit resources were measured at each net and later used as predictors in 7 *a priori* models to evaluate habitat factors that explained capture rates. An information theoretic approach was used to build and subsequently rank models for 3 groups (all mature-forest birds during the post-breeding season, hatch-year only, after-hatch-year only) and 6 species of interest [Ovenbird (*Seiurus aurocapillus*), Worm-eating Warbler (*Helmitheros vermivorous*), Red-eyed Vireo (*Vireo olivaceus*), Hooded Warbler

(*Wilsonia citrina*), Scarlet Tanager (*Piranga olivacea*), and Wood Thrush (*Hylocichla mustelina*)]. Overall, models reflecting habitat structure (low vegetation, average canopy height) best explained variation in capture rates of mature-forest juveniles and post-breeding adults. Capture rates were negatively related to low vegetation and positively related to canopy height for all groups and species of interest except Scarlet Tanager and Red-eyed Vireo. The collective weight of evidence (i.e., summed weights for models containing the variable) for low vegetation across the 3 groups ranged from 88-97%, suggesting that low vegetation was an important variable. Although birds during the post-breeding period may use early successional habitats because they provide dense cover, extremely dense low vegetation may inhibit movements and provide cryptic locations for snakes and other predators. Instead, taller sites with comparatively less vegetation below 1.5 m may provide better protection from aerial and ground predators. Canopy height best explained use by Ovenbird, Hooded Warbler, and Wood Thrush with collective weights of evidence ranging from 76-98%. Scarlet Tanagers were positively associated with fruit, and this model best explained variation in their capture rates. Furthermore, the collective weight of evidence for fruit was 99%, strongly suggesting its importance for juvenile and post-breeding adult Scarlet Tanagers. Overall, results suggest that vegetation structure best explained use of early successional forests by many birds during the post-breeding period, although fruit may be the most important factor for Scarlet Tanager and other seasonal frugivores.

INTRODUCTION

Population declines have plagued several mature-forest species throughout eastern North America, (Robbins et al. 1989, Terborgh 1989, Askins et al. 1990, Askins 2001).

These declines stimulated much research on habitat loss and fragmentation on both the breeding and wintering grounds (Terborgh 1989, Askins et al. 1990). However, little attention has been given to the post-breeding period, which is defined as following nesting or fledging and continuing, up to 3 months, until the onset of fall migration (Pagen et al. 2000). The post-breeding period may be a particularly hazardous time for juveniles (Sherry and Holmes 1995), because they are inexperienced at foraging (Breitwisch et al. 1987, Jansen 1990, Desrochers 1992, VanderWerf 1994) and detecting and avoiding predators (Sullivan 1989, Wunderle 1991), as well as undergo their post-juvenal molt (Pyle et al. 1997). Adults may be vulnerable because of inhibited flight resulting from their pre-basic molt (Pyle et al. 1997). Not surprisingly, mortality rates can be extremely high for juveniles during the post-breeding period (Dhondt 1979, Krementz et al. 1989, Sullivan 1989, Anders et al. 1997). Recent studies suggest that juvenile survival during the post-breeding period may profoundly affect population demography (Anders et al. 1997). Consequently, unless a more thorough understanding of avian post-breeding habitat requirements is achieved, conservation strategies will be compromised.

Although habitat requirements of mature-forest birds traditionally have been assumed to be similar across much of their annual cycle, recent work illustrates they can be drastically different (Rappole and Ballard 1987, Anders et al. 1997, Vega Rivera et al. 1999, Pagen et al. 2000, Rimmer and McFarland 2000). For example, mature-forest birds often use early successional habitat at migratory stop-over sites (Moore et al. 1995) and on their wintering grounds (Petit et al. 1995), which may result from seasonal frugivory (Parrish 2000). Moore et al. (1990) documented greater use of shrub-scrub habitat by migrating birds than expected based on availability, suggesting that birds actively selected this habitat (Johnson 1980). Although shrub-scrub represented only 14% of the available habitat, it contained the highest abundance and diversity of migrants (Moore et al. 1990). On the wintering grounds, numerous studies have documented greater abundance of Neotropical migrants (including mature-forest breeders) using shrubby rather than forest habitats (Karr 1976, Terborgh 1980, Hutto 1992). Similarly, research on post-breeding ecology of mature-forest birds, although limited, has shown that young and adults of a number of species heavily utilize early successional forests (Thompson and Dessecker 1997, Anders et al. 1998, Vega Rivera et al. 1998b, Vega Rivera et al. 1999, Pagen et al. 2000, Powell et al. 2000). This shift in habitat use is often thought to reflect habitat selection based on probability of survival, as birds are no longer constrained by breeding requirements.

A common suggestion for this shift in habitat use is that birds during the post-breeding period seek out early successional habitat, in part due to fruit resources and dense cover associated with early successional forests (Desrochers 1992, Suthers et al. 2000). Dense cover and abundant food resources, generally found in early successional forests, may be especially important for survival because juveniles are extremely vulnerable to predators (Sullivan 1989, Anders et al. 1997) and migrants (juveniles and adults) must accumulate fat reserves to facilitate migration (Morton 1991, Faaborg et al. 1996). Numerous studies have documented lower foraging proficiency by juveniles relative to adults (Mueller and Berger 1970, Porter and Sealy 1982, Gochfeld and Burger 1984, Breitwisch et al. 1987, Jansen 1990, Desrochers 1992, VanderWerf 1994). This lack of foraging proficiency may result in starvation as a cause of juvenile mortality

(Krementz et al. 1989, Sullivan 1989). Juveniles may compensate for their lack of foraging proficiency by concentrating on easily captured or found food items (Breitwisch et al. 1984, Stevens 1985, Suthers et al. 2000). Fruit not only provides an easily captured and abundant food resource (Snow 1971, Wheelwright 1983), but may attract insects, further enhancing foraging opportunities in early successional forests. Abundant food resources also decrease the need to move widely in search of food, further reducing energy loss and exposure to predators. Conversely, dense cover providing protection from predators may be the primary impetus for selecting early successional habitats during the post-breeding period. Indeed, predation is frequently the primary cause of post-fledging mortality (Anders et al. 1997).

Although numerous studies invoke cover and fruit resources as underlying causes of shifts in post-breeding habitat use, none have explicitly compared the relative importance of food versus structural resources for post-breeding individuals. The goal of this study was to evaluate these 2 frequently suggested hypotheses driving habitat selection of early successional forests: (1) post-breeding birds select habitat based on fruit abundance, which provides easily accessible resources to inexperienced or molting birds, and (2) post-breeding birds select habitat based on vegetation structure and choose dense habitat that provides protection from predators.

METHODS

STUDY AREA

This study was conducted in southeast Ohio within the Zaleski State Forest and Mead-Westvaco Forest Lands (Athens, Vinton, Gallia, and Jackson counties; Appendix A). The area is characterized by rolling hills and is located within the Ohio Hills physiographic province, which is approximately 70% forested. These even-aged forests have regenerated from clearcutting in the early 1900's and are perforated by early successional forests from recent harvests. Non-forest land is concentrated in the valleys, and land uses consist of small towns, and agriculture. The vegetation is characteristic of the Mixed Mesophytic forest region (Brawn 1961). The most common tree species include yellow-poplar (*Liriodendron tulipifera*), white oak (*Quercus alba*), red oak (*Quercus rubra*), red maple (A*cer rubrum*), black gum (*Nyssa sylvatica*), sourwood (*Oxydendrum arboreum*), hickory (*Carya spp.*), white ash (*Fraxinus americana*), and sugar maple (*Acer saccharum*). Common breeding birds associated with mature forest in the study area include Red-eyed Vireo (*Vireo olivaceus*), Ovenbird (*Seiurus aurocapillus*), Worm-eating Warbler (*Helmitheros vermivorus*), Hooded Warbler (*Wilsonia citrina*), Scarlet Tanager (*Piranga olivacea*), Wood Thrush (*Hylocichla mustelina*), Eastern Wood-Pewee (*Contopus virens*), Acadian Flycatcher (*Empidonax virescens*), Black-and-white Warbler (*Mniotilta varia*), Cerulean Warbler (*Dendroica cerulea*), Carolina Chickadee (*Poecile carolinensis*), and Tufted Titmouse (*Baeolophus bicolor).*

I studied birds during the post-breeding period at 8 regenerating clearcut sites in 2002 and 12 sites in 2003 (adding 4 new sites to the original 8; Appendix B). Sites ranged from 3-7 years post harvest and were separated by at least 1 km. Regenerating clearcuts are comprised of dense vegetation and have poor visibility making avian surveys difficult. This difficulty is exacerbated during the post-breeding period, when songbirds are notably quiet and furtive (Faaborg et al. 1996, Pagen et al. 2000). Therefore, constant-effort mist-netting was conducted between 15 June and 16 August.

Mist-nets avoid problems associated with visual and auditory detection and effectively sample secretive or rarely vocal species (Karr 1981). Mist-netting also samples nearly the entire vegetative structure of early successional forests (Pagen et al. 2000), thereby reducing sampling bias (MacArthur and MacArthur 1974, Karr 1981, Remsen and Good 1996). Potential biases associated with mist-netting can result from varying capture rates due to inter- and intraspecific differences in mean flight distance and differences among nets in tension, angle, illumination, surrounding vegetative disturbance, wind, and condensation (Remsen and Good 1996).

NET PLACEMENT

I used 9 nets (12 m, 30 mm mesh) per site, and two sites were sampled simultaneously each day. Sites were sampled approximately once per week with a total of 9 visits per year. Nets were arranged systematically at each site, providing an equal sampling effort. Three parallel net lanes were separated by 50 m and extended perpendicular from the mature-forest edge with distance to any other edge at least 70 m. Within each lane a net was placed 20, 50, and 80 m from the mature-forest edge. All nets were oriented parallel to the mature forest edge (Appendix C). Nets were opened ½ hour before sunrise, closed 4.5 hours later, and cleared of birds every 30 minutes in order to minimize avian mortalities. Nets were moved between sites on a daily basis to reduce net avoidance by birds. All birds captured, except Ruby-throated Hummingbird (*Archilochus colubris*), were banded with a USGS aluminum band, and information collected included species, age, sex, molt, mass, fat, wing cord, and breeding condition. All hatch-year (HY) individuals and after-hatch-year (AHY) birds showing a wrinkled brood patch, flight feather molt, or extensive body molt (>25% of body), indicating completion of nesting were identified as post-breeding individuals (Pyle et al. 1997). Although some individuals of certain species are known to occasionally overlap breeding and molting (Jenni and Winkler 1994), the stages seldom overlap due to energy constraints (Murphy and King 1992, Butler et al. 2002).

FRUIT SAMPLING

Fruits were sampled 3 times at bi-weekly intervals from 7 July – 15 August. Sampling was conducted within two transects (1 x 12 m each) oriented parallel to and 1 m from both sides of each net (24 m^2 per net site; Levey 1988, Blake and Loiselle 1991, Suthers et al. 2000). For each plant species I recorded total number of fruits over all individual plants within the belt transect. Ripe, unripe, and spent fruits were assessed separately. Fruits that were green to pinkish in color were identified as unripe, dark pink to black fruits were ripe, and desiccated fruits were classified as spent. There was a high correlation between ripe and potential (ripe + unripe fruit) fruit ($r = 0.83$, $n = 108$). Therefore, potential fruit was used in analysis because it reflected future fruit availability (Blake et al. 1990). This was important because *Rubus*, the dominant fruiting plant, both ripens and is consumed quickly, and large quantities of fruit would have been missed if only ripe fruit was examined.

VEGETATION SAMPLING

Vegetation was sampled at each mist-net using a modified James and Shugart (1970) method. A 0.04 ha circular plot was established at the center of each net, providing 9 plots per site. Vegetation structure was measured along two 10 m transects at each net by recording the number of total vegetation hits (i.e., number of times leaves or stems touched a pole) from 0.5-3.0 m in 0.5 m increments using a telescoping pole.

Vegetation hits were identified as either low (0.5-1.5 m above the ground, hereafter low vegetation) or high (1.5-3.0 m above the ground, hereafter high vegetation). Canopy cover (cover > 5 m) was assessed every 2 m along each 10 m transect by recording the presence or absence of vegetation at the crosshairs of an ocular tube (0 = no hit, 1 = hit), and then averaged to generate an estimate of percent canopy cover. The 3 dominant sapling and shrub species within the plot also were identified. Number of small (12-23 cm diameter at breast height, dbh), medium (23-38 cm dbh) and large (>38 cm dbh) snags, residual trees, and logs longer than 1.0 m with a diameter >7.5 cm were counted. Finally, the average canopy height throughout the 0.04 ha circular plot was estimated using the telescoping pole.

DATA ANALYSIS

Prior to analysis, variables not meeting the assumption of normality were square root transformed. Because residual trees and snags were uncommon at all sites, they were not included in analysis. High vegetation was removed from analysis because it was highly correlated with average canopy height ($r = 0.71$, $n = 108$), which had the advantage of characterizing the forest above 3 m. Average canopy height and low vegetation had a modest negative correlation ($r = -0.51$, $n = 108$). Ecologically this was logical because as the canopy closes the understory gets shaded out.

Vegetation structure of early successional forests is typically heterogeneous due to patches of saplings interspersed with shrubs and bare ground. Consequently, much of the relevant variation in microhabitat features and avian captures occurred at a fine scale. To account for this, I used net-level data in hierarchical linear models with a nested design. Hierarchical linear models allow simultaneous analysis at multiple nested spatial or temporal levels (Osborne 2000). Random effects can be specified for both continuous and categorical variables, and variation can be partitioned at each level of data (Littell et al. 2002). Explanatory variables measured at nets were nested within sites. I developed a set of 7 *a priori* candidate models, based on evidence from previous studies, to explain patterns of habitat use of birds during the post-breeding period. An information theoretic approach was used to build and subsequently rank models containing food (fruit abundance) and cover (low vegetation, average canopy height) variables. Model included combinations of the variables fruit, low vegetation, and average canopy height for each of the 3 groups (all juvenile and adult post-breeding mature-forest birds, AHY post-breeders, juveniles) and 6 species of interest (Ovenbird, Worm-eating Warbler, Red-eyed Vireo, Hooded Warbler, Scarlet Tanager, Wood Thrush). I calculated delta AIC (Δ_i, Akaike's Information Criterion), and Akaike's weights (w_i) from AIC_c values (used for small sample size; Burnham and Anderson 1998) generated using a nested analysis in Proc Mixed (SAS Institute 1990). The model with the smallest AIC_c was considered the best explanatory model, however, other models with a delta AIC (Δ_i) < 2 were considered equally plausible in light of the data (Burnham and Anderson 1998).

RESULTS

I captured 590 mature-forest birds during the post-breeding period in 2002 and 1058 in 2003 (Appendices D, E, F). The total number of mature-forest birds during the post-breeding period consisted of 1165 HY and 483 AHY individuals. The most commonly captured species were Ovenbird, Worm-eating Warbler, Red-eyed Vireo, Hooded Warbler, Scarlet Tanager, and Wood Thrush (in order of decreasing abundance).

Of the 7 candidate models, capture rates of birds during the post-breeding period were best explained by the model containing only low vegetation, which explained captures of all birds nearly 3x better than the second best model (Table 2.1). Low vegetation similarly best explained captures of HY and AHY birds and was 2.2x and 1.4x, respectively, more plausible than the second best model. In both cases, the model containing both low vegetation and average canopy height were considered equally plausible (ΔAIC < 2). In fact, the 3 groups had collective weights of evidence (i.e., summed weights for models containing the variable) ranging between 88-97% for low vegetation, suggesting it was an important variable. Interestingly, these groups displayed an inverse relationship with low vegetation (Fig. 2.1).

The same 7 candidate models used to identify important variables for post-breeding groups also were applied to the 6 species of interest (Table 2.1). Canopy height ranked within the top 2 models for all individual species except Scarlet Tanager. Specifically, it was identified as the top model for Ovenbird, Hooded Warbler, and Wood Thrush, where increased capture rates were associated with increased canopy height (Fig. 2.2). For Ovenbird, the model containing both fruit and low vegetation was equally plausible in light of the data. For Wood Thrush, low vegetation also ranked closely. Still, the collective weight of evidence for canopy height ranged from 76-98%, emphasizing its importance for these species. The model containing low vegetation was the top model for Worm-eating Warbler and Red-eyed Vireo (Fig. 2.3). In most cases, the model containing low vegetation and canopy height were considered equally plausible in light of the data (ΔAIC < 2). The importance for low vegetation was revealed by the high collective weights of evidence (88% for Worm-eating Warbler and

93% for Red-eyed Vireo). Red-eyed Vireo showed a positive relationship while Worm-eating Warbler was negatively related to low vegetation. The model containing fruit best explained capture rates for Scarlet Tanager, and the collective weight of evidence for fruit was 99%, providing strong support for its importance. Fruit abundance was positively related to capture rates of Scarlet Tanager (Fig. 2.4).

DISCUSSION

A number of studies have documented mature-forest birds moving into early successional forests during the post-breeding period, and some have suggested that dense cover and/or abundant food resources explain patterns of habitat selection (Anders et al. 1998, Vega Rivera et al. 1998b, Marshall et al. 2003). However, few have explicitly studied the underlying reasons for this shift (but see Vega Rivera et al. 1998b). I not only documented substantial use of early successional forests by mature-forest birds during the post-breeding period, but also examined underlying causes of this habitat shift. In general, birds during the post-breeding period were negatively associated with low vegetation and positively associated with average canopy height.

As suggested by others, vegetation structure was the most important factor associated with post-breeding bird use of regenerating forests in my study (Vega Rivera et al. 1998b, Bayne and Hobson 2001). Interestingly, higher capture rates of mature-forest birds during the post-breeding period were associated with less dense low vegetation. For example, capture rates were 1.5x and 2.5x greater in nets surrounded by sparse vegetation (<50 vegetation hits) than those with dense vegetation (>150 vegetation hits) for all juveniles and adult post-breeders and AHY post-breeders respectively. Extremely dense patches of low vegetation may inhibit foraging movements by birds, while providing cryptic locations for snakes, which are often a primary predator in early successional habitats (Thompson and Burhans 2003). As shrubs and saplings get taller they begin to shade out the lowest vegetation and may provide better protection from aerial and ground predators. Because low vegetation structure had a moderate negative correlation with average canopy height, there is the possibility that birds were selecting microhabitat based on canopy height. In fact, capture rates were nearly 2x higher in nets associated with a high canopy (>4.5 m) compared to a low canopy (<2.5 m) for Ovenbird and over 6x higher for Wood Thrush. Although the model containing both canopy height and low vegetation structure was never the top model, the two variables explained a substantial amount of variation in capture rates of several groups (juvenile and adult post-breeders, juveniles, AHY post-breeders, Worm-eating Warbler, Red-eyed Vireo, and Wood Thrush). These data suggest that vegetation structure is the primary feature attracting many mature-forest post-breeding birds to early successional forests.

Whereas the abundance of mature-forest juveniles and post-breeders appeared to be explained better by vegetation structure than fruit resources, fruit was the most important variable when explaining captures of Scarlet Tanager. Tanager capture rates were 2.5x greater in nets with high (>600) compared to low (<100) fruit abundance. This comes as little surprise because Scarlet Tanagers are known to be highly frugivorous outside the breeding period (Mowbray 1999). In fact, 81% of tanagers that we captured during the post-breeding period in 2003 had fruit stains on their bill. In a pilot study, I found that older clearcuts (10 years post-harvest) with closed canopy and limited fruit were seldom used by Scarlet Tanagers during the post-breeding period, and only 2 birds were captured in 1023 net hours at 3 sites. Although the relationship with fruit was strongest for Scarlet Tanagers, I also documented fruit on the bills of Wood Thrush, Ovenbird, and Red-eyed Vireos, which are also known to consume fruit outside of the breeding period (Parrish 2000). For Ovenbirds the second ranked and equally plausible model contained fruit. Fruit at all sites was dominated by *Rubus* species, and small-gaped birds may be unable to capitalize on this temporally abundant but large food resource (Martin 1985). Arthropods also are attracted to fruit, which may further attract post-breeding birds.

My findings support the frequent suggestion that post-breeding use of early successional forests by mature-forest breeders is a response to both vegetation structure and abundant fruit resources (Anders et al. 1998, Vega Rivera et al. 1998b). Birds during the post-breeding period are extremely vulnerable to predators because HY birds are inexperienced and AHY birds have limited flight capabilities while they molt their flight feathers (Vega Rivera et al. 1998a). This vulnerability may cause the breeding habitat of many species becoming unsuitable during the post-breeding season. To reduce their risk of predation, post-breeding birds may select habitat where they are able to forage and rest in the relative safety of dense cover (Anders et al. 1998). Several studies have found that juvenile birds experience high mortality rates (Sullivan 1989, Anders et al. 1997, A.M. Maxted unpub data). For example, Anders et al. (1997) reported 58% mortality of radio-tagged HY Wood Thrush (51% from depredation) during the first 4 weeks post-fledging and A.M. Maxted (unpublished data) reported 61% mortality rates of Yellow-breasted Chats (*Icteria virens*) and Gray Catbirds (*Dumetella carolinensis*) 8 weeks after fledging. Predation rates are frequently highest during the first week post-fledging when birds were still learning to fly and the third week when they gained independence and foraged conspicuously (Sullivan 1989, Anders et al. 1997, Powell et al. 2000). Shortly after achieving independence, juvenile birds may disperse into thicker habitats, presumably to reduce their predation risk. In fact, several studies have documented a sharp decline in mortality for HY (Anders et al 1997) and AHY (Powell et al. 2000) individuals immediately following a shift into denser habitat. Thick habitats may be riparian thickets, edges, or early successional forests and have been labeled 'safe havens' (Anders et al. 1997). Regenerating clearcuts have comparable leaf area to a mature forest compressed into a few meters above the ground (Keller et al. 2003), and may provide the greatest benefits in terms of reduced depredation.

Another important outcome of this study was documentation of heavy use of early successional forests by birds during the post-breeding period. Most of the species known to breed in mature forests in my study area were captured in the early successional plots during the post-breeding season – 31 species in all. In fact, the only species known to breed in the region that were not captured included White-breasted Nuthatch (*Sitta carolinensis*), Pileated Woodpecker (*Dryocopus pileatus*), Northern Parula (*Parula americana*), and Ruffed Grouse (*Bonasa umbellus*). Although Northern Parula and Ruffed Grouse heavily use early successional forests during the post-breeding period (Thompson and Dessecker 1997, Pagen et al. 2000), parulas are uncommon in the study region (Peterjohn 2001) and grouse are too large to be captured with our mist-nets. Similar to my findings, others have captured both a high diversity of mature-forest birds and high numbers of Ovenbird, Worm-eating Warbler, and Red-eyed Vireo in early successional forest stands during the post-breeding period (Pagen et al. 2000, Marshall et al. 2003). Noteworthy captures from my study included several Cerulean Warbler

(*Dendroica cerulea*), Louisiana Waterthrush (*Seiurus motacilla*), and Eastern Wood-Pewee (*Contopus virens*). Two hatch-year Cerulean Warblers were observed foraging together at a site suggesting early successional habitats are used by Cerulean Warbler family groups or flocking juveniles (A.C. Vitz, personal observation). Similar to the findings of Marshall et al. (2003), I regularly captured a juvenile and adult of the same species in a net suggesting regenerating forests are frequently used by family groups of mature-forest birds. There is one striking contrast to the Marshall et al. (2003) study. Whereas the majority of mature-forest birds documented during the post-breeding period by Marshall et al. (2003) were AHY individuals, most captured birds in my study were HY individuals (71%). This difference may have been the result of variation in annual productivity. Because I found HY birds heavily using early successional forests, availability of this habitat may have important implications for recruitment.

The large number of mature-forest birds captured during the post-breeding period is likely not attributed to breeding activity in regenerating forests. All of the regenerating clearcuts were ≤ 7 years post harvest, and breeding surveys conducted over 2 years at all sites detected very few forest birds (A.D. Rodewald, unpublished data). My study sites will probably remain unsuitable as breeding habitat until they reach ~10 years post harvest, and at that point Ovenbird, Wood Thrush, and Worm-eating Warbler may begin using them for breeding (Pagen et al. 2000). Furthermore, > 85% of mature-forest birds captured in the regenerating stands had post-breeding characteristics. Of the 15% lacking post-breeding characteristics, most also lacked breeding characteristics (i.e., brood patch or cloacal protruberance) and were probably nonbreeding individuals (i.e., floaters). A strategy for floaters may be to forage in early successional forests in order to reduce predation risk and aggression from conspecifics. Only a few captured mature-forest birds were in breeding condition (mostly Hooded Warbler) suggesting that birds breeding near the edge may forage in early successional stands, but those captures were omitted from analysis.

One potentially important factor that was not examined in this study was invertebrate resources. As part of another study I sampled arthropods at the site level and found high variability among sites (coefficient of variance > 36). Unfortunately, these data could not be modeled at the net level. Early successional forests may have a higher abundance of arthropods than mature-forests (Janzen 1973, Jokimäki et al. 1998, Keller et al. 2003). Lepidopterans, heavily preyed upon by birds, seem to be especially high in regenerating stands (Keller et al. 2003). Furthermore, evidence exists that arthropods prefer to graze on young leaves (Coley 1983) and leaves of early successional species (Edwards-Jones and Brown 1993, Farji-Brener 2001) due to high nutrition value and low levels of secondary compounds. Thus, the possibility remains that birds may select early successional habitats, at least partly, due to high arthropod abundance.

To my knowledge, this study documented the greatest species diversity and abundance of mature-forest birds found in regenerating clearcut stands. This clearly illustrates the importance of early successional forests for birds during the post-breeding period and supports their consideration in conservation activities. While my study suggests that reasons for this habitat shift vary by species, vegetation structure and fruit resources both appear to play important roles. My results demonstrate that animals must be studied across their life cycle to identify key habitats and resources. Most studies on breeding mature-forest species focus on the importance of large forest tracts for breeding

(Rosenberg et al. 1999). By disregarding the post-breeding season, studies fail to recognize that early successional forests are heavily used during the post-breeding period may even improve survival and recruitment of juveniles into the population. My study suggests that maintenance of early successional forests may be an important strategy for forest bird conservation. Future research should evaluate if access to early successional forests decreases mortality during the post-breeding season.

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Table 2.1 Model statements describing microhabitat features in relation to group and species capture rates in regenerating clearcuts in southeast Ohio in 2002 and 2003. Best supported models have a smaller delta AIC (Δ_i), and larger Akaike weights (ω_i).

Model statements	K	AIC_c	Δ_i	ω_i
All birds				
Lowveg[a]	5	253.20	0.00	0.720
Canopy Lowveg	6	255.30	2.10	0.252
Canopy[b]	5	259.70	6.50	0.028
Fruit Lowveg	6	273.80	20.60	0.000
Fruit[c]	5	274.90	21.70	0.000
Lowveg canopy fruit	7	275.70	22.50	0.000
Fruit Canopy	6	277.10	23.90	0.000
HY birds				
Lowveg	5	245.80	0.00	0.604
Canopy Lowveg	6	247.40	1.60	0.272
Canopy	5	249.00	3.20	0.122
Fruit	5	258.80	13.00	0.001
Fruit Lowveg	6	260.20	14.40	0.000
Fruit Canopy	6	260.70	14.90	0.000
Lowveg canopy fruit	7	261.40	15.60	0.000
AHY birds				
Lowveg	5	146.10	0.00	0.565
Canopy Lowveg	6	146.80	0.70	0.398
Canopy	5	152.50	6.40	0.023
Fruit Lowveg	6	154.40	8.30	0.009
Lowveg canopy fruit	7	156.00	9.90	0.004
Fruit Canopy	6	160.70	14.60	0.000
Fruit	5	164.40	18.30	0.000
Ovenbird				
Canopy	5	382.40	0.00	0.387
Fruit Lowveg	6	383.80	1.40	0.192
Lowveg canopy fruit	7	384.20	1.80	0.157
Fruit Canopy	6	384.90	2.50	0.111
Canopy Lowveg	6	385.00	2.60	0.106
Lowveg	5	387.10	4.70	0.037
Fruit	5	389.80	7.40	0.010

Table 2.1 (continued)

Worm-eating Warbler				
Lowveg	5	120.30	0.00	0.597
Canopy Lowveg	6	122.10	1.80	0.243
Canopy	5	123.90	3.60	0.099
Fruit Lowveg	6	126.20	5.90	0.031
Lowveg canopy fruit	7	127.90	7.60	0.013
Fruit Canopy	6	128.30	8.00	0.011
Fruit	5	129.30	9.00	0.007
Red-eyed Vireo				
Lowveg	5	143.70	0.00	0.563
Canopy Lowveg	6	144.60	0.90	0.359
Canopy	5	148.10	4.40	0.062
Fruit	5	152.70	9.00	0.006
Fruit Canopy	6	153.00	9.30	0.005
Lowveg canopy fruit	7	154.40	10.70	0.003
Fruit Lowveg	6	154.90	11.20	0.002
Hooded Warbler				
Canopy	5	99.60	0.00	0.735
Lowveg	5	102.80	3.20	0.148
Canopy Lowveg	6	104.60	5.00	0.060
Fruit Lowveg	6	105.80	6.20	0.033
Lowveg canopy fruit	7	108.00	8.40	0.011
Fruit	5	109.30	9.70	0.006
Fruit Canopy	6	109.30	9.70	0.006
Scarlet Tanager				
Fruit	5	85.90	0.00	0.536
Fruit Lowveg	6	88.00	2.10	0.188
Fruit Canopy	6	88.00	2.10	0.188
Lowveg canopy fruit	7	89.90	4.00	0.073
Canopy	5	93.00	7.10	0.015
Lowveg	5	98.80	12.90	0.001
Canopy Lowveg	6	100.20	14.30	0.000
Wood Thrush				
Canopy	5	45.80	0.00	0.401
Canopy Lowveg	6	46.30	0.50	0.313
Fruit Canopy	6	47.90	2.10	0.140
Lowveg canopy fruit	7	48.10	2.30	0.127
Lowveg	5	52.80	7.00	0.012
Fruit Lowveg	6	54.10	8.30	0.006
Fruit	5	62.00	16.20	0.000

[a]Number of Low vegetation hits (0.5-1.5 m) measured at each net. [b]Average canopy height within 0.04ha circular plot at each net. [c]Number of fruit per net.

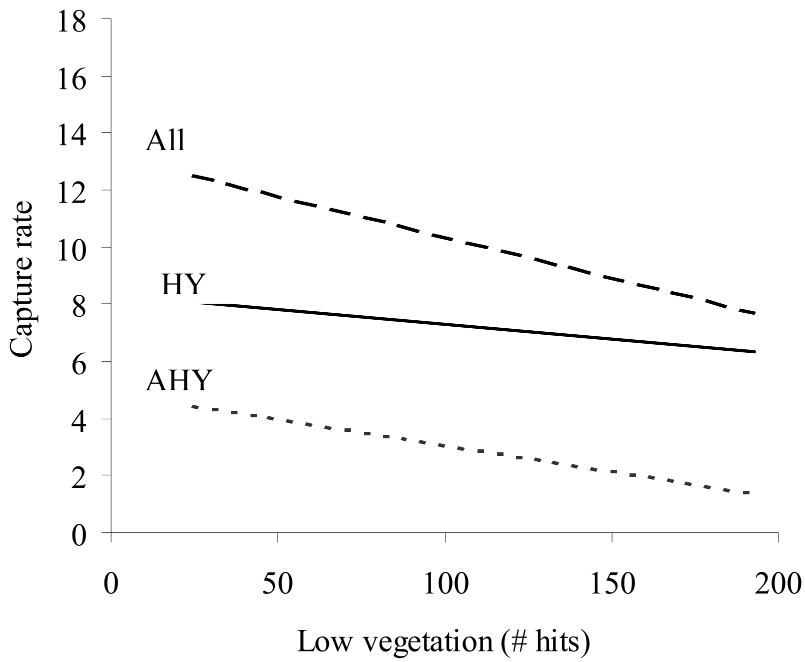

Figure 2.1. The relationship between low vegetation (number of vegetation hits 0.5–1.5 m) and captures (per 100 net hours) of all birds, HY, and AHY birds in southeast Ohio, 2002-2003.

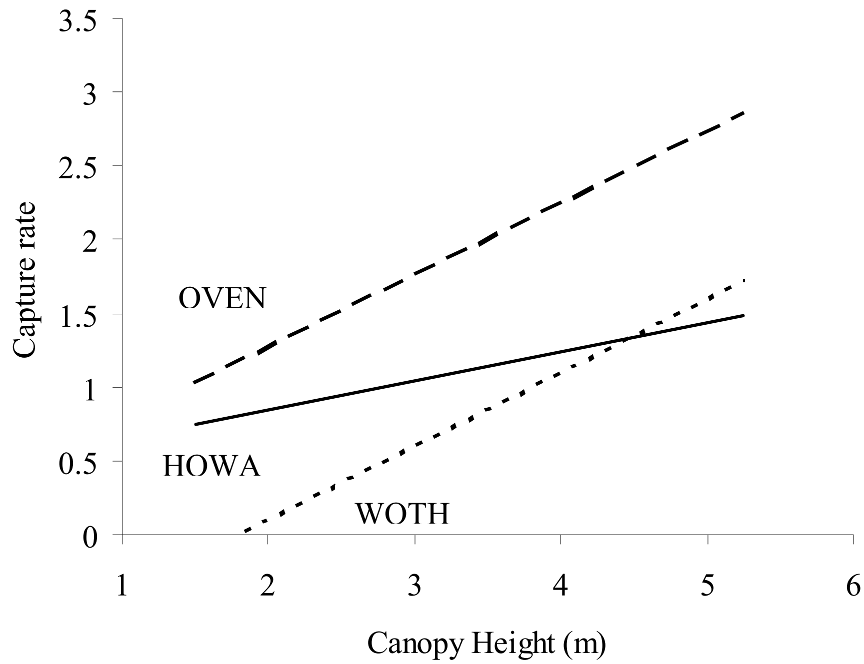

Figure 2.2. Captures of birds per 100 net hours compared to canopy height for Ovenbird, Hooded Warbler, and Wood Thrush in southeast Ohio, 2002-2003.

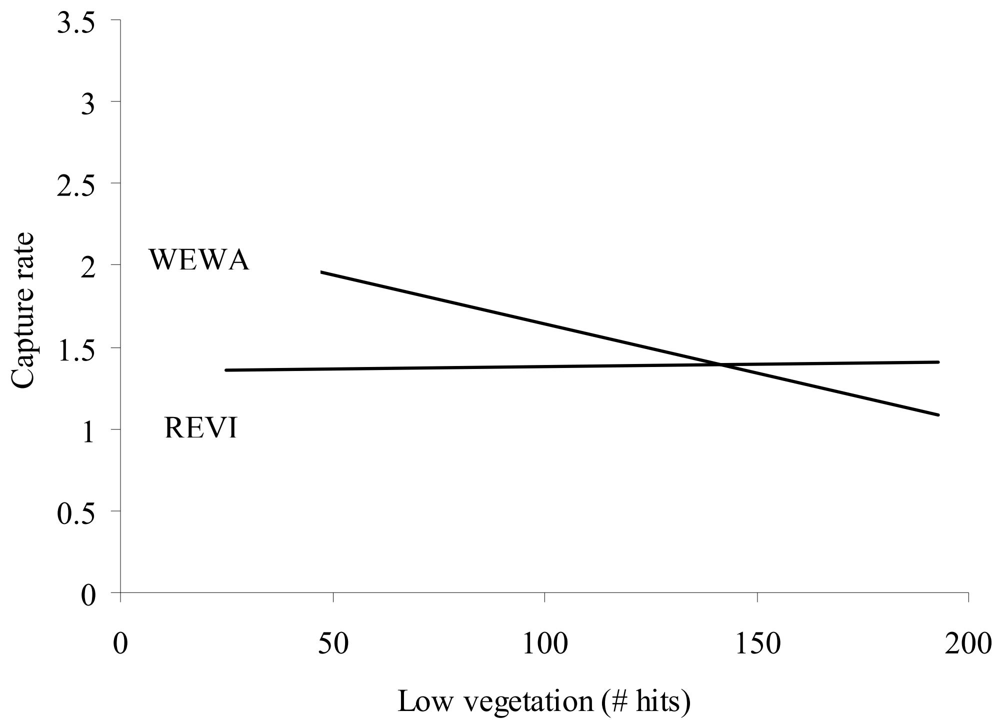

Figure 2.3. Capture rates (per 100 net hours) of Worm-eating Warbler and Red-eyed Vireo with respect to low vegetation (number of vegetation hits 0.5–1.5 m) in southeast Ohio, 2002-2003.

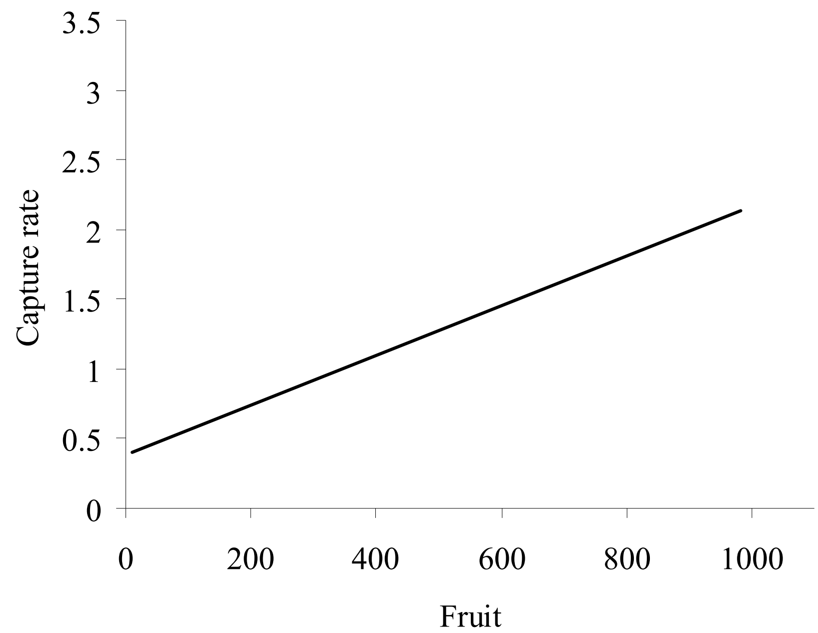

Figure 2.4. Capture rates of Scarlet Tanagers per 100 net hours compared to average fruit per net in southeast Ohio, 2002-2003.

CHAPTER 3

Area and edge sensitivity of mature-forest birds during the post-breeding period

Abstract: For decades, clearcuts were widely regarded as detrimental to birds associated with mature forest. However, recent studies have demonstrated that regenerating clearcuts can provide habitat for many avian species associated with mature forest during the post-breeding period. No study has evaluated the sensitivity of post-breeding birds to edges or size of cuts, yet these features can be directly manipulated by wildlife and forest managers. I examined how capture rates of mature-forest birds during the post-breeding period were related to stand size and distance to the mature forest edge and evaluated if habitat features explained patterns of habitat use. I selected 12 regenerating hardwood clearcuts that represented small (4-9 ha) and large (13-18 ha) stands in southeast Ohio. Sites ranged from 3-7 years post-harvest and were separated by at least 1 km. Constant effort mist-netting (9 nets per site) was utilized between 15 June – 16 August in 2002 and 2003 to quantify bird abundance, and vegetation and food variables were measured at each net. A split-plot analysis of variance, where the whole-plot unit (site) consisted of 3 split-plot units (distance categories), was used to test for differences in capture rates with stand size and distance to the mature-forest edge. I used multiple `analysis of variance to test for differences among groups and individual species and habitat variables with respect to stand size and distance from the mature forest edge while controlling for overall experiment-wise error rates. I captured 1648 mature-forest birds during the post-breeding period in 7331 net hours over 2 years. Capture rates were significantly greater in small than large clearcuts, and this effect was most pronounced for Scarlet Tanager (*Piranga olivacea*), Wood Thrush (*Hylocichla mustelina*) and Hooded Warbler (*Wilsonia citrina*). Interestingly, captures of mature-forest birds during the post-breeding period increased with distance to the mature forest edge (from 20-80 m), and the apparent preference for interiors of clearcuts was strongest in large clearcuts. These patterns cannot be attributed to habitat differences, as food and vegetation variables did not vary with stand size or distance from the edge. Overall, the results show that birds heavily use regenerating clearcuts during the post-breeding period, but that individuals may be sensitive to edges and size of cuts. Managers seeking to create early successional forests that provide valuable habitat for both early and late successional species may need to consider size and shape of clearcuts.

INTRODUCTION

Human-induced changes in disturbance regimes over the last two centuries have substantially altered forested ecosystems in eastern North America and, in particular, have reduced amounts of early-successional habitats. Concomitantly, wildlife associated with early successional forests have shown regional and range-wide population declines (Hunter et al. 2001, Thompson and DeGraaf 2001). This is particularly important because a surprising number of forest wildlife species in North America depend on regular disturbance (Askins 1993, Brawn et al. 2001). For example, Hunter et al. (2001) recognized 128 avian species in eastern North America that are associated with disturbance-maintained habitats. Some of these species, including shrubland birds, require disturbance to be regularly applied to relatively large areas of the landscape (Rudnicky and Hunter 1993, Annand and Thompson 1997, Robinson and Robinson 1999, Costello et al. 2000). Currently, forest harvesting, especially via even-aged techniques such as clearcutting, is one of the most efficient methods to create early successional habitat in eastern forests (Conner et al. 1979, Thompson and Fritzell 1990, Keller et al. 2003), but large-scale forest clearing raises questions concerning habitat loss and fragmentation of mature forest habitat. One of the central challenges to managing appropriate amounts of seral stages within a landscape will be to balance the needs of early and late successional species, as the two groups respond differently to management practices and may differ widely in what is perceived as a "suitable" landscape.

Traditionally, clearcuts have been viewed as having largely negative influences on birds associated with mature forests. For example, habitat edges created by clearcutting can be detrimental to breeding birds due to increased nest predation and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*; Hagan et al. 1996, King et al. 1996). Widespread timber harvesting could negatively affect breeding birds by reducing the size of mature-forest patches (Ambuel and Temple 1983). Numerous studies have demonstrated that small forest tracts have lower abundance, diversity, and reproductive success of breeding birds than large forest tracts (Whitcomb et al. 1981, Ambuel and Temple 1983, Blake and Karr 1984, 1987, Robbins et al. 1989).

A striking contrast is that recent studies demonstrated that many mature-forest birds select early successional habitat during the post-breeding season, which begins with fledging of the young and lasts until fall migration (Rappole and Ballard 1987, Morton

1991, Baker 1993, Vega Rivera et al. 1998b). The combination of dense vegetation cover and abundant fruit resources seems to promote use of shrub patches by fledgling and post-breeding birds, including Wood Thrush (*Hylocichla mustelina)*, Red-eyed Vireo (*Vireo olivaceus)*, Scarlet Tanager (*Piranga olivacea)*, Ovenbird (*Seiurus aurocapillus)*, Hooded Warbler (*Wilsonia citrina)*, and Worm-eating Warbler (*Helmitheros vermivorus*; Anders et al. 1998, Vega Rivera et al. 1998b, Pagan et al. 2000, Marshall et al. 2003). One frequently invoked explanation for use of early successional forests by mature-forest birds during the post-breeding period is that dense vegetation structure decreases predation risk. Indeed, post-breeding season birds are especially vulnerable to predation, and mortality rates can be extremely high for post-breeding birds, especially inexperienced juveniles (Sullivan 1989, Anders et al. 1997). Post-breeding birds also may select early-successional forests for their abundant fruit resources. Fruit comprises a majority of the diet for many migrating (Parrish 2000) and overwintering (Rappole 1995) passerines, and the same may be true for post-breeding individuals (Martin et al. 1951, Vega Rivera et al. 1999).

Because habitats used by breeding early-successional and late-successional birds during the post-breeding period appear similar, there would seem to be a real opportunity to meet both of their needs within the same stands. However, habitat selection by post-breeding birds may be constrained by edge and area-sensitivity, which is true for many species during the breeding season. Like their mature forest counterparts, small patches of early successional forests have a high ratio of edge to interior habitat. Forest edges created by clearcutting are abrupt (Matlack and Litvaitis 1999) and may alter the microclimate (Matlack 1993), vegetation structure (Chen et al. 1992, Fraver 1994, Euskirchen et al. 2001), food supply (Burke and Nol 1998, Zanette et al. 2000) and predator community (Gates and Gysel 1978, Whitcomb et al. 1981, Brittingham and Temple 1983, Wilcove 1985, Yahner and Scott 1988, Paton 1994, Donovan et al. 1995, Flaspohler et al. 2001). Birds during the post-breeding period may be attracted to edges, or small early successional stands if birds (1) regularly move between mature forest and shrublands, (2) prefer the greater vertical diversity of the habitat, and (3) encounter a greater diversity of plant and animal foods along edges (due to increased heterogeneity). Conversely, interior early successional habitat (or large early successional stands) may attract post-breeding birds if edges (1) concentrate predators (e.g., abundant perching sites for raptors), (2) contain fewer fruits or reduced arthropod numbers or activity due to reduced sun exposure (via shading by overstory trees), (3) contain less foliage or stem volume than interior areas, or (4) promote conflicts with late breeding conspecifics in the forest. After-hatch-year (AHY) and hatch-year (HY) birds during the post-breeding period may respond differently to edge and patch size within early successional forests because AHY birds are not only dominant over HY individuals, but may have different dietary preferences, foraging abilities, and vulnerability to predators (Wunderle 1991).

Currently, the sensitivity of post-breeding birds to patch size or edges of regenerating forests is completely unknown. Information on avian response to patch size is particularly important when evaluating the appropriate composition and configuration of a forested landscape for bird conservation. I evaluated the extent to which mature-forest birds during the post-breeding period show area or edge sensitivity when using early successional forests created through clearcutting.

METHODS

Study Area

This study was conducted in southeast Ohio within the Zaleski State Forest (Athens and Vinton Counties) and Mead-Westvaco Forest Lands (Vinton, Gallia, Athens, and Jackson Counties; Appendix A). The region is within the Ohio Hills physiographic province and is characterized by rolling hills. Land cover is composed of approximately 70% forest dominated by mature even-aged stands perforated by early successional stands. Non-forest land is concentrated in the valleys, where land use consists of small towns and agriculture. The vegetation is typical of the Mixed Mesophytic forest region (Brawn 1961). The most common tree species include: yellow-poplar (*Liriodendron tulipifera*), white oak (*Quercus alba*), red oak (*Quercus rubra*), red maple (*Acer rubrum*), black gum (*Nyssa sylvatica*), sourwood (*Oxydendrum arboreum*), hickory (*Carya spp.*), white ash (*Fraxinus americana*), and sugar maple (*Acer saccharum*). Common mature-forest breeding birds are Red-eyed Vireo, Ovenbird, Worm-eating Warbler, Hooded Warbler, Scarlet Tanager, Wood Thrush, Eastern Wood-Pewee (*Contopus virens*), Acadian Flycatcher (*Empidonax virescens*), Black-and-white Warbler (*Mniotilta varia*), Cerulean Warbler (*Dendroica cerulea*), Carolina Chickadee (*Poecile atricapillus*), and Tufted Titmouse (*Baeolophus bicolor)*.

I studied the abundance of mature-forest birds during the post-breeding period in 8 hardwood regenerating clearcuts in 2002 and 12 in 2003 (adding 4 sites to the original 8; Appendix B). Constant-effort mist-netting was used to document abundance between 15 June and 16 August in 2002 and 2003. Sites were equally divided into small (4-9 ha) and large (13-18 ha) sizes (4 each in 2002, 6 each in 2003), and resembled a square in shape. All sites ranged from 3-7 years post harvest and were separated by at least 1 km.

Early successional forests are notoriously difficult to sample for birds due to poor visibility, and this problem is exacerbated during the post-breeding period when songbirds are notably quiet and furtive (Faaborg et al. 1996, Pagen et al. 2000). Mist-netting avoids both visual and auditory biases, and effectively samples secretive or rarely vocal species (Karr 1981). Furthermore, mist-netting is an especially effective method for detecting birds in early successional forests because the low structure (i.e. canopy ca. 2-5 m tall) allows sampling across all or most of the vegetative structure (Pagen et al. 2000), thereby reducing sampling bias associated with this method. Nonetheless, biases associated with mist-netting remain (MacArthur and MacArthur 1974, Karr 1981, Remsen and Good 1996). These include varying capture rates due to interspecific and intraspecific differences in mean flight distance and differences among nets in tension, angle, illumination, surrounding vegetative disturbance, wind, and condensation, all of which can affect capture rates (Remsen and Good 1996).

Net Placement

I used 9 nets (12 m long, 2.6 m high, 30 mm mesh) per site, and two sites were sampled simultaneously each morning. Sites were sampled approximately once per week with a total of 9 visits per year. Nets were arranged systematically at each site, providing an equal sampling effort. I created 3 net lanes separated by 50 m and extending perpendicular from the mature-forest edge. Within each lane a net was placed 20, 50, and 80 m from the mature-forest edge and the distance to any other edge was at least 70 m. In addition, all nets were oriented parallel to the mature-forest edge (Appendix C). Nets were opened 0.5 hour before sunrise, were closed 4.5 hours later, and were cleared of birds every 30 minutes. Nets were moved between sites on a daily basis to reduce net avoidance by birds. All birds captured (except hummingbirds) were banded with a USGS aluminum band, and information collected including species, age, sex, molt, mass, fat, wing cord, and breeding condition. Post-breeding individuals included all hatch-year individuals and after-hatch-year birds showing a wrinkled brood patch, flight feather molt, or extensive body molt ($\geq$ 25% of body) indicating completion of nesting (Pyle et al. 1997). Although some species occasionally overlap molting with breeding (Jenni and Winkler 1994) or migration (Leu and Thompson 2002), this is uncommon due to energy constraints (Murphy and King 1992, Butler et al. 2002).

Microhabitat Sampling

Fruit abundance, arthropod abundance, and vegetation structure were examined in association with each site and distance to edge in order to assess habitat differences between large and small regenerating stands and with distance from the mature forest edge within stands. Fruit was sampled at biweekly intervals between July 7-August 15 (3 times per season). Each sampling effort included a complete count of fruit within two transects (1 x 12 m each) oriented parallel to and 1 m from both sides of each net (24 m^2 per net; Levey 1988). All fruits were identified and classified as ripe, unripe, and spent. Because *Rubus* fruit progress from unripe to spent quickly, large quantities of fruit may be overlooked if only ripe fruit was analyzed. Ripe and unripe fruit were combined as a measure of potential fruit (Blake et al. 1990). Because potential fruit was highly correlated with ripe fruit ($r = 0.89$, $P = <0.001$), ripe fruit was dropped from analysis.

Arthropods were sampled (bi-weekly between 7 July – 15 August) with branch clippings 3 times in the first year and 2 times in the second year. For each sampling effort, 2 clippings were associated with each net and were located along the rudimentary trail (connecting nets) 5 m on either side of each net (18 clippings per site). Branches were collected perpendicular to and 1 m from the path at a randomly selected height (0.5, 1.0, 1.5, or 2.0 m). A plastic bag was placed over the branch and the branch was clipped into the bag (Majer et al. 1990). Samples were transported to the lab where they were frozen to immobilize insects for collection and preservation (Johnson 2000). Using foreceps arthropods were carefully separated from the vegetation. Biomass (fresh) was measured from the collected arthropods because a prey's food value is closely related to its mass (Krebs and McCleery 1984, Karasov 1990, Johnson 2000), and a ratio was obtained from the arthropod to clipped vegetation biomass. Because weather likely influenced the distribution and availability of arthropods (Prescott and Middleton 1988), arthropod surveys were performed during late mornings (after 10:00) with no precipitation, little wind and comparable temperatures. Branch clipping was an appropriate technique because they effectively captured sessile and flying arthropods and sampled the majority of the vegetative structure (Majer et al. 1990, Johnson 2000).

Vegetation structure including low vegetation hits (0.5-1.5 m, hereafter low vegetation structure), high vegetation hits (1.5-3.0 m, hereafter high vegetation structure), and average canopy height were measured within a 0.04 circular plot centered at each net. Two 20 m perpendicular transects were established and total numbers of stem and leaf hits along a 3 m telescoping pole were recorded at 2 m intervals along each transect. Canopy cover (cover > 5 m) was assessed directly overhead every 2 m along each 20 m transect by recording the presence or absence of vegetation at the crosshairs of an ocular tube (0 = no hit, 1 = hit), and then averaged to generate an estimate of percent canopy cover. Within the 0.04 ha circular plot I identified the 3 most common saplings and shrubs and counted number of small (12-23 cm diameter at breast height, dbh), medium (23-38 cm dbh) and large (>38 cm dbh) snags, residual trees, and logs longer than 1.0 m with a diameter >7.5 cm.

Data Analysis

I standardized bird captures for each site by calculating captures per 100 net hours. Because data were collected over 2 years, I tested for yearly differences in capture rates of the mature-forest group and for species that were analyzed separately (Ovenbird, Worm-eating Warbler, Red-eyed Vireo, Hooded Warbler, Scarlet Tanager, and Wood Thrush; Proc Glm, SAS 1990). Additionally, I also tested for year differences in capture rates for each distance category from the mature-forest edge (Proc Glm, SAS 1990). If no differences were found ($P > 0.05$), data were averaged over years.

I analyzed the relationships between stand size and distance to the mature forest edge had on capture rates of mature-forest birds during the post-breeding period (all species combined) using a split-plot analysis of variance (Proc Mixed, Littell et al. 2002), where the whole-plot unit (site) consisted of 3 split-plot units (distance categories). This allowed me to test for relationships with stand size, distance from the edge, and their interaction within a single model. To examine responses of 6 commonly captured species (Ovenbird, Worm-eating Warbler, Red-eyed Vireo, Hooded Warbler, Scarlet Tanager, and Wood Thrush), I used a multivariate analysis of variance (MANOVA) to control for experiment-wise error rates. One MANOVA was used to test for differences among the

3 distance classes and another was used for stand size. *A posteriori* univariate analysis of variance identified which individual species showed strongest responses to both stand size and distance from the mature forest edge. This same approach was used to examine differences between HY and AHY birds in their response to size and edge.

High vegetation structure was excluded from data analysis because it was correlated with average canopy height ($r = 0.62$, $P < 0.001$), and canopy height had the advantage of assessing structure above 3 m. Similar to previous analyses, MANOVAs were used to analyze differences in vegetation structure (low vegetation structure, average canopy height), fruit abundance, and arthropod abundance with distance from the edge (20 m, 50 m, 80 m), and another was used to test for differences in these same variables between small and large regenerating stands. Separate tests by year were performed when analyzing food and cover variables because arthropod abundance varied by year, and 4 additional sites were used in the second year. All statistical analyses were performed using Statistical Analysis Systems Software (SAS Institute 1990).

RESULTS

Over 2 years during the post-breeding period, I captured 1648 mature-forest birds of 31 species with 7331 net hours, averaging 22.8 $\pm$ 1.8 SE captures/100 net hours. I captured 590 birds in 2932 net/hours in 2002, and 1058 birds were captured in 4409 net/hours in 2003 (Appendix D). The six most commonly captured species included Ovenbird, Worm-eating Warbler, Red-eyed Vireo, Hooded Warbler, Scarlet Tanager, and Wood Thrush (in order of decreasing abundance), and represented 62% of the total number of mature-forest post-breeding captures.

Because there were no annual differences in capture rates at 20 m ($F_{1,14} = 0.18$, $P = 0.680$), 50 m ($F_{1,14} = 2.49$, $P = 0.137$), or 80 m ($F_{1,14} = 0.20$, $P = 0.658$) from the mature-forest edge, data over the 2 years were averaged. Capture rates of mature-forest birds during the post-breeding period were positively related to distance from the mature forest edge (Split-plot, $F_{2,20} = 3.55$, $P = 0.048$; Fig. 3.1a). Interestingly, the interaction between distance to the edge and stand size with total captures of mature-forest birds was nearly significant, showing a higher percentage of birds captured away from the edge in large than small stands ($F_{2,20} = 2.77$, $P = 0.087$; Fig. 3.2). Distance to edge did not significantly affect captures for any individual species (Fig. 3.1b), but did for AHY birds. After-hatch-year birds were captured significantly more as distance from the edge increased (MANOVA Wilks' Lambda $F_{2,33} = 4.03$, $P = 0.006$; ANOVA $F_{2,33} = 5.14$, $P = 0.011$), but this pattern was not evident for HY birds ($F_{2,33} = 1.55$, $P = 0.227$; Fig. 3.1a).

Capture rates in the 8 stands sampled used in both years did not differ by year and were combined for analysis ($F_{1,14} = 1.63$, $P = 0.223$). Significantly higher capture rates of mature-forest birds were found in small compared to large stands (Split-plot $F_{1,10} = 6.90$, $P = 0.025$; Fig. 3.3a). Stand size was marginally related to captures of HY and AHY birds (Wilks' Lambda $F_{1,10} = 3.19$, $P = 0.089$), and the *a posteriori* univariate tests revealed significantly higher capture rates in small regenerating stands for HY birds ($F_{1,10} = 7.01$, $P = 0.024$) but not AHY birds ($F_{1,10} = 2.76$, $P = 0.128$; Fig. 3.3a). Overall, the 6 most commonly captured species had higher capture rates in small stands (Wilks' Lambda $F_{1,10} = 5.49$, $P = 0.041$; Fig. 3.3b). Univariate tests revealed that this relationship held true for Scarlet Tanager ($F_{1,10} = 7.35$, $P = 0.022$), Wood Thrush ($F_{1,10} = 5.60$, $P = 0.039$), and Hooded Warbler ($F_{1,10} = 4.52$, $P = 0.059$), but not for Red-eyed

Vireo ($F_{1,10} = 1.13$, $P = 0.313$), Worm-eating Warbler ($F_{1,10} = 0.12$, $P = 0.733$), or Ovenbird ($F_{1,10} < 0.01$, $P = 0.975$).

Microhabitat characteristics, including low vegetation, average canopy height, arthropod abundance, and fruit abundance, did not vary with distance from the mature-forest edge in 2002 (Wilks' Lambda $F_{2,21} = 0.75$, $P = 0.902$) nor 2003 (Wilks' Lambda $F_{2,9} = 0.62$, $P = 0.750$). Similarly, small and large sites did not differ in vegetation structure, arthropod abundance, and fruit abundance in 2002 (Wilks' Lambda $F_{2,6} = 0.96$, $P = 0.534$) or 2003 (Wilks' Lambda $F_{2,10} = 0.74$, $P = 0.591$; Table 3.1).

DISCUSSION

Overall capture rates for mature-forest birds during the post-breeding season were significantly higher in small than large regenerating stands. This pattern was most pronounced for HY birds, Wood Thrush, Red-eyed Vireo, Hooded Warbler, and Scarlet Tanager. For instance, capture rates per 100 net hours for Scarlet Tanagers were over 4 times greater in small compared to large stands. Habitat variables examined (i.e., fruit, arthropods, vegetation structure) failed to explain the apparent selection of small clearcuts as post-breeding habitat.

In an interesting contrast to this preference for small regenerating clearcuts, I found that mature-forest birds during the post-breeding period were captured more frequently as distance from the mature-forest edge increased. Although capture rates increased with distance in both stand sizes, this relationship was most pronounced in large stands. Avoidance of edges could be explained several ways, though I have no empirical evidence for these possibilities. Edge avoidance may be an effective strategy to reduce competitive interactions with late-breeding conspecifics defending territories near the edge. Another possible explanation is that mature-forest birds during the post-breeding period heavily use the interior of early successional patches during the early morning hours when interior of regenerating stands receive more direct solar radiation than the edge. Increased sunlight may promote morning arthropod movement while providing physiological advantages for juveniles and post-breeding adults. In fact, molting birds lose a considerable amount of energy through heat loss (Murphy 1992). However, my findings did not support this because the percentage of birds captured in the stand interior did not change with time of day (A.C. Vitz, unpublished data). Alternatively, mature-forest birds during the post-breeding period may avoid edges if edges concentrate predators as frequently found during the breeding season (Whitcomb et al. 1981, Wilcove 1985). Forest edges provide abundant perches for hawks to utilize and scan for potential prey. In fact, perches may largely dictate availability of prey within a habitat for forest raptors and clearcuts with perches are used significantly more than those lacking perches (Widen 1994). Furthermore, perching opportunities within the study sites were limited because the majority of sites lacked residual trees. Forest hawks such as Coopers (*Accipiter cooperii*), Sharp-shinned (*Accipiter striatus*), and Broad-winged (*Buteo platypterus*) Hawks were common (A.C. Vitz, pers obs). Anders et al. (1997) documented that at least 3 of their 49 radio-tagged post-breeding Wood Thrush were depredated by raptors. An increase in predators may quickly reduce habitat quality because birds during the post-breeding period are thought to be extremely vulnerable to predators due to reduced flight capabilities for AHY birds (Vega Rivera et al. 1998a), and inexperienced at detecting and evading predators for HY birds (Sullivan 1989).

Area-sensitivity and edge avoidance are well documented for birds and have been demonstrated in species associated with grasslands (Johnson and Temple 1990, Herkert 1994, Vickery et al. 1994, Winter and Faaborg 1999), shrublands (Rudnicky and Hunter 1993), wetlands (Benoit and Askins 2002), and forests (Whitcomb et al. 1981, Robbins et al. 1989). Despite extensive documentation of area and edge sensitivity in breeding birds, the generality of this phenomenon throughout the avian life cycle is largely unknown (but see Doherty and Grubb 2002). This study suggests that during the post-breeding season, mature-forest birds may be sensitive to size of regenerating cuts and prefer small stands. At the same time, though, birds may avoid mature forest edges.

Dense cover and abundant food resources are largely thought to explain use of early successional forests by mature-forest birds during the post-breeding period (Anders et al. 1998, Vega Rivera et al. 1998b, Pagen et al. 2000). However, I demonstrated that vegetation structure, fruit resources and arthropod resources did not differ with either stand size or distance from the mature forest edge, and do not seem to explain the different capture rates. These findings are important because they suggest factors other than cover and food resources help to explain post-breeding habitat use.

Species that utilize both mature and early successional forests during the post-breeding period may prefer small stands because they permit increased access to both habitats. I suggest this may, at least partially, explain the significantly higher capture rates of Scarlet Tanager in small stands. I observed tanagers returning to the mature forest after foraging on fruit, which is consistent with Vega Rivera et al. (2003) findings that adult post-breeding Scarlet Tanagers were frequently located in both mature and early successional forests. Higher capture rates in small stands also may be a result of a concentration effect. Small clearcuts surrounded by mature forest generally have more mature forest habitat (more mature-forest birds) in the immediate landscape than large cuts. If mature-forest birds are indeed selecting early successional habitat, then higher capture rates in small stands would be expected. I plan to examine this possibility when landscape-level data become available (expected Spring 2004).

These results are important because they not only demonstrate substantial use of early successional forests by mature-forest species during the post-breeding period, but suggest that size of the regenerating stand strongly affects use. However, caution is advised when interpreting these data because habitat use (Garshelis 2000) or bird density (Van Horne 1983, Vickery et al. 1992) may be a poor indicator of habitat quality. Although I found no difference in weights of captured birds between small and large stands (Appendices G, H, I), I was unable to evaluate if stand size affected survivorship.

Management Implications

Managing a forested landscape for both late and early successional breeders involves the maintenance of different seral-staged forests. Creating early successional forests has generally been viewed as decreasing breeding habitat for mature-forest species, but these shrub-sapling dominated stands may provide critical habitat for mature-forest birds during the post-breeding period. Clearly, many mature-forest species use regenerating clearcuts during the post-breeding season and this presents an exciting opportunity for forest managers to simultaneously meet the needs of mature-forest species while creating habitat for early successional breeders. However, post-breeding birds may be sensitive to the size of an early successional forest patch, and my findings suggest that they prefer small cuts. If this preference is linked to survival or condition, then large cuts that are generally favored by early successional breeders may not serve mature-forest post-breeders well. Future research should compare survivorship and energetic condition of post-breeding birds across a range of clearcut sizes.

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		Size					
		Small			Large		
Variables[a] (SE)	Year	20 m	50 m	80 m	20 m	50 m	80 m
Arthropods	2002	0.0009(0.0004)	0.0004(0.0001)	0.0005(0.0001)	0.0005(0.0001)	0.0005(0.0001)	0.0005(0.0001)
	2003	0.0003(0.0001)	0.0002(0.0001)	0.0003(0.0001)	0.0002(0.0001)	0.0002(0.0000)	0.0002(0.0001)
Low	2002	247.00(34.68)	303.50(12.80)	320.00(57.97)	391.25(29.75)	306.75(50.71)	377.50(47.74)
Vegetation	2003	325.00(5.00)	352.50(44.50)	333.00(49.00)	403.00(64.00)	439.50(14.50)	338.50(6.50)
Canopy	2002	2.85(0.24)	2.623(0.46)	2.59(0.40)	2.33(0.19)	2.52(0.11)	2.12(0.13)
Height	2003	3.60(0.41)	3.36(0.44)	3.32(0.38)	2.96(0.26)	2.97(0.16)	2.96(0.27)
Fruit	2002	738.58(232.11)	637.33(200.08)	922.83(425.95)	615.25(200.09)	410.00(68.30)	601.92(123.52)
	2003	811.11(156.11)	454.44(110.03)	629.67(197.30)	836.94(271.21)	608.61(131.08)	771.72(182.26)

[a]Microhabitat variables: Arthropods, arthropod biomass divided by clipped branch mass; Low vegetation, number of low vegetation hits (0.5-1.5 m) measured at each net; Canopy height, average canopy height within 0.04ha circular plot at each net; Fruit, number of fruit per net.

Table 3.1 Mean (SE) values for microhabitat variables in small (4-9 ha) and large (13-18 ha) regenerating clearcuts at 20, 50, and 80 m from the mature forest edge, 2002 and 2003.

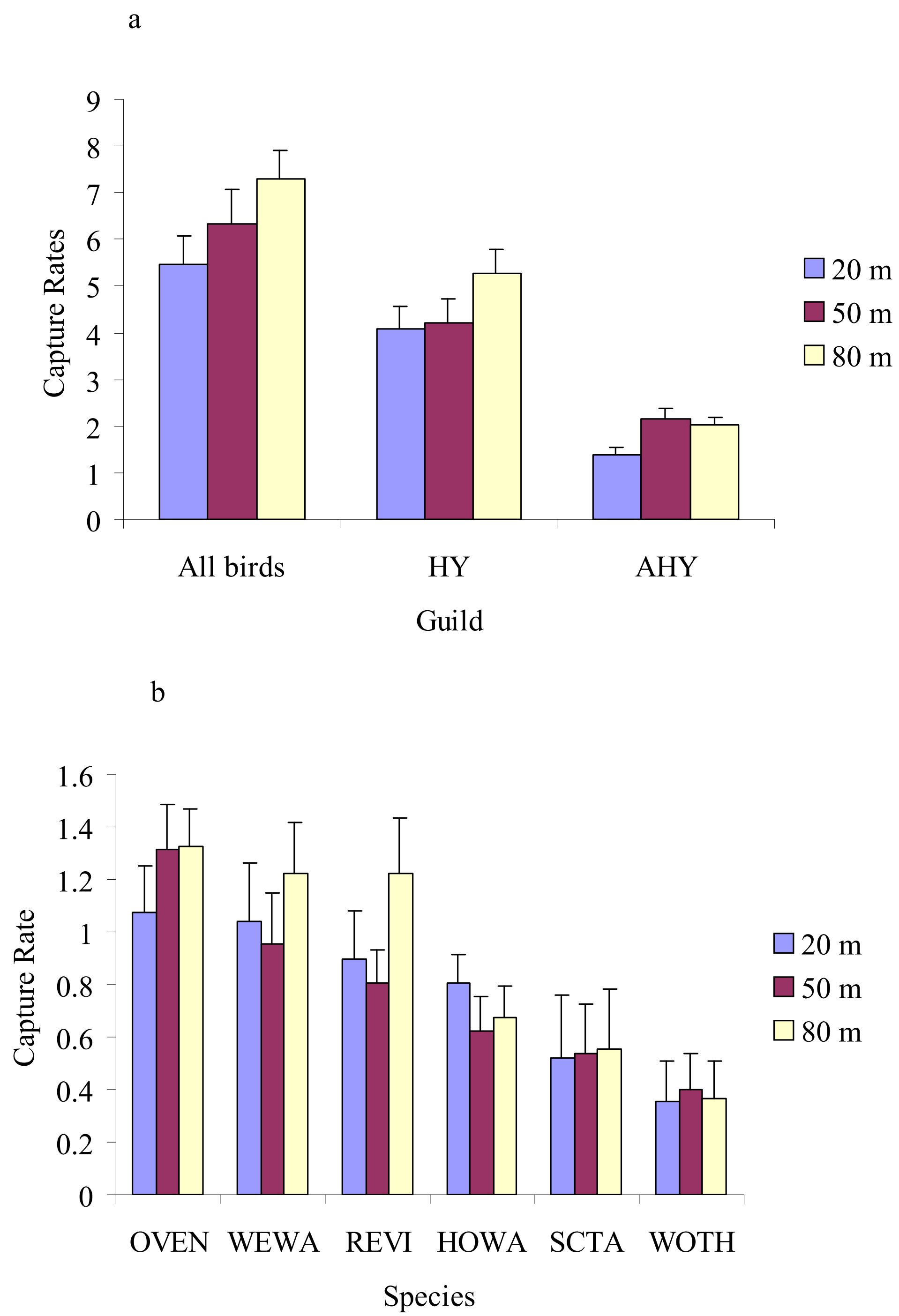


Figure 3.1. Capture rates of mature forest (a) groups, and (b) species during the post-breeding period with respect to distance from the mature forest edge in southeastern Ohio regenerating clearcuts, 2002 and 2003. Capture rates are standardized per 100 net hours. See Table 2.1 for species codes.

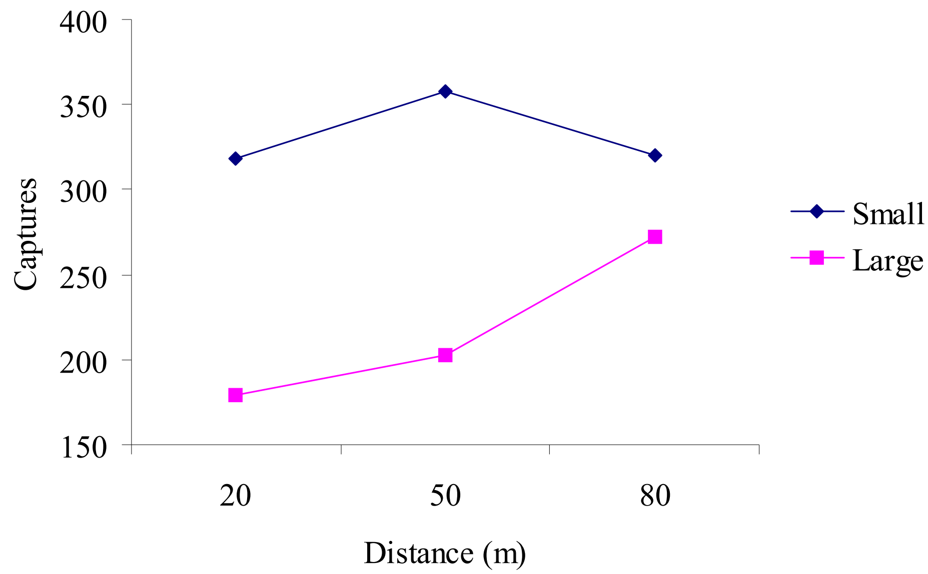
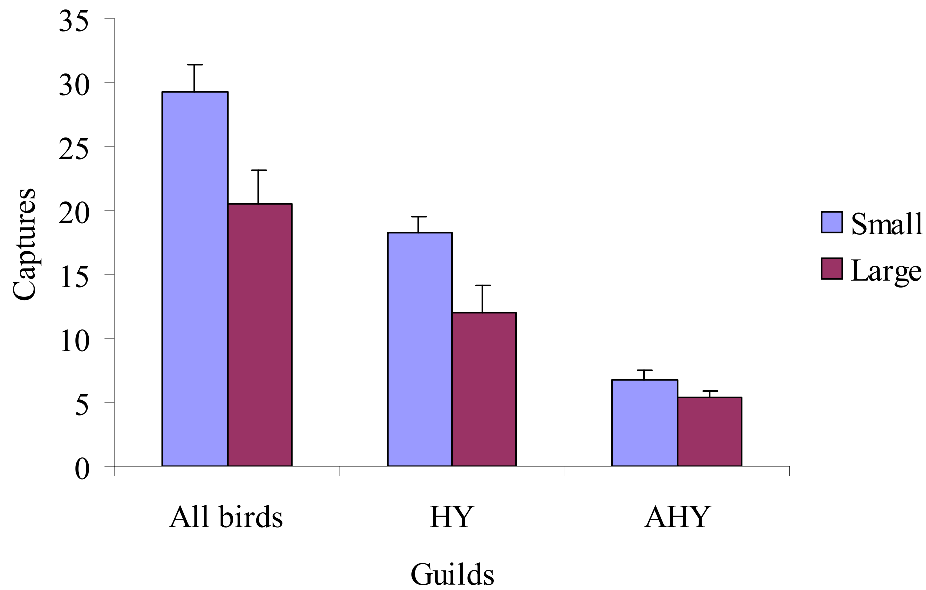


Figure 3.2. Total number of captures of mature-forest birds during the post-breeding period with respect to distance and stand size in regenerating clearcuts in southeast Ohio, 2002 and 2003. Small stands ranged from 4-9 ha, and large stands ranged from 13-18 ha.

a



b

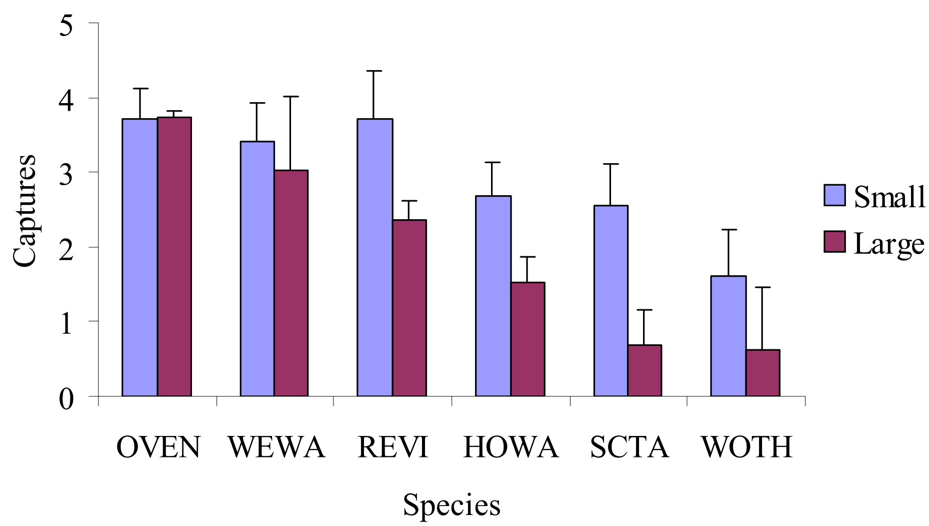
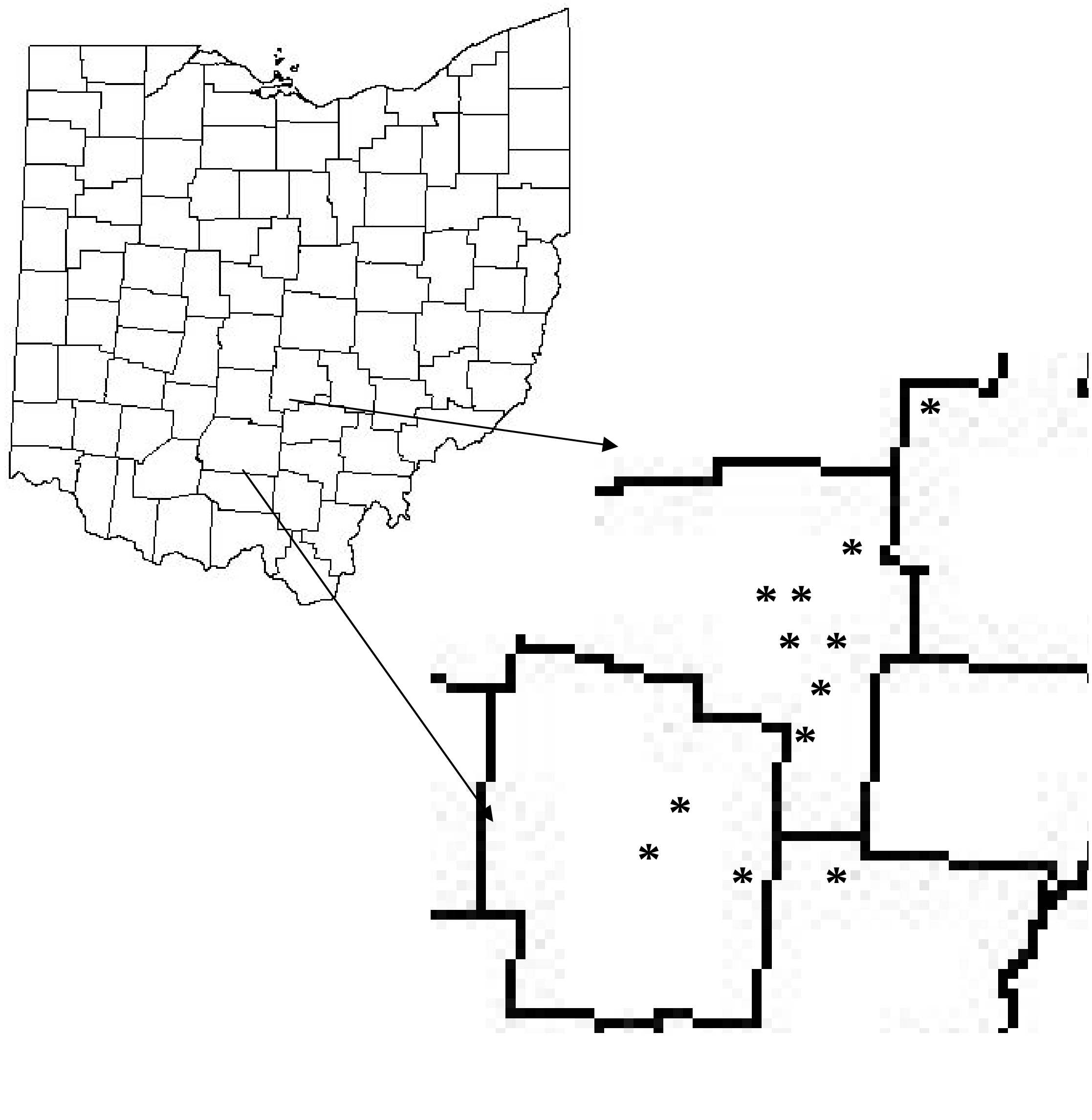


Figure 3.3. Capture rates (per 100 net hours) of mature-forest (a) groups, and (b) species during the post-breeding period with respect to size of the regenerating stand. Small regenerating stands ranged from 4-9 ha, and large ranged from 13-18 ha. Species codes are listed in Table 2.1.

APPENDIX A. Location of regenerating clearcut sites within Athens, Vinton, Gallia, and Jackson counties, Ohio, USA

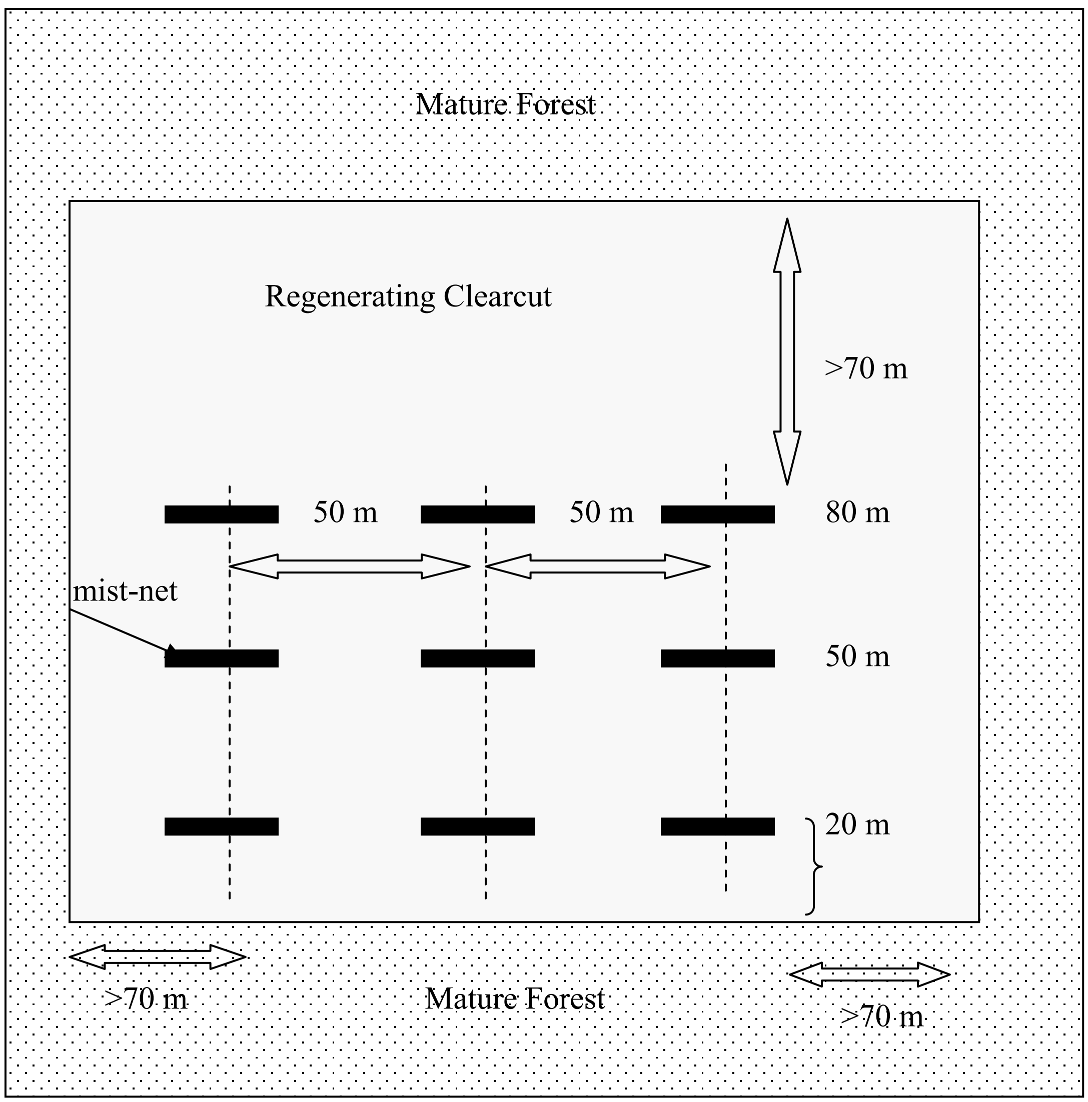


APPENDIX B. Location, size, and year of cut of 12 mist-netting sites in regenerating clearcuts in southeast Ohio, USA.

Site	Site Number	County	Lattitude	Longitude	Size (ha)	Year Cut
Connaut Rd[1,2]	3	Athens	39º23'N	82º17'W	5.67	1996
CCC[1,2]	4	Vinton	39º17'N	82º20'W	7.69	1997
Will Tract 2[1,2]	6	Vinton	39º15'N	82º24'W	5.67	1996
Sand Hill[1,2]	7	Jackson	39º05'N	82º35'W	13.76	1996
Cemetery[1,2]	8	Jackson	39º04'N	82º36'W	13.35	1996
Gomer Davis[1,2]	9	Jackson	38º59'N	82º28'W	14.57	1998
Mead Gate[1,2]	10	Gallia	38º59'N	82º22'W	13.76	1997
Green Gate[1,2]	11	Vinton	39º13'N	82º36'W	4.05	1996
REMA[2]	12	Vinton	39º09'N	82º23'W	15.66	1999
Will Tract 3[2]	13	Vinton	39º15'N	82º25'W	6.89	1996
Bobcat[2]	14	Vinton	39º08'N	82º24'W	18.09	1997
Kick Gate[2]	15	Vinton	39º12'N	82º22'W	9.31	1999

[1]Data collected in the 2002 summer.
[2]Data collected in the 2003 summer.

APPENDIX C. Systematic placement of mist-nets at 12 regenerating clearcuts. Within each site, 3 net lanes were established perpendicular to a common mature-forest edge. Each lane consisted of a net 20, 50, and 80 m away from the mature-forest edge with the distance to any other edge at least 70 m. All sites were surrounded by mature-forest and each mist-net was situated parallel to the mature-forest edge.



APPENDIX D. Number of captures of post-breeding mature-forest birds in 8 and 12 regenerating clearcuts in Southeast Ohio in 2002 and 2003, respectively. KEWA were removed from analysis because they are known to breed in regenerating clearcuts (Thompson and Fritzell 1990).

Species	Species Code	2002 Captures	2003 Captures
Acadian Flycatcher (*Empidonax virescens*)	ACFL	9	27
American Redstart (*Setophaga ruticilla*)	AMRE	7	16
American Robin (*Turdus migratorius*)	AMRO	29	8
Black-and-white Warbler (*Mniotilta varia*)	BAWW	20	37
Black-billed Cuckoo (*Coccyzus erythropthalmus*)	BBCU	2	3
Blue Jay (*Cyanocitta cristata*)	BLJA	0	6
Black-throated Green Warbler (*Dendroica virens*)	BTNW	1	1
Carolina Chickadee (*Poecile carolinensis*)	CACH	30	26
Cerulean Warbler (*Dendroica cerulea*)	CERW	1	4
Downy Woodpecker (*Picoides pubescens*)	DOWO	13	23
Eastern Phoebe (*Sayornis phoebe*)	EAPH	11	14
Eastern Screech-Owl (*Otus asio*)	EASO	0	1
Eastern Wood-Pewee (*Contopus virens*)	EAWP	3	12
Eastern Tufted Titmouse (*Baeolophus bicolor*)	ETTI	25	24
Hooded Warbler (*Wilsonia citrina*)	HOWA	71	86
Kentucky Warbler (*Oporornis formosus*)	KEWA	49	68
Louisiana Waterthrush (*Seiurus motacilla*)	LOWA	3	10
Ovenbird (*Seiurus aurocapillus*)	OVEN	81	191
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	RBGR	1	1
Red-bellied Woodpecker (*Melanerpes carolinus*)	RBWO	2	1
Red-eyed Vireo (*Vireo olivaceus*)	REVI	72	138
Ruby-throated Hummingbird (*Archilochus colubris*)	RTHU	19	61
Scarlet Tanager (*Piranga olivacea*)	SCTA	40	78
Summer Tanager (*Piranga rubra*)	SUTA	0	2
Worm-eating Warbler (*Helmitheros vermivora*)	WEWA	67	155
Wood Thrush (*Hylocichla mustelina*)	WOTH	26	56
Whip-poor-will (*Caprimulgus vociferous*)	WHIP	1	1
Yellow-billed Cuckoo (*Coccyzus americanus*)	YBCU	2	2
Yellow-throated Vireo (*Vireo flavifrons*)	YTVI	5	4
Yellow-throated Warbler (*Dendroica dominica*)	YTWA	0	1
Total		590	1058

APPENDIX E. Number of captures of post-breeding mature-forest species by site in 8 regenerating clearcuts in Southeast Ohio in 2002.

	Captures at Sites (2002)								
Species[a]	**3**	**4**	**6**	**7**	**8**	**9**	**10**	**11**	Totals
ACFL	1	0	1	2	2	0	1	2	9
AMRE	3	0	0	0	0	2	0	2	7
AMRO	4	7	0	4	11	0	1	2	29
BAWW	1	2	8	3	1	2	0	3	20
BBCU	0	0	0	0	1	0	1	0	2
BTNW	0	1	0	0	0	0	0	0	1
CACH	4	9	4	7	2	0	2	2	30
CERW	0	0	0	0	0	0	0	1	1
DOWO	2	1	0	5	5	0	0	0	13
EAPH	2	8	0	0	1	0	0	0	11
EAWP	0	0	0	1	1	1	0	0	3
ETTI	5	2	3	5	5	1	0	4	25
HOWA	19	13	12	1	5	10	6	5	71
KEWA	10	2	1	8	6	6	8	8	49
LOWA	0	1	0	1	0	0	1	0	3
OVEN	11	5	18	10	14	8	9	6	81
RBGR	0	0	0	0	0	0	1	0	1
RBWO	0	0	0	1	1	0	0	0	2
REVI	3	19	13	2	11	5	4	15	72
RTHU	0	3	1	5	3	0	4	3	19
SCTA	6	21	1	1	2	1	0	8	40
WEWA	10	5	23	1	4	8	8	8	67
WOTH	10	1	7	0	2	2	2	2	26
WPWI	0	0	0	0	0	0	1	0	1
YBCU	0	1	0	0	1	0	0	0	2
YTVI	1	0	0	2	2	0	0	0	5
Total	92	101	92	59	80	46	49	71	590

[a] Full species names can be found in Appendix D.

APPENDIX F. Number of captures of post-breeding mature-forest species by site in 12 regenerating clearcuts in Southeast Ohio in 2003.

	Captures at Sites (2003)												
Species[a]	**3**	**4**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	Totals
ACFL	4	3	3	2	4	1	1	1	2	2	1	3	27
AMRE	10	1	0	0	0	0	0	1	0	0	1	3	16
AMRO	1	2	0	0	1	0	0	3	1	0	0	0	8
BAWW	1	6	7	1	4	0	2	3	3	0	4	6	37
BBCU	0	0	0	1	0	1	0	0	1	0	0	0	3
BLJA	1	0	0	2	0	0	0	2	0	0	0	1	6
BTNW	0	0	1	0	0	0	0	0	0	0	0	0	1
CACH	3	3	1	4	0	1	1	0	4	6	0	3	26
CERW	1	1	1	0	0	0	0	0	0	0	0	1	4
DOWO	1	1	2	2	5	1	1	3	0	4	0	3	23
EAPH	2	3	1	0	0	0	0	2	0	2	0	4	14
EASO	0	0	1	0	0	0	0	0	0	0	0	0	1
EAWP	2	2	1	4	1	0	0	0	0	0	1	1	12
ETTI	3	1	3	3	1	2	2	1	2	5	0	1	24
HOWA	9	14	13	1	3	7	2	9	9	6	7	6	86
KEWA	16	2	4	5	3	6	6	6	5	2	8	5	68
LOWA	2	3	0	2	0	0	1	0	2	0	0	0	10
OVEN	32	15	17	7	22	9	20	13	14	9	19	14	191
RBGR	0	0	1	0	0	0	0	0	0	0	0	0	1
RBWO	0	0	0	0	0	0	1	0	0	0	0	0	1
REVI	11	24	20	6	7	7	3	12	24	9	6	9	138
RTHU	1	8	2	2	9	5	1	4	10	6	5	8	61
SCTA	9	19	10	4	1	2	1	8	7	4	2	11	78
SUTA	0	0	0	0	0	0	0	0	0	0	0	2	2
VEER	0	0	0	0	0	0	0	0	0	0	1	0	1
WEWA	16	10	16	1	5	15	6	24	17	8	26	11	155
WOTH	6	7	12	3	4	4	2	2	3	10	1	2	56
WPWI	0	0	0	0	0	0	0	0	0	0	0	1	1
YBCU	0	0	0	0	2	0	0	0	0	0	0	0	2
YTVI	1	2	0	0	0	0	0	1	0	0	0	0	4
YTWA	0	1	0	0	0	0	0	0	0	0	0	0	1
Total	132	128	116	50	72	61	50	95	104	73	82	95	1058

[a] Full species names can be found in Appendix D.

APPENDIX G. The mean mass and mass/wing chord ratio by site for Ovenbird, Worm-eating Warbler, and Red-eyed Vireo in southeastern Ohio in 2002 and 2003.

	OVEN[a]		WEWA[a]		REVI[a]	
Site[b]	Mass (g) (SE)	Mass/Wing (SE)	Mass (g) (SE)	Mass/Wing (SE)	Mass (g) (SE)	Mass/Wing (SE)
3	18.31 (0.200)	0.256 (0.003)	12.86 (0.20)	0.190 (0.003)	16.88 (0.59)	0.217 (0.007)
4	18.13 (0.280)	0.252 (0.004)	12.43 (0.19)	0.182 (0.003)	16.15 (0.15)	0.210 (0.002)
6	17.83 (0.232)	0.249 (0.003)	13.19 (0.16)	0.193 (0.003)	16.32 (0.20)	0.211 (0.003)
7	18.55 (0.49)	0.261 (0.007)	13.85 (0.85)	0.202 (0.002)	16.18 (0.32)	0.203 (0.003)
8	18.29 (0.17)	0.257 (0.003)	13.50 (0.28)	0.203 (0.005)	16.69 (0.27)	0.213 (0.003)
9	18.30 (0.26)	0.257 (0.003)	13.04 (0.22)	0.188 (0.003)	16.62 (0.41)	0.216 (0.005)
10	18.39 (0.18)	0.254 (0.003)	12.78 (0.19)	0.187 (0.004)	15.79 (0.26)	0.201 (0.003)
11	18.23 (0.27)	0.255 (0.005)	13.02 (0.18)	0.192 (0.003)	16.05 (0.29)	0.207 (0.004)
12	17.97 (0.31)	0.246 (0.003)	13.16 (0.23)	0.194 (0.003)	15.92 (0.22)	0.208 (0.003)
13	17.62 (0.22)	0.246 (0.003)	12.89 (0.31)	0.192 (0.005)	16.09 (0.37)	0.211 (0.005)
14	19.03 (0.76)	0.260 (0.010)	13.12 (0.27)	0.196 (0.004)	16.80 (0.55)	0.217 (0.007)
15	18.08 (0.24)	0.252 (0.003)	13.22 (0.24)	0.195 (0.003)	15.94 (0.36)	0.211 (0.004)

[a]Species names can be found in APPENDIX D.
[b]Site numbers can be found in APPENDIX B.

APPENDIX H. The mean mass and mass/wing chord ratio by site for Hooded Warbler, Scarlet Tanager, and Wood Thrush in southeastern Ohio in 2002 and 2003.

	HOWA[a]		SCTA[a]		WOTH[a]	
Site[b]	Mass (g) (SE)	Mass/Wing (SE)	Mass (g) (SE)	Mass/Wing (SE)	Mass (g) (SE)	Mass/Wing (SE)
	10.32	0.161	26.94	0.291	45.76	0.448
3	(0.13)	(0.002)	(0.57)	(0.006)	(0.97)	(0.009)
	10.35	0.161	26.72	0.293	45.62	0.443
4	(0.16)	(0.002)	(0.21)	(0.002)	(1.57)	(0.014)
	10.45	0.163	27.62	0.297	46.99	0.452
6	(0.17)	(0.003)	(0.66)	(0.008)	(0.64)	(0.006)
	9.50	0.153	28.18	0.307	48.50	0.453
7	(0.00)	(0.000)	(0.97)	(0.009)	(2.50)	(0.023)
	9.53	0.150	27.50	0.293	48.83	0.466
8	(0.29)	(0.004)	(0.289)	(0.005)	(1.26)	(0.015)
	10.50	0.166	28.75	0.315	44.50	0.435
9	(0.24)	(0.004)	(1.25)	(0.008)	(0.67)	(0.006)
	10.71	0.164	27.5	0.301	43.00	0.422
10	(0.36)	(0.005)	(0.00)	(0.000)	(1.76)	(0.015)
	10.54	0.166	27.77	0.304	46.00	0.450
11	(0.31)	(0.005)	(0.619)	(0.006)	(1.04)	(0.016)
	9.90	0.156	26.08	0.292	44.17	0.425
12	(0.56)	(0.007)	(0.71)	(0.007)	(1.01)	(0.004)
	10.42	0.160	28.17	0.295	46.00	0.464
13	(0.22)	(0.002)	(0.44)	(0.018)	(0.94)	(0.006)
	10.43	0.165	26.75	0.285	51.00	0.505
14	(0.33)	(0.005)	(0.25)	(0.003)	(0.00)	(0.000)
	10.20	0.162	26.78	0.296	45.00	0.431
15	(0.14)	(0.002)	(0.51)	(0.004)	(2.00)	(0.014)

[a]Species names can be found in APPENDIX D.
[b]Site numbers can be found in APPENDIX B.

APPENDIX I. The mean mass and mass/wing ratio of the 6 species of interest in small (4-9 ha) and large (13-18 ha) regenerating clearcut stands in southeast Ohio in 2002 and 2003.

	Small		Large	
Species[a]	Mass (g) (SE)	Mass/Wing (SE)	Mass (g) (SE)	Mass/Wing (SE)
OVEN	18.03 (0.11)	0.252 (0.002)	18.42 (0.14)	0.256 (0.002)
WEWA	12.94 (0.12)	0.191 (0.002)	13.24 (0.15)	0.195 (0.003)
REVI	16.23 (0.14)	0.211 (0.001)	16.33 (0.17)	0.210 (0.003)
HOWA	10.38 (0.05)	0.162 (0.001)	10.10 (0.21)	0.159 (0.003)
SCTA	27.33 (0.25)	0.296 (0.002)	27.46 (0.39)	0.299 (0.005)
WOTH	45.90 (0.27)	0.448 (0.004)	46.67 (1.31)	0.451 (0.013)

[a]Species names can be found in APPENDIX D.

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