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Post-fledging ecology and survival of neotropical migratory songbirds on a managed Appalachian forest

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POST-FLEDGING ECOLOGY AND SURVIVAL OF NEOTROPICAL MIGRATORY SONGBIRDS ON A MANAGED APPALACHIAN FOREST

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ABSTRACT

POST-FLEDGING ECOLOGY AND SURVIVAL OF NEOTROPICAL MIGRATORY SONGBIRDS ON A MANAGED APPALACHIAN FOREST

TIM DELLINGER

During the post-fledging period, some juvenile songbirds appear to require early successional habitats at some level, suggesting that disturbance (whether natural or anthropogenic) in the landscape is important. Previous studies of juvenile Wood Thrushes (*Hylocichla mustelina*) have found them in early successional areas in which adults do not nest. My objective was to determine how juvenile Wood Thrushes used areas harvested through various silvicultural techniques within a forested landscape. I examined settled areas, habitat use, survival, and daily movements of 55 radio-tagged juvenile Wood Thrushes on a managed forest in the central Appalachian mountains of West Virginia during 2004 to 2005.

I tagged individuals as nestlings and as juveniles, and radio-tracked birds in the natal and post-natal period. I used Global Positioning Systems to record the location of each bird on a daily basis and sampled habitat variables at these locations. All locations were assigned to one of three landcovers (mature forest, sawtimber harvests, and early successional areas) on a digitized map of the study site. I examined the proportion of daily locations within each landcover. I measured the size of harvests and related size and age to use by juvenile Wood Thrushes.

Once independent from adults, most individuals preferred early successional areas, in particular large, older clearcuts, >13-ha in size and 7-11 years post harvest. Overall, radio-tagged Wood Thrushes tended to move from open areas to those with a denser understory as they transitioned from being dependent on adults to being independent. Survival was similar among cover types (n*atal*: P = 0.7, *mature forest* 91%, *sawtimber harvest* 80%, *early successional area* 88%; *post-natal*: 100% among all cover types).

Radio-tagged juvenile Wood Thrushes on my study remained in the natal areas approximately 3 weeks before moving to post-natal sites. Similar to other studies, some individuals were located in up to 4 separate post-natal sites prior to migration or transmitter battery failure. Sizes of and duration within settled areas were similar to those documented in previous studies but distances between settled sites were shorter (*natal to initial post-natal:* $\overline{x}$ =

760 m; *initial to subsequent*: $\overline{x} = 930$ m), as were daily movements between consecutive locations, suggesting juvenile Wood Thrushes on my study site did not need to move long distances to find suitable habitat. Among first post-natal settled areas occupied at least 5 days in which $\geq$ 80% of locations were within one cover type, settled areas were smallest in early successional areas (0.8 ha), intermediate in mature forest (1.0 ha), and largest in sawtimber harvests (2.8 ha) ($P = 0.01$); however, settled areas within sawtimber harvests averaged smallest among subsequent settled areas with this criteria.

I examined mist-net captures of songbirds between two silvicultural methods that create early-successional patches, clearcuts and deferment cuts. In late-July and late-August 2004 and 2005, I sampled three clearcuts and three deferment cuts similar in size (14.7 – 16.2 ha) and age (5 – 8 years) on my study site. No overall differences ($P > 0.05$) in abundance, species richness, or diversity were detected between the two treatments for adult or juvenile captures. Of the two species with the highest captures, significantly more juvenile Hooded Warblers (*Wilsonia citrina*) were captured ($P < 0.05$) in clearcuts than in deferment cuts, while juvenile Chestnut-sided Warblers (*Dendroica pensylvanica*) were captured more often in deferment cuts ($P < 0.05$). Early successional patches are important in the post-fledging ecology of Wood Thrushes as well as other migratory songbirds. My results do not indicate clearcuts or deferment cuts are more favorable to all birds, rather each treatment was important to at least one guild or species. Thus, both harvest types appear suitable for use by land managers interested in creating early successional habitats for songbirds.

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CHAPTER 1

INTRODUCTION

INTRODUCTION

Information on habitat use, post-fledging and pre-migration movements, as well as survival of hatch-year birds is needed to aid in the development of conservation plans for Neotropical migratory songbirds. While nesting success data often have been relied upon in recent years to assess source-sink dynamics associated with various landscape attributes, a complete picture of recruitment is lacking in the absence of information on survival during the post-fledging period, particularly the time young birds become independent from adults. During this period, various studies have reported some species of juvenile songbirds shift to habitats dissimilar to that used by breeding adults. For example, observational studies examining post-breeding habitat use of adult forest-nesting species have noted the presence of juveniles among adults in dense edge habitats (Bayne and Hopson 2001, Harris and Reed 2002, Rodewald and Brittingham 2002, Rush 2004). Further evidence that juvenile songbirds may use habitats dissimilar to that of their parents has been provided by studies that have addressed habitat use by hatch year migratory birds through the use of mist nets to sample songbirds within early successional habitats (Rappole and Ballard 1987, Pagen *et al*. 2000, Marshall et al. 2003, Vitz and Rodewald 2005). Those studies observed both adults and fledglings in early successional areas. However, proportion of sampled early successional habitat used, duration of use, and distance between daily movements cannot be fully addressed by mark-recapture studies.

RADIO-TRACKING

Vega Rivera (1998) described independent hatch-year birds as difficult to observe, a fact which has resulted in a paucity of information about many species during this period. Radio-tracking, however, allows observers to more easily monitor such animals. Furthermore, radio-tracking provides information on settled area size, daily movements, habitat use, and survival without requiring recapture.

Cochran and Lord (1963) first described the radio-tracking method, which was initially performed on rabbits, skunks, and raccoons. One of the first studies to radio-track songbirds used a 4.7 g transmitter on an American Robin (*Turdus migratorius*). This transmitter was 7.4% of the individual's total body weight; additionally the transmitter antenna was 1 m long and the battery lasted only 32 hours (Graber and Wunderle 1966). With the advent of smaller electronic components, smaller lightweight transmitters with greatly improved battery duration are now being used. Today Wood Thrushes, which average 30 g lighter than American Robins, are tagged with 1.1 g transmitters that have a 15 cm antenna and a battery life of $\geq$ 10 weeks (personal observation).

Thus the development and availability of lightweight radio-transmitters for research have increased the ability to gather habitat use information for various species in the post-fledging period. For example, tagged juvenile Eastern Meadowlarks (*Sturnella magna*) in Illinois moved into agricultural habitat rarely used by breeding adults (Kershner *et al*. 2004). In Costa Rica, Cohen and Lindell (2004) reported tagged juvenile White-throated Robins (*Turdus assimilis*) moved from breeding areas in coffee plantations or pasture to forested areas. These authors went on to suggest bird species may need different habitats, or perhaps the quality of various habitats may become more or less important over the course of their lifecycles. Radio-tagged juvenile Swainson's Thrushes (*Catharus ustulatus*) in California were found to use vegetation types different from those of nesting adults (White *et al*. 2005). Moreover tagged juvenile Ovenbirds (*Seiurus aurocapilla*) in New Hampshire moved to areas with fewer mature trees and more vertical structure than available at nest sites or random sites (King *et al*. 2006). Most of our current knowledge about the post-fledging ecology of juvenile songbirds is based on the Wood Thrush (*Hyocichla mustelina*). In the earliest of these modern studies, Vega Rivera et al. (1998) radio-tagged 42 Wood Thrush juveniles over 3 years in eastern Virginia. Radio-tagged juveniles departed relatively open natal areas and relocated to habitats with less canopy cover, fewer mature trees, and denser understory. Additionally, post-natal areas were closer to roads and canopy openings, and farther from mature forests. The average age of fledglings when they departed the natal area was 32.5 days, which is about 20 days after fledging (Ehrlich et al. 1988). The authors determined the average distance between the natal and post-natal sites to be 1.5 km, the mean distance between daily locations to be 101 m, and the average size of post-natal areas used to be 2.8 ha. They hypothesized that juveniles may depart their natal areas for any of the following reasons: to begin migration, select future breeding territories, socialize with other juveniles, avoid intraspecific competition with adult Wood Thrushes, or optimize foraging while completing prebasic molt. They concluded that foraging optimization and socialization to avoid predators were the likely causes.

In another study, Anders et al. (1998) examined natal and post-natal habitat use and home range size in the Ozark Mountains of Missouri. During 1994 and 1995, they tagged 49 Wood Thrush nestlings and determined that juveniles occupied early to mid-successional post-natal sites that were dissimilar to the mature forest habitat of their natal areas. The distance from the natal area to the post-natal area was 2.08 km, which is slightly greater than that reported by Vega Rivera et al. (1998). Using a 95 % minimum convex polygon based on an average of 17 locations, the Missouri study reported natal home range sizes ranged from 2.6 to 24.8 ha. The first post-natal settled area averaged 1.5 ha and subsequent settled areas were 0.2 ha. Anders et al. (1998) noted that juvenile movements between home ranges were in a generally southern direction.

Lang et al. (2002) investigated how management strategies for endangered Red-cockaded Woodpeckers (*Picoides borealis*) might impact adult and juvenile Wood Thrushes in Georgia. These management practices typically involved removing the mid- and understory vegetation through forest thinning and prescribed burning in ~20 ha stands of loblolly pine (*Pinus taeda*). Their study monitored the movements and habitat use of 74 hatch-year Wood Thrushes 2 years before silvicultural treatments, 2 years after, and concurrently on an unmanaged control area. The authors' findings were similar to the two previously mentioned studies in regard to both time in the natal area (avg. 25 days) and the distance between the natal and post-natal areas (2.2 km). However, in contrast, post-natal vegetation types used before and after treatment and in control sites suggested that juveniles preferred areas similar to their natal areas of mature mixed forests with moderate overstory. Thus, Lang et al. (2002) concluded that small scale thinning and burning had little impact on habitat use and movements of juvenile Wood Thrush.

In the most recent study, Fink (2003) examined habitat use during the natal and post-natal periods in a largely agricultural region with little intact forest. The 3-year study radio-tracked 78 fledging Wood Thrushes and classified daily locations as natal, post-natal settled, or post-natal wandering. Fink (2003) concluded juveniles in the post-natal period remained in areas with higher shrub density, fewer large trees, and in closer proximity to grassland and row-crops than at natal locations. Furthermore, among post-natal movements, locations classified as wandering had lower densities of woody shrubs, larger diameter trees, and were typically farther from forest edges than settled locations, suggesting birds had not found suitable habitat.

OBJECTIVES

While similarities among the results of the above-mentioned studies begin to explain the ecology during the hatch year of one forest interior species, their differences suggest further study is essential in understanding management priorities. For that reason we examined habitat use and settled area size of juvenile Wood Thrush through the use of radio-tracking on an intensely managed forest in West Virginia. We also attempted to investigate the habitat requirements, settled area size, and juvenile survival of three additional Neotropical migratory forest interior species: Black-throated Blue Warbler (*Dendroica caerulescens*), Black-and-white Warbler (*Mniotilta varia*), and Ovenbird (*Seiurus aurocapilla*). The Central Appalachians contain some of the largest intact, forested areas in the Eastern United States (Smith 1995) and are recognized as an important area for conservation of songbird populations (Rich et al. 2004). West Virginia, specifically, is approximately 80% forested, with 4.74 million ha designated as timberland (Milauskas 2003). However, given that timber revenue is important to the economy of many eastern states—especially in West Virginia where over 29,000 people are employed in the forest products industry (Milauskas 2003)—and that logging on public and private lands will continue, it is important to document the effects of various harvesting methods on juvenile Neotropical migrants as well as other songbird populations.

The overall purpose of this study was to examine post-fledging habitat requirements and juvenile survival in the context of forest disturbance. The specific objectives were to:

1. identify natal and post-natal areas and quantify their habitat characteristics through vegetation measurements and/or silvicultural history;
2. quantify the average patch size and distance to nearest edge of early successional areas used,

3. quantify overall Wood Thrush survival rates as well as survival within each cover type during the natal and post-fledging/pre-migration period,
4. identify minimum convex polygon settled area size and daily movements of juvenile Wood Thrushes during the natal and post-natal periods and contrast them with previous studies, and
5. determine if settled area size varied among cover types.

Furthermore, to investigate community-level responses within early successional habitats, our objectives were to:

6. compare songbird use of clearcuts and deferment cuts during the post-fledging period by comparing avian abundance, species richness, and diversity between the two harvest types, and
7. examine differences in the use of both harvest types by juveniles and adults of three habitat guilds.

STUDY SPECIES

Our primary focal species, the Wood Thrush, is a mid-sized (40 – 50 g) migratory songbird that breeds in the eastern United States and southeastern Canada (Roth *et al*. 1996). It typically constructs its nest an average of 3 m above the ground within the interior and edges of deciduous and mixed forests (Harrison 1975, Roth *et al*. 1996). The female usually lays 2 – 4 eggs, incubation lasts about 13 days, and fledging occurs at 12 – 15 days post-hatching (Harrison 1975, Roth *et al*. 1996). Adults typically have two clutches, however triple brooding is occasionally reported (Roth et. al 1996, Friesen *et al*. 2001). Females in a Virginia study remained with fledglings 13 days before departing to begin incubation of the next brood, whereas males remained with all fledglings until their independence and departure from the natal area at 19 days post-fledging (Vega Rivera *et al*. 2000). In their final broods of the same study, fledglings were divided between the male and female, and either left or remained on the natal area subject to where the adult chose its molting site. As reported above, this woodland species has been the subject of most post-fledging studies primarily due to the ease in finding nests and its medium size allowing it to carry a transmitter with a relatively long life. However investigation into use of various silvicultural techniques and the preferred age of early successional areas are lacking.

Ovenbirds are large ground-nesting warblers (14 - 28 g) that inhabit deciduous or mixed forests in northern and northeastern North America during the breeding season (Van Horn and Donovan 1995). Usually 4 – 5 eggs are laid in the well-camouflaged nest and incubation lasts about 13 days (Ehrlich *et al*. 1988, Van Horn and Donovan 1995). Adults typically have only one clutch, however two broods have been reported (Ehrlich *et al*. 1988, Van Horn and Donovan 1995). Once chicks fledge at 8 – 10 days after hatching (Ehrlich *et al*. 1988), they still cannot fly; young Ovenbirds instead jump and flutter, or hop along the forest floor for up to 10 days before reaching the early flying stage (Van Horn and Donovan 1995). Only one radio-tracking study has examined juvenile Ovenbird ecology (King *et al*. 2007) and we hoped to add information from a dissimilar area.

Black-and-white Warblers (*Mniotila varia*) (9 - 15 g) also are ground nesters and found throughout much of the eastern and central United States and Canada (Kricher 1995). Nests are often located along hillsides or ravines (Harrison 1975) in open-woods, second-growth and mature forests (Kricher 1995). Usually 5 eggs are laid and incubated by the female for 10 days before hatching (Ehrlich *et al*. 1988). Chicks fledge at 8 – 12 days post-hatching although are not yet proficient in flight (Kricher 1995). Some mist-net studies indicate juvenile Black-and-

White Warblers are found in early successional habitat in the post-fledging period (e.g. Marshall *et al*. 2003), however no radio-tracking information is known to exist.

Black-throated Blue Warblers (*Dendroica caerulescens*) are small (8 – 12 g) migrants that breed in deciduous and mixed forests of the northeast United States, southern Canada, and in the higher elevations of the Appalachian Mountains (Holmes 1994). The nest is usually within 1 – 1.5 m of the ground within dense shrubs (Holmes 1994). The incubation period lasts 12 – 13 days and young usually fledge 11 – 12 days after hatching (Ehrlich *et al*. 1988). Immediately after young birds fledge, Holmes (1994) reported they often remain in the breeding territory in the low understory, however young are flying well 10 – 14 days after fledging. The only information available for the period when young are independent from adults is from mist-net studies (e.g. Rimmer and McFarland 2000, Marshall *et al*. 2003). Currently there are no published accounts of radio-tagged juveniles.

2003 PILOT STUDY

Due to our lack of experience in radio-tagging hatch-year individuals that were only a few weeks old and had a small body mass, we conducted a pilot study in 2003 to hone techniques and develop the effective telemetry methods for our study site. Nests of 14 Wood Thrush pairs, two Ovenbird pairs, three Black-throated Blue Warbler pairs, and two Black-and-white Warbler pairs were located and monitored. Nestlings fledged successfully from seven of the 14 Wood Thrush nests, all Black-and-white Warbler and Ovenbird nests; all monitored Black-throated Blue Warbler nests, however, failed during incubation. We radio-tagged seven nestling Wood Thrushes from five of the monitored nests. We attempted to radio-tag a nestling from each Black-and-white Warbler nest but could not achieve a proper harness fit on birds from either site, and thus no individuals were tagged. One nestling perished during the tagging attempt, most likely due to stress. Young birds fledged sooner than anticipated at both Ovenbird nests, and also were not tagged.

Three sizes of radio-transmitters used on the four focal species were purchased from Blackburn Transmitters of Nacogdoches, TX. The smallest transmitter was intended for use on Black-throated Blue and Black-and-white Warblers. It weighed 0.32 g, which was within 3.5 % of both species' total body weights, and had an estimated battery life of 21 days. The 0.45 g transmitter was intended for use on Ovenbirds, and had an estimated 45 days of battery life. Wood Thrushes were tagged with a 1.1 g transmitter with a battery life of >60 days. The 0.45 g and 1.1 g transmitters weighed 3 % of Ovenbirds' and Wood Thrushes' total body weights, respectively. Ranges and battery lives of all three sizes of transmitters were determined by attaching them to Wood Thrushes because we were unable to tag individuals of the other species. The 1.1 g transmitters were detected from as far away as 1,350 m; the maximum range of the 0.45 g and 0.32 g transmitters were 400 m and 270 m respectively. The duration of battery life was 15 days, 35 days, and >55 days for the lightest to heaviest transmitters.

To attach the transmitter to an individual, a leg-loop harness (Rappole and Tipton 1991) was made of lightweight cotton embroidery floss, 1.0 mm in diameter (Fedy et al. 2002), and attached when the nestling was estimated to be within 3 days of fledging. Embroidery floss is comprised of several strands, and occasionally during 2003 one or a few strands would become entangled on the feet of a young bird and slow the tagging process. To expedite this process and also ensure the transmitter—which has a relatively short battery life compared to the life span of the bird—is shed as soon as possible, we used 0.7 mm diameter dissolvable sutures in 2004 and 2005. Doerr and Doerr (2002) reported that dissolvable sutures lasted on average 149 days (SD = 89 days), a duration which was well beyond the battery life of our transmitters. Also we found tagging to be less difficult before 10:00 am; nestlings seemed less likely to kick, and thus it was easier to slip the harness loops over the thighs. While Rappole and Tipton (1991) stated that after some practice a transmitter could be attached in a matter of seconds, our tagging time varied greatly during the pilot study, requiring nearly 10 minutes on some individuals. However, as familiarity of tagging increased, time required to safely fit a harness was significantly decreased to less than one minute.

The pilot study enabled us to identify limitations and potential problems of radio-tracking highly mobile species in mountainous terrain. Specifically, our asynchronous triangulation method and Global Positioning System equipment introduced unacceptable error. In asynchronous triangulation one observer first determined two receiving locations based on the strength of the transmitter signal, then recorded the Universe Transverse Mercator (UTM) coordinates for the first location and the compass bearing from that receiving point in the direction of the radio-tagged bird. The observer then drove to the second receiving station and recorded the compass bearing and UTM coordinates. The UTM coordinates and corresponding compass bearings then were entered into a Microsoft Excel spreadsheet for each tagged bird. Those spreadsheets then were input into Program LOCATE (Kie et al. 1996), which determined the point of intersection of the two bearings in UTM coordinates, and theoretically indicated the actual location of the radio-tagged bird. Our major concern with this method was that the time lapse between collection of the first and second signal was typically > 5 minutes, which was sufficient time for radio-tagged individuals of a highly mobile species to be in a different location when the second signal was collected. Furthermore, telemetry signals often bounced within the steep slopes and deep ravines of the study site and did not intersect. Lastly, UTM coordinates collected with Garmin III GPS units were too variable, being inaccurate by >100 m at times. Because of these concerns we abandoned triangulation and instead homed in to each radio-tagged bird's location daily. Furthermore, we used GPS units with sub-meter accuracy and corrected UTM coordinates through base stations. These changes in methodology allowed us to accurately identify and mark each individual's location and return later to quantify vegetative characteristics.

During our mist-net examination of community-level response between different harvest types in the pilot study we also discovered another source for juveniles of our focal species. Of 46 species netted, 52 % were forest interior species, with both juvenile and adult Wood Thrushes, Ovenbirds and Black-and-white Warblers being the most frequently captured. Thus, even though their natal area was unknown, we elected to radio-tag hatch-year individuals of the focal species captured during the mist-net study in 2004 and 2005 to increase our sample size and provide information on older individuals.

COVER TYPE USE BY TWO WARBLER SPECIES

In 2004 and 2005 we tagged two Neotropical migratory warbler species for which no radio-tagging reports exist in the scientific literature (see Chapter 2 for attachment method) (Appendix A). These three individuals were netted during our examination of songbird use of deferment cuts and clearcuts (see Chapter 4).

OVERVIEW OF CHAPTERS

This thesis has been written in the form of four chapters. The first chapter provides justification for my research, a literature review of previous studies, and information from the pilot study. The second chapter examines survival and cover type use of juvenile Wood Thrushes while dependent on their parents and after independence from parents. The third chapter compares natal and post-natal settled area sizes and daily movements of radio-tagged juvenile Wood

Thrushes to other studies and within cover types. The last chapter examines community-level responses within stands harvested using two silvicultural techniques. The first chapter is written in the style of *The Condor*. The remaining chapters are written in and will be submitted to the following scientific journals:

Chapter 2 – *The Condor*

Chapter 3 – *The Condor*

Chapter 4 – *Forest Ecology and Management*

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CHAPTER 2

COVER TYPES AND HABITAT USE BY JUVENILE WOOD THRUSHES ON A MANAGED APPALACHIAN FOREST

Abstract. Recent studies suggest that when juvenile Wood Thrushes (*Hylocichla mustelina*) become independent from their parents they may require forests in earlier successional stages than they did while dependent. My objectives were to identify natal and post-natal areas used by juvenile Wood Thrushes, to quantify their habitat characteristics, and to relate habitat characteristics to survival on a managed forest. I radio-tagged 62 Wood Thrushes during 2003 to 2005 in the central Appalachian mountains of West Virginia. I assigned telemetry locations to the natal or post-natal period, sampled habitat variables at these locations, and categorized each location as mature forest, sawtimber harvest, or early successional patch. During the natal period, juveniles preferred mature forest. Once independent from adults, early successional areas were preferred by most juveniles, specifically clearcuts >13-ha in size and 7-11 years post harvest. Within each cover type, juveniles tended to move from open areas to those with a denser understory as they transitioned from natal to post-natal period. Survival was similar among cover types. Areas of early regeneration in various sizes and ages are apparently important to juvenile Wood Thrushes in the post-fledging / pre-migration period and should be maintained by land managers.

INTRODUCTION

Early successional habitats are declining in the eastern United States as farmlands revert to forest and as land development occurs (Askins 2001); as a result, many associated bird species also are declining. Regenerating areas appear to be important to other habitat guilds as well. Recent studies have documented adult and juvenile migratory birds of mature forest guilds in early successional areas during post-breeding (Vega Rivera et al.1999, Vega Rivera et al. 2003, Marshall et al. 2003, Vitz and Rodewald 2005) post-fledging (Anders et al.1998, Vega Rivera et al. 1998a, Fink 2003, Marshall et al. 2003, Vitz and Rodewald 2005), and migration (Pagen et al. 2000, Rodewald and Brittingham 2004). For juvenile songbirds, post-fledging/pre-migration information was virtually lacking in the literature until the advent of small, lightweight radio-transmitters; studies are currently emerging on survival and habitat use during the post-fledging period. Juveniles of four forest interior species have been studied (King et al. 2006, Mattsson et al. 2006, White et al. 2005) and four studies have focused on Wood Thrushes (*Hylocichla mustelina*) (Anders et al. 1998, Vega Rivera et al. 1998a, Lang et al. 2002, Fink 2003). Each observed similar survival rates. Most mortality occurred the first week of fledging when tagged juveniles were near the ground and were not proficient flyers, and again later when first independent from adults.

Three of the four studies (Anders et al. 1998, Vega Rivera et al. 1998a, Fink 2003) reported that after independence from parents, juveniles used early successional habitats (e.g. old fields, roadside thickets, forest edges, tree fall gaps, and small clearcuts 1-8 ha in size) that were dissimilar to adult breeding habitat. Juveniles move to early successional areas because of different habitat requirements at their particular stage of life (White et al.

2005). These requirements may include an abundance of soft mast producing species such as blackberries (*Rubus* spp.) (Anders et al. 1998, Vega Rivera et al. 1998a). Many soft mast producing species typically fruit during mid to late summer, which coincides with the post-fledging period. Soft mast concentrated in relatively small areas would require little energy and foraging time, and would benefit young birds that are not yet proficient foragers and must build up enough fat reserves to begin migration. Both Anders et al. (1998) and Vega Rivera et al. (1998a) observed juvenile Wood Thrushes consuming soft mast in early successional areas.

However, abundant soft mast may be only a by-product of a different post-independence requirement: dense vegetation for predator avoidance (Fink 2003). High mortality rates are considered common during the post-fledging period (Baker 1993). Dense understory patches provide concealment and may help reduce the risk of predation, especially from avian predators. Fink (2003) reported that the probability of juvenile Wood Thrush survival increased in areas with high shrub density; likewise Anders et al. (1997) observed that after young birds had moved to dense habitats the probability of predation was zero.

In contrast, post-fledging Wood Thrushes in Georgia did not always select denser habitats when independent. Instead, Lang et al. (2002) suggested the juveniles may have been found in post-fledging habitats similar to what was used while still dependent on their parents. Fledglings from areas with somewhat dense understory cover (i.e., burned areas or areas from which large diameter trees had been removed) remained in similar habitats as juveniles. Likewise, individuals from habitats with more open cover moved to comparable areas once independent. This type of divergence among the findings of studies may be the result of dissimilar habitat matrices and associated disturbance history. Understanding movement and habitat use patterns during the post-fledging period is essential in identifying common habitat and conservation needs throughout the breeding range of Wood Thrushes.

Although forest management can fragment or remove breeding habitat for many mature forest songbird species (Thompson et al. 1995), natural or anthropogenic early successional patches may be important to juveniles. Furthermore, cover provided by patches of dense regeneration also may be crucial to some species of post-breeding adults during heavy molt (Vega Rivera et al. 1998b, Vitz and Rodewald 2005). Currently no information exists for post-fledging habitat use on lands with active forest management. If post-fledging habitat is not adequate, juvenile survival could be reduced with important implications for source/sink dynamics of a population. For this reason, I examined habitat use of juvenile Wood Thrushes using radio telemetry on an intensively managed forest in West Virginia. Unlike previous studies of juvenile Wood Thrushes, slightly more than 50% of the landscape in my study had some type of silvicultural treatment within the past 15 years, and early successional patches ranged in size from small roadside clearings of < 1 ha up to 29 ha timber harvests.

The objective of this study was to examine post-fledging habitat requirements and juvenile survival of Wood Thrushes in the context of silvicultural practices that made patches of regeneration of various sizes and ages available to young birds. My specific objectives were to:

1. identify natal and post-natal areas and quantify their habitat characteristics through vegetation measurements and/or silvicultural history; and

2. quantify survival rates during the post-fledging/pre-migration period and relate them to habitat use.

The null hypotheses were that radio-tagged Wood Thrushes would use habitats proportional to their availability on the landscape and that survival would be similar across habitats. However, based on recent studies, I predicted that during the natal period birds would most often be located in the relatively open mature forest and that later, during the post-natal period, as they tried to meet their own food and cover demands, they would be found in denser areas. Furthermore, I predicted that survival would be higher in such areas.

METHODS

STUDY AREA

This study was conducted on the 3411 ha MeadWestvaco Wildlife and Ecosystem Research Forest (MWERF) and the 1705 ha MeadWestvaco Panther Run Tract (PRT) in southwestern Randolph County, West Virginia (Fig. 1). The MWERF and PRT were established in 1994 and 2001 respectively, to provide sites for long-term research on the effects of intensive forest management practices on wildlife and other ecosystem elements. Based partly on elevation, the MWERF was equally divided into two blocks of 1705.5 ha. The lower elevation block was used in this study, as it was logistically closer and more similar in elevation to the PRT. The elevation of this block ranges from 707-1012 m, while 16 km to the north the PRT is 634-914 m. The woody vegetation on the MWERF and PRT can be characterized as second growth hardwood forest initially harvested 80-90 years ago. The MWERF is composed primarily of cove hardwoods and mixed mesophytic communities (Braun 1950), with northern and Allegheny hardwoods present in the higher elevations (Engle 2007). The PRT is composed primarily of xeric oak-hickory forests.

Both sites have many patches of regenerating forest areas (Table 1). Sawtimber, diameter-limit, and clearcuts were the typical harvesting methods. In 2004, 40 even-aged harvest units were present on the study areas and ranged from 6.1 to 29.2 ha in size.

RADIO-TAGGING AND TRACKING

Nest searching occurred throughout the study areas from June through August 2003, and May through August of 2004 and 2005. When a nest was discovered, the stage (building, incubation of eggs, or brooding of nestlings) was ascertained at that time or during subsequent visits. Nests were monitored every 3 days or less, if hatching or fledging was eminent (Ralph et al. 1993). Nestlings were radio-tagged 2 – 3 days prior to fledging. Most (92 %) were returned to the nest after tagging; those that could not be returned were placed in woody vegetation above the ground near the nest. When nestlings fledged earlier than anticipated, the immediate vicinity of the nest site was observed from a distance to locate the fledgling. Once located, it was captured with a mesh 61 cm diameter hoop net, radio-tagged, then released near the capture site.

As a complement to radio-tagged nestlings, juvenile Wood Thrushes were captured with mist-nets during the post-natal period as part of a study examining songbird use of regeneration units during the post-fledging period (T. Dellinger, Chapter 4). Captures occurred from 21 July to 18 August 2004, and 1 August to 29 August 2005. All tagged birds were released at the capture site.

Nearly all Wood Thrushes were tagged with a 1.1 g transmitter with a battery life of > 60 days. These transmitters weighed 3% of the Wood Thrushes' total body weight. A 0.3 g and a 0.5 g transmitter was used on two Wood Thrushes tagged in July 2003, each with a battery life of 15 and 35 days respectively. To attach the transmitter, we used a leg-loop harness (Rappole and Tipton 1991) made of 0.7 mm diameter dissolvable sutures. Doerr and Doerr (2002) reported that dissolvable sutures lasted on average 149 days (SD = 89 days).

Using a 150-152 MHz antenna and T1000 Wildlife Materials, Inc. receiver, observers collected a daily location for each bird. In July-October 2003, daily locations were gathered by a single observer through asynchronous triangulation from the nearest road and were used only in survival analyses. During June-September of both 2004 and 2005, Wood Thrushes were tracked by homing in on radio signals on foot and each location was marked with plastic flagging for subsequent vegetation measurements. Additionally, using a Trimble XT GPS unit, the UTM coordinates of the site where the bird was first observed were recorded with a minimum of 80 fixes obtained for each location. Ninety-eight percent of all fixes were averaged, differentially corrected with GPS Pathfinder© Office 2.9 software, and entered into ArcView 3.2™. Thirty-three locations could not be differentially corrected with the GPS Pathfinder© Office 2.9 software due to various reasons both known (e.g., expired base station files) as well as unknown. I kept those locations in the data set based on the accuracy of the Trimble XT GPS unit on the study site because among all differentially corrected locations, the raw uncorrected location was < 8 m from the corrected location.

Occasionally radio-tagged individuals could not be found when they initially moved to a new location. Thus, I searched for a lost bird for at least 2 days and nights before considering it to have left the study area and scanned for previous lost individuals during these times as well. I began searching for such birds from their last known location, driving roads radiating outward from that location while scanning via a receiver with a roof-mounted omnidirectional antenna. When a radio-tagged bird was not found during the day, an observer searched again after sunset via roads. At night, signals of Wood Thrushes could be detected from greater distances than during daytime tracking, presumably because the birds were stationary while roosting above the forest floor. In addition to searching both study sites, I also searched for radio signals in the area between the two study sites.

For most individuals, two distinct spatial clusters of locations were apparent representing two periods: the period when the fledgling was dependent on its parents for food and received some protection from them, and the independence period when the individual was on its own. Assignment of locations to a period was based on age of the fledgling and proximity of the location to the natal nest. The dependence period locations typically occurred close to the nest and are referred to as the natal area. The parents chose the nest site location and thus the habitat in the natal area. Fledglings generally remained on the natal area for the first 3 weeks out of the nest. The independence period locations are referred to as the post-natal area. These areas are of special interest because they represent the habitats actually used by the juvenile birds and may contain elements required for their survival during this time. Juveniles remained in the post-natal areas for up to 7 weeks before their transmitter batteries died or they moved out of the study area, presumably as they began their fall migration.

HABITAT USE

I examined habitat use at two spatial scales (landscape and habitat surrounding individual telemetry locations) to compare natal and post-natal areas. Similarities and differences between these scales may have important conservation implications when managing for all life stages of the Wood Thrush.

At the landscape scale, three dominant cover types (mature forest, sawtimber harvests, and early successional areas) were digitized on both the MWERF and PRT based on stand data and field observations and represented cover type availability (Table 1). Each telemetry location was assigned to a cover type. Stands that originated in the 1920s and received select harvest through the 1980s were considered mature forest. This cover type was characterized as having a closed canopy and open understory. Sawtimber harvests were stands that consisted mainly of closed canopy areas, with some canopy gaps and often dense understory and ground cover. This cover type was the result of selectively harvesting only large diameter trees in a stand (typically > 30 cm diameter at breast height), leaving 14-16 m^2/ha BA or 70-80% of the original stand. Early successional areas included roadside thickets as well as large even-aged harvests. In 2004, all sawtimber harvests were $\leq$ 14 years post-harvest and all even-aged harvests were $\leq$ 10 years post-harvest.

Because early successional habitats were highly variable, I further divided early successional habitats into three categories based on age and type of regeneration areas (Table 1). Even-aged harvests were divided by age: old harvests (7 to 11 years post-harvest) and young harvests (3 to 6 years post-harvest). Old harvests were typically pole forests with < 8 m canopy height composed primarily of fire cherry (*Prunus pensylvanica*), red maple (*Acer rubrum*), and black birch (*Betula lenta*), with a dense understory along skid roads. In 2004, there were seven and six old harvests on the PRT and MWERF, respectively. Young harvests were primarily composed of dense brambles and saplings that averaged < 4 m high. There were 12 young harvests on the PRT, and 13 on the MWERF in 2004. Disturbed areas made up the third early successional category and were small shrubby areas along gas wells and roadsides. These small, often linear patches were mowed every 2-3 years to prevent the establishment of trees. They were comprised primarily of blackberry (*Rubus* spp) brambles and small hardwood saplings.

Using all locations on and off of the study areas for each radio-tagged individual, I calculated the proportion of daily locations within each dominant cover type, as well as within the three early successional categories. For the early successional categories, only individuals located within an early successional patch at least 2 days in either period was included; hence five individuals/locations were omitted during the natal period and three in the post-natal. Only one location in this cover type may have been the result of a bird fleeing from observers while being radio-tracked.

To examine if bird locations in mature forest or sawtimber harvest were closer to cover type borders, I calculated distance to nearest edge for every location within those cover types on the study area with ArcMap 9.0™. Similarly, I calculated the distance to forest edge of locations in young and old harvests.

On a finer scale, I quantified vegetation surrounding daily telemetry locations after the respective birds no longer used the area. For all locations that were not in the early successional cover type, I used a vegetation density board (Nudds 1977) to determine the amount of vegetative concealment. The percent cover was estimated in 20% increments and assigned a value of 1-5 for each 0.5 m interval of the 3 m board from 10 m away in a randomly determined direction.

I also collected detailed vegetation information at a randomly selected subset of the telemetry locations (373 of 1650 locations) for each tagged bird. Detailed vegetation sampling could not be quantified at all daily locations for each radio-tagged bird due to the large number of locations recorded and to limitations in both time and personnel. Most were from clusters of daily locations representing a small use area of approximately 2 ha.

Sixteen variables (Table 2) were measured using methods modified from James and Shugart (1970) and BBIRD protocols (Martin et al. 1997) in a 0.04 ha circular plot centered on the location at which the bird was observed. Ground and canopy cover were measured by ocular estimation at 20 regularly spaced intervals along two 22.6-m lines, arranged along the cardinal directions perpendicular to one another, which defined the circular plot (Noon 1981). Within the plot, percent slope, aspect, and all trees and snags greater than 7.6 cm diameter at breast height (d.b.h.) were identified and measured. All woody stems within a 5 m radius from the center of the plots also were quantified.

STATISTICAL ANALYSES

I used a Chi-square contingency table analysis to test the hypothesis that the proportion of telemetry locations in each cover type was the same during the natal and post-natal periods. I omitted the six individuals radio-tagged in 2003 due to uncertain accuracy of individual locations and included all 2004 and 2005 locations on and off of the study areas.

Cover type use and availability analyses included only locations on MWERF and PRT during 2004 and 2005 because availability could not be determined for locations off the study areas. I compared the proportion of locations of each bird found in each cover type to the amount of each cover type present on each study area with Chi-square Goodness-of-Fit Tests (Neu et al. 1974). I conducted this analysis separately for natal and post-natal periods, and thus a greater number of birds were used for natal calculations than for post-natal because some individuals left the study area once they were independent of their parents. I calculated cover type proportions separately for MWERF and PRT, as well as for each year, due to differences in availability of cover types at each site and in each year. Additionally, I determined cover type availability in spring and again in late summer to account for new harvests that occurred in mid-summer. I assumed all tagged birds to be statistically independent and thus each Chi-square test for goodness-of-fit statistic and its degrees of freedom were summed to obtain an overall value for each period (White and Garrott 1990). I constructed Bonferroni 95% confidence intervals to determine which cover types were not used in proportion to their spatial availability by individuals on the MWERF and PRT (Neu et. al 1974).

I used Student's *t*-tests for three distance to nearest edge comparisons within each period: for locations within mature forest and sawtimber harvests, between mature forest and sawtimber harvests, and between young and old harvests. Within young harvests, I compared distance to forest edge of natal and post-natal locations; no natal locations occurred in older harvests. For onsite post-natal locations within clearcuts, I used linear regression to test for increasing or decreasing trends in distance to edge versus harvest size and age. I used polynomial regression to relate clearcut size and age to number of locations and number of individuals using each stand in each year during the post-natal period. Independent variables included in the regression model were stand size, stand age, and stand age^2. Alpha ≤ 0.05 was considered significant.

I used Wilcoxon rank-sum tests to compare the estimated concealment of each 0.5 m level of the vegetation density board between natal and post-natal locations (Kilgo et al. 1996). Wilcoxon rank-sum test p-values <0.008 were considered significant after applying a Bonferroni correction for the number of statistical tests.

Before analysis of vegetation variables, I tested them for normality with the Shapiro-Wilk's test at the 95% confidence level. None of the habitat variables were normally distributed and thus were transformed prior to analysis: slope using square root, percent ground covers and canopy layers using arcsine square root, and densities of seven size classes of woody vegetation using a log-transformation. While these transformations decreased the variance and reduced outliers, all variables remained non-normally distributed. Normality probability plots of all transformed habitat variables suggested their distributions were tolerably close to normality and not serious enough to drop from the analysis. All means given are mean ± standard error (SE) of raw data.

I used one-way analysis of variance (ANOVA) (Dowdy and Wearden 1991) to compare vegetation variables among cover types within natal and post-natal locations to identify common habitat features. After applying a Bonferroni adjustment, $P \leq 0.003$ was considered significant.

I used a one-way multivariate analysis of variance (MANOVA) (Barker and Barker 1984) to compare overall differences between the habitat characteristics present at the natal and post-natal locations for each cover type. The independent variable was *period* (natal or post-natal) and the dependent variables were the 16 habitat variables described above. When MANOVA showed a significant difference, I used Student's *t*-tests with $P \leq 0.003$ to identify the specific variables that differed between natal and post-natal sites for each cover type. For MANOVA, significance was set at $P \leq 0.05$.

Also based on significant differences in MANOVA, I determined which of the 16 vegetation variables were most important in separating natal and post-natal areas by using step-wise discriminate function analysis (DFA) (McGarigal 2000) to develop a model from the transformed variables for each cover type. Step-wise DFA evaluates the importance of individual variables and removes unimportant variables from the model. The entry and stay alpha levels were set at 0.15 for the step-wise DFA.

Using data collected from all radio-tagged fledglings in 2003-2005, I calculated survival rates during the post-fledging period with the Kaplan-Meier estimator (Kaplan and Meier 1958) modified to allow for staggered entry of animals into the study (Pollock et al. 1989a, 1989b). Overall survival rate was the probability that a bird survived until the end of the post-fledging period. I also determined survival for each cover type, within each period. All individuals that used in proportion to or greater than availability of a cover type, based on Bonferroni's 95% confidence intervals results, were used in the survival calculation. The cover type survival estimate was the probability that individuals survived until the end of the natal or post-natal period within a given cover type and within a given period. To test for differences between cover type survival estimates in each period, I used a log-rank test (Savage 1956, as described in Pollock et al. 1989a).

RESULTS

I radio-tagged 62 Wood Thrushes during 2003 to 2005. Seven were nestlings from five nests in 2003, 17 were tagged from 13 nests as nestlings or within 2 days of fledging in 2004, 28 were tagged from 25 nests as nestlings or within 2 days of fledging in 2005. These individuals are referred to as fledglings. For nests (n = 3) from which two sibling Wood Thrushes were radio-tagged, I considered movements of each to be independent of its sibling. This assumption was validated by the fact that I did not observe fledglings together during the natal period, and in the post-natal period all siblings' daily locations were separated by at least 1 kilometer. Nests were located in all three cover types, 33 in mature forest, nine in sawtimber, and one in an even-age harvest. The remaining ten individuals were captured in even-age harvests with mist-nets and radio-tagged during the post-natal period, three in 2004 and seven in 2005. These individuals are called juveniles.

HABITAT USE

Cover Types. I identified cover type for 1650 locations of 47 radio-tagged individuals in 2004 and 2005. Distribution of daily locations among the cover types differed between natal and post-natal periods ($\chi^2 = 272.08$, $df = 2$, $P<0.001$). Fifty-nine percent of daily natal locations were in mature forest (Fig. 2). The majority of post-natal locations were in sawtimber harvests (43%) and early successional areas (37%). Over the course of the season however, cover type use appeared to differ. Among natal locations, most were in mature forest throughout the season, while early successional use surpassed sawtimber use in early July and peaked in late August (Fig. 3). Among post-natal locations, use of sawtimber cuts declined from early July to early August, as early successional habitat use increased (Fig. 3). By late August early succession use dropped and most locations were again in sawtimber harvests until migration began or the transmitters expired.

Natal locations of 37 radio-tagged fledglings occurred on the study area and were used to compare use and availability of cover types. During the natal period, daily locations were not in cover types proportional to availability ($\chi^2=990.08$, $df = 74$, $P<0.0001$). Mature forest was used more than expected based on availability and sawtimber harvests were used less than expected (Fig. 4). Bonferroni 95% confidence intervals calculated for the proportion of time each bird spent in each cover type showed mature forest was preferred by a greater number of individuals (54%) in the natal period

(Fig. 5). Sawtimber harvests and early successional areas were avoided during this period by 65% and 62%, respectively, of individual tagged birds.

During the post-natal period, 35 Wood Thrushes could be used in cover type use and availability analyses; 25 were fledglings and ten were juveniles. Use and availability of cover types differed in the post-natal period (χ^2=628.19, *df* = 70, *P*<0.0001). Early successional areas were used more often than expected based on availability and mature forest less than expected (Fig. 4). Bonferroni 95% confidence intervals constructed for this period suggested much individual variability (Fig. 5). Early successional areas were the most preferred cover type (37% of post-natal individuals) and cover types with a relatively dense understory (i.e., early successional areas and sawtimber harvests) were equally the least avoided cover types. In contrast, mature forest, with a somewhat open understory compared to the other cover types, was avoided by over half of individuals and preferred by only four tagged birds.

Early Successional Categories. Over both periods, 38 of 47 tagged Wood Thrushes used early successional areas and 36 were located in at least one early successional category >1 day. Thus, of 464 early successional locations, 456 were used in analysis. Radioed birds used different categories of early successional patches during the natal and post-natal periods (χ^2= 83.32, *df* = 2, *P*<0.001) with disturbed areas used more during the natal period and old harvests during the post-natal period (Fig. 6.). Young harvests were used most often during both periods, 60% and 53%, respectively (Fig. 6).

In the natal period, 14 of 37 radio-tagged Wood Thrushes were located >1 day in an early successional patch, all on the PRT. Although most daily locations were in young harvested stands (60% of 123 locations; Fig. 6), more individuals used disturbed areas (9 of

14 individuals). Specifically, I located five fledglings within two young harvests and nine birds in disturbed areas. The mean size of the two clearcuts used was 15.7 ha and the mean post-harvest age was 5 years (Table 3), with one of the stands used both years. Use and availability of early successional categories differed during the natal period (χ^2=447.53, df = 28, P<0.001). Young and old harvests were used less than expected, and disturbed areas were used more than expected (Fig. 7). Bonferroni 95% confidence intervals for the proportion of time each bird spent in each category (Fig. 8) indicated all individuals completely avoided the old harvests and 64% preferred disturbed areas.

Thirty (21 fledglings and nine juveniles) of 41 tagged individuals were located in early successional patches >1 day during the post-natal period. Young and old harvests each had more daily locations than disturbed areas (Fig. 6). Eleven and five harvest stands were used on the PRT and MWERF, respectively, and six of the 16 were used both in 2004 and 2005 by multiple radio-tagged birds. Used harvests at both study areas were similar in size, 6-20 ($\bar{x}$ = 15.5) ha on the PRT and 10-16 ($\bar{x}$ = 12.3) ha on the MWERF. Proportion of telemetry locations in a stand increased with harvest size (r^2 = 0.34, F = 4.37, P = 0.05, n = 21; Fig. 9) as did proportion of individuals (r^2 = 0.31, F = 4.17, P = 0.06, n = 21) (Fig. 10). I detected a quadratic relationship approaching significance between stand age and use for proportion of locations (r^2 = 0.34, F = 3.81, P = 0.07, n = 21; Fig. 11) and proportion of individuals (r^2 = 0.31, F = 3.35, P = 0.09, n = 21; Fig. 12). Most locations and individuals were in stands 6 - 8 years post-harvest.

Use and availability of early successional categories of onsite individuals (14 fledglings and nine juveniles) also differed during the post-natal period (χ^2=407.06, df= 46, P<0.001). Old harvests were used more than expected while young harvests were used less than expected (Fig. 8). Although Bonferroni 95% confidence intervals indicated over 50% of individuals avoided disturbed areas and young harvests, all three early successional categories were preferred by at least some individuals in the post-natal period (Fig. 9). More tagged Wood Thrushes preferred both age categories of harvests more than disturbed areas.

Telemetry locations within mature forest were farther from the forest edge than locations within sawtimber harvests during both periods (Table 4). The average distance from edge at which birds were located in young and old harvests was nearly identical during the post-natal period. Post-natal locations in young harvests were farther from the forest edge than natal locations. Within clearcuts, the distance to edge of post-natal locations decreased with increasing harvest size ($r^2 = 0.08$, $F = 5.95$, $P = 0.02$, $n = 205$; Fig. 13) and increased with harvest age ($r^2 = 0.08$, $F = 6.44$, $P = 0.01$, $n = 205$; Fig. 14).

Vegetation Density Board. I measured vegetation density at 1175 daily locations for 47 individuals located in mature forest or sawtimber in 2004 and 2005. In mature forest, locations during the post-natal period occurred in more dense vegetation than in the natal period, with significant differences at the 2.5 m and 3.0 m intervals (Table 5). In sawtimber harvests, vegetation density did not differ between the two periods. I detected no differences in vegetation density between mature forest and sawtimber locations during the natal or post-natal periods.

Vegetation Characteristics of Natal vs. Post-natal. Locations in mature forest had differences in habitat between the natal and post-natal periods (MANOVA: Wilks' $\lambda = 0.8054$, F=1.87, df=16 and 124, $P = 0.03$). Stepwise DFA for mature forest sites selected aspect, high canopy layers, and herbaceous ground cover as the variables best separating the two periods (Table 6). Only herbaceous ground cover and high canopy were significant in post-hoc *t*-tests (Table 6). Natal locations had a southward facing aspect while post-natal sites were more south-southeasterly (Table 7). Also natal sites had more high canopy cover and herbaceous ground cover.

Locations in sawtimber differed in habitat characteristics between periods (Wilks' $\lambda = 0.7503$, $F = 2.33$, df = 16 and 112, $P < 0.01$). However, univariate analysis found snag density to be the only specific variable that differed (Table 6) with natal areas containing more snags (Table 7). Snag density also was identified as the most important variable to differentiate natal and post-natal sites in stepwise DFA. Three additional discriminating variables were sapling density, leaf litter ground cover, and mid-high canopy. Natal areas had greater amounts of mid-high canopy, whereas more leaf litter ground cover and saplings were present on post-natal sites. The four variables combined explained 22% of the variance among sawtimber sites.

Early successional areas (all age and size categories combined) differed between natal and post-natal periods (Wilks' $\lambda = 0.6795$, $F = 2.54$, df = 16 and 86, $P < 0.01$). Only low-mid canopy differed in *t*-tests between periods (Table 6). Stepwise DFA identified three additional variables, high canopy, percent slope, and pole density, although low-mid and high canopy layers were the best discriminators. Natal sites had steeper slopes, less pole density and more high canopy, while more low-mid canopy layer was present at post-natal locations (Table 7).

Vegetation characteristics of locations in disturbed areas did not differ overall between periods (Wilks' $\lambda = 0.2764$, $F = 1.96$, $df = 16$ and 12, $P = 0.12$). The habitat at locations in young harvests also did not differ overall between periods (Wilks' $\lambda = 0.4922$, F =1.87, *df* = 16 and 29, *P* = 0.07).

Vegetation Characteristics Among Cover Types. Among natal locations (n = 151) of 37 individuals tagged during 2004 and 2005, ANOVA identified seven of 16 vegetation variables that were similar among cover types ($P \geq 0.003$) (Table 7). Generally, natal sites had a south facing aspect with relatively high amounts of leaf litter ground cover and small quantities of bare, herbaceous, and woody debris covers and snag density. High amounts of low canopy layer also were similar among natal cover types. Locations of 41 individuals during the post-natal period (n = 222) tended to be on moderate, southerly-facing slopes with sparse herbaceous and bare ground cover and high amounts of low-mid canopy layer.

Seven variables were identified by ANOVA ($P \geq 0.003$) as similar among natal locations in the three categories of early successional vegetation (n = 30) (Table 8); each had similar steep slopes and small amounts of bare ground, herbaceous/fern, and woody debris ground cover, and snag density. All natal sites had moderate quantities of leaf litter and low-mid canopy. Post-natal sites (n = 73) were similar across categories in that they were on steep, south-southeasterly facing slopes with small percentages of herbaceous, bare, and woody debris ground covers. Moreover, post-natal early successional areas shared high amounts of low canopy cover.

SURVIVAL

Sixty-two individuals, radio-tagged during 2003-2005, had an overall Kaplan-Meier survival estimate of 80% over the post-fledging period. Fifteen birds were censored because the harness broke prematurely and an additional one because a smaller transmitter with significantly less battery life was used. None of the batteries within the transmitters were believed to have expired prematurely; the average battery life was 48.9 days.

Nine individuals were believed to have been depredated based on condition of the transmitter or feather remains. Of the depredated nestlings, six were found within the first 2 days after they were radio-tagged. Remains of four of the six were located within 10 m of the nest, suggesting they may have been killed just before or after fledging. These individuals were from nests of each cover type: one from a nest in mature forest, two from sawtimber cuts, and one from an early successional area. Another individual from a nest in mature forest, was located 70 m downslope of the nest and appeared to have been depredated by ants or died from exposure and was subsequently scavenged by ants, as the carcass remained mostly intact. The last individual depredated prior to or just after fledging, was located 230 m from its nest site in mature forest, in an unidentified hawk's nest in another stand of mature forest. The remaining three depredated fledglings were killed at 11, 12, and 20 days post-fledging, respectively. The transmitter and a few feathers of the first were located in an even-age harvest 173 m from the site of the nest in mature forest. The remains of another were dissected from an owl pellet located in a sawtimber harvest 272 m from the mature forest nest site. The last bird was located 2,520 m from the nest site in a Cooper's Hawk (*Accipter cooperii*) nest 22 days after fledging; both Wood Thrush nest and Cooper's hawk nest were in mature forest. For the nine individuals, mortality occurred in mature forest for four, in sawtimber for three, and in early successional for two individuals.

Analysis of survival within cover types was based on the 47 individuals for which cover type preference could be determined. No radio-tagged Wood Thrushes were identified as depredated during the post-natal period, thus the Kaplan-Meier survival estimate was 1.00 for each cover type. In the natal period, birds that used or preferred mature forest (n = 29) and early successional areas (n= 14) had a Kaplan-Meier survival estimate of 0.91 and 0.88 respectively. A slightly lower survival estimate of 0.80 was calculated for natal period birds that used or preferred sawtimber harvests (n = 13). Comparison of natal survival among the three cover types was not significantly different (χ^2=0.80, *df* = 2, *P*=0.68).

DISCUSSION

NATAL PERIOD

I found that within as few as 2 days after fledging, radioed juveniles moved into a young harvest or disturbed area. One explanation for this behavior is that juveniles followed adults into these areas (Vega Rivera et al. 2000). Use of disturbed areas does not seem unusual for adults of an interior/edge species such as the Wood Thrush; however, for a forest species to spend several days in a large clearcut seems counter-intuitive. One explanation for this behavior is that after their final brood of the season has fledged and before migration begins, adults experience a molt that greatly reduces their flying ability. They have been observed to move into areas with dense saplings at this time, presumably for predator avoidance (Vega Rivera et al. 1998b). Occasionally they are still caring for fledglings at this time, which follow them into the clearcuts.

Another reason juveniles moved into young harvests or a disturbed area may have been simply that so many early successional patches were in close proximity to the nest sites. All nest sites were < 500 m ($\bar{x}$ = 98.0; range 10 to 485) from the nearest early successional patch, and slightly more than a third of the radio-tagged fledglings moved into these nearby areas. However, I did not detect all radio-tagged birds in early successional areas even when such areas were relatively close to the natal area. Furthermore, birds that did use early successional areas did not always use those closest to the nest. For example some individuals passed over strips of disturbed areas < 50 m from the nest site en route to settling in a clearcut 80 m beyond.

What drew radioed individuals to use or not use a specific early successional patch in the natal period remains unclear, however one characteristic common to all but one early successional patch used, is that all were upslope or at a higher elevation than the nest site. Similar to the advantage of being in the forest canopy, an upslope position may have helped in evading predators. This advantage may have held true particularly in disturbed areas. Fledglings could have hidden in dense regeneration from potential predators approaching upslope, or could have glided downslope if flushed from the dense vegetation and still remained in the natal area. For individuals in young harvests the vastness of the dense regeneration likely provided sufficient concealment in all directions.

POST-NATAL PERIOD

During the post-natal period I found juveniles in vegetation similar to that described by others, namely: in dense habitats created by clearcuts 1 – 8 ha in size (Anders et al. 1998), along roadsides and forest edges (Vega Rivera 1998a, Fink 2003), and in forests where most large trees had been harvested (Anders et al. 1998, Fink 2003). Compared to mature forest, these cover types had more saplings, more low canopy layers, more herbaceous ground cover, fewer snags, and less upper-high canopy layers. Although juveniles used all categories of early successional patches, most preferred clearcuts. Of 40 clearcuts available at the beginning of the study in 2004, 16 were used. The majority of radioed birds used cuts 6 – 8 years post-harvest; no radioed individuals were found in recent harvests $\leq$ 2 years post-harvest and even cuts in their third post-harvest growing season were seldom used. Patchy low vegetation within dense slash (i.e. undecomposed coarse woody debris left from logging operations) may have made recent harvests unfavorable.

Harvest size appeared to be important in determining use by post-natal fledglings. More daily locations and radio-tagged individuals were in large harvests (13.9 – 19.8 ha) than smaller cuts (6.1- 11.1 ha); all but four harvests used by fledglings were >13 ha in size. Greater proportions of locations and individuals in large harvests is contrary to the results of Vitz and Rodewald (2005), who found greater capture rates of juvenile mature forest songbirds in smaller (4.0 to 9.3 ha) over larger harvests (13.3 – 18.1 ha) in the post-natal period. They speculated that juveniles using both mature forest and early successional areas might prefer smaller harvests because of increased access to both habitats. Because I observed radioed individuals only a few minutes each day, individuals could possibly have used both cover types in a single day. I did suspect an individual that remained in a 5 year old harvest moved to mature forest near dusk to roost with conspecifics in taller trees. Yet individuals were located at different times each day, and most tagged birds within clearcuts were usually within a small use area in the harvest on consecutive days.

Vitz and Rodewald (2005) also found a relationship approaching significance between harvest size and distance to edge. They found a greater percentage of mature forest species were captured farther from the edge in larger rather than smaller harvests. My data show the converse, that radioed birds were located closer to the edge in larger harvests. This effect may be due in part to fewer locations in smaller relative to larger cuts;

however, locations near the edge of larger harvests may support their hypothesis that both early successional and mature forest are used daily. As harvests become older they may offer more preferred habitat characteristics of both cover types, as individuals tended to be farther from the edge with each additional post-harvest year. Habitat characteristics of old clearcuts shared with areas in younger harvests close to the forest edge are high stem density and some vertical stratification, although not to the degree of that found in mature forest.

NATAL VERSUS POST-NATAL SITES

Similar to previous studies (Fink 2003, Vega Rivera et al. 1998a, Anders et al. 1998), I found an overall shift in cover type preference between the natal and post-natal periods, with denser understories used more in the post-natal period as well as early successional areas preferred over sawtimber harvests in this period. Survival was similar among cover types.

All previous studies have described vegetation differences between natal and post-natal settled areas (Anders et al. 1998, Lang 2002, Fink 2003); however, the comparisons were made without respect to cover type. In contrast, I compared vegetation characteristics within cover types and within early successional categories between both periods, and discovered a more complete picture of the juvenile tendency to move from semi-open to dense habitat.

Mature forest had the most open understory of the three cover types, yet juveniles sought out denser areas within it; however, the type of vegetation used for concealment differed by period. Natal sites within mature forest had more herbaceous ground cover, such as ferns, which most likely provided cover for young birds that were not yet proficient flyers. In contrast, post-natal sites had less herbaceous ground but denser saplings. Patches of high sapling density used were probably located in canopy gaps, because high canopy layers often were absent from these locations.

Vegetation differences between natal and post-natal use areas within sawtimber harvests appeared to be related to the age of the stand post-harvest. Thirty-five percent of individuals located in sawtimber harvests in the natal period used cuts < 3 years post-harvest, while in the post-natal period only cuts that were last harvested in early to mid-1990s were used. During sawtimber harvests some non-harvested trees and poles usually were damaged from logging equipment and from felled trees, these trees/poles subsequently died yet remained standing as snags in the immediate years following the harvest. Thus, the most likely source of higher snag density on natal than post-natal sites, as identified by statistical analyses, was use of young sawtimber cuts < 3 years post-harvest in the natal period. In contrast, on post-natal sites a significant lack of snags relative to natal sites suggests perhaps some deteriorated and eventually fell. Over time with the presence of numerous harvest-related canopy gaps, multivariate analysis identified a significantly higher density of saplings on post-natal sites, which usually were species such as birch (*Betula* spp.), American beech (*Fagus grandifolia*), and maple (*Acer* spp.). While leaf litter was the dominant ground cover on both natal and post-natal sites, natal areas tended to have higher amounts of bare ground, herbaceous plants and ferns, and woody debris than post-natal areas; incidentally these other ground covers were the likely result of recent logging disturbance and lack of a dense sapling understory. This may explain why DFA identified leaf litter as an important discriminator between natal and post-natal sites in sawtimber harvests.

Within early successional areas, specifically young harvests, the trend of moving to denser areas in the post-natal period was reversed, as natal sites were on average denser than post-natal sites. Examining only individuals that used the same young harvest in both periods verifies that in the natal period these birds were located in areas with more saplings than in the post-natal period. Again, it is possible young birds are linked to these denser areas in the natal period by following experienced adults that require cover and that are undergoing heavy molt and are incapable of flight. Closer scrutiny of sapling size in the vegetation data showed post-natal sites had three times as many large saplings 2.5 cm to 7.6 cm and > 80 fewer saplings < 2.5 cm than natal locations. The larger diameter saplings were taller than the surrounding vegetation and could possibly have been used for night roosts, or as cover, or even as landmarks for young birds moving within the clearcut. In the natal period radioed birds in young harvests remained closer to the forest edge potentially allowing roosting opportunities within nearby mature trees.

The abundance of soft mast, often cited as an explanation for the use of early successional areas, did not fully explain the movement from natal to post-natal areas. Most individuals moved into an early successional area before soft mast was abundant (i.e. before *Rubus* was ripe). Furthermore, softmast occurred throughout all cover types and I observed individuals consuming soft mass within each cover type, suggesting the availability of this food type may not have been a limiting factor.

SURVIVAL

The majority of deaths in my study occurred 2 days after fledging, and thus the trend I detected in overall juvenile survival rates was similar to that reported by most other authors in that survival was higher in the denser post-natal areas (Anders et al. 1998, Fink 2003).

Higher mortality during the natal period may be the result of juvenile inexperience in evading predators, particularly in the initial days after fledging when young birds are incapable of extended flight (Vega Rivera et al. 2000). Thus, as suggested by other authors (Anders et al. 1998, Vega Rivera et al. 2000, Fink 2003, Vitz and Rodewald 2005), moving into denser vegetation would appear to have a survival advantage for poor fliers. However, I found no difference in survival rates among birds located in mature forest, sawtimber harvests, and early successional areas, a result that contradicted my prediction of survival being highest in the densest areas. One explanation for this result is that it is possible large areas of early successional vegetation are not necessary for adequate concealment of juveniles, and that the smaller patches formed beneath canopy gaps in mature forest were sufficient for this purpose. The survival rates I detected, however, were high throughout both periods, and thus inference about the habitat as related to these rates may be limited. One possible cause of higher mortality in the natal period, in particular the first few days after tagging, could have been increased predation due to techniques involved in radio-tagging nestlings. Our methods violated the nest monitoring protocol first suggested by Ralph et al. (1993) and subsequently followed by a majority of nest monitoring studies (Martin et al. 1997) by allowing observers to behave in ways that may have attracted predators to the nest. Specifically when we radio-tagged a nestling, we left a dead end trail at nests; left human scent at nests by the touching the nest tree, nest, and nestlings with our bare hands; often disturbed areas around nests with a ladder; allowed adults to give alarm calls for the duration of the tagging process; failed to ascertain that no hawks or corvids were watching us before we removed nestlings; did not check “dummy” nests; and were near nests when young were close to fledging.

CONSERVATION IMPLICATIONS

Wood Thrush fledglings are not capable of extended flight until about 7 days after fledging (Vega Rivera et al. 2000). Thus, to provide cover for juvenile Wood Thrushes before migration, some early successional areas should be created and maintained through canopy disturbance. Preferably, large regeneration areas with 3 – 6 m high canopy should be maintained through a rotation that ensures clearcuts 6 – 8 years old are present at all times. But if large harvests are not desired or needed, land managers should maintain some smaller early successional patches in places such as along roadsides or within canopy gaps. While I observed juveniles to prefer large clearcuts, they also used such smaller patches, apparently with no increased mortality. Sawtimber harvests, while of uncertain benefit to the long-term health of the forest, apparently also provide suitable habitat for juveniles, especially after a period of regeneration has created areas of dense sapling growth.

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Table 1. Available proportions of cover types and early successional categories on MeadWestvaco Wildlife and Ecosystem Research Forest (MWERF) and Panther Run tract (PRT) in Randolph County, West Virginia in 2004-2005.

	Percent of land cover			
	MWERF		**PRT**	
	2004	**2005**	**2004**	**2005**
Mature Forest	68.3	64.1	34.1	30.8
Sawtimber Harvests	12.9	12.7	51.3	49.6
Early Successional	18.9	23.2	14.6	19.7
Disturbed Areas	1.9	1.6	13.5	10.1
Young Harvests (3 – 6 yrs post-harvest)	69.5	71.7	79.0	60.5
Old Harvests (7 – 11 yrs post-harvest)	28.6	26.7	7.4	29.5

Table 2. Description of detailed habitat variables collected at a subset of all locations on MeadWestvaco Wildlife and Ecosystem Research Forest (MWERF) and Panther Run tract (PRT) in Randolph County, West Virginia in 2004-2005.

Variable	**Description and sampling method**
% Slope	Incline at daily location measured via clinometer
Aspect	Azimuth downhill from daily location
Ground Cover	Percent ground cover based on ocular readings at 20 locations within an 11.3 m radius of the daily location
Herbaceous/Fern	Percent coverage of grass or herbaceous species
Leaf litter	Percent coverage of litter
Woody debris	Percent coverage of woody debris
Bare	Percent cover of bare ground
Canopy Height Classes:	Percent cover of 6 canopy classes identified through a ocular reading at 20 locations within an 11.3 m radius of the daily location
Low	woody stems 0.5 to 3.0 m in height
Low-mid	woody stems 3.1-6.0 m in height
Mid	woody stems 6.1-12.0 m in height
Mid-high	woody stems 12.1-18.0 m in height
High	woody stems 18.1-24.0 m in height
Upper-high	woody stems greater than 24.0 m in height
Stem Densities	Total count per species of all saplings and trees
Sapling	Small trees, shrubs, or woody stems < 7.6 cm in diameter within 5 m of center of the daily location
Pole	Trees with a diameter breast height (d.b.h.) between 7.6 cm and 22.9 cm within an 11.3 m radius of the daily location
Tree	Trees with a d.b.h. > 22.9 cm within an 11.3 m radius of the daily location
Snag	Dead trees with a d.b.h. > 7.6 cm within an 11.3 m radius of the daily location

Table 3. Average size (ha) and age (years post-harvest) of young and old clearcut stands used by radio-tagged Wood Thrushes in Randolph County, West Virginia in 2004-2005.

		Natal			**Post-natal**		
		n	**$\bar{x}$ ± SE**	**Range**	***n***	**$\bar{x}$ ± SE**	**Range**
Young Harvests	Size	2	15.7 ± 0.26	15.4 -15.9	8	15.7 ± 0.71	11.1 - 17.9
	Age	2	4.3 ± 1.25	3 - 6	8	5.1 ± 0.39	3 - 6
Old Harvests	Size				8	13.2 ± 1.52	6.06 - 19.8
	Age				8	8.9 ± 0.63	7 – 11

Table 4. Average distance ($\bar{x}$ ± SE) to the nearest edge of daily locations of radio-tagged Wood Thrushes in Randolph County, West Virginia in 2004-2005.

	No. Birds	**No. Locations**	**$\bar{x}$ ± SE**	**Range**	**No. Birds**	**No. Locations**	**$\bar{x}$ ± SE**	**Range**	***T***	***P***
	Mature Forest				**Sawtimber Harvests**					
Natal	31	443	76.1 ± 2.6	0.4 – 257.3	16	178	45.0 ± 2.0	1.8 – 138.7	5.49	< 0.01
Post-natal	23	117	104 ± 11.7	2.4 – 880.0	26	253	64.3 ± 3.4	0.1 – 305.7	2.15	0.03
	Young Harvests				**Older Harvests**					
Natal	5	74	37.3 ± 3.3	1.9 – 116.3						
Post-natal	11	104	64.6 ± 4.2	4.8 – 174.8	14	101	65.4 ± 5.1	3.0 – 219.5	-0.36	0.72

Table 5. Means and standard errors for each height interval of the vegetation density board measured at daily locations of radio-tagged Wood Thrushes in Randolph County, West Virginia in 2004 and 2005. Values are an index of percent coverage: 1 = 0-20%, 2 = 21-40%, 3 = 41-60%, 4 = 61-80%, 5 = 81-100%. Significance was set at $P \leq 0.008$ to account for Bonferroni correction.

Interval Height	**Natal**	**Post-natal**	**Wilcoxon rank-sum Test**	***P***
Mature Forest				
n	442	172		
0.5	2.11 ± 0.07	2.13 ± 0.12	52148.0	0.68
1.0	2.06 ± 0.07	2.09 ± 0.11	52786.0	0.95
1.5	2.01 ± 0.07	2.23 ± 0.12	55295.0	0.18
2.0	2.22 ± 0.07	2.62 ± 0.13	57555.0	0.01
2.5	2.24 ± 0.07	2.90 ± 0.13	60282.0	<0.0001
3.0	2.39 ± 0.07	2.99 ± 0.13	60621.0	<0.0001
Sawtimber Harvest				
n	178	383		
0.5	2.27 ± 0.12	2.29 ± 0.08	49657.5	0.83
1.0	2.10 ± 0.11	2.36 ± 0.08	46790.5	0.06
1.5	2.02 ± 0.10	2.38 ± 0.08	45831.0	0.01
2.0	2.15 ± 0.10	2.52 ± 0.08	45758.0	0.01
2.5	2.25 ± 0.11	2.58 ± 0.08	45885.5	0.02
3.0	2.51 ± 0.12	2.70 ± 0.08	47225.0	0.11

Mature Forest and Sawtimber Comparisons

	Natal		**Post-natal**	
	Wilcoxon rank-sum Test	*P*	Wilcoxon rank-sum Test	*P*
0.5	57123.5	0.32	45370.0	0.13
1.0	56200.5	0.61	44053.5	0.02
1.5	56684.5	0.44	45162.0	0.11
2.0	55313.5	0.98	48186.0	0.83
2.5	55890.5	0.74	50673.0	0.09
3.0	57004.5	0.37	50596.0	0.10

Table 6. Significant (P<0.003) vegetation variables of natal and post-natal comparisons of daily locations of radio-tagged Wood Thrushes in Randolph County, West Virginia in 2004-2005, with *t*-tests and variables retained by discriminant function analysis as most important to distinguish between periods.

Vegetation Variable	**t**	***P***	**DFA Correlation Coefficient**
Mature Forest			
Aspect			0.0176
Herbaceous/Fern ground cover	3.51	0.0006	0.0690
High canopy	3.48	0.0007	0.0794
Sawtimber Harvests			
Leaf litter ground cover			0.0275
Mid-high canopy			0.0357
Sapling density			0.0521
Snag density	3.44	0.0011	0.1034
Early Successional Areas			
Slope			0.0467
Low-mid canopy	-4.33	<.0001	0.1304
High canopy			0.1137
Pole density			0.0252

Table 7. Means and standard errors of vegetation variables quantified during the natal and post-natal periods in each cover type for radio-tagged Wood Thrushes in Randolph County, West Virginia in 2004-2005.

Vegetation Variable	**Mature Forest**		**Sawtimber Harvests**		**Early Successional Areas**	
	Natal	**Post-natal**	**Natal**	**Post-Natal**	**Natal**	**Post-Natal**
% Slope [b]	29.7 ± 1.6	32.0 ± 2.3	34.1 ± 2.0	30.4 ± 1.2	42.0 ± 2.7	33.1 ± 1.8
Aspect [ab]	180.3 ± 9.9	166.2 ± 12.5	193.3 ± 14.8	214.6 ± 11.3	132.7 ± 16.0	181.7 ± 13.4
Ground cover (%)						
Herbaceous/Fern [ab]	11.3 ± 1.4	5.4 ± 1.1	11.5 ± 2.2	9.8 ± 1.3	17.2 ± 3.9	11.6 ± 1.7
Leaf litter [a]	70.4 ± 2.1	78.1 ± 2.0	71.7 ± 2.6	76.6 ± 1.6	59.3 ± 3.5	67.7 ± 2.0
Woody debris [a]	9.4 ± 1.0	8.0 ± 1.0	9.7 ± 1.5	8.3 ± 0.9	13.2 ± 1.9	14.6 ± 1.4
Bare [ab]	5.8 ± 0.8	4.9 ± 1.0	4.3 ± 1.1	3.4 ± 0.5	8.3 ± 2.1	4.0 ± 0.6
Canopy cover (%)						
Low[a]	69.2 ± 2.4	67.6 ± 3.5	79.0 ± 3.5	79.3 ± 2.3	80.7 ± 4.0	91.9 ± 1.3
Low-mid [b]	73.5 ± 2.1	73.5 ± 2.9	81.9 ± 2.6	81.1 ± 1.8	49.8 ± 4.7	73.8 ± 3.0
Mid	75.5 ± 2.2	74.2 ± 3.1	77.9 ± 3.6	73.0 ± 2.3	29.3 ± 6.2	21.7 ± 3.8
Mid-high	80.1 ± 2.0	77.3 ± 3.3	77.2 ± 3.8	69.0 ± 2.5	27.8 ± 5.8	11.2 ± 2.8
High	76.7 ± 2.5	62.8 ± 3.5	64.0 ± 4.4	54.8 ± 3.2	25.8 ± 5.5	8.4 ± 2.3
Upper-high	41.2 ± 3.0	32.1 ± 3.7	29.1 ± 4.3	23.3 ± 2.8	11.2 ± 3.9	3.5 ± 1.2
Stem density (no./plot)						
Sapling	67.6 ± 5.0	81.1 ± 9.0	89.9 ± 8.9	127.6 ± 8.4	223.4 ± 27.1	215.4 ± 14.5
Pole	8.1 ± 0.5	9.8 ± 0.8	8.6 ± 0.8	8.4 ± 0.5	3.9 ± 0.7	5.0 ± 0.8
Tree	7.3 ± 0.4	6.9 ± 0.4	6.4 ± 0.5	6.3± 0.3	2.6 ± 0.5	1.0 ± 0.3
Snag [a]	1.7 ± 0.2	1.8 ± 0.3	1.8 ± 0.4	0.7 ± 0.1	1.1 ± 0.5	0.3 ± 0.1

[a] Vegetation characteristics similar among cover types during the natal period.
[b] Vegetation characteristics similar among cover types during the post-natal period.

Table 8. Means and standard errors of vegetation variables quantified on early successional sites during the natal and post-natal periods of radio-tagged Wood Thrushes in Randolph County, West Virginia in 2004-2005.

Vegetation Variable	**Disturbed Areas**		**Young Harvests**		**Old Harvests**
	Natal	**Post-natal**	**Natal**	**Post-Natal**	**Post-Natal**
% Slope [bc]	40.9 ± 2.7	36.2 ± 5.7	43.1 ± 5.1	32.2 ± 2.3	32.6 ± 3.0
Aspect [c]	144.4 ± 23.5	132.3 ± 30.9	119.4 ± 21.8	179.9 ± 20.5	206.7 ± 20.7
Ground cover (%)					
Herbaceous/Fern [ab]	11.3 ± 5.3	18.1 ± 4.9	23.9 ± 5.4	11.3 ± 2.3	9.1 ± 2.5
Leaf litter [a]	57.5 ± 4.7	55.4 ± 5.2	61.4 ± 5.3	66.1 ± 2.7	75.4 ± 2.8
Woody debris [ab]	16.6 ± 3.0	14.6 ± 4.3	9.3 ± 2.0	17.7 ± 2.2	11.1 ± 1.7
Bare [ab]	13.1 ± 3.3	8.1 ± 2.3	2.9 ± 1.3	3.1 ± 0.9	3.2 ± 0.7
Canopy cover (%)					
Low [b]	70.3 ± 5.9	83.5 ± 4.4	92.5 ± 3.2	95.9 ± 1.1	91.1 ± 2.2
Low-mid [a]	60.3 ± 5.7	68.9 ± 8.3	37.9 ± 6.4	64.4 ± 5.0	86.8 ± 2.6
Mid	53.1 ± 7.3	51.5 ± 8.2	2.1 ± 2.1	6.9 ± 3.5	24.8 ± 6.6
Mid-high	51.6 ± 6.5	42.7 ± 9.3	0.7 ± 0.7	6.3 ± 3.1	2.1 ± 1.5
High	42.7 ± 6.6	31.2 ± 9.7	1.4 ± 1.4	4.5 ± 2.3	2.1 ± 1.0
Upper-high	20.0 ± 6.5	12.7 ± 5.1	1.1 ± 1.1	1.4 ± 1.0	1.6 ± 0.9
Stem density (no./plot)					
Sapling	116.9 ± 18.7	135.1 ± 22.9	345.1 ± 30.2	277.0 ± 20.7	182.3 ± 21.7
Pole	6.0 ± 0.9	6.1 ± 1.4	1.4 ± 0.5	1.3 ± 0.5	8.7 ± 1.7
Tree	4.9 ± 0.6	3.6 ± 0.8	0.1 ± 0.1	0.6 ± 0.4	0.3 ± 0.2
Snag [a]	2.1 ± 1.0	1.2 ± 0.4	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1

[a] Vegetation characteristics similar among early successional categories during the natal period.

[b] Vegetation characteristics similar among early successional categories during the post-natal period.

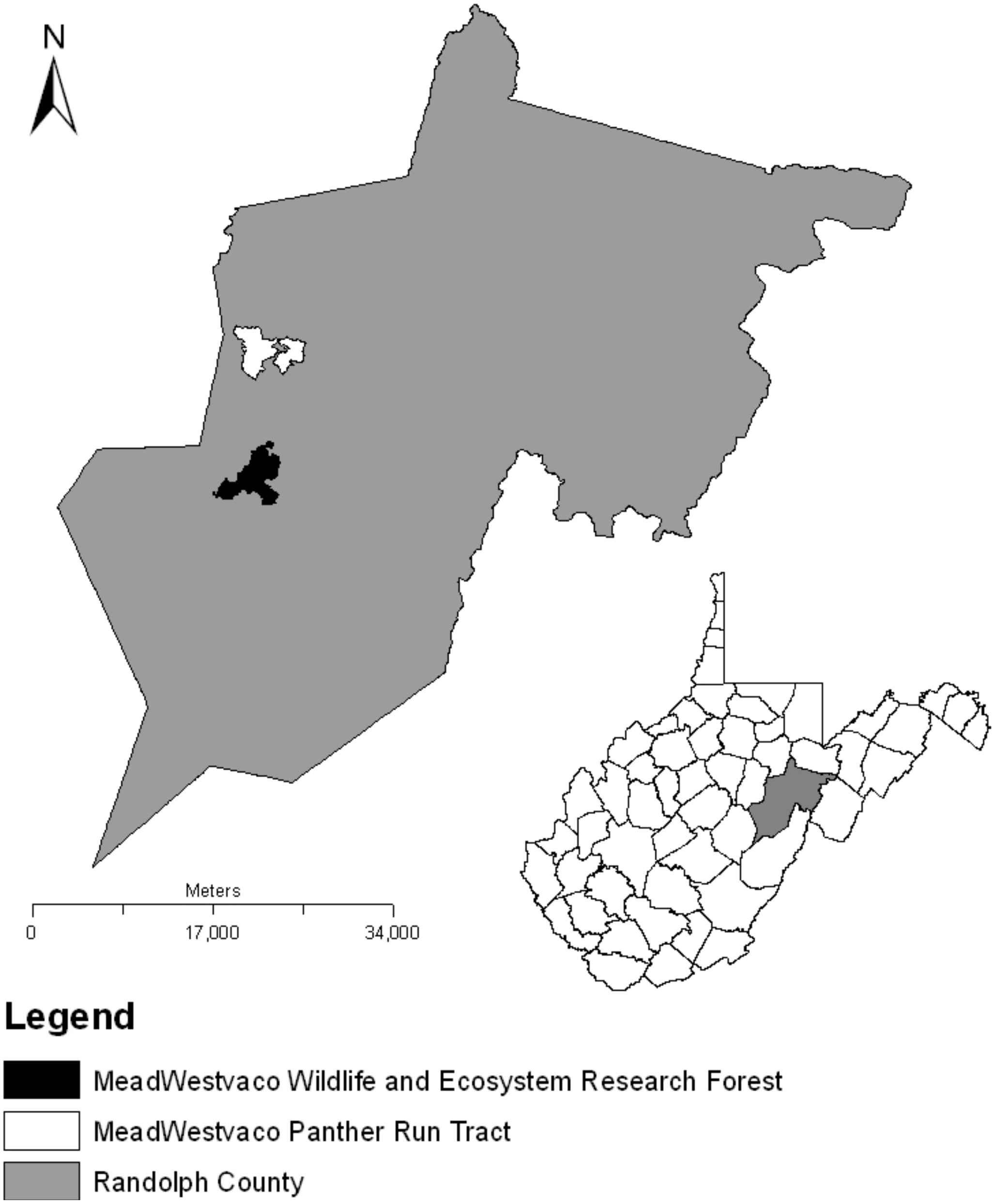

Figure 1. Locations of the MeadWestvaco Wildlife and Ecosystem Research Forest and the Panther Run Tract in Randolph County, West Virginia.

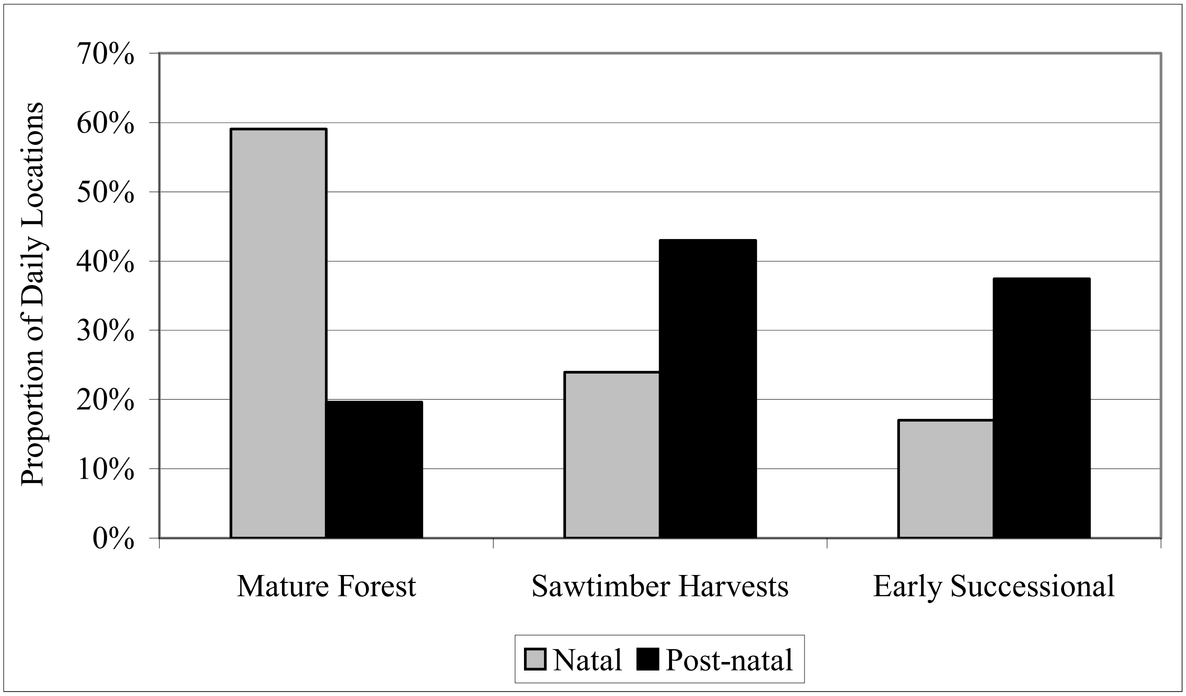

Figure 2. Percent of daily locations for radio-tagged Wood Thrushes during the natal (n = 37) and post-natal (n = 41) periods in Randolph County, West Virginia, 2004 and 2005.

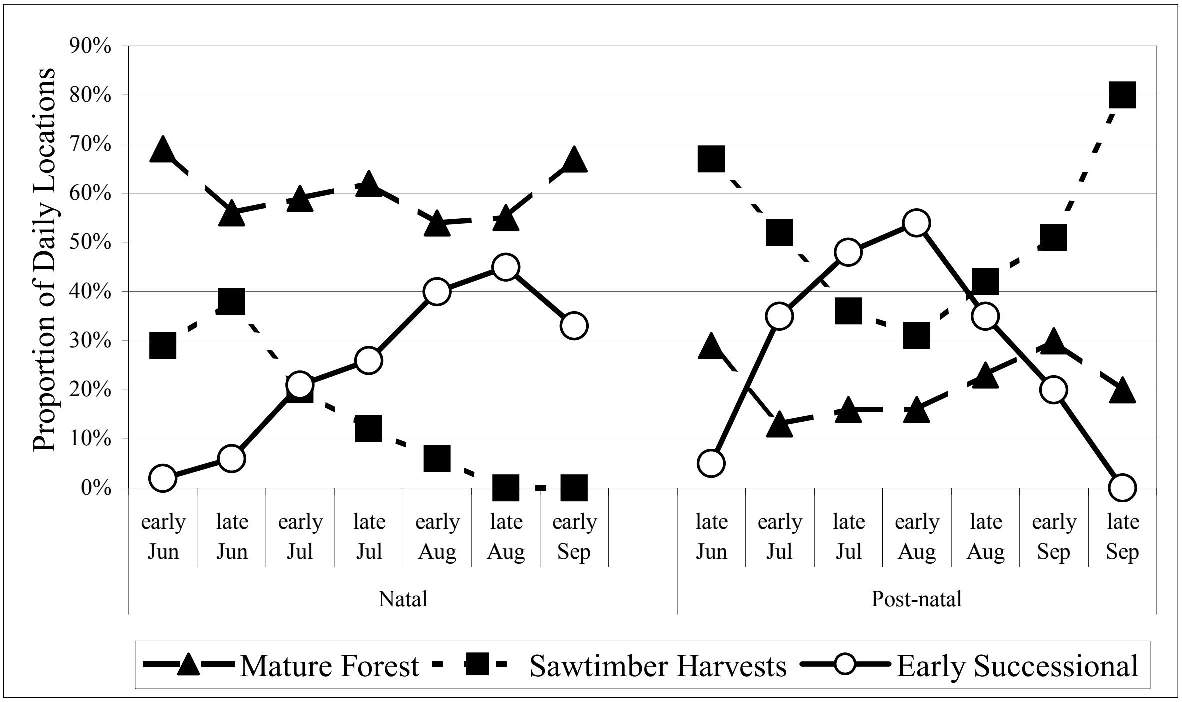

Figure 3. Temporal use of cover types in the natal and post-natal periods in Randolph County, West Virginia during 2004 and 2005. Early refers to days 1 – 15 and late to all subsequent days of each month.

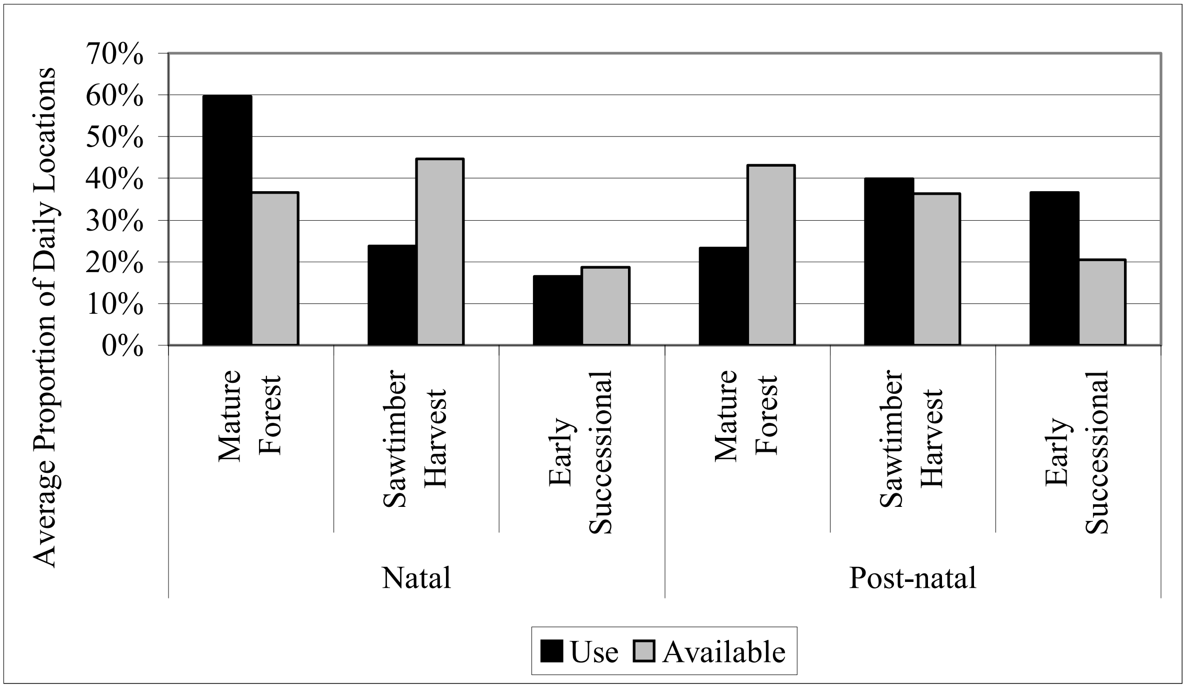

Figure 4. Average proportion of locations within each cover type and the proportion of each available cover type during the natal (n = 37 individuals) and post-natal (n = 35 individuals) periods in Randolph County, West Virginia, 2004 and 2005.

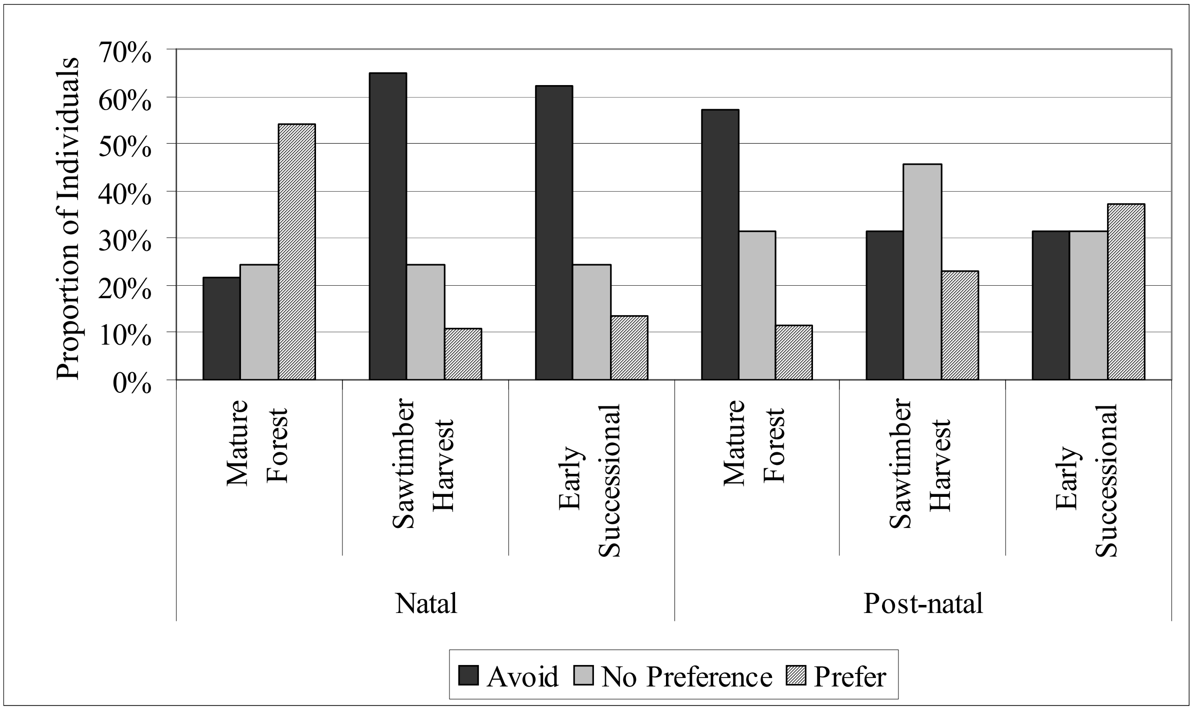

Figure 5. Based on Bonferroni 95% confidence intervals results, proportions of juvenile Wood Thrush that preferred or avoided each cover type during the natal and post-natal periods in Randolph County, West Virginia, 2004 and 2005.

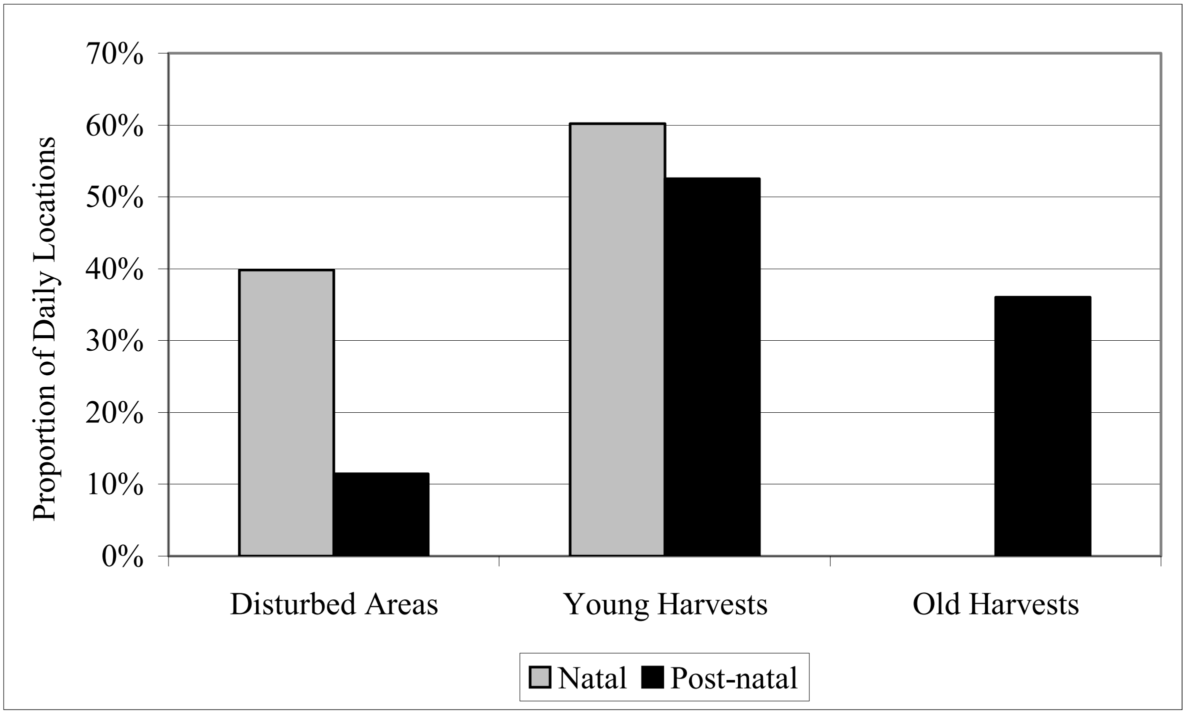

Figure 6. Proportions of daily Wood Thrush locations for 36 individuals within each early successional category during natal and post-natal periods in Randolph County, West Virginia, 2004 and 2005.

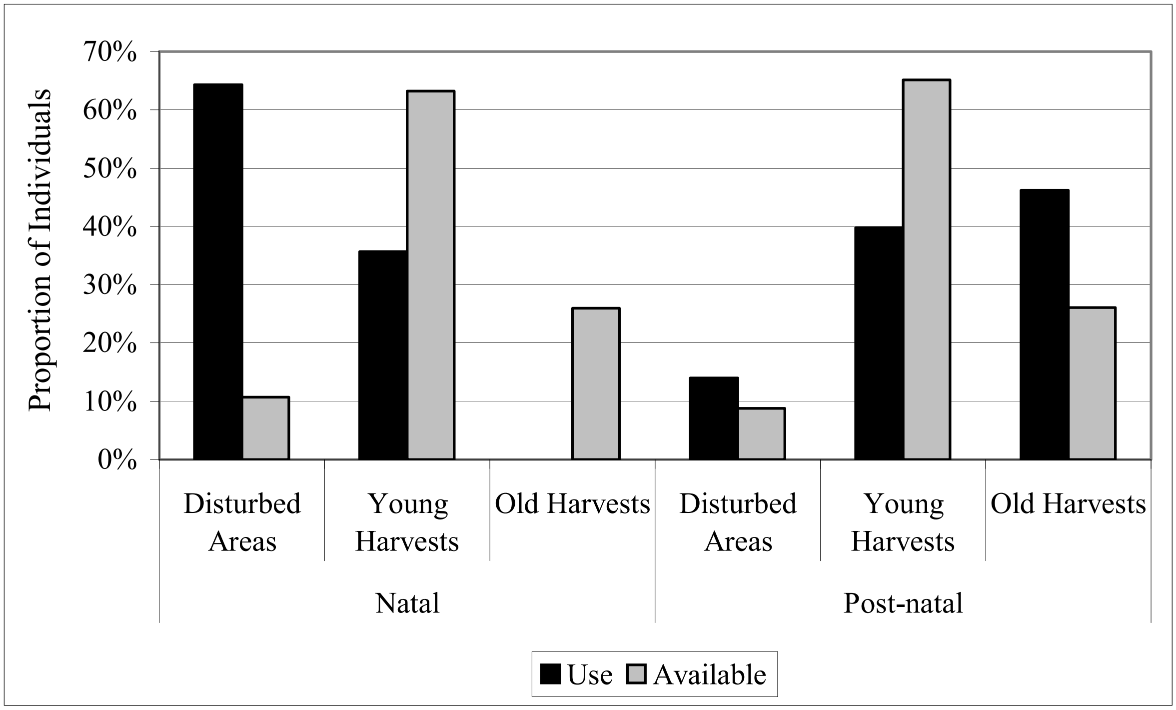

Figure 7. Average proportion of Wood Thrush locations within each early successional category and the proportion of each available category during the natal (n = 14 individuals) and post-natal (n = 23 individuals) periods in Randolph County, West Virginia, 2004 and 2005.

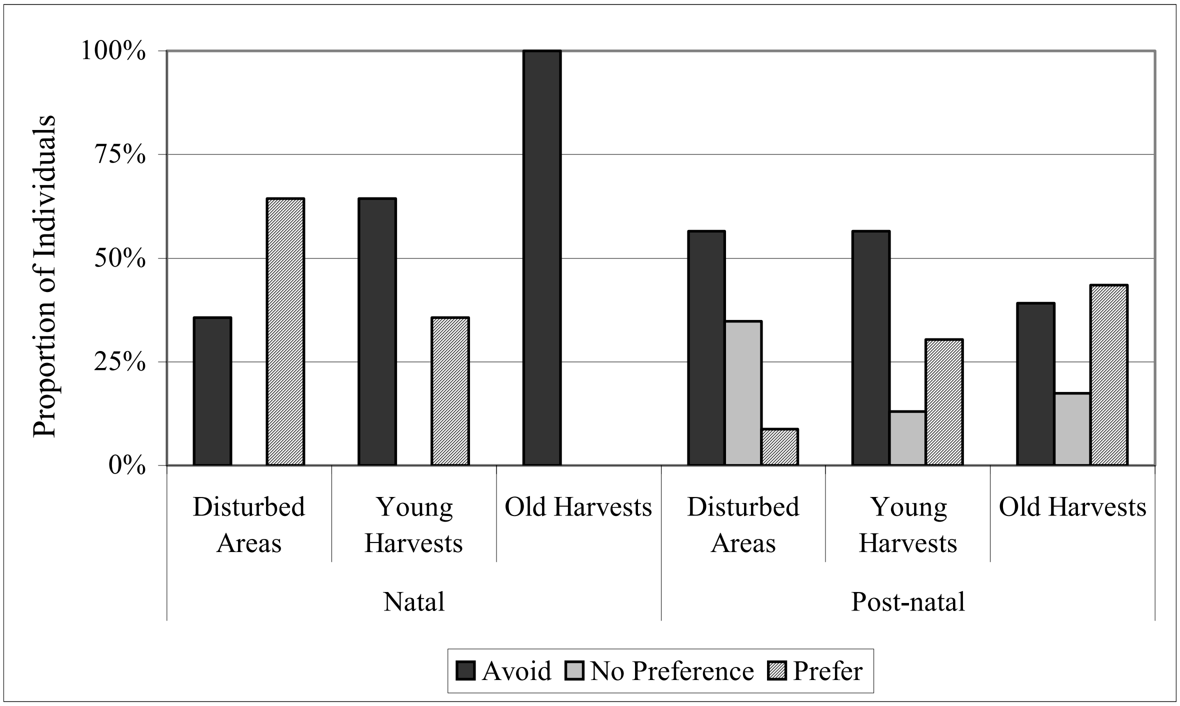

Figure 8. Based on Bonferroni 95% confidence intervals results, proportions of juvenile Wood Thrush that preferred or avoided each early successional category during the natal and post-natal periods in Randolph County, West Virginia, 2004 and 2005.

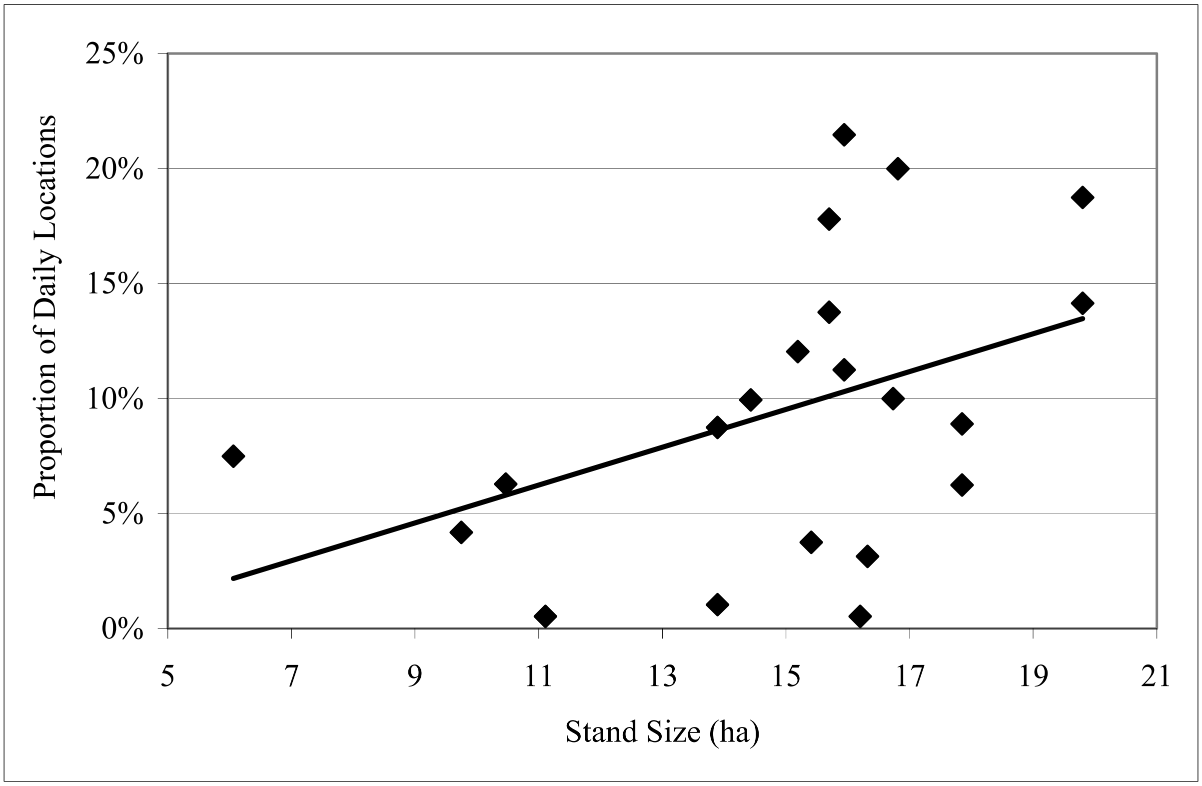

Figure 9. Proportion of daily juvenile Wood Thrush locations (*n* = 271) (*dependent variable*) within 16 clearcuts of various sizes (*independent variable*) used during the post-natal period in Randolph County, West Virginia, 2004 and 2005 ($r^2 = 0.34$, $P = 0.05$).

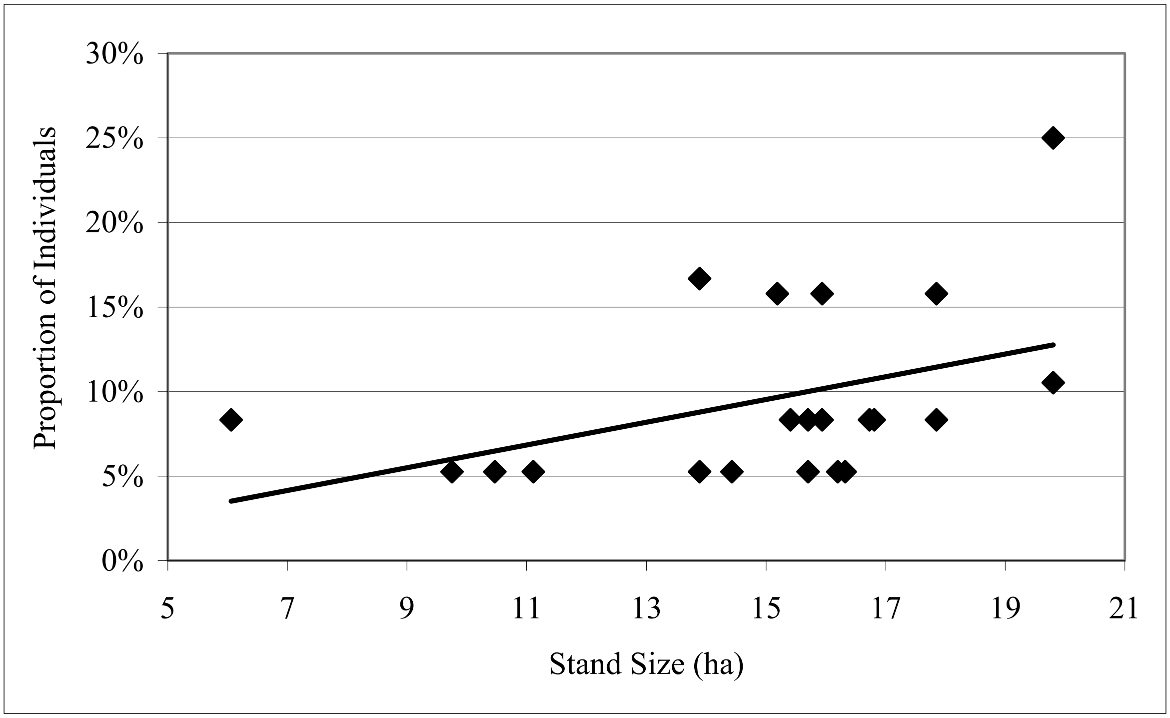

Figure 10. Proportion of radio-tagged juvenile Wood Thrushes (*dependent variable*) within 16 clearcuts (*independent variable*) of various sizes used during the post-natal period in Randolph County, West Virginia, 2004 and 2005 ($r^2 = 0.31$, $P = 0.06$).

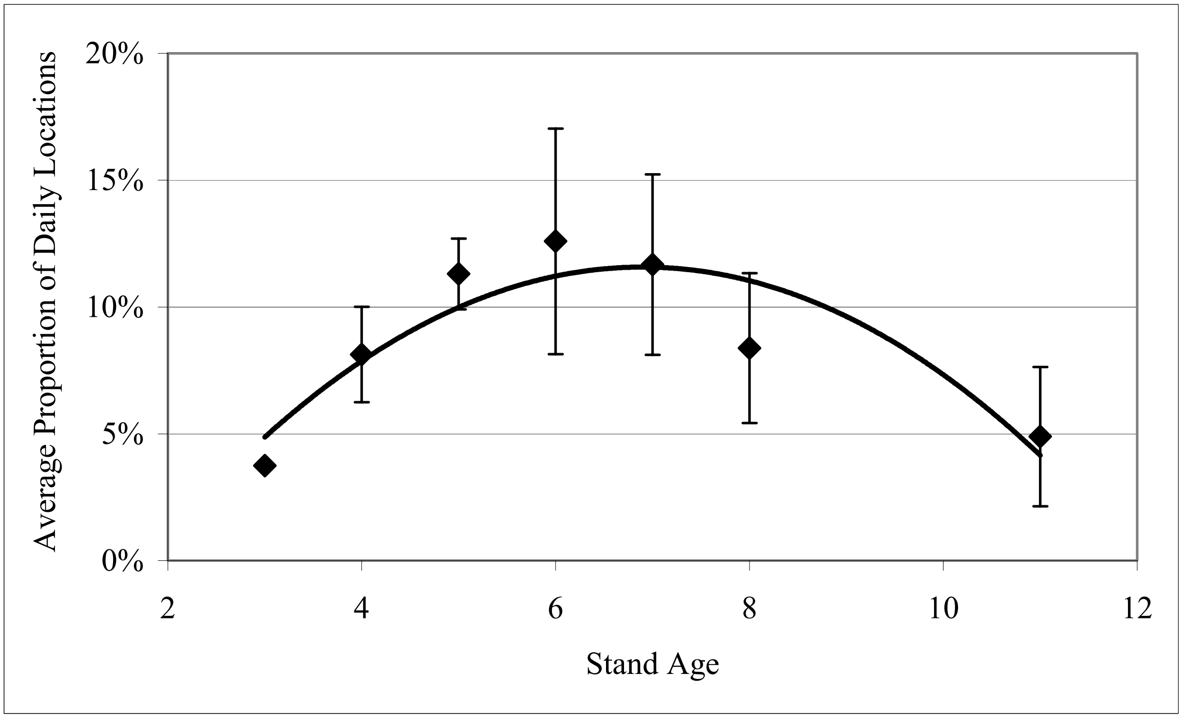

Figure 11. Average proportion and standard errors of radio-tagged juvenile Wood Thrush post-natal daily locations (n = 271) (*dependent variable*) in early successional harvests of various ages (years post-harvest) (*independent variable*) in Randolph County, West Virginia, 2004 and 2005 ($r^2 = 0.34$, $P = 0.07$).

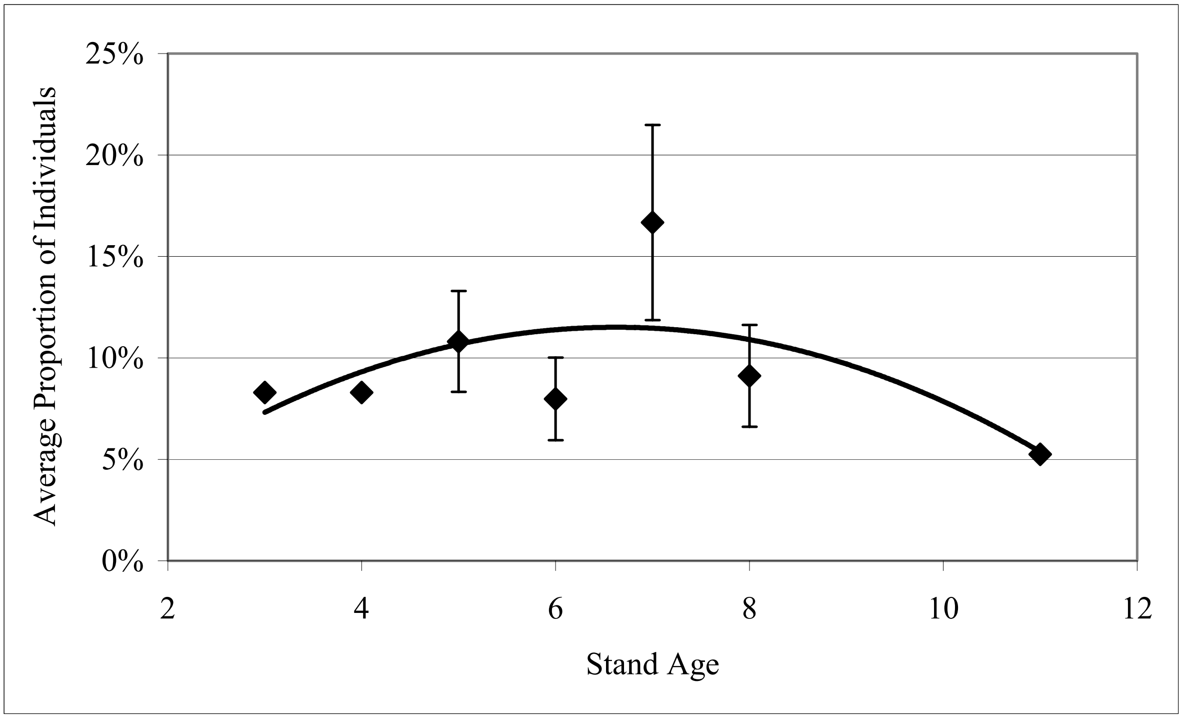

Figure 12. Average proportion and standard errors of radio-tagged juvenile Wood Thrushes (*dependent variable*) within 16 clearcuts (*independent variable*) of various ages (years post-harvest) used during the post-natal period in Randolph County, West Virginia, 2004 and 2005 ($r^2 = 0.31$, $P = 0.09$).

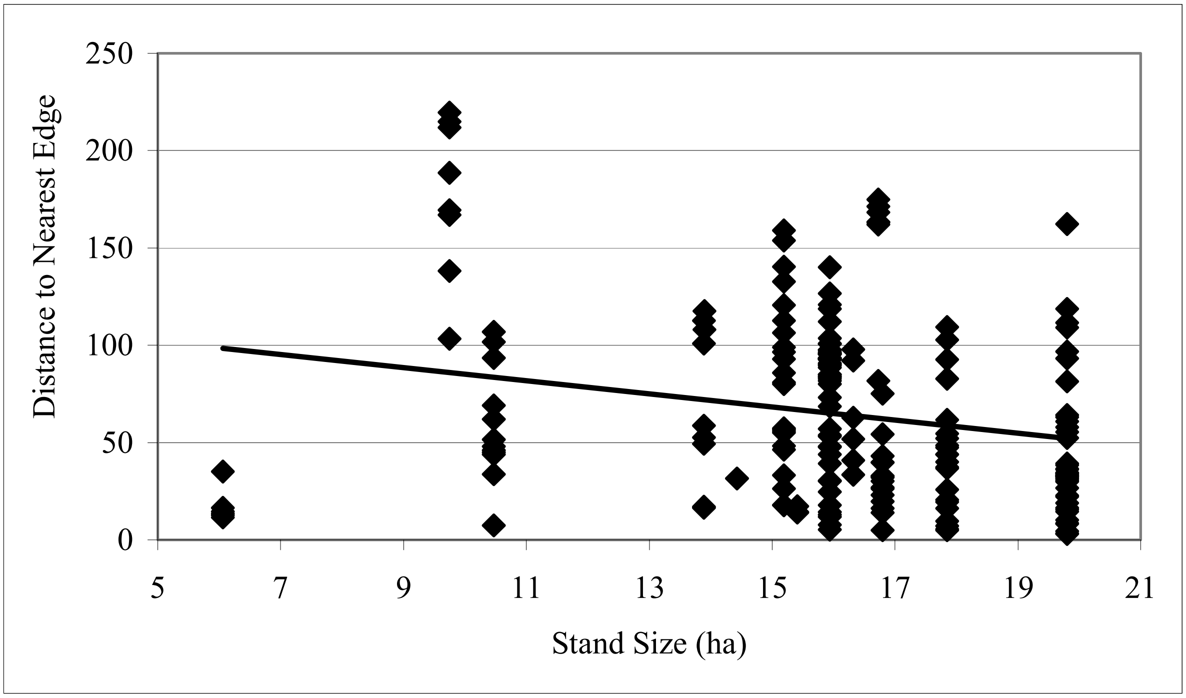

Figure 13. Distance to the nearest edge (m) (*dependent variable*) of onsite daily locations (n = 205) of 22 Wood Thrushes in 16 clearcuts of various sizes (*independent variable*) used during the post-natal period in Randolph County, West Virginia, 2004 and 2005 ($r^2 = 0.08$, $P = 0.02$).

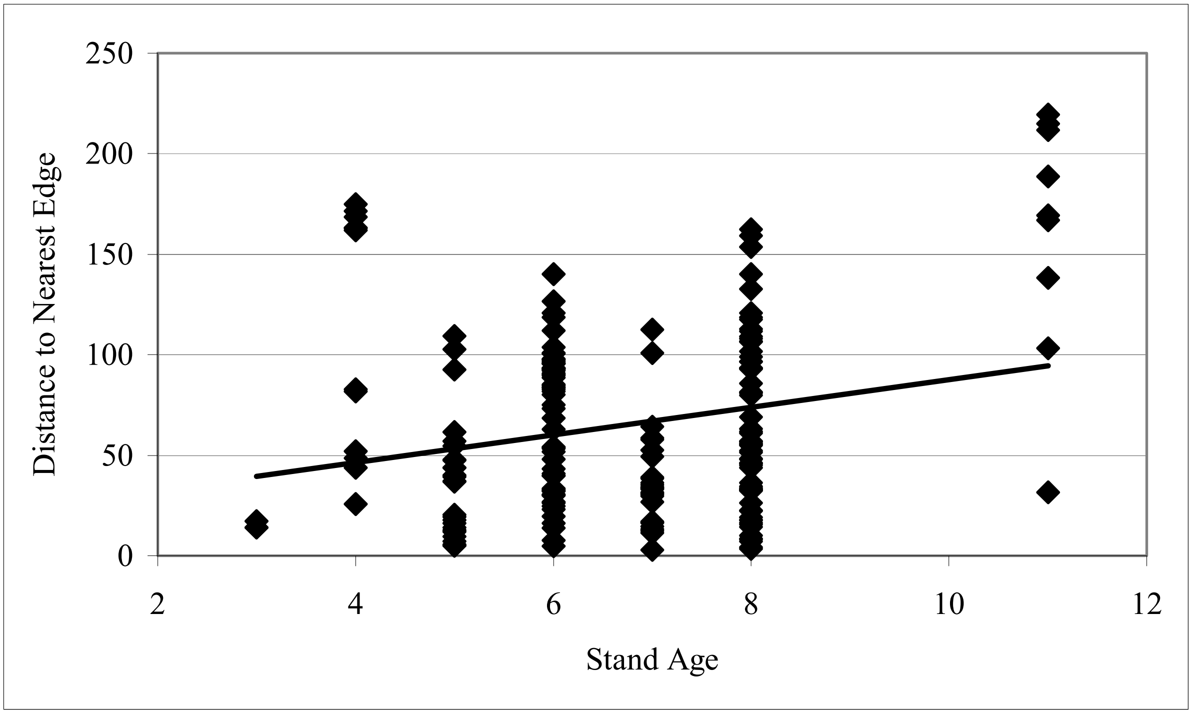

Figure 14. Distance to the nearest edge (m) (*dependent variable*) of onsite daily locations (n = 205) of 22 juvenile Wood Thrushes in 16 clearcuts of various ages (*independent variable*) used during the post-natal period in Randolph County, West Virginia, 2004 and 2005 ($r^2 = 0.08$, $P = 0.01$).

CHAPTER 3

POST-NATAL HABITAT AND MOVEMENTS OF JUVENILE WOOD THRUSHES ON A MANAGED APPALACHIAN FOREST

Abstract. Recent studies have documented movements and settled area sizes of juvenile Wood Thrushes (*Hylocichla mustelina*) during the several week period between the time they become independent from their parents and the onset of migration. Up to five settled areas can be established, often several hundred meters apart. I examined the movements and settled areas of 55 juvenile Wood Thrushes within mature forest, sawtimber harvests, and early successional areas on a managed forest in the central Appalachian mountains of West Virginia during 2004 to 2005. Juveniles remained in the natal area approximately 3 weeks before moving into sites with dense cover. Settled area size and duration were similar to those documented in previous studies but distances between settled areas were shorter, as were daily movements between consecutive locations. Among first post-natal settled areas occupied at least 5 days in which $\geq$ 80% of locations were within one cover type, settled areas were smallest in early successional areas (0.8 ha), intermediate in mature forest (1.0 ha), and largest in sawtimber harvests (2.8 ha); however, settled areas within sawtimber harvests averaged smallest among subsequent settled areas with these criteria. Juveniles preferred harvested stands to mature forest areas, but it is unclear if they preferred even-aged harvests or sawtimber harvests, or perhaps if their habitat requirements changed throughout the period prior to migration. A large proportion of sawtimber harvests on the study site may have influenced the high use, because proportionally twice as many exploratory locations were in sawtimber harvests than clearcut. Regardless, cover and resources may have been concentrated in both types of harvested areas, causing young birds to require a smaller area than would be needed within mature forest to meet their daily requirements prior to migration.

INTRODUCTION

For some Neotropical songbirds the time between independence from parents and the onset of migration can be as long as 2 months (Vega Rivera *et al*. 1998), particularly for individuals from initial and mid-season clutches. During this period individuals must complete prebasic molt while becoming adept at flying, evading predators, and acquiring food resources. Wood Thrushes (*Hylocichla mustelina*) follow this pattern, with some individuals remaining up to 2 months in areas 0.5 to 2.2 km from the natal area (Anders *et al*. 1998, Vega Rivera *et al*. 1998, Lang *et al*. 2002, Fink 2003).

Various hypotheses have been suggested explaining juvenile Wood Thrushes' movement patterns, with the foremost being predator avoidance. Most recent studies examining post-natal movements of juvenile Wood Thrushes generally suggest individuals move through various land covers, often settling in areas with dense vegetation for protection from predators (Anders *et al*. 1998, Vega Rivera *et al*. 1998, Fink 2003, Dellinger Chapter 2). Fink (2003) classified post-natal movement locations in central Missouri into two categories: those in which an individual was settled within a settled area, and those in which it was simply wandering about the landscape. He concluded settled locations were in areas of denser vegetation, typically near the forest edge in areas fragmented by agriculture. Conversely, some dense areas, such as clearcuts, are generally considered movement barriers to breeding adults, and therefore perhaps young birds are moving about the landscape using areas breeding birds do not; thus an intraspecific competition hypothesis is a second possible explanation (Vega Rivera *et al*. 1998). The optimal foraging hypothesis also has been suggested, as researchers have noted abundant soft mast in post-natal areas (Anders *et al*. 1998, Vega Rivera *et al*. 1998). Vega Rivera *et al*. (1998) noted a seasonal shift from early successional areas to mature forest in late fall, a time when presumably *Rubus* spp. were gone but hardwood species were fruiting (i.e. *Nyssa sylvatica*). Another hypothesis, premigratory socialization with conspecifics, also has been suggested (Vega Rivera *et al*. 1998). Specifically, Vega Rivera *et al*. (1998) described juveniles from different nests in Virginia moving to a common post-natal grouping site. However, movements about the landscape may be simply the commencement of migration (Anders *et al*. 1998). Anders *et al*. (1998) found individuals moved in a southerly direction after leaving the area of parental dependence in the Missouri Ozarks. Lastly, young birds may move through the landscape scouting potential breeding territory for the following season (Baker 1993).

My objective was to examine movement patterns and settled area characteristics of juvenile Wood Thrushes on a highly structured landscape that included areas of large even-aged harvests, partial harvests, and un-harvested areas. My specific objectives were to:

1. quantify settled area size and daily movements of radio-tagged juvenile Wood Thrushes prior to and after independence from their parents for the purpose of comparison to those documented by previous studies and on less disturbed landscapes.
2. examined post-independence movements that were within and outside settled areas,
3. as well as cover type use on these sites over the course of the post-independence/pre-migration period. Unlike previous studies of juvenile Wood Thrushes, slightly more than 50% of the combined landscape investigated had some large silvicultural treatment within the past 15 years.

METHODS

STUDY AREA

This study was conducted on the 3411 ha MeadWestvaco Wildlife and Ecosystem Research Forest (MWERF) and the 1705 ha MeadWestvaco Panther Run Tract (PRT) in southwestern

Randolph County, West Virginia (Fig. 1). The MWERF and PRT were established in 1994 and 2001, respectively, to provide sites for long-term research on the effects of intensive forest management practices on wildlife and other ecosystem elements. Based partly on elevation, the MWERF is equally divided into two blocks of 1705.5 ha. The lower elevation block was used in this study as it was logistically closer and similar in elevation to the PRT. The elevation of this block ranges from 707 m to 1012 m, while 16 km to the north the PRT is 634 m to 914 m. The MWERF is composed primarily of cove hardwoods and mixed mesophytic communities (Braun 1950), with northern and Allegheny hardwoods present in the higher elevations (Engle 2007). The PRT is composed primarily of oak-hickory (*Quercus* spp.- *Carya* spp.) forests. Both can be characterized as second growth hardwood forests. Since 2001, about 3% of each site has been harvested annually as part of a long-term, landscape-level project. Thus both sites have many patches of regenerating forest areas; the oldest cuts were 10 years post-harvest in 2004. Sawtimber, partial-harvests, and even-aged harvests were the typical harvesting methods.

Based on stand data and personal observations, I digitized roads and the following three dominant cover type categories using ArcView 3.2 ™: mature forests, sawtimber harvests, and early successional patches (Table 1). Areas termed mature forest were initially harvested 80-90 years ago although they received diameter-limit cutting through the 1980s. Sawtimber harvests were defined as areas in which large diameter trees (typically > 30 cm diameter at breast height) were selectively harvested, leaving 70-80% of the original stand in place. These areas had many canopy gaps and often dense understory and ground cover. The majority of PRT had received a sawtimber cut by 2004, while the MWERF had considerably less. Early successional areas included roadside thickets as well as large even-aged harvests. These areas had high sapling density and vegetation usually was 2 to 8 m tall.

RADIO-TAGGING AND TRACKING

I searched for nests throughout the study areas from May through August of 2004 and 2005. When I discovered a nest, I ascertained the stage (building, incubation of eggs, or brooding of nestlings) at that time or during subsequent visits. I monitored nests every 3 days or less if hatching or fledging was eminent. Nestlings were radio-tagged 2 – 3 days prior to fledging. I returned most (92%) to the nest after tagging, and those that could not be returned due to their fleeing behavior I placed in woody vegetation above the ground near the nest. When nestlings fledged earlier than anticipated, I observed the immediate vicinity of the nest site from a distance to attempt to identify the fledgling's location. I captured recent fledglings with a mesh 24" diameter hoop net, radio-tagged them, and then released them near the capture site.

As a complement to radioed nestlings, I captured juvenile Wood Thrushes with mist-nets during the post-natal period as part of a study examining songbird use of regeneration units during the post-fledging period (T. Dellinger, Chapter 4). Captures occurred from 21 July to 18 August 2004 and 1 August to 29 August 2005. I released all tagged birds at the capture site.

I tagged all Wood Thrushes with a 1.1 g transmitter with a battery life of > 60 days (Blackburn Transmitters, Nacogdoches, TX). These transmitters weighed 3% of the Wood Thrushes' total body weight. To attach the transmitter to individuals, I constructed leg-loop harnesses (Rappole and Tipton 1991) from 0.7 mm diameter dissolvable sutures that lasted on average 149 days ± 89 days (Doerr and Doerr 2002).

Using a 150-152 MHz antenna and T1000 Wildlife Materials, Inc. receiver, observers located each bird daily. During June-September of 2004 and 2005, we tracked Wood Thrushes by homing in on radio signals on foot and marked each site with plastic flagging for subsequent vegetation measurements. Additionally, using a Trimble XT GPS unit, I recorded the UTM coordinates of the site where the bird was first observed with a minimum of 80 fixes obtained for each location. Fixes were averaged and differentially corrected with GPS Pathfinder Office 2.9 software. For each radioed bird, I created a shapefile in ArcView 3.2™ with all daily locations. All locations were placed within one of three digitized cover type categories.

Occasionally, radio-tagged individuals could not be found when they moved to a new location. Thus, I searched for a lost bird for at least 2 days and nights before considering it to have left the study area. I scanned for previous lost individuals during these times as well. I began searching for such birds from their last known location driving roads radiating outward from that location while scanning via a receiver with a roof-mounted omnidirectional antenna. When a radio-tagged bird was not found during the day, an observer searched again after sunset via roads. At night, signals of Wood Thrushes could be detected from greater distances than during daytime tracking, presumably because the birds were stationary while roosting above the forest floor. In addition to searching both study sites, I also searched for radio signals in the area between the two study sites.

I assigned each daily location to one of two periods based on age of the chick and proximity to the nest: the period when the fledgling was dependent on its parents for food and received some protection from them, and the independence period when the individual was meeting its entire daily requirements on its own. The dependence period locations were typically near the nest where the chick first hatched and are referred to as the natal area. The parents chose the nest site location and thus the habitat in the natal area. Young birds generally remained on the natal area for the first 3 weeks out of the nest. The independence period locations are referred to as the post-natal area. These areas are of special interest because they represent the habitats actually being selected by the juvenile birds and may contain elements required for their survival. Juveniles remained in the post-natal areas for up to 7 weeks before their transmitter batteries died or they moved out of the study area, presumably as they began their fall migration. For most radio-tagged individuals, two distinct spatial clusters were apparent, representing these two periods. Furthermore, most clusters were greater than 300 m apart, typically because individuals made a large single movement. Natal, initial, and occasionally, subsequent post-natal settled areas were identified through consecutive tracking for most individuals. For some radioed birds, I could not identify the first post-natal settled area either because the juveniles were captured with mist-nets, or because they could not be located for a number of days after departing the natal area.

All post-natal locations were classified as settled, wandering or exploratory. I considered settled areas to be clusters of at least three locations within 100 m of an initial location (Fink 2003). Occasionally tagged birds did not settle into a post-natal area within 3 days of leaving a previous settled area (natal or post-natal). Some were moving directionally away from a settled area while others moved hundreds of meters in seemingly random directions; I term these movements wandering locations. Lastly, some individuals in settled areas departed that area for up to 3 days and then returned. These locations were typically > 300 m from the previous day's location and I labeled these as exploratory movements.

I determined settled area size using 95% minimum convex polygons (Mohr 1947) to compare to previous studies (Anders *et al.* 1998, Vega Rivera *et al.* 1998), using Animal Movements Program (Hooge and Eichenlaub 1997) in ArcView 3.2. The azimuth from one settled area to the next was found by first creating a point shapefile based on a settled area's center of mass using XTools (DeLaune 2000) in ArcView 3.2, combining points of all settled areas per individual, and then using "simple movements" tool from Hawth's Tools (Beyer 2004) in ArcMap 9.0. All azimuths were classified as a cardinal or subcardinal direction. Also based on the settled area center of mass, I determined the distance between consecutive settled areas using "create polyline from point file" tool in Animal Movements Program (Hooge and

Eichenlaub 1997) in ArcView 3.2. Additionally I used the “create polyline from point file” tool to calculate the distance between consecutive daily movements for settled, wandering, and exploratory locations. For nests (*n* = 3) from which two sibling Wood Thrushes were radio-tagged, I considered the settled area and movements of each to be independent of its sibling. This assumption was validated by the fact that I did not observe fledglings together during the natal period, and in the post-natal period all siblings’ daily locations were separated by at least 1 kilometer.

STATISTICAL ANALYSIS

I used a one-way chi-square analysis to examine the direction radioed birds moved from one settled area to the next. The proportion of the cardinal and subcardinal directions fledglings were observed to move were compared to expected values of equal proportions in each direction. I used chi-square contingency table analyses to test the hypotheses that the proportion of post-natal locations in each cover type was the same between the initial and subsequent settled areas and between settled and non-settled locations. To determine if settled area size varied among cover types, I evaluated settled areas occupied at least 5 days, a period beyond which mean size did not increase. Each settled area was classified within one cover type if $\geq$ 80% of locations were within that cover type; all other settled areas occupied $\geq$ 5 days were considered to be in an ecotone. Settled area size and duration (days) were compared among cover types/ecotone areas for initial and subsequent settled areas with a one-way analysis of variance (ANOVA). All means are given with the standard error and alpha $\leq$ 0.05 was considered significant.

RESULTS

I radio-tagged 55 Wood Thrushes in 2004 and 2005. Of these, 17 were tagged from 13 nests as nestlings or within 2 days of fledging in 2004, and 28 were tagged from 25 nests as nestlings or within 2 days of fledging in 2005. These individuals are referred to as fledglings. The remaining ten individuals were captured with mist-nets and radio-tagged during the post-natal period: three in 2004, and seven in 2005. These individuals are called juveniles.

Five of the 55 fledglings were depredated either just before or after fledging, and thus I collected no telemetry data on these. Two additional fledglings were depredated on their natal settled area; another was killed either prior to leaving or on the first day of the post-natal period. The transmitter harness broke and fell off five fledglings during the natal period, and off nine radioed birds (7 fledglings and two juveniles) during post-natal movements. Overall, 47 fledglings and juveniles were radio-tracked from 5 to 74 days ($\bar{x} = 38.9 \pm 2.9$). We did not recapture or resight any of the 2004 radio-tagged Wood Thrushes in 2005.

SETTLED AREAS

The 32 nestlings (from 29 nests) that we were able to track through the natal period remained on their natal settled area on average 21.6 ± 0.7 (range 13 – 31) days after fledging. Among siblings tagged from the same nest, one pair departed the natal area the same day, while one sibling from each of the other two nests remained in the natal area longer, 5 and 12 days. Mean size of natal settled areas was 3.1 ± 0.4 ha (Table 2).

During the post-natal period, 68 settled areas were identified for 39 juvenile Wood Thrushes. Seventeen individuals had one post-natal settled area, 16 were tracked to two sites, five used three sites, and four post-natal settled areas were identified for one individual. Initial post-natal settled area size averaged 1.6 ± 0.3 ha for 26 tracked birds, and were occupied an average of 12.6 ± 1.5 days (Table 2).

The natal and first post-natal settled areas were separated by an average of 760.0 ± 107.8 m (range 151.3 m – 2680.9 m). A majority of first post-natal settled areas, 23 of 26, were > 300 m from the natal settled area. Three individuals settled in areas closer (range 151–204 m) to the natal areas. All three were located in 3-6 year old clearcuts during the natal period and after 1 to

7 days of exploratory movements, returned to a different section of the same clearcut for the post-natal period. Arrival from natal to the initial post-natal settled area occurred in 2.7 ± 0.5 days (range 1 – 9 days), although 14 of 26 individuals required only 1 day. The average direction birds moved from the natal area to their first post-natal settled area was 200.1 ± 21.1˚, but did not differ from random ($\chi^2 = 4.2$, $df = 7$, $P = 0.8$).

I identified 29 subsequent settled areas following the initial post-natal settled area for 22 radioed birds; average size and duration of use were 1.1 ± 0.3 ha and 8.7 ± 1.2 days, respectively (Table 2). Based only on individuals that we could locate for $\geq$ two consecutive post-natal settled areas, mean distance between consecutive post-natal settled areas was 930.8 ± 137.9 m (range 33.0 - 2995.2 m) and arrival from one post-natal settled area to another took on average 2.3 ± 0.5 days (range 1 – 9 days). The average bearing radioed birds moved from one post-natal settled area to the next was 191.3 ± 19.4˚, similar to movements from the natal area to the first post-natal settled area. The direction individuals moved from one post-natal settled area to the next did not differ from random directions ($\chi^2 = 2.7$, $df = 7$, $P = 0.9$).

DAILY MOVEMENTS

The average distance between consecutive daily locations was similar among settled areas. Based on 708 successive movements of 47 radio-tagged Wood Thrushes, average movements within natal settled areas was 72.6 ± 2.4 m (range 0.4 - 677.7 m). Within the initial post-natal settled areas the mean distance was 87.6 ± 4.1 m (range 0.2 – 608.7 m) based on 293 consecutive movements of 26 radioed birds, and among subsequent post-natal settled areas the average distance was 86.1 ± 5.8 m (range 0.4 – 964.5 m) for 234 consecutive movements of 22 individuals.

Several radioed birds (16 of 39) that settled into a post-natal settled area performed at least one exploratory movement. Most juveniles were located while on these forays, however some radioed birds were re-located only after returning to the settled area 1-3 days later, hence of 32 exploratory movements 25 were monitored. Exploratory movements that were located were > 300 m from the previous day's location except for one (273.5 m); average exploratory movement was 561.3 ± 50.9 m (range 273.5 – 1326.2 m) from the previous day's location.

Post-natal wandering movements (n = 115) were identified for 28 tagged Wood Thrushes before either settling into a settled area or leaving the study area. Of these, two birds wandered and did not settle into a settled area during the post-natal period on or around our study site. The mean distance of a daily wandering movement was 508.2 ± 51.8 m (range 1.0 – 2629.0 m).

COVER TYPE USE

Initial vs. Subsequent Post-natal Settled areas. Of 35 radio-tagged birds, 28 fledglings and seven juveniles, 329 locations were in an initial settled area and 287 were in subsequent settled areas. Distribution of daily locations among the cover types differed between initial and subsequent post-natal settled areas ($\chi^2 = 19.2$, df = 2, $P < 0.001$). Twice as many initial settled area locations were in sawtimber harvests than in early successional areas, the next most used cover type (Fig. 2). Locations in subsequent settled areas were nearly equal in proportion in sawtimber harvests and early successional patches.

Settled vs. Non-settled Locations. Based on 41 juveniles/fledglings, we collected 758 locations in settled areas and 140 locations of exploratory or wandering movements. For comparison to settled sites, I combined wandering and exploratory locations into a single movement category I termed non-settled locations due to the small sample size of exploratory locations. Distribution of settled and non-settled locations in the three dominant cover types differed ($\chi^2 = 21.5$, df = 2, $P < 0.001$). Proportionally, settled locations were similar in early successional patches and sawtimber harvests (Fig. 3). However among non-settled sites, most locations were in sawtimber harvests, with mature forest next, and early successional patches having the fewest non-settled locations.

Post-natal settled area size among cover types. Twenty-one initial settled areas were used at least 5 days, with six settled areas occurring in ecotone areas and 15 primarily in one cover type (Table 3). The number of days in initial settled areas did not differ among cover types or ecotone areas (ANOVA: $F = 0.14$, $P = 0.93$). Size of initial settled areas located in ecotone areas or one of the three cover types was significantly different ($F = 4.77$, $P = 0.01$). The smallest mean settled area was in early successional areas, with mature forest and ecotone patches next largest, and sawtimber harvests encompassed the greatest area (Table 3).

Twenty-five subsequent settled areas were occupied 5 days, 22 were primarily in one cover type and three were in ecotone areas. The number of days within a cover type/ecotone patch did not differ among subsequent settled areas ($F = 0.57$, $P = 0.64$). Significant differences also were not detected in subsequent settled area size ($F = 0.50$, $P = 0.69$).

DISCUSSION

Among previous studies examining juvenile Wood Thrush movements, my sample size is second only to Fink (2003) in number of individuals radio-tagged and individuals tracked in the post-natal period. My study confirmed that several previous conclusions regarding movements of juvenile Wood Thrushes also hold true in an area with intensive forest management. Similar to earlier studies, I found that juvenile Wood Thrushes remained on their natal settled areas the first 3 weeks after fledging (Anders *et al*. 1998, Vega Rivera *et al*. 1998, Lang *et al*. 2002, and Fink 2003) (Table 4). These areas were associated with adult breeding habitats that generally were in mature forest stands (Dellinger Chapter 2). Also comparable to previous studies (Anders *et al*. 1998, Fink 2003), most post-natal daily locations were in areas associated with denser understories. Furthermore, settled area sizes during both periods, as well as duration within post-natal settled areas, were similar to earlier published studies (Anders *et al*. 1998, Vega Rivera *et al*. 1998, and Fink 2003) (Table 4).

Despite similarities in the overall pattern of movements and cover type use between juveniles in other studies and mine, the large-scale silvicultural disturbances at my study area appeared to have had some influence on behavior, primarily by providing large tracts of suitable habitat. Early successional areas and sawtimber harvests had high proportions of settled locations and small settled areas. Cover and resources may have been concentrated in these areas, which could have resulted in birds using a smaller area to meet their daily requirements than would have been needed in an area of more sparsely distributed resources.

The high density of large early succession areas may have resulted in birds not needing to move great distances between such patches. Evidence supporting this is provided by the fact that compared to distances between settled areas reported in previous accounts both natal and initial, as well as between subsequent post-natal were closer on our study (Table 4). Specifically, both Anders *et al*. (1998) and Lang *et al*. (2002) report a mean of > 2 km, Vega Rivera *et al*. (1998) has a mean of 1.5 km, and Fink (2003) lists an average of 0.83 km separating natal and initial post-natal settled areas, whereas on our study area the average was less, 0.76 km. The distance between subsequent post-natal settled areas also averaged less (Table 4); Vega Rivera *et al*. (1998) reported a mean of 1.5 km compared to 0.9 km on our study. Furthermore, fewer non-settled locations were in early successional areas than in sawtimber harvests or mature forest patches; most birds we radio-tracked did not wander through or explore early successional areas while transitioning or returning to a settled area. Desrochers and Hannon (1997) also found songbirds in the post-fledging period seemingly to prefer moving through forest over moving through open areas such as fields and clearcuts.

My data lend further insight to the six hypotheses of causal mechanisms of post-dependence/pre-migratory movements. First, similar to Lang *et al*. (2002) and Fink (2003), directional analyses of individuals moving from natal to the post-natal settled areas did not support the commencement of migration hypothesis of individuals gradually moving south. Moreover, between settled areas, directions of movement observed with the highest frequency on our study site were equal between north, northwest and southeast.

Socialization of conspecifics was observed, albeit loose and temporary. Unlike Vega Rivera *et al*. (1998), who observed radioed young up to 30 minutes and observed 39 of 42 with a conspecific, we typically observed individuals < 10 minutes daily. However, we also noted when conspecifics were nearby and observed 27 of 41 tagged birds with a conspecific in the post-natal period. Some degree of socialization also existed among tagged Wood Thrushes, in the sense that occasionally individuals moved together within an area. I observed two birds from different nests together for 5 consecutive days in 2005. Additionally, I noted radioed birds near each other in 2004 and in 2005. In both instances, one individual was wandering and one was settled in either a natal or initial post-natal settled area.

Similar to Lang *et al*. (2002) and Fink (2003) we did not relocate any second-year individuals returning to a settled area the following year although we roughly nest searched settled areas within sawtimber harvests and mature forest stands in 2005 where radioed birds had been tracked in 2004. Thus, our data did not support the movement hypothesis of juveniles searching for potential breeding territories.

Additionally, similar to Anders *et al*. (1998) and Fink (2003), intraspecific competition was not observed. However, although adult birds in my study were not marked, I made two indirect observations of what I perceived as adults of two clutches moving fledglings to the same clearcut, in a manner similar to that observed by Vega Rivera *et al*. (1999). The first occurrence was of a juvenile moving into a particular clearcut > 130 m from the nest site 18 days post-fledging where it remained 4 days, while its two late-season siblings from a second brood moved into the same cut 4 days post-fledging. The behavior of following their parents may explain why at such a young age these two radio-tagged siblings moved upslope to a clearcut, crossing a 10 m wide gravel road with little cover along the way. For individuals of early broods that moved to a large harvest, it is unclear if the adults were merely accompanying the juveniles in early successional areas, or to the territory boundary, or if the adult behavior might have been unrelated to that of the juveniles. More information is needed on the movement interactions of adult and juvenile Wood Thrushes among early successional habitats.

With the majority of radioed birds preferring early successional areas during mid to late summer (Dellinger Chapter 2) when several soft mast species were producing fruit, support for the optimal foraging hypothesis may be valid. We noted on occasion tagged individuals eating the fruit of *Rubus* spp. and *Prunus pensylvanica*. Furthermore, fruit stains occasionally were visible on the feathers surrounding the mandible in Wood Thrush and other species captured in mist-nets in large even-aged harvests (Dellinger Chapter 4). Likewise, and similar to movements noted by Vega Rivera *et al*. (1998), some individuals shifted from early successional areas to areas with mature trees in early autumn where they were observed consuming fruit in the canopies of *N. sylvatica* and *P. serotina*.

Predator avoidance may likely have been the primary factor motivating juvenile movements in the post-natal period. Post-fledging survival estimates did not differ between mature forest, sawtimber harvests and early successional areas; however, young Wood Thrushes preferred harvested areas with denser understories to mature forest areas (Dellinger Chapter 2). Raptors depredated at least three radioed individuals on their natal settled areas. Anders *et al*. (1998) and Fink (2003) also reported hawks depredating radioed individuals on natal settled areas during their studies. Denser vegetation would impede raptors hunting ability and may provide cover for birds inexperienced in predator evasion (Anders *et al*. 1998, Vega Rivera *et al*. 1998, Fink 2003). Soft mast producing species such as *Rubus* spp. may be an additional benefit in these areas (Anders *et al*. 1998, Vega Rivera *et al*. 1998, Fink 2003), although many individuals moved to harvested stands prior to the mast ripening (Dellinger Chapter 2).

While it is clear that juveniles primarily used harvested stands among settled locations, what remains unclear is whether even-aged or sawtimber harvests were preferred. Both types were used more than was spatially available among settled and non-settled locations, however early successional areas were preferred by more individuals (Dellinger Chapter 2). High use of sawtimber harvests we observed possibly was due to the large tracts harvested by this technique on the PRT and surrounding areas. However, high availability does not explain why the majority of settled areas (39%) also were in this cover type on the MWERF where this harvest type was much less abundant. Conversely, the high use of early successional patches, particularly on the PRT, suggested sawtimber was not the overall preferred cover type for settled locations. In general, stands harvested by both methods probably were used because both techniques resulted in areas with dense understories, a habitat characteristic that may fulfill the primary habitat required by juvenile Wood Thrushes.

CONSERVATION IMPLICATIONS

Juvenile Wood Thrushes may benefit from maintaining even-aged cuts between 5 and 10 years old or by implementing sawtimber cutting, improvement cutting, or crop tree management. These forest management activities appear to mimic various sizes and types of natural canopy disturbances and provide the dense vegetation required for concealment and/or resource procurement at this stage in the avian life cycle. However, maintaining some areas in an older seral stage would encourage reproduction by providing nesting habitat required by breeding adults.

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Table 1. Available proportion of cover types in Randolph County, West Virginia in 2004-2005.

	Percent of land cover			
	MWERF		PRT	
	2004	2005	2004	2005
Mature Forest	68.3	64.1	34.1	30.8
Sawtimber Harvests	12.9	12.7	51.3	49.6
Early Successional Areas	18.9	23.2	14.6	19.7

Table 2. Average sizes and number of days occupied of settled areas of radio-tagged Wood Thrushes in Randolph County, West Virginia in 2004-2005.

	No. Birds	**No. Settled areas**	**$\bar{x}$ Area (ha)**	**Range (ha)**	**$\bar{x}$ Days**
Natal	32	32	3.1 ± 0.4	0.2 – 10.0	21.6 ± 0.7
Post-natal (PN)	39	68	1.3 ± 0.2	0.002 – 6.1	11.1 ± 0.9
First PN	26	26	1.6 ± 0.3	0.002 – 4.4	12.6 ± 1.5
Subsequent PN	22	29	1.1 ± 0.3	0.005 – 6.2	8.7 ± 1.2

Table 3. Average size and number of days occupied of radio-tagged Wood Thrush settled areas that were either in ecotone patches or had at least 80% of the settled area locations in one cover type and were occupied at least 5 days in Randolph County, West Virginia in 2004-2005.

	Initial			**Subsequent**		
	n	**$\bar{x}$ days**	**$\bar{x}$ size**	**n**	**$\bar{x}$ days**	**$\bar{x}$ size**
Mature Forest	1	12	1.0	4	13 ± 5.5	1.5 ± 0.8
Sawtimber Harvests	10	15.5 ± 2.8	2.8 ± 0.3	11	8.4 ± 1.8	0.9 ± 0.2
Early Successional Areas	4	13 ± 3.5	0.8 ± 0.4	7	11.6 ± 2.7	1.4 ± 0.8
Ecotone Patches	6	15 ± 2.5	1.5 ± 0.4	3	11.7 ± 3.2	2.2 ± 1.7

Table 4. Comparison of various parameters of settled areas in Randolph County, West Virginia in 2004-2005 to previous studies. N = natal period, PN = post-natal period

	Dellinger	Anders[1]	Lang[2]	Vega Rivera[3]	Fink[4]
Total number of radio-tagged Wood Thrushes	55	49	37	42	78
Average no. days in natal area	21.6	22.3	24.5	~20.5	22.3
Average natal settled area size (ha)	3.1	4.5			
Average distance between N and PN sites (m)	0.8	2.1	2.2	1.5	0.8
Average distance between consecutive PN settled areas (m)	0.9			1.5	
Average initial PN home-range size (ha)	1.6	1.5		2.8	
Average subsequent PN home-range size (ha)	1.1	~0.2			
Average daily movement distance in natal areas (m)	73		>117		
Average daily movement distance within PN settled area (m)	85			101	
Average no. days in initial PN settled area	12.6				12.9
Average no. days in subsequent settled area	8.7				9
Range of days wandering from N to PN settled areas	1 to 9				1 to 8

[1] Anders et al. 1998
[2] Lang et al. 2002
[3] Vega Rivera et al. 1998
[4] Fink 2003

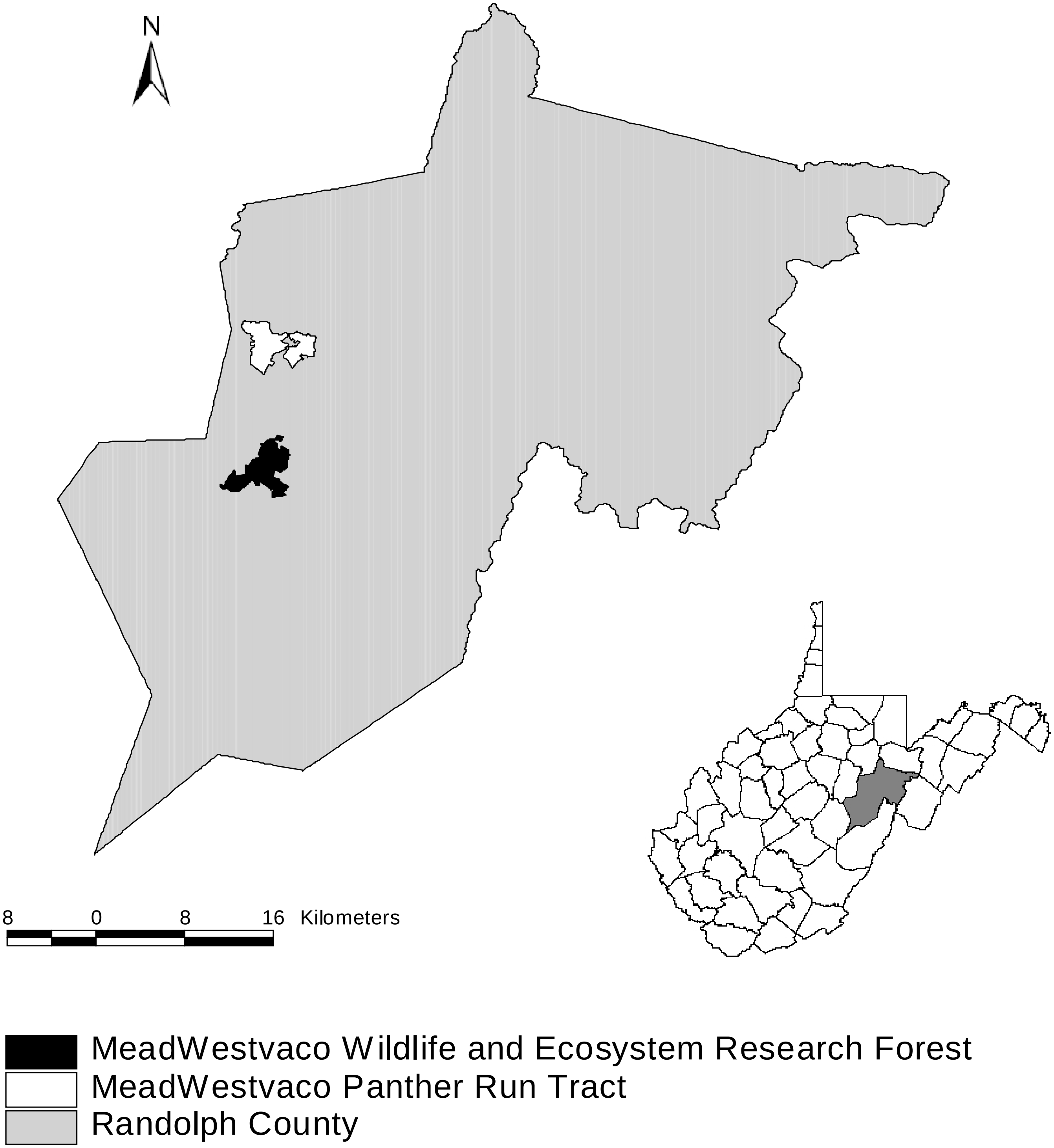

Figure 1. Locations of the MeadWestvaco Wildlife and Ecosystem Research Forest and the Panther Run Tract in Randolph County, West Virginia.

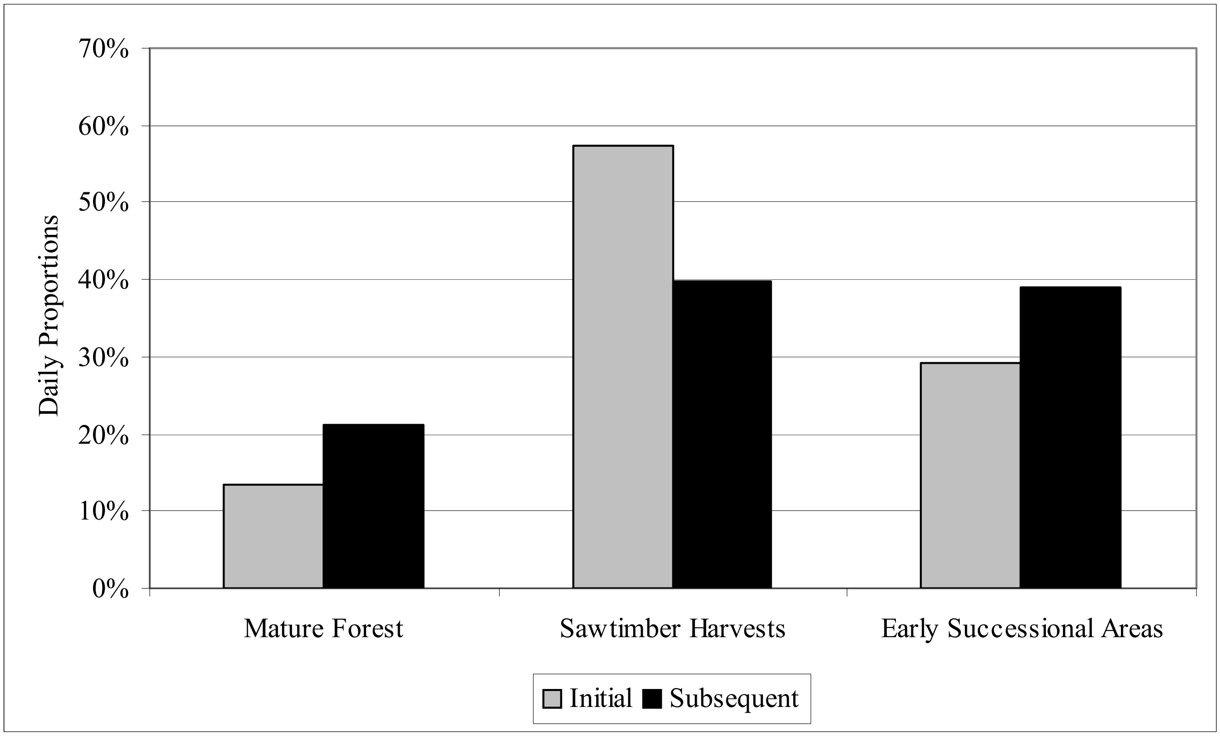

Figure 2. Proportions of post-natal daily Wood Thrush locations within cover types for settled area categories, 2004-2005, Randolph County, West Virginia.

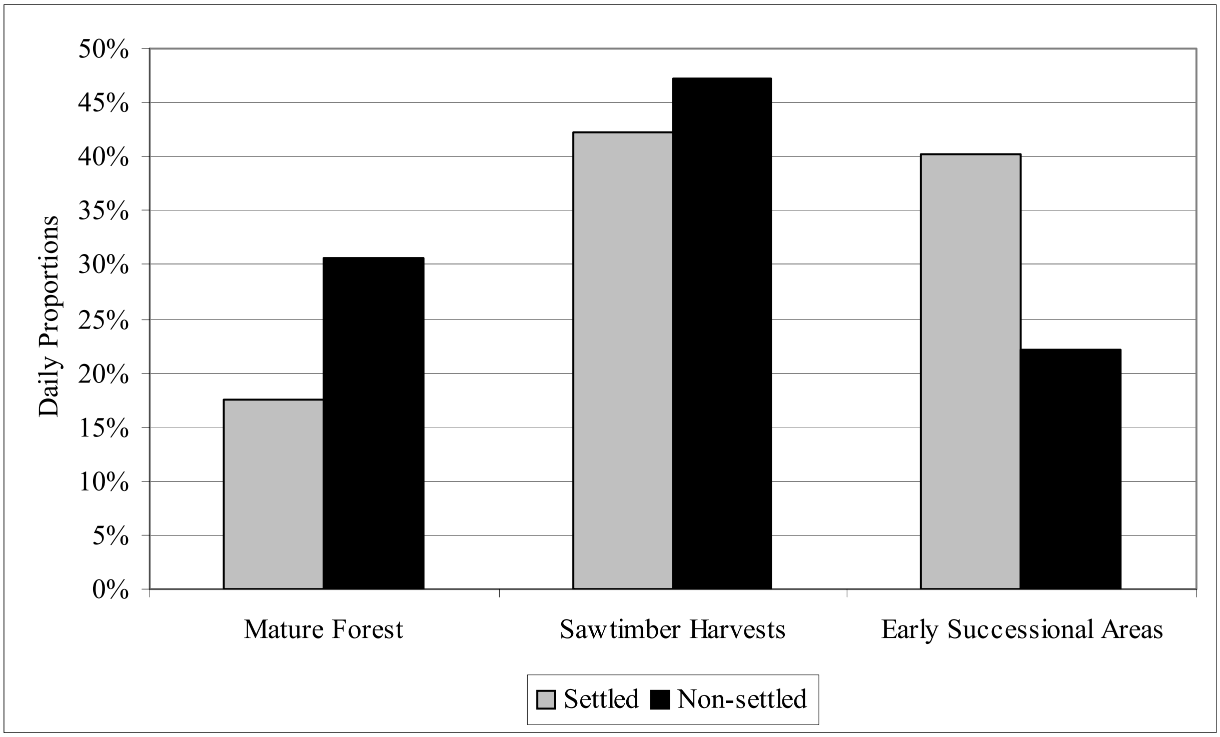

Figure 3. Proportions of post-natal daily Wood Thrush locations within cover types for movement categories, 2004-2005, Randolph County, West Virginia.

CHAPTER 4

USE OF CLEARCUTS AND DEFERMENT CUTS BY SONGBIRDS DURING THE POST-FLEDGING PERIOD

ABSTRACT

Early-successional patches are important to both shrubland and mature forest birds during the post-fledging period when adults are finished breeding and young are fledged. We compared mist-net captures of songbirds between two silvicultural methods that create early-successional patches, clearcuts and deferment cuts. In late-July and late-August 2004 and 2005, we sampled birds using mist-nets in three clearcuts and three deferment cuts similar in size (14.7 – 16.2 ha) and age (5 – 8 years) in Randolph County, West Virginia. No overall differences ($P > 0.05$) in abundance, species richness, or diversity were detected between the two treatments for adult or juvenile captures. For early successional species, more adults ($P = 0.04$) and juveniles ($P = 0.03$) were captured in deferment cuts than in clearcuts. Juvenile interior-edge species—those that typically need some mature trees but are not necessarily tied to the forest interior—were captured more often in clearcuts ($P < 0.05$) than in deferment cuts. Significantly more juvenile Hooded Warblers (*Wilsonia citrina*) were captured ($P < 0.05$) in clearcuts, while juvenile Chestnut-sided Warblers (*Dendroica pensylvanica*) were captured more often in deferment cuts ($P < 0.05$). Our results do not indicate clearcuts or deferment cuts are clearly more favorable to all birds, rather each treatment was important to at least one guild or species. Thus, both harvest types appear suitable for use by land managers interested in creating early successional habitats for songbirds.

Keywords: Clearcut; Deferment cut; Post-fledging; Songbirds; Silviculture; West Virginia;

1. Introduction

Juvenile and adult bird species of various habitat assemblages either pass through or remain several days in early-successional habitats during the post-fledging and post-breeding periods, respectively (Rappole and Ballard 1987, Anders *et al.* 1998, Vega Rivera *et al.* 1998a, Vega Rivera *et al.* 1999, Pagen et al. 2000, Fink 2003, Marshall *et al.* 2003, Vega Rivera *et al.* 2003, Rodewald and Vitz 2005, Vitz and Rodewald 2005, T. Dellinger, unpubl. data). During the post-breeding/post-fledging period, adults and juveniles may be more vulnerable to avian predators than they are at other times, largely because adults may be in heavy molt during this period and possibly cannot maintain sustained flight or perform evasive maneuvering, and juveniles are inexperienced in escaping predators and in foraging (Anders *et al.*1997, Vega Rivera *et al.*1998b). Dense vegetation and plentiful soft mast in early-successional patches may be important in providing food and cover prior to migration to both juveniles and adults. For these reasons, anthropogenic activities that create patches of early-successional vegetation ranging in size from disturbed areas along roadsides to large multi-hectare timber harvests may benefit songbirds during these periods. Researchers have begun to examine various aspects of post-fledging use of early-successional areas including optimal size and shape of timber harvests for different songbird guilds (Rodewald and Vitz 2005, Vitz and Rodewald 2005). We have found no published studies that examined post-fledging bird response to residual canopy in even-age harvests.

Our study focused on two commonly used even-aged methods, clearcuts and deferment cuts. Typically within clearcut harvests, all trees >2.5 cm in diameter are removed (Smith et al. 1997), although occasionally small groups of residual canopy trees are left. In contrast, deferment cutting, also known as a two-age harvesting, irregular shelterwood, or shelterwood with reserves, retains some mature trees (basal area of approximately 4.5 m^2 per ha) that are evenly distributed across the harvested area to diminish the negative visual impacts present in a clearcut (Smith et al. 1997). After the establishment of regeneration, two height strata are present, high overstory trees and a low scrub-shrub layer. Smith *et al*. (1989) reported that abundance and richness of available tree stems in this lower layer did not differ from that of clearcuts and thus concluded that deferment cuts were silviculturally comparable to clearcuts, .

Miller *et al*. (1995) considered deferment cuts to be important tools for enhancing vertical structure of harvested stands. The increased structural diversity of deferment cuts may be important to some songbird species during the post-fledging period by providing more varied food items while maintaining the dense understory cover typically found in clearcuts. Specifically, hard and soft mast producing trees such as black cherry (*Prunus serotina*) and oaks (*Quercus* spp.) often are retained in deferment cuts. Duguay *et al*. (2001a) measured higher amounts of bark-dwelling invertebrates, a food resource for some birds, in deferment cuts than in clearcuts approximately 15 years post-harvest.

Previous studies have investigated songbird use of clearcuts and deferment cuts during the breeding season. Weakland (2000) found deferment cuts initially had negative impacts on the abundance of Red-eyed Vireos (*Vireo olivaceus*) and Black-throated Green Warblers (*Dendroica virens*), although she concluded that overall this harvest treatment did not negatively affect most forest songbirds. Duguay *et al*. (2001b) reported greater nest parasitism in and around deferment harvests than in clearcuts or mature forest areas, although abundance and daily nest-survival rates did not differ. Dellinger (2005) found that when nesting within even-aged harvests, Veeries (*Catharus fuscescens*) and Wood Thrushes (*Hylocichla mustelina*) tended to place their nests within 11.3 m of a tall tree such as those remaining in deferment cuts. No studies have examined songbird use of these two harvest types after the breeding season. Our objective was to compare songbird use of clearcuts and deferment cuts during the post-fledging period by comparing avian abundance, species richness, and diversity between the two harvest types. Furthermore, we looked for differences in the use of both harvest types by juveniles and adults of three habitat guilds.

2. Methods

This study was conducted in southwestern Randolph County, West Virginia on the 3413 ha MeadWestvaco Wildlife and Ecosystem Research Forest (MWERF) and the 1705 ha MeadWestvaco

Panther Run Tract (PRT) located 16 km north of the MWERF. The MWERF and PRT were established in 1994 and 2001 respectively, to provide sites for long-term research on the effects of industrial forest management practices on wildlife and other ecosystem elements. The elevation of the MWERF ranged from 744 to 1180 m, while the PRT was 634 to 914 m. This region had an average growing season, or frost-free period, of 150 days per year (Smith 1995). The woody vegetation on the MWERF and PRT were second growth hardwood forest that were initially harvested 80-90 years ago. The MWERF is composed primarily of cove hardwoods and mixed mesophytic communities (Braun 1950), with northern and Allegheny hardwoods present in the higher elevations (Engle 2007). The PRT was composed primarily of xeric oak-hickory forests. Both sites had many patches of regenerating forest areas due to past or recent harvesting events. Specifically high-grading or diameter-limit cutting and clearcutting were typical harvesting methods on timberlands in Randolph County from the 1930s to 1995. All clearcuts used in this study had 1-2 small groups of residual canopy trees with groups composed of <20 trees and encompassing areas of <0.1 ha. Within deferment cuts residual canopy trees, 7-20% of the original stand, were scattered throughout the harvested area.

2.1 Experimental Design

From regenerating stands, we selected three clearcuts and three deferment harvests. All harvest stands were irregular in shape and separated by at least 400 m. Each clearcut was paired with a deferment cut based on similarity in age, size, and elevation (Table 1), and the resulting three pairs were used as a block in statistical analyses. At the beginning of the study in 2004, the youngest block was 5 years post-harvest; the remaining two were 7 years post-harvest.

Vegetative characteristics were measured on one sampling plot for each stand in 2004. Plots were placed 10 m away from a randomly selected net location (see below) in a random direction. Trees greater than 22.9 cm diameter at breast height (d.b.h.) were tallied on an 11.3 m radius plot and woody stems < 7.6 cm d.b.h. were counted within a 5 m radius plot centered on the random location (Martin *et al*. 1997). The number of stems that yield soft mast were totaled on the 5 m radius plot. Soft mast producing species were: *Cornus florida, Crataegus* spp., *Lindera benzoin, Prunus alleghaniensis, P. serotina, Rubus* spp., *Sambucus canadensis, Sassafras albidum, Smilax* spp., and *Vitus* spp. Stand basal area was measured at one to three random locations within each harvest stand with a 10 basal area factor prism (M. McDermott *pers. comm.*). Vegetation data were not statistically analyzed due to small sample size and represent a qualitative description of study stands.

Mist-netting

We mist-netted each stand twice in 2004 and in 2005, one day in mid-July and one day in mid-August, to sample early and late in the post-fledging period. These times were chosen based on spring arrival and egg-laying dates of migrant songbirds (Hall 1983) to ensure that most species had bred at least once.

Nine 30-mm mesh nets were used during each sample: two 6 m × 2.6 m and seven 12 m × 2.6 m. All nets were positioned at least 100 m from the nearest edge within the regenerating stand. Typically, six to seven nets were set up on old skid roads, parallel to the roadside, with the remainder placed within the dense regeneration of the harvested areas on narrow paths that had been trimmed with machetes. All nets were open 4 h per visit beginning 30 minutes after sunrise on days with no precipitation and little or no wind. Because we were netting during the latter part of the breeding season while some adults still might have been incubating, brooding, or feeding nestlings or recent fledglings, nets were checked every 15 to 20 minutes to minimize the time adult birds were not caring for their young and juveniles were separated from their family or post-fledging group.

Sex and age were determined for each bird captured based on plumage attributes, molt, breeding characters, and feather wear (Pyle 1997). All captures were identified as hatch-year (juvenile) birds that fledged during the current breeding season or after hatch-year (adult) individuals that were ≥ 1 year old. Adult females without brood patches and adult males were released at the processing site; brooding females and juveniles were released near the point of capture. Wing chord and mass were recorded as described by Ralph et al. (1993), and individuals were banded with a United States Geological Survey leg band.

Data Analysis

Each species was assigned to a nesting habitat guild (early-successional, interior-edge, or forest-interior) based on personal observations, field guides and species accounts (e.g. Hall 1983, Ehrlich *et al*. 1988, Dunn and Garrett 1997) (Table 2). The interior-edge guild included species that typically need some mature trees but are not necessarily tied to the forest interior. Age groups were analyzed separately because juveniles and adults may respond differently to the presence of residual overstory trees.

We calculated the degree of similarity in bird species composition between clearcuts and deferment cuts for each age class and for overall captures using the percent similarity index (Nur *et al*. 1999). The coefficient ranges from 0, completely dissimilar, to 100, completely similar and measured percentage overlap of species between the treatments. The Shannon diversity (H') index (Pielou 1975) was used to measure heterogeneity between treatments. Species richness was the total number of species captured. Evenness (*J*) was calculated as H' / ln [species richness] (Pielou 1969). Values of *J* range between 0 and 1, with 1 representing highest evenness.

Net hours were identical for each stand and month so number of captures was not adjusted per net hour. For each age class, we calculated abundance as the number of captures overall, for each habitat guild, and for the two most numerous species captured. Abundance variables were analyzed with a Poisson regression (PROC GENMOD; SAS Institute, 2001) that compared treatment effects while accounting for block, month, and year effects. Abundance variables were log transformed to avoid errors in variance-covariance computation estimates. Model terms were block × year, treatment, month, and month × treatment. Month was included in the model because we were not concerned with recaptures for our relatively small study and we wanted to account for possible adult increases at the end of the breeding season. We used one-way analysis of variance (PROC GLM; SAS Institute, 2001) accounting for block, month, and year effects to compare richness, H', and *J*. Species richness was square root transformed before analyses. Differences were considered significant at $P \leq 0.05$.

3. Results

Although more basal area was present in deferment cuts, number of sapling stems and fruit-bearing stems was generally similar among stands with more variability among stands within a harvest type than between the two harvest types (Table 1).

3.1 Overall captures

Overall, 339 individual birds of 40 species were captured and identified during the study, 164 from clearcut harvests and 175 from deferment harvests (Table 1). Regardless if an individual's age was known, the similarity index between the two treatments was 57%, with 21 species common to both treatments. Only individuals that could be identified as adult or juvenile were used in further analyses ($n = 324$) (Table 2).

3.2 Adult captures

Over 2 years, we captured 68 adults in clearcuts and 81 in deferment cuts, but mean abundance did not differ between treatments (Table 3). Species richness ranged from 0-6 in clearcuts and 2-9 in deferment cuts; mean richness did not differ between treatments. Similarity index between the treatments was 53%. One clearcut site had no adult captures in August 2005, therefore it could not be included in diversity or evenness comparisons. Shannon diversity (H′) values and evenness (*J*) values were similar between treatments (Table 3).

Abundance of forest-interior and interior-edge species did not differ between treatments (Table 3). Early-successional species abundance differed with more captures in deferment cuts than clearcuts.

Two species, the Chestnut-sided Warbler (CSWA) and Hooded Warbler (HOWA), made up 41% and 30% of all adult captures in clearcuts and deferment cuts, respectively (Table 2). Abundance of neither species differed between the two harvest treatments.

3.3 Juvenile captures

We captured 90 juvenile songbirds within clearcuts and 85 from deferment cuts during the 2 year study; mean abundance did not differ (Table 3). Species richness ranged from 2-8 in clearcuts and 1-9 in deferment cuts and mean richness did not differ among the treatments. Similarity between clearcuts and deferment cuts for juvenile captures was 51%. There were no differences in Shannon diversity (H′) and evenness (*J*) values between treatments.

Abundance of two habitat guilds, early-successional and interior-edge, differed significantly between clearcuts and deferment cuts (Table 3). Contrary to our expectations, early-successional species were more abundant in deferment cuts, while interior-edge species were more abundant in clearcuts.

As with adult captures, juvenile CSWA (22%) and HOWA (11%) were the most common species captured. Abundance of both species differed between treatments, with more captures of CSWA in deferment cuts and more HOWA in clearcuts (Table 3). Among juvenile captures, Black-throated Green Warblers were the third most numerous (Table 2), partially as a result of 12 individuals netted simultaneously in two adjacent mist-nets, and represented the largest capture event of any species at one time.

4. Discussion

Our results did not identify either treatment as clearly “better” for songbirds. Both harvest types were used by at least one guild or individual species. In general, the bird community did not differ markedly between clearcut and deferment harvests. They shared 53% of species for adults and 51% for juveniles. For both adults and juveniles, overall individuals captured, species richness, Shannon’s diversity, and evenness were similar between the two harvest types. Similarity in vegetative structure in the understory between the two treatments may explain the lack of overall differences. It is possible that differences were present in the upper strata of the canopy where we were unable to sample. Mist-netting is an efficient technique for sampling birds in regenerating areas, especially clearcuts (Pagen *et al*. 2000), but any birds foraging in the tops of the residual trees were not captured. However, our primary question concerned use of the shrub layer, therefore this bias did not influence our results.

The possibility of the trees present throughout deferment cuts and groups of trees in clearcuts being used as predator perches did not appear to deter use of either harvest type. Adult captures of forest-interior and interior-edge guilds were similar between the two harvest types. Juveniles of the interior-edge guild were more abundant in clearcuts and both age classes of the early-successional guild were more abundant in deferment cuts suggesting that amount and spatial arrangement of residual trees may differentially influence use by some guilds. In general, both harvest types in our study provided dense understory vegetation (Table 1).

As expected, our study stands were used extensively by early successional species during the post-fledging period, and by CSWA’s in particular. More importantly, birds that typically nest in mature forest also made extensive use of both types of early successional harvests.

We suspect that HOWA nested within even-aged harvests at our study site and that we netted family groups within these harvests. Hooded Warblers were the most abundant non-early successional species captured in clearcut and deferment harvests, and adults were captured in all six stands sampled (Table 1). Some individuals captured in late July still showed breeding characteristics, a full brood patch in females and cloacal protuberance in males. Furthermore, adults were recaptured at their original banding sites (Table 1) suggesting a long tenure in these stands: a female 38 days post-capture from a deferment cut and a male 1 year post-capture in a clearcut. All nets were ≥ 100 m from the nearest edge. Our observations are consistent with those of other researchers who have noted HOWA's in atypical habitats. For example, Duguay *et al*. (2001b) monitored four HOWA nests located in 15 year-post harvest deferment cuts and clearcuts on the Monongahela National Forest in West Virginia. Point count surveys during the breeding season documented males singing within these harvest types on our study site and on the Monongahela National Forest (R. Dellinger pers. comm., M. McDermott pers. comm.). Marshall *et al*. (2003) noted a variety of habitats are used by this species and described HOWA's as habitat generalists along the succession gradient. Other non-early successional species occasionally observed breeding in early successional areas include Worm-eating Warblers, Ovenbirds, and Kentucky Warblers (*Oporornis formosus*) (Pagen et *al*. 2000). Likewise, Dellinger (2005) reported monitoring Wood Thrush and Veery nests in clearcuts and deferment cuts in West Virginia. During the breeding season, HOWA's are associated with canopy gaps in mature forest and forage in low, dense woody vegetation (DeGraaf and Rappole 1995). Perhaps the residual trees within both harvests provided enough overstory to make these harvests suitable as nesting habitat, in particular the groups of residual trees in clearcuts where captures were higher. Thus it is possible that this species will breed in habitats along a broad forest succession continuum in the central Appalachians, and is not limited to tree fall gaps or selectively logged areas contrary to many published habitat associations for this species. Further research is recommended of breeding and post-breeding early-successional habitat use of HOWA in the central Appalachians, including why deferment cuts were used less often than clearcuts.

Early successional habitats are declining in the eastern United States as farmlands revert to forest and as land development occurs (Askins 2001); consequently many early-successional species also are declining due to loss of breeding habitat. Given the relative importance of early-successional habitats to many species from various guilds, land managers should work toward a proper balance of maintaining mature forest breeding habitat for forest-interior species while also creating and maintaining early-successional areas. Although the number of stands sampled was low, our data suggest that presence of overstory canopy trees did not appreciably affect the post-fledging bird community using the shrub layer in clearcut and deferment harvests. Thus, land managers can use either harvest technique as a tool for creating early successional habitats; however, to ensure suitable habitat is available for all species, we recommend using both methods in an area.

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Table 1. Stand descriptions, vegetation measurements sampled in 2004, and mist-net captures of juvenile and adult songbirds in 3 clearcuts and 3 deferment cuts during July-August 2004 and 2005 in Randolph County, West Virginia.

	Clearcut			Deferment Cut		
	1	2	3	1	2	3
Stand Characteristics						
Tract[a]	MWERF	PRT	PRT	MWERF	MWERF	MWERF
Block	1	2	3	1	2	3
Yrs post-harvest as of 2004	5	7	7	5	7	7
Size (ha)	16.0	14.7	15.6	16.2	14.7	14.7
Elevation (m)	2840	2720	2460	3020	2980	2720
Basal area m^2 / ha [b]	0.00	0.29	0.86	1.72	4.88	2.30
# saplings < 7.6cm in 5m radius plot	338	147	148	383	98	226
# trees > 22.9cm dbh in 11.3m radius plot	0	0	0	0	1	2
# soft mast bearing stems in 5m radius plot	272	117	55	271	41	135
Adult captures						
Total individuals	22	26	20	45	10	26
Species richness	11	10	14	18	5	14
Forest-interior [c]	3 (3)	1 (1)	3 (3)	9 (6)	0	3 (3)
Interior-edge [c]	11 (5)	18 (5)	9 (6)	23 (8)	4 (2)	11 (6)
Early-successional [c]	8 (3)	7 (4)	8 (5)	13 (4)	6 (3)	12 (5)
Juvenile captures						
Total individuals	35	14	41	41	19	25
Species richness	16	6	12	17	9	10
Forest-interior [c]	10 (5)	0	13 (2)	7 (5)	4 (4)	8 (4)
Interior-edge [c]	16 (7)	10 (4)	17 (6)	15 (7)	4 (2)	8 (4)
Early-successional [c]	9 (4)	4 (2)	11 (4)	19 (5)	11 (3)	9 (2)
Chestnut-sided Warbler captures						
Total adult	4	1	1	8	1	3
Total juvenile	6	0	5	14	6	8
Recaptured adult	1	0	0	0	0	0
Recaptured juvenile	0	0	0	1	0	0
Hooded Warbler captures						
Total adult	6	13	3	6	2	4
Total juvenile	3	5	5	3	0	3
Recaptured adult	0	1	0	1	0	0
Recaptured juvenile	0	0	0	0	0	0

[a] MWERF=MeadWestvaco Wildlife and Ecosystem Research Forest; PRT=Panther Run Tract

[b] M. McDermott pers comm.

[c] Number of individuals, with number of species in parenthesis.

Table 2. Common names, scientific names, guild assignments, and numbers of individuals per treatment for adult and juvenile songbirds captured in 3 clearcuts and 3 deferment cuts in Randolph County, West Virginia, July-August 2004 and 2005.

Species	Habitat Guild[a]	Clearcut		Deferment Cut	
		Adult	Juvenile	Adult	Juvenile
Blue-winged Warbler (*Vermivora pinus*)	ES				1
Carolina Wren (*Thryothorus ludovicianus*)	ES		1		
Chestnut-sided Warbler (*Dendroica pensylvanica*)	ES	6	11	12	28
Common Yellowthroat (*Geothlypis trichas*)	ES	2	1		
Eastern Towhee (*Pipilo erythrophthalmus*)	ES	4	7		1
Field Sparrow (*Spizella pusilla*)	ES	4		2	
Gray Catbird (*Dumetella carolinensis*)	ES	1	3	7	6
Indigo Bunting (*Passerina cyanea*)	ES	5		7	2
Mourning Warbler (*Oporornis philadelphia*)	ES				1
Northern Cardinal (*Cardinalis cardinalis*)	ES			1	
Song Sparrow (*Melospiza melodia*)	ES			1	
Traill's Flycatcher (*Empidonax traillii*)	ES			1	
White-eyed Vireo (*Vireo griseus*)	ES	1	1		
Black-and-white Warbler (*Mniotilta varia*)	FI	1	1		3
Blackburnian Warbler (*Dendroica fusca*)	FI	1		1	1
Black-throated Blue Warbler (*Dendroica caerulescens*)	FI		2	2	2
Black-throated Green Warbler (*Dendroica virens*)	FI		15	1	1
Blue-headed Vireo (*Vireo solitarius*)	FI			1	
Cerulean Warbler (*Dendroica cerulea*)	FI				1
Least Flycatcher (*Empidonax minimus*)	FI	1	1		
Magnolia Warbler (*Dendroica magnolia*)	FI		3	4	4
Ovenbird (*Seiurus aurocapillus*)	FI			1	5
Scarlet Tanager (*Piranga olivacea*)	FI	1			
Tennessee Warbler (*Vermivora peregrina*)	FI			1	2
Winter Wren (*Troglodytes troglodytes*)	FI		1		
Worm-eating Warbler (*Helmitheros vermivorus*)	FI	3		1	
American Redstart (*Setophaga ruticilla*)	IE	3	2	1	
American Robin (*Turdus migratorius*)	IE		1		
Black-billed Cuckoo (*Coccyzus erythropthalmus*)	IE			1	
Black-capped Chickadee (*Poecile atricapilla*)	IE		2	3	1
Canada Warbler (*Wilsonia canadensis*)	IE	3	5	3	6
Cedar Waxwing (*Bombycilla cedrorum*)	IE	1		6	2
Dark-eyed Junco (*Junco hyemalis*)	IE				1
Hooded Warbler (*Wilsonia citrina*)	IE	22	13	12	6
Northern Parula (*Parula americana*)	IE	1			
Red-eyed Vireo (*Vireo olivaceus*)	IE	3	10	2	4
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	IE	1		1	
Tufted Titmouse (*Baeolophus bicolor*)	IE			1	
Veery (*Catharus fuscescens*)	IE	3	5	6	3
Wood Thrush (*Hylocichla mustelina*)	IE	1	5	2	4
	Total	68	90	81	85

[a] Habitat guild assignment based on field guides, species accounts, and personal observations: ES = early-successional; IE = interior-edge; FI = Forest-interior.

Table 3. Mist-net captures of adult and juvenile songbirds in clearcuts and deferment cuts in Randolph County, West Virginia, July-August 2004 and 2005.

	Clearcut			Deferment Cut				
	N	$\bar{x}$	SE	n	$\bar{x}$	SE	Test Statistic[a]	
Adult captures								
Total individuals	68	5.7	0.97	81	6.8	1.33	$X^2 = 0.42$	0.52
Species richness	21	3.8	0.53	26	5.0	0.79	$F = 0.92$	0.38
Shannon's Index		1.2	0.14		1.4	0.17	$F = 1.61$	0.26
Evenness		0.7	0.08		0.9	0.03	$F = 3.29$	0.13
Forest-interior	7	0.6	0.20	12	1.0	0.41	$X^2 = 1.72$	0.19
Interior-edge	38	3.5	0.61	38	3.2	0.80	$X^2 = 0.18$	0.67
Early-successional	23	2.1	0.51	31	2.6	0.45	$X^2 = 4.10$	0.04
Chestnut-sided Warbler	6	0.5	0.28	12	1.0	0.35	$X^2 = 1.98$	0.16
Hooded Warbler	22	2.0	0.57	12	1.0	0.33	$X^2 = 1.57$	0.21
Juvenile captures								
Total individuals	90	7.5	1.87	85	7.1	1.32	$X^2 = 0.01$	0.93
Species richness	20	4.3	0.59	22	4.7	0.69	$F = 0.91$	0.38
Shannon's Index		1.2	0.13		1.3	0.16	$F = 1.07$	0.35
Evenness		0.8	0.05		0.8	0.05	$F = 0.51$	0.51
Forest-interior	23	1.9	1.16	19	1.6	0.47	$X^2 = 2.34$	0.13
Interior-edge	43	3.6	0.71	27	2.3	0.52	$X^2 = 10.06$	<0.01
Early-successional	24	2.0	0.34	39	3.3	0.73	$X^2 = 4.94$	0.03
Chestnut-sided Warbler	11	0.9	0.34	28	2.3	0.61	$X^2 = 11.03$	<0.01
Hooded Warbler	13	1.1	0.26	6	0.5	0.26	$X^2 = 6.67$	<0.01

[a] X^2 is Wald X^2 from Poisson regression; *F* is from analysis of variance

Appendix A. Capture dates and movement information of juvenile Neotropical migratory warbler species radio-tagged in 2004-2005, Randolph County, West Virginia.

Species	**Individual**	**Date captured**	***Number of days located/over days radio-tracked**	**Comments**
Ovenbird (*Seiurus aurocapillus*)	480	22 July 2004	0	Individual never relocated
	492	17 Aug 2004	0	Signal detected 3 hrs post sunset in regeneration unit where bird was captured; bird never relocated.
	547	29 Aug 2005	0	Signal detected in early afternoon and 2 hrs after sunset in regeneration unit where captured; bird never relocated.
Black-throated Blue Warbler (*Dendroica caerulescens*)	515	23 July 2005	1/1	Signal detected in regeneration unit where captured on previous day. On second day post-capture, located transmitter which had fallen off.
Black-and-White Warbler (*Mniotilta varia*)	019	16 Aug 2004	5/6	Over the period of a week, bird was located along periphery and within the regeneration unit where captured.
	059	25 July 2005	3/8	Individual was not located again in the regeneration unit where captured; instead it had moved west into a sawtimber harvest.

* excludes capture day

Figure B-1. Recently fledged Wood Thrush (*Hylocichla mustelina*) radio-tagged in 2004 on the MeadWestvaco Wildlife and Ecosystem Research Forest in Randolph County, West Virginia.

Figure B-2. Juvenile Black-throated Blue Warbler (*Dendroica caerulescens*), radio-tagged in 2005 on the MeadWestvaco Wildlife and Ecosystem Research Forest in Randolph County, West Virginia.

Figure B-3. Mature Forest cover type on the MeadWestvaco Wildlife and Ecosystem Research Forest and Panther Run Tract in Randolph County, West Virginia. These areas were last harvested 70 – 90 years ago, and typically had a closed canopy and fairly open understory.

Figure B-4. Sawtimber harvest cover type 8 years post-harvest, on the MeadWestvaco Wildlife and Ecosystem Research Forest and Panther Run Tract in Randolph County, West Virginia.

Figure B-5. Young Harvest (clearcut) early successional category found on the MeadWestvaco Wildlife and Ecosystem Research Forest and Panther Run Tract in Randolph County, West Virginia.

Figure B-6. Deferment cut found on the MeadWestvaco Wildlife and Ecosystem Research Forest and Panther Run Tract in Randolph County, West Virginia.

Figure B-7. Disturbed area early successional category found on the MeadWestvaco Wildlife and Ecosystem Research Forest and Panther Run Tract in Randolph County, West Virginia.

Figure B-8. Old Harvest early successional category found on the MeadWestvaco Wildlife and Ecosystem Research Forest and Panther Run Tract in Randolph County, West Virginia.

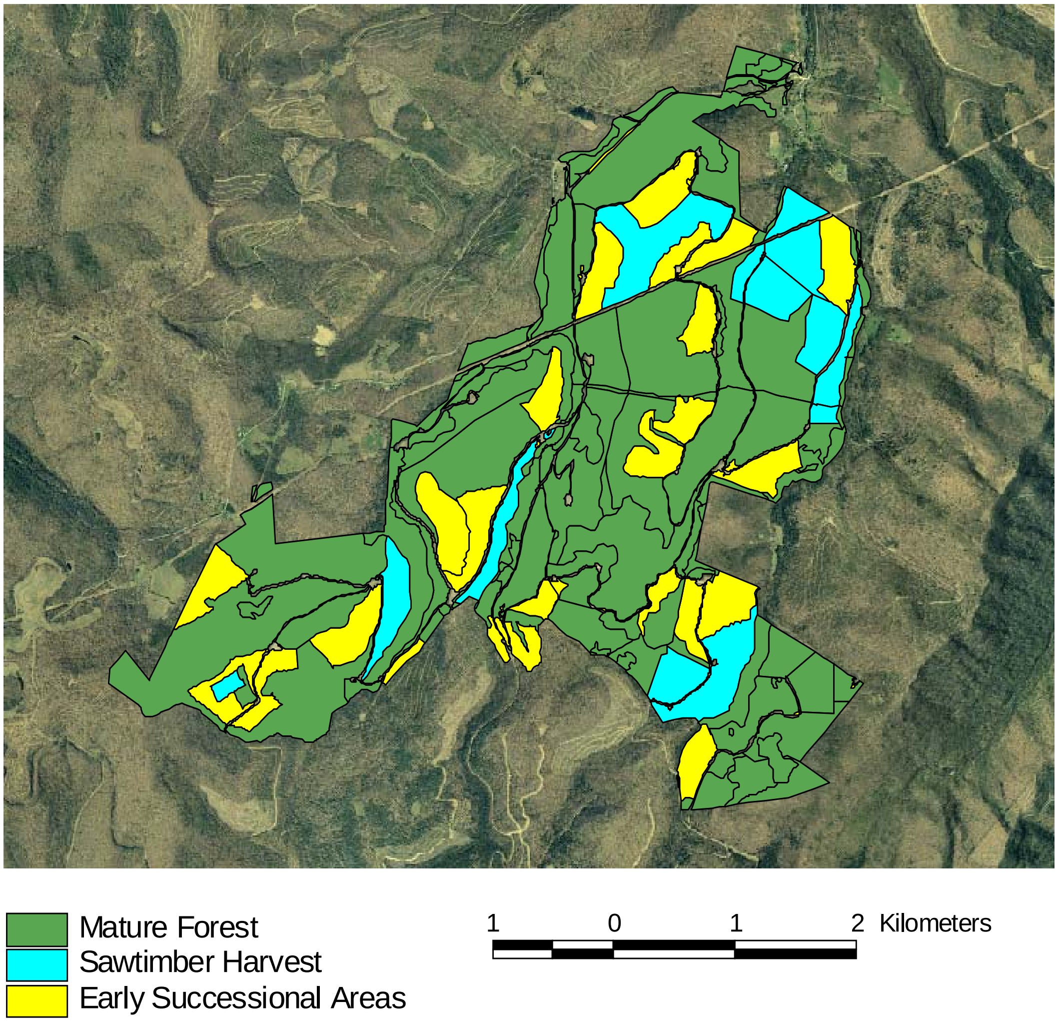

Figure B-9. Digitized land cover types on the MeadWestvaco Wildlife and Ecosystem Research Forest in Randolph County, West Virginia.

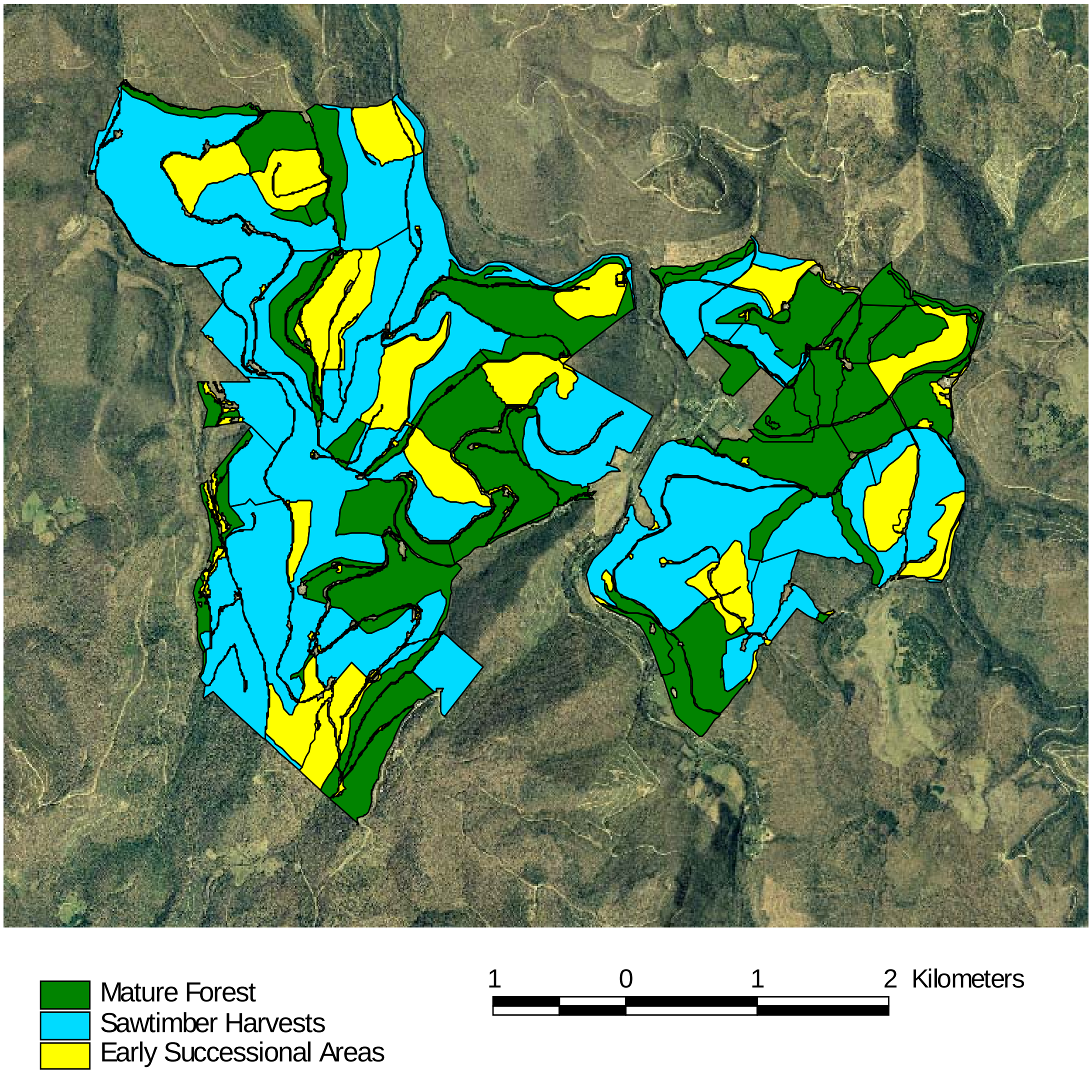

Figure B-10. Digitized land cover types on the MeadWestvaco Panther Run Tract in Randolph County, West Virginia.

Figure B-11. Vegetation density board used to quantify concealment at non-early successional locations of radio-tagged Wood Thrushes in Randolph County, West Virginia, 2004 and 2005.

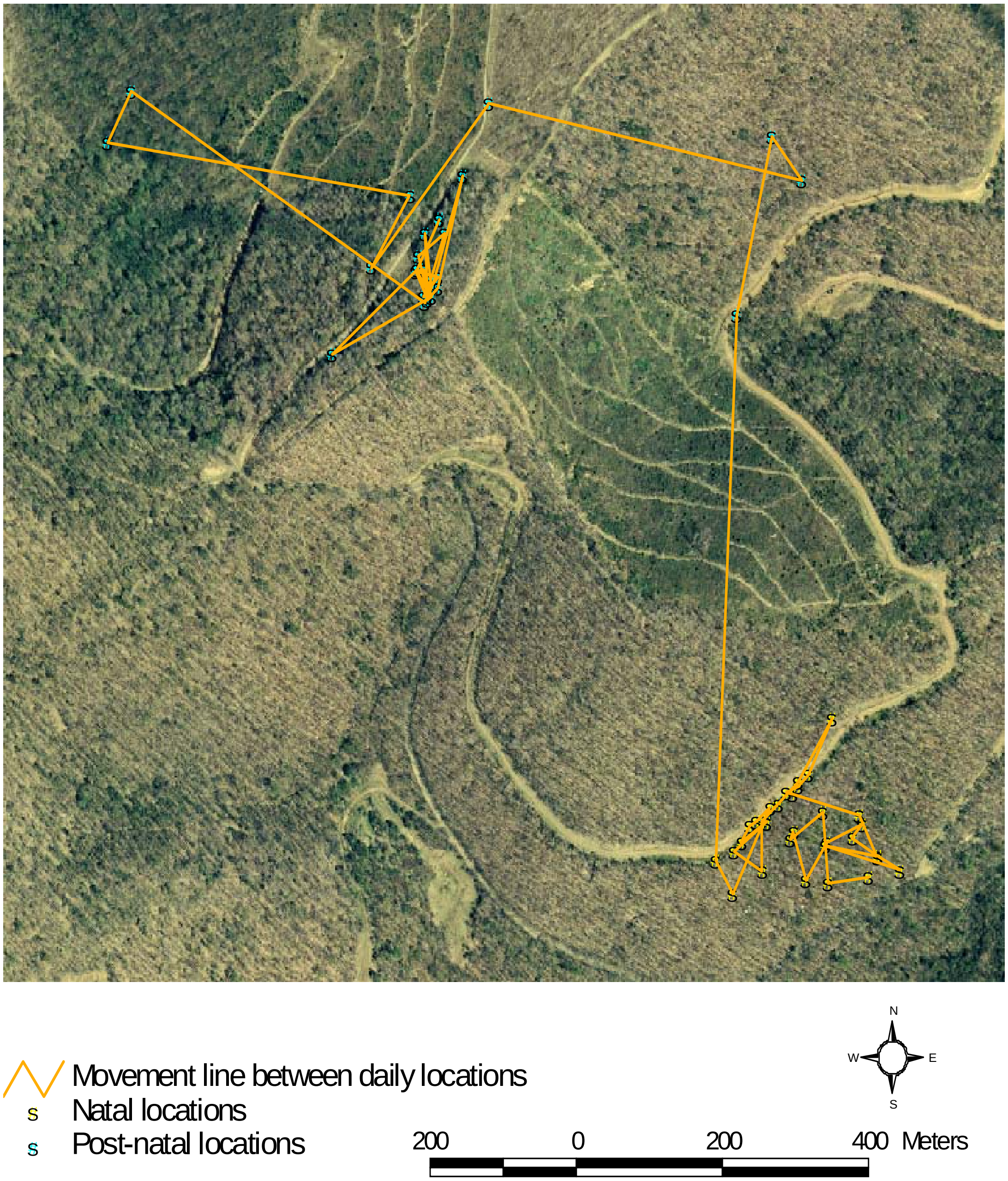

Figure B-12. Distances between consecutive daily locations were calculated within ArcView 3.2 using Animal Movements extension.

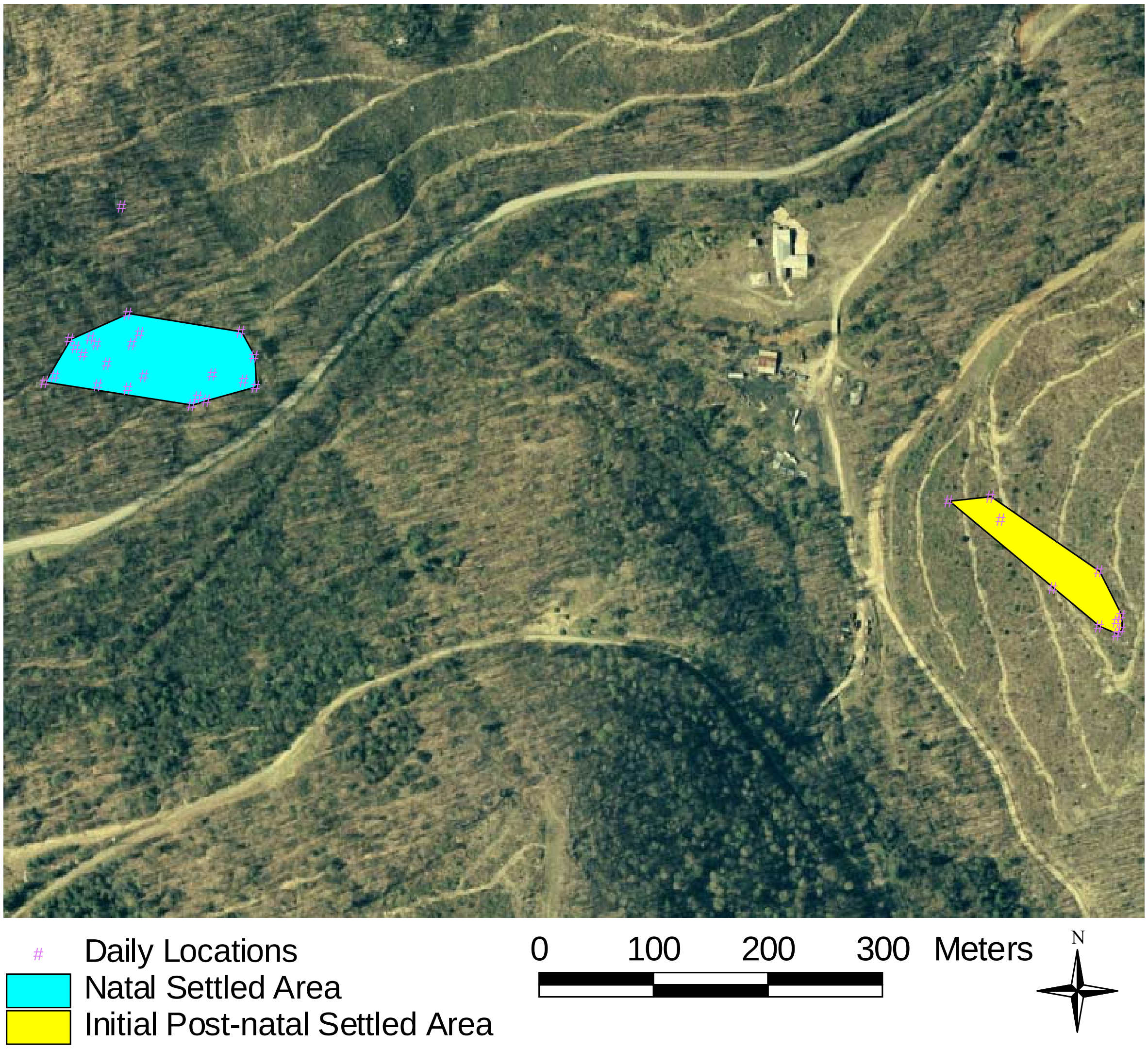

Figure B-13. Settled area sizes for natal and post-natal sites were determined by 95% minimum convex polygons using Animal Movements extension in ArcView 3.2.