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WOOD THRUSH MOVEMENTS AND HABITAT USE: EFFECTS OF FOREST MANAGEMENT FOR RED-COCKADED WOODPECKERS

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ABSTRACT.—We monitored adult and juvenile breeding-season movements and habitat use of radio-tagged Wood Thrushes (*Hylocichla mustelina*) at the Piedmont National Wildlife Refuge, central Georgia, USA. We investigated the effects that management for Red-cockaded Woodpeckers (*Picoides borealis*), thinning and burning >30 year old loblolly pine (*Pinus taeda*) habitat, had on Wood Thrushes, a ground-foraging and midstory-nesting species. Adult Wood Thrush pairs regularly moved long distances between nesting attempts (range 1 to 17,388 m). The only experimental effect we found on adult movements was a decrease in weekly emigration rates (Ψ) from thinned and burned compartments after silvicultural management. Adult males preferred riparian hardwoods with sparse to moderate cover and those preferences increased following management. Juveniles remained near their nest site ($\bar{x} = 177$ m, SE = 113) for an average 24 days (SE = 6.3), and then dispersed a mean 2,189 m (SE = 342). Before dispersal, juveniles preferred upland hardwood–pine mixed habitat ($P < 0.05$) with moderate overstory cover ($P < 0.05$). We found no management effects on dispersal distances or predispersal habitat use. However, juveniles from thinned and burned compartments dispersed to hardwood habitats with dense cover, whereas birds from control compartments dispersed to pine-dominated habitats with sparse cover. All juveniles dispersed to areas with habitat similar to what they used before dispersal. Small-scale thinning and burning for Red-cockaded Woodpeckers may have had little effect on Wood Thrush habitat use and movements because typical movements were often larger than the scale (stand or compartment) targeted for management. Received 6 February 2001, accepted 24 July 2001.

RESUMEN.—Monitoreamos con radio-telemetría los movimientos y el uso de hábitat durante la época reproductiva de adultos y juveniles de *Hylocichla mustelina* en el Refugio Nacional de Vida Silvestre Piedmont, en Georgia central, EEUU. Investigamos los efectos que tiene el manejo del bosque (entresaca y quema de hábitat de *Pinus taeda* con más de 30 años de edad) orientado a la conservación de *Picoides borealis* sobre *H. mustelina*, una especie que se alimenta en el suelo y que nidifica a media altura del bosque. Las parejas adultas de *H. mustelina* por lo general se movieron largas distancias entre los intentos de nidificación (rango 1 a 17,388 m). El único efecto experimental que encontramos en los movimientos de adultos fue una disminución en las tasas semanales de emigración (Ψ) desde los sectores entresacados y quemados luego del manejo silvicultural. Los machos adultos prefirieron los bosques ribereños con poca a moderada cobertura, y estas preferencias incrementaron luego del manejo. Los juveniles permanecieron cercanos al sitio de nidificación ($\bar{x} = 177$ m, ES = 113) por un promedio de 24 días (ES = 6.3) y luego se dispersaron una media de 2,189 m (ES = 342). Antes de la dispersión los juveniles prefirieron hábitat no-ribereno mixto de bosque y pino ($P < 0.05$) con moderada cobertura del dosel ($P < 0.05$). No encontramos

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efectos del manejo sobre las distancias de dispersión o sobre el uso del hábitat previo a la dispersión. Sin embargo, los juveniles de sectores entresacados y quemados se dispersaron a hábitats de bosque con cobertura densa, mientras que las aves de los sectores de control se dispersaron a hábitats con escasa cobertura dominados por pinos. Todos los juveniles se dispersaron hacia áreas con hábitat similar al que usaron antes de dispersarse. Las acciones de entresaca y quema de pequeña escala orientadas al manejo de *P. borealis* pueden haber tenido poco efecto sobre el uso de hábitat y los movimientos de *H. mustelina* porque sus movimientos típicos fueron generalmente mayores que la escala (rodal y sector) elegida para manejo.

WOOD THRUSHES (*Hylocichla mustelina*) in Georgia are estimated as having one of the highest rates of population decline, 3.2% per year, during 1966 to 1989 (B. Peterjohn unpubl. data). At that rate, Georgia's Wood Thrush population declined 50% between 1966 and 1989. Weinberg and Roth (1998) found a direct relationship between forest patch size, reproductive success, and return rates for Wood Thrushes in Delaware. In Georgia, the size and number of contiguous forest tracts increased (Odum and Turner 1990) during the same time the Wood Thrush population declined. Might forest management practices, such as removal of mid- and understory vegetation to promote overstory growth, degrade habitat quality necessary for maintaining Wood Thrush populations that prefer undisturbed contiguous forest habitat? We posit that as one possible explanation.

Changes in breeding-ground vegetation structure may affect avian behavior including daily movement or habitat use. American Redstarts (*Setophaga ruticilla*) changed foraging maneuvers in areas with different vegetation structure (Maurer and Whitmore 1981). Behavioral changes, caused by compromising habitat quality, could ultimately affect reproductive success or survival. For example, Black-throated Blue Warblers (*Dendroica caerulescens*) decreased their nesting attempts in preferred nesting areas when foliage was removed (Steele 1993). By studying movements and habitat use in an experimental setting, researchers may be able to detect changes in behavior before effects on reproduction or survival.

Small-scale (~50 ha) forest thinning and prescribed burns are used to provide preferred habitats for Red-cockaded Woodpeckers (*Picoides borealis*). Red-cockaded Woodpeckers use older (>40 years), open pine habitat with sparse understory for colony sites and foraging (Jackson 1977, Richardson and Costa 1998).

Wood Thrushes nest in the midstory and forage on the ground (Roth et al. 1996). Because Wood Thrushes prefer areas with denser mid- and understory for nesting and foraging (Roth et al. 1996), habitat needs for Wood Thrushes may conflict with forest thinning and burning used to enhance Red-cockaded Woodpecker habitat. We studied the effects that thinning and burning loblolly pine (*Pinus taeda*) forest (to create foraging habitat for endangered Red-cockaded Woodpeckers) have on movements and habitat use of Wood Thrushes. We chose to study Wood Thrushes because their habitat needs potentially conflict with Red-cockaded Woodpeckers, their relative abundance at our study site, their size (large enough to carry radio-transmitters), and because their populations were declining in Georgia. Having not found any overall effects of Red-cockaded Woodpecker management on survival or reproductive success (Lang 1998, Powell et al. 2000), our objectives for this paper were to determine effects silviculture for Red-cockaded Woodpeckers has on Wood Thrushes' movements and habitat use.

METHODS

STUDY AREA

We conducted our study at Piedmont National Wildlife Refuge, Jones and Jasper Counties, Georgia, USA. Piedmont National Wildlife Refuge had a mixture of young and mature (60 to 70 year old), pine-hardwood forests including loblolly pine, oaks (*Quercus* spp.), hickories (*Carya* spp.) and sweetgum (*Liquidambar styraciflua*). Flowering dogwood (*Cornus florida*), was the primary midstory species. Piedmont National Wildlife Refuge is managed for forest wildlife, including a population of Red-cockaded Woodpeckers, and is divided into 35 management compartments (~400 ha each). To create Red-cockaded Woodpecker foraging habitat, Piedmont National Wildlife Refuge managers selectively harvest pine stands up to 50 ha in size within targeted management compartments on an 80 to 100 year rotation

(Piedmont National Wildlife Refuge 1982). Managers use thinning to maintain a basal area of 11 to 18 m² ha⁻¹, and prescribed winter burns every three to five years to prevent hardwood encroachment. Areas managed specifically for Red-cockaded Woodpecker colonies are thinned to a basal area of 6 m² ha⁻¹ (Richardson and Costa 1998). Because ~50 ha stands are targeted for management within each ~400 ha compartment only a portion of the compartment gets thinned or burned.

EXPERIMENTAL DESIGN

We used a before–after controlled intervention design (Carpenter et al. 1989, Eberhardt and Thomas 1991) to determine effects that thinning and burning loblolly pine forest for Red-cockaded Woodpeckers had on Wood Thrushes. We chose two compartments (one experimental and one control) within a broader seven-compartment study (three experimental and four control) to conduct our telemetry operations in (Powell et al. 2000). Although other portions of our research were replicated (see Powell et al. 2000), sample size requirements and field logistics prevented replication of our movement and habitat-use experimental units. We monitored Wood Thrush movements and habitat use for two years before silvicultural treatment (1993 and 1994 breeding seasons) and two years after silvicultural treatment (1995 and 1996 breeding seasons) on experimental compartments and concurrently for four years on control compartments (1993 to 1996 breeding seasons). Management compartments were our study units, and “experimental” or “control” refers to the treatment type. No thinning or burning was conducted on study compartments eight or more years before our study, with the exception of removing trees infested with the southern bark beetle (*Dendroctonus frontalis*) to avoid outbreaks. Refuge managers thinned and burned stands within experimental compartments between September 1994 and April 1995. Piedmont National Wildlife Refuge has a fixed management plan so we were not able to choose our study compartments randomly. We maintained temporal controls to protect against errors of interpretation that could occur without a completely randomized design (Eberhardt and Thomas 1991). Whereas we only radio-tagged adults on one treatment and one control compartment, we radio-tagged juveniles on multiple compartments to increase our sample size, and pooled data within experimental and control compartments for comparisons of treatment effects.

Within each compartment we established two study plots, each 500 × 1,000 m (50 ha), containing two parallel transects 250 m apart, running lengthwise. We oriented the plots roughly perpendicular to streams and habitat gradients to give a fair repre-

sentation of vegetation types and silvicultural treatments.

FIELD METHODS

Capture.—We conducted field research from early April to September in 1993 to 1996. Three methods were employed to capture Wood Thrushes: systematic mist-netting, target-netting, and hand capture of juveniles. We used nets placed along our transect lines as our primary capture tool from May to July between sunrise and 1000 EST. To supplement our sample, we used 8 to 10 “target” mist nets near nests or in known territories, netting sunrise to 1000 EST and late afternoon until sunset. To help lure Wood Thrushes into target nets, we used decoys and playback calls. We captured juveniles as they fledged with a net or by hand. We attempted to document fidelity of second-year Wood Thrushes to a natal dispersal location by target netting for three to four days at several known juvenile dispersal locations (where radio-marked juveniles had first moved after leaving their nest site). We banded all birds with an aluminum federal band and placed radio transmitters on a subsample (Powell et al. 2000). More details on capture methods can be found in Powell et al. (2000).

Radio telemetry.—We attached radio transmitters (1.6 g, battery life ~45 days; Holohil Systems Ltd., Corp, Ontario, Canada) to adult male and female thrushes as equally as possible on one experimental and one control compartment (1993: 10 males, 3 females; 1994: 17 males, 15 females, 11 juveniles; 1995: 17 males, 15 females, 15 juveniles; 1996: 15 males, 15 females, 11 juveniles) using a thigh harness (Rappole and Tipton 1991, Powell et al. 1998, 2000). For juveniles, we adjusted the thigh harness loop size to obtain a proper fit, leaving room for growth. The 1.6 g transmitter is ~5% of Wood Thrush body weight ($n = 374$, $\bar{x}_{\text{adult}} = 46$ g, $SE = 0.2$; $n = 74$, $\bar{x}_{\text{fledgling}} = 40$ g, $SE = 1.1$). Although we assumed radios would not affect juvenile survival or behavior (Cochran et al. 1967, Cochran 1980, Rappole et al. 1989, Powell et al. 1998), we only radio-tagged half the juveniles from each nest. We marked adults in late-April to mid-June and marked juveniles throughout the season. We used a six-element truck-mounted antenna for general locations and a three-element hand-held antenna to determine exact locations. When we could not find marked birds from the ground, we used aerial telemetry to relocate them.

To map movements, we established a series of geographic reference points using a global-positioning system (GPS) receiver, differentially corrected, and recorded a daily distance and angle from a geographic reference point to a radio-marked Wood Thrush location. At each bird's location, we documented the canopy type (upland hardwood, riparian hardwood, pine, and co-dominant pine–hardwood

mix), and cover class (cover class: 1 to 10% cover = sparse, 11 to 33% cover = moderate, 34 to 100% cover = dense), most abundant midstory species and midstory cover class (2 m to canopy), and understory cover class (ground to 2 m) within a 10 m radius of the Wood Thrush's location.

Study plot habitat sampling.—From 1993 to 1996, we measured vegetation on all study plots in late July and early August, while plants were in full foliage, at 40 m intervals along our study plot transects. Within a 10 m radius at each interval, we recorded canopy type; the most abundant midstory species; and cover class of overstory, midstory, and understory. We also measured basal area of softwoods and hardwoods (10-basal area factor prism), vertical cover ≤ 2 m (density board with 20 rows and 5 columns of 100 cm² squares), and canopy cover (concave densiometer).

STATISTICAL METHODS

Daily location.—We used adult and juvenile daily telemetry locations to calculate their distances from the nest and used that parameter to test our hypotheses about changes in Wood Thrush daily activity. We used a three-factor linear model (PROC GLM; SAS Institute 1990) to examine whether average daily distance from the nest differed between time (pre-treatment [1993, 1994] and post-treatment [1995, 1996]), treatment (experimental and control), or their interaction. Factors included time, treatment, and individual Wood Thrush (nested within time and treatment classes). We used sums-of-squares appropriate for unbalanced designs (SAS Institute 1990; type III model) and the mean-square for the individual as the error term to test for time and treatment effects. We used Satterthwaite's adjustment to estimate appropriate degrees-of-freedom (Milliken and Johnson 1984). We used a two-factor linear model to test for differences in daily distance from the nest between sexes (adults only), and the mean-square for the individual as the error term to test for differences between sexes. For adults, only observations of individuals >20 m from the nest were included in those analyses. We considered any observations of adults ≤ 20 m from the nest to be "at the nest" for our analyses because those birds were not foraging or engaged in territorial defense (L. A. Powell and J. D. Lang pers. obs.).

Additionally, we present the difference of the mean differences between experimental and control compartments ($\bar{x}_{\text{experimental before silviculture}} - \bar{x}_{\text{control before silviculture}}$) - ($\bar{x}_{\text{experimental after silviculture}} - \bar{x}_{\text{control after silviculture}}$) and their 95% confidence intervals. Positive confidence intervals represent greater movement on control compartments, negative confidence intervals represent greater movements on experimental compartments, and confidence intervals overlapping zero are not different from one another.

Adult within-year emigration.—Using program SURVIV (White 1983), we estimated weekly binomial probability of adults leaving the study compartments (~ 400 ha each) as a measure of within-year emigration (ψ). Using the log-odds ratio approach (White and Garrott 1990) we estimated α_i , the relationship between experimental and control compartment emigration, before and after treatment. That is equivalent to testing time \times treatment interaction in an optimal impact study design (Green 1979) when replications are not available (Eberhardt and Thomas 1991; E = experimental, C = control; B = before treatment, A = after treatment):

$$\alpha_B = \log\left(\frac{\psi_E^B}{\psi_C^B}\right) \quad \alpha_A = \log\left(\frac{\psi_E^A}{\psi_C^A}\right)$$

Because estimates of emigration were independent, we used a z-test to detect a change in α_i after silvicultural treatment.

Female inter-nest movements and juvenile movements.—We used distances moved (1) by females between consecutive nesting attempts, (2) by adults during emigration from study compartments (we define emigration as any movement away from our study compartments, including inter-nest movements of adult males and females, as well as postbreeding movements before migration), and (3) by juveniles dispersing from the nest site to estimate probability of female inter-nest movements, adult emigration distances, and juvenile dispersal distances among several distance intervals. We used a 1,000 sample bootstrap simulation (Buckland et al. 1993) to reduce bias of estimates of movement and associated confidence intervals. We define adult within-year dispersal as any movement away from a nesting area during the breeding season, before migration. And, for our study we define juvenile dispersal as a large-scale movement (>700 m) from the capture site, usually the nest, without returning. We chose 700 m because we never observed a juvenile returning after moving 700 m away from their capture site. Our documentation of juvenile dispersal should not be confused with natal dispersal, defined as movement from the birth site to the area where reproduction is first attempted (Greenwood and Harvey 1982). We used a linear model (PROC GLM; SAS Institute 1990) to detect an experimental effect (time \times treatment interaction) on female inter-nest movements, adult emigration distances, juveniles' time to dispersal, and juvenile dispersal distances. Additionally, we tested juvenile predispersal movements (daily locations), distance from capture site, and distance from initial dispersal location for a silvicultural treatment effect (time \times treatment interaction) using a three-factor ANOVA. Factors included treatment, time, and individual juvenile (nested within treatment and time classes). We pooled 1995 and 1996 data for after-dispersal tests.

HABITAT

Vegetative changes due to silvicultural treatment.—We used PROC GLM (SAS Institute 1990) to test for an effect of silviculture (time \times treatment interaction) on basal area, canopy cover, and mid- and understory foliage density.

Habitat preference: Adult and juvenile.—We estimated habitat preference with compositional analysis (Aebischer et al. 1993), and we used a MANOVA model to test for a silvicultural treatment effect on habitat use versus abundance (time \times treatment interaction; J. Bittle pers. comm.). Although canopy cover types did not change throughout the study, we used a year-specific estimate of habitat abundance to reduce observer bias. Habitat preference was calculated as the log-ratio of habitat use (proportion of times found in each vegetation type) to habitat abundance (proportion of study area with each vegetation type). Positive values indicate a preference (i.e. higher use than abundance) for a vegetation type. We used t values to detect significant differences among ranked vegetation types at $\alpha \leq 0.05$. Because females were often at the nest, we used males only for our adult habitat-preference analysis.

Habitat use comparisons: Juvenile.—We used log-linear models, within PROC CATMOD (SAS Institute 1990), to compare use of overstory type and over-, mid-, and understory percentage cover classes for silvicultural treatment effects, individual effects (nesting individuals within test groups), and differences in years both before and after dispersal. Using chi-square tests, we compared use of midstory species between random sites and juvenile locations before dispersal, use before and after dispersal, and use on treated to nontreated sites. For all of our analyses, we considered $\alpha \leq 0.05$ statistically significant.

RESULTS

MOVEMENTS

Adult daily location.—Males ranged farther from the nest (maximum distance, 624 m) than females (maximum distance, 539 m). Excluding "at nest" locations, females (least-squared mean, all years pooled = 135.6 m, $n = 45$, SE = 9.1) tended to be located farther from nest sites than males (least-squared mean = 106.9 m, $n = 41$, SE = 7.4; $P = 0.12$). Females were at the nest during 70% (95% CI: 67–73%) of our observations, and males only 36% (95% CI: 33–40%; $\chi^2 = 193.2$, $df = 1$, $P = 0.001$). Males and females were found <100 m from the nest during approximately 50–60% of all observations (Fig. 1).

Adult within-year emigration.—We recorded 63 instances of male and female emigration from

study compartments (including known re-nesting locations); the mean distance dispersed between nests or after the end of the nesting period was 3,353 m ($n = 63$, SE = 452). Most adults made two to three movements of ≥ 1 km throughout the breeding season. Male and female Wood Thrushes had similar rates of within-year emigration (Table 1; $\chi^2 = 0.309$, $df = 4$, $P = 0.98$). About 30% of adults moved <1 km and about 20% moved 1 to 2 km; Wood Thrushes emigrated up to 17 km from our study sites (Fig. 2A).

Female movements between nests.—Within a breeding season, females moved from 1–17,388 m (median = 251 m) between nest sites (Fig. 2B). In all cases except one, radio-tagged pairs remained together during movements to re-nest, including five nesting attempts by one pair. Most females (~80%) moved <1 km to re-nest (Fig. 2B). We found no differences in the distances moved by females when re-nesting after successful or failed nesting attempts ($F = 1.92$, $df = 1$ and 36, $P = 0.17$; successful: $n = 8$, $\bar{x} = 424$ m, SE = 343; failed: $n = 30$, $\bar{x} = 1130$ m, SE = 364).

Juvenile movements and dispersal.—The average predispersal daily movements were 131 m in 1994 ($n = 9$, SE = 10), 208 m in 1995 ($n = 15$, SE = 10), and 117 m in 1996 ($n = 10$, SE = 15). Juvenile dispersal occurred between three and four weeks after fledging ($n = 24$, $\bar{x} = 24.5$ days, SE = 6.27). There was a trend toward dispersing later in 1995 than in 1994 or 1996 ($F = 3.43$, $df = 2$, $P = 0.06$; 1994 $n = 4$, $\bar{x} = 22.0$ days, SE = 1.47; 1995 $n = 9$, $\bar{x} = 28.2$ days, SE = 2.72; 1996 $n = 6$, $\bar{x} = 20.2$ days, SE = 2.34). Three juveniles did not disperse, 1 in each 1994, 1995, and 1996. Average dispersal distance for juveniles was 2,189 m ($n = 34$, SE = 342). Juvenile dispersal probabilities were bimodal, with probabilities of dispersing 0 to 1 km (~35%) and 1 to 2 km (~30%) higher than all other categories except 4 to 5 km (~20%, Fig. 2C).

After dispersal, juveniles remained within 172 m in 1994 ($n = 8$, SE = 47), 360 m in 1995 ($n = 8$, SE = 33), and 390 m in 1996 ($n = 6$, SE = 40) of their dispersal location, until transmitter battery failure. However, three juveniles made a second long-distance movement (~5 km) 18 to 20 days after dispersal. The farthest distance traveled by a juvenile was 6,524 m. The average daily distance moved was 140 m ($n = 35$, SE = 9).

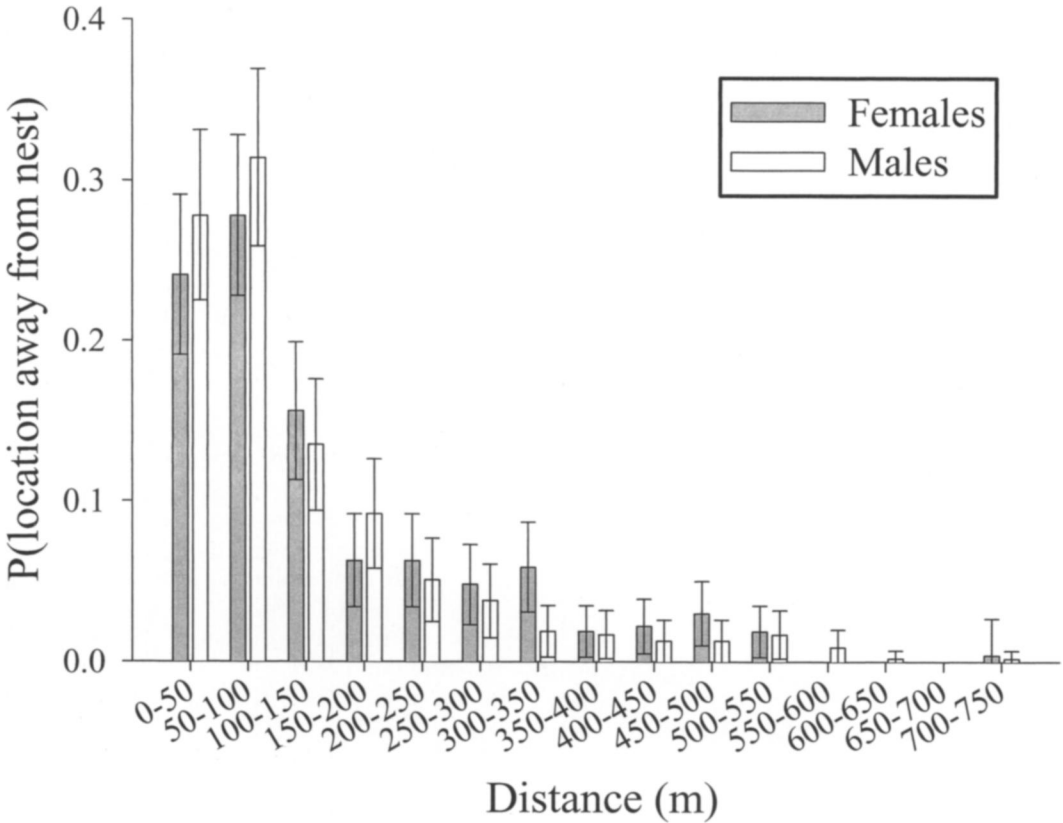


FIG. 1. Distances male and female Wood Thrushes were found from the nest during daily telemetry locations at the Piedmont National Wildlife Refuge, central Georgia, during 1993 to 1996 breeding seasons.

We did not recapture any second-year birds returning to their juvenile dispersal areas. We recaptured two second-year Wood Thrushes banded as hatch-year birds on our study plots.

One second-year male was recaptured 3,600 m from his initial capture location and one second-year female was recaptured within 300 m of her original capture location.

TABLE 1. Estimates and SE of weekly emigration (probability of leaving ~400 ha study compartment) for 63 adult male and female Wood Thrushes on experimental^a and control compartments at the Piedmont National Wildlife Refuge, central Georgia, during two time periods, 1993 to 1994 (before silvicultural treatment) and 1995 to 1996 (after silvicultural treatment). Sex-specific model was selected by likelihood ratio test and AIC comparison. Estimates and SE of α , a relationship between experimental and control emigration (Ψ), are given for each time period.

Sex	Time	Experiment Ψ (SE)	Control Ψ (SE)	α^b (SE)	$\alpha\bar{x}_{before} - \alpha\bar{x}_{after}$ (CI)
Male	Before	0.150 (0.095)	0.055 (0.061)	1.113 (0.904)	
Male	After	0.084 (0.047)	0.119 (0.068)	-0.390 (0.758)	1.503 (-0.809 to 3.815)
Female	Before	0.162 (0.066)	0.070 (0.050)	0.948 (0.910)	
Female	After	0.083 (0.032)	0.130 (0.043)	-0.511 (0.454)	1.459 (-0.534 to 3.452)
Pooled	Before	0.156 (0.044)	0.060 (0.027)	1.056 (0.575)	
Pooled	After	0.083 (0.021)	0.125 (0.030)	-0.452 (0.318)	1.508 (0.220 to 2.769)

^a Experimental compartments received thinning and burning for Red-cockaded Woodpecker management (silvicultural treatment) between the 1994 and 1995 breeding seasons, whereas control compartments remained untreated.

^b $\alpha = \log(\Psi_e/\Psi_c)$.

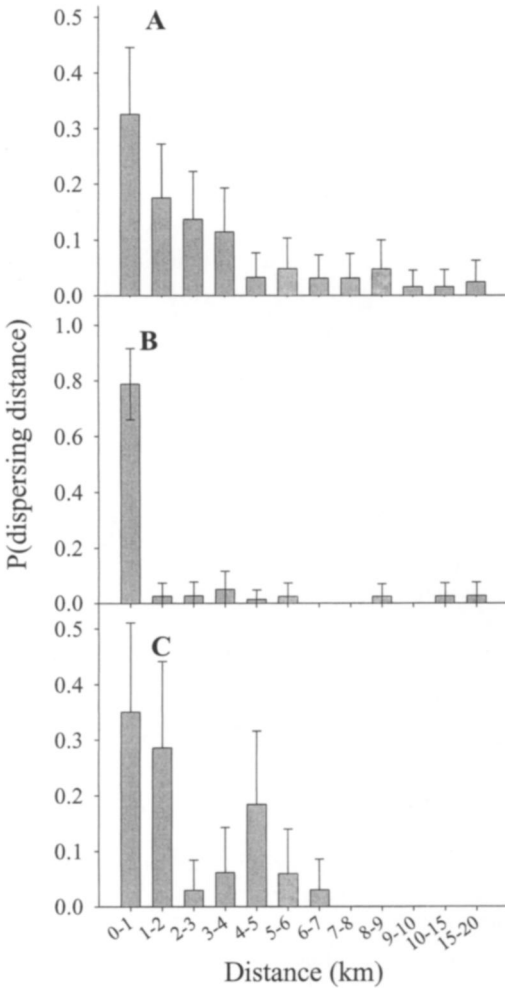


FIG. 2. Distances moved by (A) adults emigrating from a study compartment, (B) renesting females, and (C) dispersing juveniles at the Piedmont National Wildlife Refuge, central Georgia, during 1993 to 1996 breeding seasons.

HABITAT USE AND PREFERENCE

Adult males.—We observed 68 adult radio-tagged males from 0 (never relocated after release) to 111 days after marking (remarked once; mean monitoring interval = 39 days). Adult male Wood Thrushes used all forest overstory vegetation types at Piedmont National Wildlife Refuge (Table 2). In general, we found adult males most often in sparse or moderate forest vegetation (Table 2). Rank of habitat use versus habitat abundance for adult male Wood Thrushes was riparian hardwood (RH) > upland hardwood (UH) > pine and riparian

TABLE 2. Overstory, midstory (2 m to below canopy layer) and understory (0–2 m) habitat use (%) by radio-marked adult male Wood Thrushes at the Piedmont National Wildlife Refuge, central Georgia, during two time periods, 1993 to 1994 (before silvicultural treatment*) and 1995 to 1996 (after silvicultural treatment). Canopy type: Pine = P, riparian hardwood = RH, upland hardwood = UH; percent cover class: 1 to 10% = sparse, 11 to 33% = moderate (mod), 34 to 100% = dense.

Time	Year	Canopy type				Midstory				Understory					
		P	P/RH	P/UH	RH	UH	Sparse	Mod	Dense	Sparse	Mod	Dense			
Before	1993	21	2	38	1	37	71	20	9	83	15	2	—	—	—
Before	1994	40	11	17	15	16	11	56	33	44	48	8	41	35	23
After	1995	32	14	15	20	18	36	41	23	79	19	2	49	35	16
After	1996	16	12	40	18	15	60	33	6	94	4	2	55	31	14

* Silvicultural treatment, thinning and burning for Red-cockaded Woodpecker management, was conducted between the 1994 and 1995 breeding seasons.
 † Data not available.

hardwood mix (P/RH) > pine and upland hardwood mix (P/UH) > pine (P). Adult males exhibited significant preferences for RH over P/UH ($P = 0.02$) and UH over P/UH ($P = 0.01$).

Juveniles.—We observed 28 radio-tagged juveniles from 3 to 27 times (mode = 15) before dispersal. Juvenile rank habitat use versus habitat abundance was P/UH > P/RH > RH > P > UH, with P/UH significantly preferred and UH significantly underutilized ($P < 0.05$). Juveniles preferred moderate overstory (>2 m) percentage cover class (11–30%), and avoided sparse (0–10%) overstory ($P < 0.05$). Juveniles used more dense overstory percentage cover in 1995 and 1996 ($F = 7.45$, $df = 6$ and 42 , $P < 0.001$) than in 1994. Of the three most common midstory tree species (dogwood, sweetgum, and loblolly pine), juveniles used areas with dogwood more frequently than expected ($\chi^2 = 77.8$, $df = 2$, $P = 0.001$).

SILVICULTURAL EXPERIMENT

Vegetation changes.—The stands on experimental compartments selected for pine thinning and hardwood removal had different vegetative structure than other portions of the study compartments. Thinned areas had higher basal area of softwoods ($15.7 \text{ m}^2 \text{ ha}^{-1}$ [average basal area in 1994 and 1995, prethinning and post-thinning] vs. $10.0 \text{ m}^2 \text{ ha}^{-1}$ [1994 and 1995, areas not thinned], $F = 39.2$, $df = 1$ and 603 , $P < 0.001$), less basal area of hardwoods ($4.1 \text{ m}^2 \text{ ha}^{-1}$ vs. $10.9 \text{ m}^2 \text{ ha}^{-1}$, $F = 64.5$, $df = 1$ and 607 , $P < 0.001$), less canopy density ($F = 56.62$, $df = 1$ and 595 , $P < 0.001$), and less dense understorey (0–0.3 m: $F = 11.13$, $df = 1$ and 600 , $P < 0.001$; 1–2 m: $F = 4.57$, $df = 1$ and 605 , $P = 0.03$) than not-thinned forest areas. We did not detect an effect of our treatment on softwood basal area, but we did find hardwood basal area was significantly reduced on treated compartments (Powell et al. 2000). Thinning decreased percentage canopy cover (time \times treatment interaction, $F = 15.24$, $df = 1$ and 595 , $P < 0.001$). We also found evidence of understorey percentage cover (1–2 m) decreasing due to thinning (time \times treatment interaction, $F = 2.96$, $df = 1$ and 605 , $P = 0.09$). Midstory cover tended to increase on treated compartments (Powell et al. 2000). In 1995, after burning, average diameter at breast height (DBH) on

burned areas was greater than nonburned areas of experimental compartments (16.1 vs. 12.8 cm, $F = 19.14$, $df = 1$ and 417 , $P < 0.001$). For details of treatment effects on the vegetation, please see Appendices A and B.

Some areas of Piedmont National Wildlife Refuge have been burned repeatedly because of their proximity to good fire breaks; other areas within compartments may never receive burning. During all years, the historically burned areas of experimental compartments had less hardwood basal area ($\bar{x} = 6.3$ vs. $11.1 \text{ m}^2 \text{ ha}^{-1}$, $F = 40.0$, $df = 1$ and 607 , $P < 0.001$), less dense understorey, 0–30 cm ($F = 16.7$, $df = 1$ and 600 , $P < 0.001$) and 30–50 cm ($F = 17.5$, $df = 1$ and 605 , $P < 0.001$), and less canopy volume ($F = 9.03$, $df = 1$ and 595 , $P = 0.003$) than areas on experimental compartments not historically burned.

Adult movements.—We did not detect a difference in adult Wood Thrushes daily distance from the nest among years (female: $F = 0.241$, $df = 1$ and 55 , $P = 0.78$; male: $F = 0.470$, $df = 1$ and 51 , $P = 0.54$) or between experimental and control compartments (female: $F = 0.030$, $df = 1$ and 58 , $P = 0.86$; male: $F = 0.063$, $df = 1$ and 53 , $P = 0.80$), but distance varied among individual males ($F = 5.831$, $df = 32$ and 372 , $P < 0.001$) and females ($F = 2.644$, $df = 33$ and 193 , $P < 0.001$). We also found no treatment effect on daily distances moved by adults (Table 3; time \times treatment interaction; females: $F = 2.240$, $df = 2$ and 56 , $P = 0.11$, males: $F = 0.791$, $df = 2$ and 51 , $P = 0.45$). The mean difference between experimental and control compartments in daily distance moved was not different from zero (males: $\bar{x}_{\text{before-after 1995}} = -16 \text{ m}$ (95% CI: -114 to 82), $\bar{x}_{\text{before-after 1996}} = 55 \text{ m}$ (95% CI: -38 to 148); females: $\bar{x}_{\text{before-after 1995}} = -33 \text{ m}$ (95% CI: -145 to 79), $\bar{x}_{\text{before-after 1996}} = 89 \text{ m}$ (95% CI: -16 to 194)).

After thinning and burning, weekly probability of leaving a study compartment increased on control compartments and decreased on experimental compartments for both sexes combined (pooled sexes: $z = 2.295$, $P = 0.02$). We found no difference in females' inter-nest movements between experimental and control compartments from 1994 to 1996 ($F = 2.79$, $df = 1$, $P = 0.10$) or due to the treatment (time \times treatment interaction, $F = 0.69$, $df = 1$, $P = 0.41$).

TABLE 3. Least-squared mean^a daily distance (m) of male ($n = 41$ individuals, 474 daily observations) and female ($n = 45$ individuals, 269 daily observations) Wood Thrushes from their nest site at the Piedmont National Wildlife Refuge, central Georgia, during two time periods, 1994 (before silvicultural treatment) and 1995 to 1996 (after silvicultural treatment).

Time	Year	Treatment	Male		Female	
			\bar{x}	SE	\bar{x}	SE
Before	1994	Pooled	111	19	113	20
After	1995	Pooled	126	13	143	15
After	1996	Pooled	91	10	143	13
Before	1994	Experimental	142	38	132	41
After	1995	Experimental	135	13	153	22
After	1996	Experimental	81	10	109	19
Before	1994	Control	121	18	108	24
After	1995	Control	98	24	96	26
After	1996	Control	115	19	174	19

^a Milliken and Johnson 1984.

Juvenile movements.—We detected no experimental effect on predispersal movements (time \times treatment interaction, $F = 2.49$, $df = 1$ and 29.61 , $P = 0.12$). Juvenile predispersal movements did differ among experimental and control compartments ($F = 9.26$, $df = 1$ and 30.69 , $P = 0.005$) and among years ($F = 8.92$, $df = 1$ and 30.86 , $P < 0.001$). In 1995, we located juveniles on treated compartments farther from their capture site than all other years and compartments (Table 4; $\bar{x}_{\text{before-after 1995}} = -105$ m (95% CI: -177 to -33)). We did not detect a difference in number of days to dispersal, among experimental and control compartments ($F = 0.11$, $df = 1$, $P = 0.74$), or due to the treatment (time \times treatment interaction, $F = 2.57$, $P = 0.13$). We also found no difference in juvenile dispersal distances between experimental and control compartments ($P = 0.67$), among years ($P = 0.25$), or in relation to treatment (time \times treatment interaction, $P = 0.25$). And, we did

not find any differences in postdispersal movement between time (before or after silvicultural treatment; $F = 2.71$, $df = 2$ and 23.89 , $P = 0.11$), between study units (experimental and control, $F = 0.009$, $df = 1$ and 23.37 , $P = 0.92$) or related to treatment (time \times treatment interaction, $F = 0.005$, $df = 1$ and 23.9 , $P = 0.94$).

Adult male habitat use.—We did not detect an effect of time (before and after treatment; $F = 0.90$, $df = 4$ and 53 , $P = 0.46$) or experimental and control designation ($F = 1.11$, $df = 4$ and 53 , $P = 0.36$) on vegetation type used. However, there was a trend toward an interaction between time and treatment ($F = 2.10$, $df = 4$ and 53 , $P = 0.09$, Table 2). Adults did use thinned pine habitats and burned areas after treatment for foraging and nesting (Table 2). But, adult males tended to use burned or thinned pine overstory on experimental compartments less after treatment (Fig. 3A) and used riparian hardwood overstory (none thinned, some

TABLE 4. Mean distance radio-tagged juvenile Wood Thrushes were found from their capture site, before dispersal, at the Piedmont National Wildlife Refuge, central Georgia, during the 1994 (before silvicultural treatment) and 1995 to 1996 (after silvicultural treatment) breeding seasons.

Time	Year	Treatment type ^a	Mean distance from capture site (m) ^b	SE	n
Before	1994	Control	97	19	3
After	1995	Control	161	11	8
After	1996	Control	— ^c	—	—
Before	1994	Experimental	140	16	3
After	1995	Experimental	309	25	5
After	1996	Experimental	117	15	10

^a Experimental compartments received thinning and burning for Red-cockaded Woodpecker management (silvicultural treatment) between the 1994 and 1995 breeding seasons, whereas control compartments remained untreated.

^b Least-squares means (Milliken and Johnson 1984).

^c No nests survived.

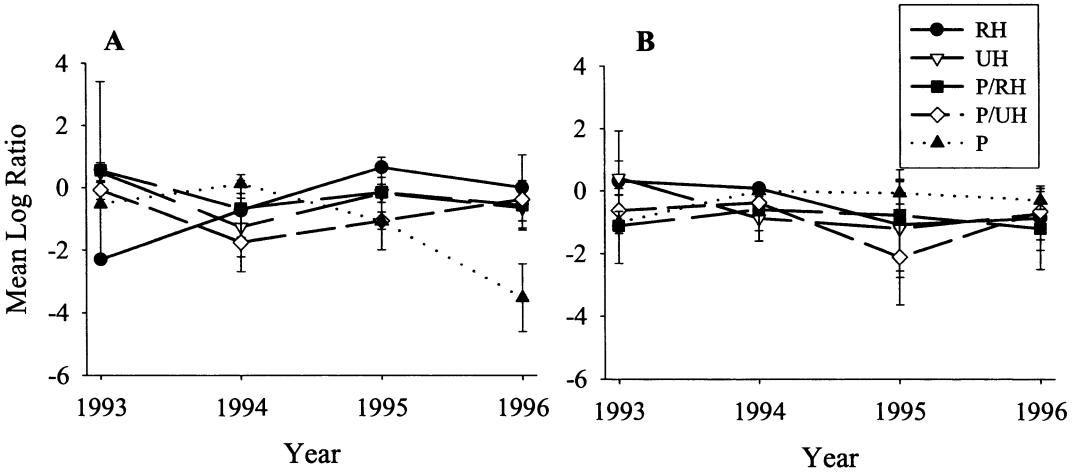


FIG. 3. Log-ratios (proportion used/habitat abundance) for five overstory types used by adult male radio-tagged Wood Thrushes on (A) experimental and (B) control compartments during 1993, 1994 (presilvicultural treatment) and 1995, 1996 (postsilvicultural treatment) at Piedmont National Wildlife Refuge, central Georgia. Positive values indicate preference for an overstory type (used in greater proportion than its abundance). Vertical bars represent 95% confidence intervals. (P = pine, RH = riparian hardwood, UH = upland hardwood, P/(RH or UH) = mix).

burned) more after treatment (Fig. 3A). On control compartments, Wood Thrush preference for pine overstory remained consistent and riparian hardwood overstory preference declined (Fig. 3B).

Juvenile habitat use.—Juveniles used different overstory types among study compartments ($F = 3.221$, $df = 5$ and 19 , $P = 0.02$; Fig. 4) and

years ($F = 2.369$, $df = 10$ and 38 , $P = 0.02$), but we did not detect an experimental effect (time \times treatment interaction, $F = 1.2$, $df = 5$ and 19 , $P = 0.34$). We found no differences in use of overstory percentage cover class between experimental and control compartments ($F = 1.427$, $df = 3$ and 21 , $P = 0.26$) or due to the treatment (time \times treatment interaction, $F =$

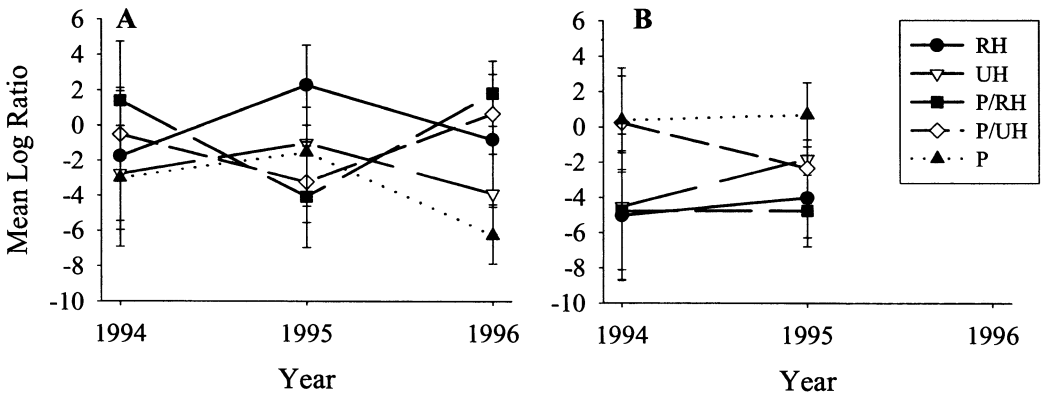


FIG. 4. Log-ratios (proportion used/habitat available) for five overstory types used by radio-tagged juvenile Wood Thrushes on (A) experimental and (B) control compartments at Piedmont National Wildlife Refuge, central Georgia, during 1994 (presilvicultural treatment) and 1995, 1996 (postsilvicultural treatment) breeding seasons. Positive values indicate preference for an overstory type (used in greater proportion than its abundance). Vertical bars represent 95% confidence intervals. No nests survived to allow radio-marking on control compartments in 1996. (P = pine, RH = riparian hardwood, UH = upland hardwood, P/(RH or UH) = mix).

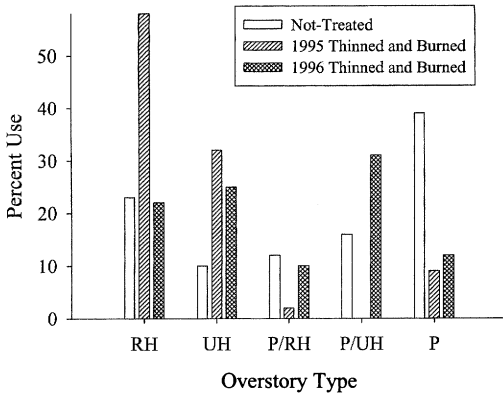


FIG. 5. Overstory type and percentage use by radio-tagged Wood Thrush juveniles after dispersal from treated and not-treated study sites during 1994 to 1996 breeding seasons, central Georgia. Not-treated sites include experimental compartments before silvicultural treatment. Juveniles from experimental compartments in 1995 and 1996 used significantly different habitat and could not be pooled. (P = pine, RH = riparian hardwood, UH = upland hardwood, P/(RH or UH) = mix).

0.583, $df = 3$ and 21 , $P = 0.63$). We detected no differences in understory (0–2 m) percentage cover class preferred ($P > 0.05$), between experimental and control compartments ($F = 0.33$, $df = 3$ and 22 , $P = 0.80$), among years ($F = 2.217$, $df = 3$ and 22 , $P = 0.11$), or due to silvicultural treatment (time \times treatment interaction, $F = 0.601$, $df = 3$ and 22 , $P = 0.62$).

During post-treatment years (1995 and 1996), juveniles from experimental compartments dispersed to areas with hardwood overstory type more frequently than to areas with pine ($\chi^2 = 40.72$, $df = 2$, $P < 0.001$; Fig. 5) and with dense overstory cover ($\chi^2 = 46.46$, $df = 2$, $P < 0.001$; Fig. 6A). We did not detect a difference in the percentage cover class of midstory ($\chi^2 = 2.06$, $df = 2$, $P = 0.35$; Fig. 6B) or understory ($\chi^2 = 0.26$, $df = 2$, $P = 0.87$; Fig. 6C) used by juveniles after dispersing from treated sites.

DISCUSSION

ADULTS

Songbird breeding-season dispersal distances are probably much greater than indicated by currently available data. Current understandings of breeding-season dispersal are based on an unrepresentative sample because, to date,

most dispersal distances have been estimated using mark-recapture methods (Opdam 1991, Haas 1995, Villard et al. 1995) or mark-resighting (Roth et al. 1996). Our radio-marked adult Wood Thrushes each made two to three long-distance movements, challenging the dogma that all Nearctic–Neotropical migrant bird dispersals during the breeding season are short because of the need to retain territories on a yearly basis (Villard et al. 1995). We recaptured several adults in close proximity (17 of 25 returns were between <100–500 m) to their capture location the previous, but other adults may have returned to locations off our study plots where they had emigrated for second or third nesting attempts during the previous year. We may have even underestimated breeding-season movements if some birds emigrated beyond our aerial telemetry search area. Because adults moved farther than juveniles during the breeding season, our movement data suggest adult dispersal may contribute more to overall dispersal within a population than previously thought (Greenwood and Harvey 1982).

In our study, conducted in contiguous forest habitat, radio-marked Wood Thrush pairs sometimes traveled several kilometers between consecutive nest locations within the same breeding season. Our data contrast with movement data of Wood Thrushes in fragmented habitats, where breeding pairs usually remained in a small woodlot during the entire breeding season (Roth et al. 1996). Rappole et al. (1989) reported long-distance movements (>1.0 km) in undisturbed wintering ground habitats that are similar to our findings on breeding grounds. Therefore, fragmentation may serve as an impediment to Wood Thrush dispersal movements during the breeding season or winter. On fragmented breeding grounds, where a 15 ha woodlot is a large forest fragment, there may be fewer nesting territories to choose from and a stronger incentive to stay or return to that area to nest. At Piedmont National Wildlife Refuge, which is ~14,000 ha of contiguous forest, it may be more profitable for Wood Thrushes to move 1 to 2 km when reneesting or choosing a territory on return migration flights.

We did follow some Wood Thrush pairs from contiguous forest of Piedmont National Wildlife Refuge to fragmented forests or residential areas. Predation events may have induced these

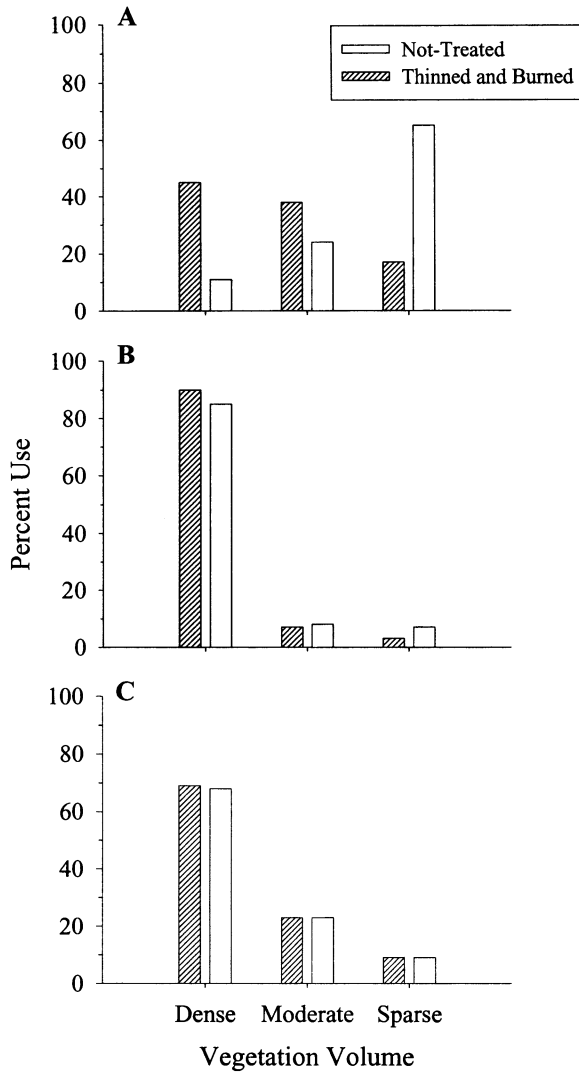


FIG. 6. Percentage cover (1 to 10% = sparse, 11 to 33% = moderate, 34 to 100% = dense) of (A) over-, (B) mid-, and (C) understorey used by radio-tagged Wood Thrush juveniles after dispersal from treated and not-treated study sites during the 1994 to 1996 breeding seasons, central Georgia. Not-treated sites include experimental compartments before silvicultural treatment.

long distance movements, or possibly the only available nesting territories were in the fragmented habitat (Jackson et al. 1989). We did not collect data to test territory availability, but lack of availability seems unlikely. Jackson et al. (1989) predicted avian pairs will disperse together if desired nesting habitat is unoccupied by competitors and most pairs we followed dispersed together. Though predation could have played a role, we did not observe pairs moving farther after a failed nesting attempt. There

may be a selective advantage to disperse, even when the first nest attempt is successful, if nest predators are present (Powell and Frasch 2000).

It is also possible placing radios on the adults caused the long distance movements. That seems unlikely though because adults did not emigrate immediately after attaching the radios, and there is no evidence that transmitters affect thrush behavior (Cochran et al. 1967, Rappole et al. 1989, Powell et al. 1998). Also, Krementz and Christie (2000), marking only

with leg bands, recaptured 11 individuals (six different species) emigrating from one stand to another within a breeding season. Some of those individuals traveled over 14 km. Perhaps long-distance dispersals by adults within a breeding season are common, but go undetected because of difficulty of documenting such movements.

Documenting changes in movement and habitat use can be critical to understanding population dynamics of a species of concern in a management context and should be considered when conducting population viability analyses. Because birds may encounter different hazard rates when moving to new areas, large-scale movement data for adults and juveniles is important for construction of spatially based avian population models (Conroy et al. 1995). Commonly, avian researchers consider study plots of close proximity independent study units. In those situations, movements of study organisms between plots could confound unit-specific demographic parameter estimates or mask effects of vegetative differences. For biologists conducting research in large forest tracts, movement patterns observed in our study could decrease ability to recapture marked individuals within a breeding season or on return flights, creating a strong negative bias in annual return rates. Our results indicate movement should not be ignored when assessing the source-sink status of a population. For example, Donovan et al. (1995) assumed that adults and juveniles were habitat faithful (returned to same source or sink habitat from year to year, and remained there). Wood Thrushes at Piedmont National Wildlife Refuge violated that assumption, because both adults and juveniles generally left the compartment in which they began the season. The probability of a female staying 20 weeks (the entire breeding season) on one Piedmont National Wildlife Refuge compartment was <20% (Table 1). Therefore, most Wood Thrushes presently use more than one ~400 ha forest-management compartment each year (or leave the refuge). From a conservation perspective, it is important to include surrounding public and private land in the management plan because those lands are also used by birds nesting on refuge property.

JUVENILES

Fledglings stayed near the nest, parents, and siblings for ~25 days, similar to patterns for

Wood Thrushes documented by others (Brackbill 1943, Knopf 1974, Nolan 1974, Anders et al. 1998, Vega Rivera et al. 1998). Juvenile average dispersal distance (2.2 km) was also similar (Anders et al. 1998, Vega Rivera et al. 1998), but juveniles at Piedmont National Wildlife Refuge dispersed in random directions (J. D. Lang unpubl. data) rather than traveling south (Anders et al. 1997) or to a juvenile grouping site (Vega Rivera et al. 1998). In Eastern Bluebirds (*Sialia sialis*), another member of the thrush family (Turdidae), female natal dispersal distances were greater than males (Plissner and Gowaty 1996). Our bimodal juvenile dispersal data (Fig. 2C) could result from a similar trend, although we were unable to identify sex of nondimorphic juvenile Wood Thrushes (Pyle et al. 1987) and were unable to recapture second-year birds where we had radio-tracked them during juvenile dispersal.

Vegetation type used by juveniles after dispersal (often off Piedmont National Wildlife Refuge) was similar to that used on the refuge before dispersal, with greater use of hardwoods. Although juvenile use of denser under- and midstory, and moderate overstory (Fig. 6) corresponds to Brackbill's (1943) findings, it is possible dispersing juveniles chose their habitat based on what was present at their natal site.

SILVICULTURAL EXPERIMENT

Adult Wood Thrushes were less likely to leave experimental compartments after thinning and burning than before, but we detected no other effects of the treatment on adult movement parameters. Adult males exhibited some tendency to increase preference for hardwood habitats and decrease preference for pine habitats following treatment (Fig. 3). Changes in forest stand structure may have increased exposure to predators (Robinson 1988, Robinson et al. 1995) or decreased food supply (Conner and Rudolph 1991), possibly explaining observed decreases in preference for pine habitat on experimental compartments after silvicultural treatment.

Juvenile Wood Thrush movement patterns and habitat use varied by management compartment and year, but changed little in response to thinning and burning for Red-cockaded Woodpeckers. We did not detect an effect of treatment on dispersal times or distances.

But in 1995, fledglings on treated compartments ranged farther from their nest than in any other years or compartments (Table 4). That may have been a short-term response to silvicultural treatment, occurring only during breeding season immediately following thinning and burning. Because vegetation type and percentage cover used by juveniles did not change in 1995 (following treatment), juveniles may have ranged farther to find preferred habitat.

Before dispersing, fledglings at Piedmont National Wildlife Refuge used habitat in proportion to abundance, with juveniles on treated compartments preferring hardwood areas and juveniles on nontreated areas using more pine. After dispersal, that pattern continued—juveniles from treated compartments chose areas with hardwood overstory significantly more than areas with pine. That suggests habitat management at the natal site may affect choices made by juveniles during dispersal.

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APPENDIX A. Vegetation data from transects within control (C) and experimental (E) forest compartments used for radio-tagging Wood Thrushes at Piedmont National Wildlife Refuge, central Georgia, during pre-silviculture (1993, 1994) and postsilviculture (1995, 1996) years.

Forest compartment	Year	Study group	Canopy composition (%)					
			RH	UH	P/RH	P/UH	P	O ^a
12	1993	E	0	19.4	0	33.3	47.3	0
12	1994	E	8.8	16.2	7.8	29.4	37.3	0.5
12	1995	E	4.0	15.0	4.0	40.0	36.0	1.0
12	1996	E	4.0	19.0	1.0	29.0	46.0	1.0
25	1993	C	0.5	16.3	0.5	54.0	28.7	0
25	1994	C	16.7	14.2	8.8	21.1	38.7	0.5
25	1995	C	3.0	19.0	4.0	29.0	45.0	0
25	1996	C	1.0	14.0	6.0	65.0	14.0	0

Forest compartment	Year	Study group	Canopy density (%)			Mean basal area (SD)	
			0–9%	10–29%	>30%	Softwood (m ² ha ⁻¹)	Hardwood (m ² ha ⁻¹)
12	1993	E	15.2	37.3	47.5	9.9 (7.3)	8.4 (7.3)
12	1994	E	25.1	24.1	50.7	11.3 (8.0)	11.3 (8.0)
12	1995	E	13.0	24.0	63.0	11.3 (9.4)	9.7 (8.3)
12	1996	E	20.0	51.0	29.0	12.6 (8.5)	13.2 (9.5)
25	1993	C	6.9	60.9	32.2	10.9 (7.5)	9.5 (7.3)
25	1994	C	38.2	40.7	21.1	10.0 (7.2)	11.4 (8.2)
25	1995	C	9.0	39.0	52.0	10.7 (7.9)	12.3 (7.1)
25	1996	C	6.0	28.0	66.0	9.4 (6.9)	11.4 (7.3)

^a Open, other canopy compositions described in text.

APPENDIX B. Vegetation data from transects within control (C) and experimental (E) forest compartments used for radio-tagging Wood Thrushes at Piedmont National Wildlife Refuge, central Georgia, during pre-silviculture (1993, 1994) and postsilviculture (1995, 1996) years.

Forest compartment	Year	Study group	Mean canopy cover (SD)%	Mean horizontal cover (%)		
				0–30 cm	31–100 cm	101–200 cm
12	1993	E	0.95 (0.10)	0.65	0.49	0.52
12	1994	E	0.96 (0.10)	0.42	0.57	0.57
12	1995	E	0.92 (0.20)	0.34	0.54	0.60
12	1996	E	0.93 (0.13)	0.28	0.46	0.59
25	1993	C	0.94 (0.07)	0.64	0.45	— ^a
25	1994	C	0.96 (0.07)	0.39	0.55	0.54
25	1995	C	0.95 (0.07)	0.29	0.43	0.45
25	1996	C	0.96 (0.07)	0.19	0.37	0.39

^a Data not available.