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EFFECTS OF FOREST MANAGEMENT ON DENSITY, SURVIVAL, AND POPULATION GROWTH OF WOOD THRUSHES

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Abstract: Loss and alteration of breeding habitat have been proposed as causes of declines in several Neotropical migrant bird populations. We conducted a 4-year study to determine the effects of winter prescribed burning and forest thinning on breeding wood thrush (*Hylocichla mustelina*) populations at the Piedmont National Wildlife Refuge (PNWR) in Georgia. We estimated density, adult and juvenile survival rates, and apparent annual survival using transect surveys, radiotelemetry, and mist netting. Burning and thinning did not cause lower densities ($P = 0.25$); wood thrush density ranged from 0.15 to 1.30 pairs/10 ha. No radiomarked male wood thrushes ($n = 68$) died during the 4 years, but female weekly survival was 0.981 ± 0.014 (SE) for females ($n = 63$) and 0.976 ± 0.010 for juveniles ($n = 38$). Apparent annual adult survival was 0.579 (SE = 0.173). Thinning and prescribed burning did not reduce adult or juvenile survival during the breeding season or apparent annual adult survival. Annual population growth (λ) at PNWR was 1.00 (95% confidence interval [CI] = 0.32–1.63), and the considerable uncertainty in this prediction underscores the need for long-term monitoring to effectively manage Neotropical migrants. Population growth increased on experimental compartments after the burn and thin (95% CI before = 0.91–0.97, after = 0.98–1.05), while control compartment λ declined (before = 0.98–1.05, after = 0.87–0.92). We found no evidence that the current management regime at PNWR, designed to improve red-cockaded woodpecker (*Picoides borealis*) habitat, negatively affected wood thrushes.

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Biologists have generally relied on observed species-area relationships to investigate the effects of silviculture on songbird demography (McComb et al. 1989, Thompson et al. 1992, Wenny et al. 1993). Studies of species abundance provide little insight into the underlying causes of the decline unless demographic parameters also are determined (Van Horne 1983, Askins et al. 1990). Therefore, focus has shifted from estimating trends in abundance to estimating demographic parameters and movement rates (Roth and Johnson 1993, Martin 1995, Robinson et al. 1995, Anders et al. 1997). How-

ever, adult and juvenile survival in the breeding season has not been estimated for forest interior songbirds in management contexts, and density and demographic parameters have rarely been studied concurrently. Such information is critical for managers who must take appropriate actions to respond to present songbird population declines (Sauer and Droege 1992, Sauer et al. 1996).

Wildlife biologists are unable to manage any area for the benefit of all species, and even species of concern in a geographic area may have competing habitat needs (Lynch and Whigham 1984). In the southern Piedmont, loblolly pine (*Pinus taeda*) and other pine species are managed for late seral stages, in particular to provide suitable habitat for endangered red-cockaded woodpeckers (*Picoides borealis*). Management for red-cockaded woodpeckers typically includes (1) implementing a harvest schedule that allows long rotation (100 years) schedules,

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(2) thinning to reduce basal area of pine overstory, (3) reduction of hardwood midstory components, and (4) prescribed burning (Jackson et al. 1984, Richardson and Costa 1997). Despite the need for red-cockaded woodpecker management, managers are concerned that this management regime may degrade hardwood midstory and understory breeding habitats for some Neotropical migrant species by increasing predator abundance along habitat edges and increasing foraging distances (Lucas 1994).

We chose the wood thrush (*Hylocichla ustulata*) as a study species because (1) it nests in hardwood midstory and understory tree species (Roth et al. 1996), (2) it is large enough to carry a radiotransmitter (Powell et al. 1998), (3) it is abundant at our study site, most importantly in areas that were slated for red-cockaded woodpecker silviculture, and (4) it is a species of concern. North American Breeding Bird Survey (BBS) data show that wood thrush populations in eastern forests have declined 1.8% per year ($P < 0.001$) during 1966–95 (Sauer et al. 1996), with the most marked decline from 1978–88 (–4.1%, $P < 0.001$; Sauer and Droege 1992). Our objectives were to determine the effect of forest thinnings and prescribed winter burns on adult and juvenile survival and density of adult wood thrushes, and predict population growth rates.

METHODS

Study Area

We conducted this study from May 1993 to September 1996 at PNWR in the southern Piedmont of Georgia. The PNWR covers 14,146 ha of which 13,580 ha (96%) are forested in 34 400-ha management compartments. Forest acreage is principally (79%) pines (*Pinus* spp.), dominated by loblolly pine (*P. taeda*). Pine stands are classed by size as reproduction, pole-size, and saw timber. Additional types are pine-hardwood (*Quercus* spp., *Carya* spp., *Liriodendron tulipifera*) mix, bottomland riparian zones (henceforth bottomland hardwood), upland hardwood, and open field. Red-cockaded woodpecker management is a primary goal at PNWR. Managers use retention shelterwood silviculture to manage pine habitat with a rotation length of 80–100 years (Piedmont NWR 1983, Richardson and Costa 1997). Under this regime, a series of preharvest pine thins and winter prescribed burns are used to reduce

midstory and understory hardwood components in areas designated for nesting red-cockaded woodpeckers.

Experimental Design

The Refuge's thinning and burning rotation schedule was fixed, so we could not randomly choose our study compartments. We selected 3 compartments as experimental units and 4 as controls in anticipation of the onset of silviculture (the intervention) midway through the study. Experimental compartments were burned and thinned between the 1994 and 1995 field seasons. Control units were not burned or thinned during our study, or the previous 8 years except for small harvests for disease- or fire-prevention. Although our study groups could not be randomized, our design includes temporal (before–after) and spatial controls (control vs. experimental) and replication (except for survival as a response), as in an optimal impact study design (Green 1979:68–70). We selected the 5 compartments C-8 (364 ha), C-11 (412 ha), C-12 (369 ha), C-23 (364 ha), and C-25 (378 ha) for initial study during 1993–96. Managers on PNWR burned and thinned C-8 and C-12 during the winter of 1994–95 (C-8: 166 ha burned, 42 ha thinned; C-12: 130 ha burned, 38 ha thinned). Treatments were not completed on a third experimental compartment when required, so we added 1 new control compartment (C-24, 348 ha), and 1 new experimental compartment (C-31, 297 ha), in 1995. Compartment 31 was thinned in winter 1995–96 (0 ha burned, 199 ha thinned), 1 year later than C-8 and C-12. Because of this staggered entry of compartments, the sample size of experimental compartments in the density experiment declined from $n = 3$ for a first-year response to $n = 2$ for a second-year response.

Field Methods

Bird surveys, vegetation sampling, and capture of birds were conducted on 2 0.5- × 1.0-km rectangular plots located in each compartment. Plots were situated to bisect streams and habitat gradients and to assure sampling of all habitat types in each experimental and control compartment. Plots on experimental compartments were situated to include areas to be affected by thinning and burning. Two 1,000-m transect lines, located 125 m from the edges of the plot, served as the baselines for bird and vegetation sampling.

We surveyed all study plots 8 times during 1993 and 16 times annually during 1994–96 commencing in mid-May to avoid counting migratory birds. We conducted surveys from sunrise to 1000 hr on rain-free days by slowly walking transects, locating male wood thrushes by vocalizations, and pacing the perpendicular distance to the transect line. At least 1 experimental and 1 control compartment were surveyed each day, and we varied the starting point to avoid temporal detection biases (Robbins 1981).

We captured wood thrushes by 3 methods. First, we used 25 nets, systematically located 40 m apart along the 1-km transect lines on all study subplots, to obtain a representative sample from all habitats used by wood thrushes (Powell 1998). Nets were opened and checked for birds from sunrise to 1000 hr for 4 days, then moved to a new compartment. Second, we targeted 8–10 nets in known wood thrush territories from sunrise to 1000 hr and 1700–2100 hr until ≥ 1 birds were captured. We closed nets in the event of heavy rain, high winds, or temperatures $>30^{\circ}\text{C}$. Third, we captured juveniles by hand or with an insect net at the nest during fledging. In this paper, we refer to all hatch-year birds as juveniles.

We determined the age of each captured wood thrush by feather and beak morphology, and sex by the presence of a brood patch or cloacal protuberance (Pyle et al. 1987). We banded each bird with an aluminum U.S. Geological Survey, Biological Resources Division (BRD) leg band; during 1993–94 we also marked birds with individually color-coded plastic leg bands. We fit a subsample of banded adults and juveniles with 1.6-g Holohill Systems, radiotransmitters (battery life of 45 days) using thigh harnesses (Rappole and Tipton 1991). As a precaution against negatively affecting an entire brood (Rappole et al. 1989, Powell et al. 1998), we only radiomarked half of the juveniles in a nest.

We marked adults with transmitters on 1 experimental (C-12) and 1 control compartment (C-25), with radiomarked males and females distributed evenly between experimental and control compartments; thus, our inferences on survival effects are not based on replication. We deployed half the transmitters (10/compartment) for adults in a staggered manner beginning on 24 April, with the remaining half deployed in mid-June. We re-marked 9 pairs of adults (3 in 1995, 6 in 1996) during the breed-

ing season after battery failure. We radiomarked juveniles throughout the season, beginning in mid-May, and attempted to radiomark juveniles on C-12 and C-25. However, nest failures on C-25 prevented adequate samples of juveniles. Therefore, we added juveniles from other control compartments (3 on C-11, 5 on C-23, 2 on C-27) to increase the radiomarked sample (C-27 was not part of the original design, but fit the requirements of a control compartment). Radiomarked birds were periodically located from sunrise to sunset using triangulation from truck-mounted antennas, followed by visual location using hand-held antennas. We determined the status of thrushes by sight or by changes in signal strength. We used aerial telemetry to locate birds that had moved from the study compartments or the PNWR.

We collected vegetation data at 40-m intervals along transect lines during July–August each year. At each sample point we determined canopy cover type, 3 dominant midstory species, tree basal area (10-factor prism), and canopy closure (concave densiometer). We ocularly estimated density of understory (0–2 m) and midstory (2 m to below canopy) vegetation in percent classes. During 1995–96, we also measured canopy height, live crown height (clinometer), and average diameter of 8 random trees at each point.

Analytical and Statistical Methods

Bird Density.—We estimated bird density from the sample counts and distances with line transect models (Buckland et al. 1993) using a likelihood ratio test of compartment-specific encounter rates. We treated repeated surveys as recommended by Buckland et al. (1993:300–301). We used the bootstrap procedure to obtain a more robust estimate of variance for each compartment (Buckland et al. 1993:119–120). To test for an effect of red-cockaded woodpecker silviculture on density (the interaction between study group and time period), we used a repeated measures linear model (SAS Institute 1991b:272–274) composed of time period (before silviculture vs. after), forest compartment within study group, study group, and study group $\times$ time period interaction. We used Pearson's R^2 statistic to correlate density with the area of each compartment's canopy cover types (Piedmont National Wildlife Refuge 1983). We also constructed a multiple regression model of canopy cover types to predict

density in each study compartment using AIC to select the best model (SAS Institute 1991c).

Survival from Radiotelemetry.—We used fates of radiomarked wood thrushes to estimate weekly survival probability during the breeding season. Because of few mortalities, we estimated a constant weekly survival rate for each study compartment in each year using program SURVIV (White 1983) to provide maximum likelihood estimates and AIC to assess whether sex-specific estimates were warranted. We evaluated the effect of red-cockaded woopecker silviculture on breeding season survival by estimating α_i as

$$\hat{\alpha}_B = \log\left(\frac{\hat{S}_E^B}{\hat{S}_C^B}\right) \quad \hat{\alpha}_A = \log\left(\frac{\hat{S}_E^A}{\hat{S}_C^A}\right) \quad (1),$$

where S denotes estimated survival, E = experimental, C = control, B = before treatment, and A = after treatment. We approximated the variance of $\hat{\alpha}_i$ using the delta method (Weir 1990: 44). Under a hypothesis of no treatment effect, the relationship (α_i) between experimental and control survival should remain the same after treatment (Green 1979: 68, Eberhardt and Thomas 1991). We defined an effect parameter, Δ_α , as the difference between α_B and α_A , which was zero if no effect occurred. We calculated a 95% CI on Δ_α , and determined whether the CI included (no effect) or did not include (effect) zero; equivalently, we also computed a z -test of the null hypothesis of no effect ($H_0: \Delta_\alpha = 0$). As noted earlier, our survival inferences were not based on spatial replication. Therefore, we also conducted a randomization test to determine if the estimates we obtained for each study group differed from that expected by chance (Carpenter et al. 1989). We conducted 1,000 bootstrap randomizations of the 4 control–experimental, before–after point estimates, and for each we computed a z -statistic that we compared to the z -statistic obtained under the observed data structure. We estimated the probability of Type I error as the proportion of randomizations in which the computed z -statistics exceeded or equaled the observed z -statistic (Edgington 1995:41).

We also computed 100-day Kaplan-Meier estimates (Pollock et al. 1989, White and Garrott 1990) for comparison to other studies and for a description of temporal variability in survival rates and survival differences between adults and juveniles. However, because of few mortal-

ities, these estimates were not used to evaluate the effects of silviculture on survival.

Survival from Recaptures.—We used capture–recapture histories and program SURVIV (White 1983) to estimate apparent annual survival and capture probability based on a Cormack-Jolly-Seber model (Pollock et al. 1990). Apparent survival estimates under this model are the product of true (demographic) survival between years and rates of return to the study compartment. Apparent annual survival is a conservative estimate of annual survival because it is also a function of emigration. To evaluate treatment impacts, we estimated α_i by direct incorporation of expression (1) in the likelihood in program SURVIV. As with breeding season survival above, we defined an effect parameter, Δ_α , as the difference between α_B and α_A , estimated its variance by the delta method (Weir 1990:44), and calculated a 95% CI for Δ_α . Lastly, we conducted a randomization test to determine if the non-random assignment of control and experimental compartments affected our results.

Population Growth.—Discrete population growth (λ), the rate of growth in a population from time t to $t+1$, is a function of annual adult survival (S^A = probability of surviving 1 year), juvenile survival (S^J = probability of surviving from the end of a breeding season to the beginning of the next breeding season), and recruitment (B = $\bar{x}$ number of females, alive at end of breeding season, produced per female):

$$\lambda = S^A + BS^J \quad (2).$$

We calculated S^A as the product of breeding season ($\hat{S}^{A,B}$) and winter ($\hat{S}^{A,W}$) survival using our estimate of female breeding season survival and estimates of adult winter survival from Conway et al. (1995). No estimates of survival exist for wood thrush juveniles on wintering grounds. Therefore, we predicted λ under 2 possibilities for winter juvenile survival (S^J), assuming that S^J equals our estimates of summer juvenile survival, or S^J equals $\hat{S}^{A,W}$; data from Conway et al. (1995).

We predicted B using the individual-based recruitment model of Powell et al. (1999), in which $\hat{B}$ is a function of our estimates of (1) female breeding season mortality, (2) nest success, (3) number of fledglings per successful nest, (4) juvenile breeding season mortality, and (5) season length and time between nesting attempts. We estimated the variance of $\hat{\lambda}$ using

Table 1. Parameter and variance estimates from other sources used in our wood thrush population model. Nest success and recruitment data were simultaneously collected during 1993–96 at the Piedmont National Wildlife Refuge, Georgia.

Parameter	Estimate	SE	Time unit	Study group	Time period
Nest success ^a	0.9591	0.0112	Daily	Control	Before
	0.9385	0.0091	Daily	Control	After
	0.9615	0.0220	Daily	Experimental	Before
	0.9534	0.0099	Daily	Experimental	After
Recruitment ^b	2.58	1.92 ^c	Yearly	Control	Before
	1.46	1.30 ^c	Yearly	Control	After
	2.11	1.52 ^c	Yearly	Experimental	Before
	2.62	1.93 ^c	Yearly	Experimental	After
Survival, winter ^d	0.900	0.027	Monthly	Not applicable	

^a From Powell (1998).
^b As predicted in Powell et al. (1999). Recruitment is defined as offspring/pair/year surviving to the end of the breeding season.
^c SD.
^d From Conway et al. (1995).

the delta method (Weir 1990:44) based on the sample estimates and standard errors for $\hat{S}^{A,B}$, $\hat{S}^{A,W}$, $\hat{S}^I$, and $\hat{B}$. To determine the amount of uncertainty in our prediction of $\hat{\lambda}$, we performed 200 repetitions of a 200-year stochastic simulation of $\hat{\lambda}_i$. During each “year” or i th simulation, we used the SAS Interactive Matrix Language’s (IML; SAS Institute 1991a) random number generator to select a value for each demographic model parameter (i.e., survival, reproduction) from a range of possible values based on our estimates and the variance of each parameter (Table 1). The demographic parameter estimates in Tables 1 and 4 represent 2 years of pooled data, and the conditional variance associated with each parameter estimate does not reflect temporal variance in population parameters; modeling populations over time requires estimates of temporal variance. We initially estimated temporal variance by subtracting the sampling variance estimate from the average variance estimate of year-specific parameter estimates (Burnham et al. 1987: 262, Link and Nichols 1994), but this resulted in negative temporal variance estimates. Therefore, we doubled the conditional or sampling variance to ensure that our model predictions were not more precise than the underlying demographic parameter estimates (J. D. Nichols, U.S. Geological Survey, Biological Resource Division, personal communication). We selected survival rates from a beta distribution to ensure parameter values <1.0 and >0.0 , and we selected fecundity rates from a normal distribution. To characterize the growth rate of the population under a specific set of model parameter values, we calculated the geometric mean $\bar{\lambda}$ as sug-

gested by Pulliam (1996) for the 200 simulations during each repetition:

$$\bar{\lambda} = \text{antilog} \left[\frac{1}{n} \sum_{i=1}^n \log(\hat{\lambda}_i) \right],$$

and computed a 95% CI (Sokal and Rohlf 1981: 421) as

$$\text{antilog} \left[\overline{\log \lambda} \pm 1.96 \sqrt{\frac{1}{n} \text{var}(\log \bar{\lambda})} \right],$$

where $\hat{\lambda}^i$ is the estimated growth rate for the i th simulation. We attempted to validate this model by comparing its output to population growth estimates from PNWR during the same years calculated with yearly compartment-specific density estimates ($\hat{D}$, Table 2), instead of survival and reproduction parameters: $\lambda_t^D = \hat{D}_{t+1}/\hat{D}_t$.

Vegetation.—To quantify the effect of the prescribed burns and thinnings on the vegetation in our study plots, we compared, at each sample point in the experimental compartments, the difference between 1994 and 1995 (pre- and post-silviculture years). Changes were analyzed with a t -test of the differences of the means of continuous variables. We also detected changes in categorical variables with a Pearson’s chi-square test.

RESULTS

Wood Thrush Density

Wood thrush density varied among compartments (Table 2; $F_{5,23} = 7.21$, $P < 0.001$) from 0.15 to 1.30 pairs/10 ha. We found no effects of time (before vs. after silviculture; $F_{1,23} = 0.63$, $P = 0.439$) or study group (experimental vs. control; $F_{1,23} = 0.16$, $P = 0.699$). We did not

Table 2. Estimated density ($\hat{D}$ = males/km²), 95% CI, and sample size of wood thrushes at Piedmont National Wildlife Refuge, Georgia, 1993–96, as determined by transect surveys of singing males.

Compartment	Study group	1993			1994			1995			1996		
		$\hat{D}$	CI	n	$\hat{D}$	CI	n	$\hat{D}$	CI	n	$\hat{D}$	CI	n
C-8	Experimental	1.58	1.22–2.05	19	2.34	0.78–7.01	21	1.50	0.83–2.74	41	1.50	0.65–3.50	16
C-12	Experimental	6.26	4.84–8.10	44	3.10	1.87–5.13	43	3.34	2.44–4.57	77	3.62	3.41–3.84	41
C-31	Experimental		— ^a			— ^a		7.52	6.42–8.80	62	13.02	8.37–20.26	87
C-11	Control	5.90	2.87–12.14	38	5.25	2.13–12.92	54	3.72	1.38–10.03	77	3.05	1.51–6.15	15
C-23	Control	8.51	6.27–11.57	57	3.81	2.83–5.12	55	3.48	2.97–4.08	76	4.02	1.32–12.21	33
C-24	Control		— ^a			— ^a		3.58	3.35–3.83	44	3.65	2.38–5.60	30
C-25	Control	4.57	2.70–7.71	32	5.13	0.61–42.90	52	3.92	3.33–4.61	92	6.25	3.71–10.52	40

^a Compartment not part of study design during 1993–94.

detect a change in density after silviculture treatments (adjusted least-squared means [$\pm$ SE]: before = 5.14 ± 0.767 males/km², after = 5.56 ± 0.767 males/km²), but density on controls declined slightly (before = 5.13 ± 0.645 males/km², after = 3.90 ± 0.645 males/km²). We found no study group $\times$ time interaction (silviculture effect; $F_{1,23} = 1.42$, $P = 0.251$). We estimated density using compartment-specific encounter rates (likelihood ratio test, $P < 0.001$) and used uniform (13 of 24 data sets), hazard (8 of 24), and half-normal (3 of 24) models; all models chosen included a cosine adjustment.

Density of males was closely related to over-story cover type. Wood thrush density was negatively correlated with compartment-specific area of saw timber-sized pine (Pearson $R^2 = -0.5326$, $P = 0.007$), but hardwoods and younger pines were not correlated with density ($P > 0.05$). Step-wise regression selected bottomland (BH) and upland (UH) hardwoods as the best model ($R^2 = 0.820$, $P < 0.001$), and upland hardwood accounted for 78.9% of the variation in density ($\hat{D} = -0.086\text{BH} + 0.122\text{UH}$).

Breeding Season Survival

We radiomarked 13 adults during 1993 (10 males, 3 females), 31 during 1994 (18 males, 13 females), 44 during 1995 (19 males, 25 females), and 43 during 1996 (21 males, 22 females). We also radiomarked 11 juveniles during 1994, 15 during 1995, and 11 during 1996 (Table 3). We marked most birds once, but we re-marked 3 male–female pairs in 1995 and 6 pairs in 1996, which allowed us to follow them for most of the breeding season. We re-marked 1 juvenile after its radio fell off prematurely.

No radiomarked male wood thrushes ($n = 68$) died during 1993–96, whereas females in our sample ($n = 63$) had a $81.8 \pm 6.7\%$ chance of surviving 100 days. Kaplan-Meier survival curves (in pairwise tests) were not different among years ($P > 0.05$), but survival curves were different between sexes when all years were pooled ($\chi^2 = 7.25$, $df = 1$, $P = 0.007$). Most female mortality occurred during the nesting period (Fig. 1). Female wood thrushes had lower weekly survival rates (female $\hat{S} = 0.981 \pm 0.014$; male $\hat{S} = 1.000 \pm 0.039$) when all 4 years were pooled together (likelihood ratio test of sex-specific model vs. pooled-sex model: $\chi^2 = 7.51$, $df = 1$, $P = 0.006$). Females were killed by avian and mammalian predators, often near active nests (Table 3).

Table 3. Sample sizes, exposure days, fates, and sources of mortality for male (M), female (F), and juvenile (J) wood thrushes radiomarked at Piedmont National Wildlife Refuge during 2 time periods (before and after red-cockaded woodpecker silviculture: 1993–94 and 1995–96) in 2 study compartment types (experimental and control).

Period	Study group	Sample size ^a			Fates (lived/died) ^a						Exposure days			F/J mortality source		
		M	F	J	M	F	J	M	F	J	M	F	J	Avian	Mammalian	Unknown
Before	Experimental	9	7	4	9/0	4/3	3/1	494	331	116				2/1	0/0	1/0
After	Experimental	21	24	17	21/0	22/2	16/1	907	765	257				0/0	1/3	1/0
Before	Control	17	9	4	17/0	8/1	3/1	632	497	681				0/1	1/0	0/0
After	Control	19	23	8	19/0	22/1	6/2	658	749	351				1/0	0/0	0/0

^a Does not include 2 males, 1 female, and 5 juveniles that were radiomarked away from 7 study compartments.

Fig. 1. Kaplan-Meier survivorship curves (White and Garrott 1990) for male, female, and juvenile wood thrushes at the Piedmont National Wildlife Refuge, Georgia, during 1993–96 (years pooled). Individuals were radiomarked using a staggered-entry format, but adults were marked earlier than juveniles. Juvenile survival curves are shown 2 ways: (A) days equals days from first radiomarking of an individual (day 0 for juveniles = May 27, day 0 for adults = April 24), and (B) day 0 equals April 24 for all groups. Both plots show the estimated probability of a wood thrush surviving 100 days during the breeding season. Plot A can be used to compare 100-day survival among age and sex groups (see dotted vertical line), while plot B shows periods of highest mortality among females and juveniles.

Female survival increased by the same proportion on control and experimental compartments during the post-treatment years (Table 4), indicating no red-cockaded woodpecker silviculture effect ($Z = 0.005$, $P = 0.996$), which agreed with our randomization tests ($P = 0.859$). The Δ_x for female survival was 0.001 ± 0.063 ; for reference, a 50% change in survival would have resulted in $\Delta_x = \pm 0.301$.

We did not observe a silviculture effect on weekly juvenile survival ($Z = 0.405$, $P = 0.685$). Point estimates for experimental compartments increased, while control estimates decreased after silviculture treatment (Table 4), again agreeing with our randomization tests ($P = 0.110$). The Δ_x for juvenile survival was -0.027 ± 0.066 . We estimated a weekly juvenile survival rate, pooled over all years and compartments, of 0.976 ± 0.010 ($n = 38$), and we estimated a 100-day Kaplan-Meier survival rate of $0.752 \pm$

Table 4. Estimates of weekly breeding season survival ($\hat{S}$) for radiomarked adult male (M), female (F), and juvenile (J) wood thrushes on experimental and control compartments at the Piedmont National Wildlife Refuge, Georgia during 2 time periods (before silviculture: 1993–94, after: 1995–96). Sex-specific model was selected for adults by likelihood ratio test and AIC comparison.

Sex or age	Time period	Experimental		Control		$\hat{\alpha}$	SE
		$\hat{S}$	SE	$\hat{S}$	SE		
M	Before	1.000	0.129	1.000	0.071	— ^a	
M	After	1.000	0.060	1.000	0.090	— ^a	
F	Before	0.974	0.038	0.977	0.040	−0.001	0.056
F	After	0.981	0.022	0.986	0.020	−0.002	0.030
M/F pooled	Before	0.987	0.021	0.991	0.018	−0.002	0.028
M/F pooled	After	0.991	0.029	0.993	0.012	−0.001	0.032
J	Before	0.947	0.051	0.974	0.026	−0.012	0.059
J	After	0.991	0.009	0.957	0.029	0.015	0.031

^a $\hat{\alpha}$ not calculated.

0.116 for all radiotagged juveniles during 1994–96. Both mortalities in 1994 occurred within 2 days of fledging, and all mortalities during 1995–96 ($n = 3$) occurred immediately following a long-distance dispersal from the nest site (15, 25, and 28 days after fledging). Avian and mammalian predators caused juvenile mortalities (Table 3), which occurred throughout the summer (Fig. 1).

Apparent Annual Survival

The best model (lowest AIC; $P = 0.239$, AIC = 46.89) to describe apparent annual survival of adult wood thrushes included homogeneous survival for birds released in 1993–95 and homogeneous recapture rates across experimental and control compartments during 1994–96 (apparent annual survival = 0.579 ± 0.173 ; recapture = 0.180 ± 0.080). To test for red-cockaded woodpecker silviculture effects, we used a model with study group-specific survival rates for wood thrushes released in 1993 (pre-silviculture returns) and 1994–95 (post-silviculture returns),

and constrained recaptured rates during 1994–96 ($P = 0.126$). Apparent survival on control compartments increased from 0.533 ± 0.296 to 0.622 ± 0.246 , while survival on experimental compartments increased from 0.207 ± 0.211 to 0.745 ± 0.433 . Although point estimates of apparent annual survival increased proportionally more on burned and thinned compartments, it was not a significant increase ($Z = 0.573$, $P = 0.567$), which agreed with the results of our randomization tests ($P = 0.381$). The Δ_a for apparent annual adult survival was 0.0 ± 1.067 .

Population Growth Model

The deterministic model (equation 2) predicted a population growth rate of $\hat{\lambda} = 1.00$ (95% CI = 0.32–1.63) when pooling parameters across time periods and study groups. Predictions of $\hat{\lambda}$ ranged from 0.898 to 1.014 (Table 5). Although much uncertainty existed in our predictions, the model usually predicted lower growth rates using adult winter survival ($\hat{S}_w^a$) estimates from Conway et al. (1995) for $\hat{S}_w^j$ than

Table 5. Predicted growth rates ($\hat{\lambda}$) of wood thrush populations using breeding season radiotelemetry data from Piedmont National Wildlife Refuge in Georgia and adult winter survival estimates ($\hat{S}_w^a$) from Conway et al. (1995). Growth rates are predicted for 4 combinations of study group and time period (before silviculture: 1993–94, after: 1995–96) categories under 2 juvenile winter survival ($\hat{S}_w^j$) assumptions: $\hat{S}_w^j$ equals $\hat{S}_w^a$ and $\hat{S}_w^j$ equals juvenile summer survival ($\hat{S}_s^j$). Growth rates are described by geometric means of a 200-year simulation.

$\hat{S}_w^j$ hypothesis	Study group	Time	$\hat{\lambda}$	95% CI
$\hat{S}_w^j = \hat{S}_w^a$	Control	Before	1.012	0.98–1.05
	Control	After	0.898	0.87–0.92
	Experimental	Before	0.937	0.91–0.97
	Experimental	After	1.012	0.98–1.05
$\hat{S}_w^j = \hat{S}_s^j$	Control	Before	1.001	0.97–1.03
	Control	After	0.933	0.91–0.96
	Experimental	Before	0.945	0.92–0.98
	Experimental	After	1.014	0.98–1.05

Fig. 2. Variation in population growth rates at Piedmont National Wildlife Refuge, Georgia. Growth rates shown are for experimental study areas after the silviculture was applied during 75 simulation years, using 2 sources of data for winter juvenile survival (summer juvenile survival and adult winter survival). Adult annual survival is estimated using breeding season and wintering (Conway et al. 1995) adult radiotelemetry data. Solid line indicates stable, non-growing populations; dashed lines indicate the 95% CI for population growth rates of experimental compartments determined from year-specific density estimates.

our estimate of summer juvenile survival (Table 5, Fig. 2).

The stochastic model predicted increasing population growth rates on the experimental compartments after the silviculture (95% CI before = 0.91–0.97, after = 0.98–1.05), and decreasing λ on control compartments (95% CI before = 0.98–1.05, after = 0.87–0.92; Table 5). For comparison, the average prediction of population growth from yearly estimates of density ($\hat{\lambda}_t^D$) was 0.995 (SD = 0.36), with $\hat{\lambda}_t^D$ on burned or thinned areas greater (1.19, SD = 0.40) than on areas not receiving silviculture (0.89, SD = 0.30; $F_{1,16} = 2.89$, $P = 0.10$).

Vegetation Changes

We did not detect a change in the basal area of softwoods due to red-cockaded woodpecker silviculture (time period $\times$ study group interaction, $P = 0.351$). However, hardwood basal area did decline during the first year after the silviculture (time period $\times$ study group interaction, $P = 0.026$), and canopy cover decreased after the silviculture (time period $\times$ study group interaction, $P = 0.014$). Understory density was

lower on experimental compartments than on controls (time period $\times$ study group interaction, $P = 0.002$) after silviculture treatment.

At thinned survey points ($n = 82$), the average softwood basal area remained the same ($P = 0.33$) and the average hardwood basal area declined by 2.02 m²/ha ($P = 0.006$). Canopy cover decreased by 11.3% ($P = 0.003$) and horizontal understory cover in the 1–2 m level decreased by 24.2% ($P < 0.001$). The density of understory ($\chi^2 = 1.65$, df = 2, $P = 0.44$) and midstory ($\chi^2 = 3.93$, df = 2, $P = 0.14$) vegetation did not change among 3 ranked density classes. In 1995, the average diameter of trees in thinned areas was slightly higher than in non-thinned areas on experimental compartments (14.7 cm vs. 13.1 cm, $P = 0.066$).

At burned survey points ($n = 82$), canopy cover decreased by 4.7% ($P = 0.001$) and horizontal understory cover in the 1–2 m level decreased by 19.8% ($P < 0.001$). The density of understory vegetation (measured 4 months after the burn) did not change ($\chi^2 = 0.48$, df = 2, $P = 0.79$). However, the midstory showed some

evidence of becoming more dense after silviculture treatment ($\chi^2 = 5.50$, $df = 2$, $P = 0.06$).

DISCUSSION

Effect of Silviculture

We found no evidence that adult and juvenile survival, density, and population growth rates were reduced by red-cockaded woodpecker silviculture. On the contrary, the stochastic model predicted that population growth rates increased on experimental compartments and decreased on control compartments after silviculture treatments. However, 95% CI for our effect parameter (Δ_a) was large, especially for apparent annual survival.

Forest thinnings and burns covered less than half of the experimental compartments, and the thinnings and burns were not drastic changes to the landscape. Wood thrushes are highly mobile species (Powell 1998) that can move easily to unaffected areas when necessary, which may explain why survival did not change after the silviculture. The high mobility of wood thrushes emphasizes the need for a study design that includes both controls and replications across time and space when studying the effects of an environmental impact (Green 1979).

Demographic Parameters

Demographic rates of wood thrushes at PNWR may be unique, as PNWR is an uncommonly large, contiguous habitat near the southern edge of the species' range. Our densities were lower than populations near the center of the species' range (Roth et al. 1996). Male breeding season survival rates were high, and pooled-sex estimates indicated a monthly breeding season survival estimate of 95.8%. We found no comparable adult survival data for the breeding season (Roth et al. 1996), but our survival estimates were higher than the monthly survival estimates in winter reported by Conway et al. (1995; 90.0%) and Rappole et al. (1989; 88.7% for sedentary birds, 44.7% for wanderers).

Ornithologists commonly report lower return rates or annual survival for females than males (Payevsky et al. 1997, Marshall et al. 1999), but the mechanism has not been confirmed. We believe our data are the first to suggest differences within the breeding season for passerines. Our data indicate that only 61% of female wood thrushes live through a 6-month breeding season, whereas 100% of males survived the same

time period. Payevsky et al. (1997) reported that males of several avian species had higher annual survival than females, but our data are the first to suggest differences within the breeding season for passerines. Return rates for female wood thrushes at PNWR are lower than males (Powell et al. 1998), but differences in philopatry could also be responsible for these observations (Marshall et al. 1999). Assuming equal survival during migration and winter, our data do not agree with Roth et al.'s (1996) report that females live up to 1 year longer than males in Delaware. Winker et al. (1990) observed a capture ratio of more than 2:1 for male and female wood thrushes on wintering grounds, and our own banding data (L. Powell and J. Lang, unpublished data) suggest higher numbers of males on breeding grounds. Differential rates of survival, assuming a 50:50 sex ratio at birth, would account for such biased sex ratios. Sex-specific survival estimates are critical for parameterization of more realistic population models (Noon and Sauer 1992), as pooled-sex survival estimates would overestimate the true survival of females at PNWR.

Most female mortalities occurred during the nesting period, and all mortalities during that period occurred at or very near the nest site. This is not surprising, as females are more than twice as likely as males to be found at the nest site (Powell 1998). This trend is comparable to female waterfowl that are more susceptible to predation during nesting periods (Losito et al. 1995, Reynolds et al. 1995, Flint and Grand 1997). The attentiveness of female songbirds to eggs and nestlings probably causes higher mortality during this period, especially during the latter part of the nesting period when inexperienced, younger females are breeding (McCleery and Perrins 1988), and females may be more prone to defend a nest against predators (Forbes et al. 1994). Female and juvenile mortalities occurred during early June to late July, and we did not record many mortalities of females and juveniles during August and early September. This period of low mortality also corresponds to a dramatic move to denser habitat by adults during the post-nesting period, and juveniles used similar, dense habitats during the post-dispersal period (Lang 1998, Powell 1998). Juvenile mortalities occurred either before dispersal or immediately following dispersal, so it appears that mortality decreased as juveniles became familiar with their dispersal

habitat. Nesting habitats and dispersal habitats were quite different (Lang 1998).

Juvenile survival rates at PNWR were higher than an Ozark wood thrush population monitored in a large, contiguous habitat (Anders *et al.* 1997), even though our juvenile survival estimates included monitoring during potentially high-risk dispersal and post-dispersal periods that Anders *et al.* (1997) did not monitor. Predator densities may be higher in the Ozarks than at the PNWR, and Ozark habitat structure or dispersal patterns may leave juveniles more susceptible to predation.

Population Growth Model

Silviculture treatments did not have a negative effect on population growth rates at PNWR. The higher $\hat{\lambda}$ on experimental compartments after the burning and thinning was largely due to differences in juvenile survival and nest success, although we detected no significant positive effect of red-cockaded woodpecker silviculture on the individual parameters (Lang 1998). Our modeling exercise underscores the necessity for more research on juvenile songbird survival in management contexts.

Although the wood thrush population in Georgia is apparently declining (Sauer *et al.* 1996), our results indicate that the PNWR population may be stable. However, our model predicted considerable variation in $\hat{\lambda}$ among study compartments and years. In the Great Smoky Mountains, another large, contiguous forest like PNWR, Simons and Farnsworth (1996) predicted an average wood thrush population growth rate of 1.10. However, they did not simultaneously obtain survival estimates in the field for adult and juvenile wood thrushes—a critical piece of the population growth model. The large variances we report for population growth rates after extensive data collection and parameter estimation underscore the caution that should be used when classifying populations as sources or sinks from point estimates with no variance component.

Although growth rates predicted by our stochastic model are within the range of population growth rates predicted from density estimates ($\hat{\lambda}_t^D$), the prediction of $\hat{\lambda}_t^D$ for experimental areas was almost 20% greater than the model's mean prediction. At least 2 factors could account for the discrepancy between the predictions. First, our stochastic model contains

many assumptions, including constant juvenile survival during the first year and no mortality during migration. Field estimates for these parameters do not exist for songbirds, and the parameters are critical for accurate predictions of population growth rates. Second, predictions of $\hat{\lambda}_t^D$ may be affected by between-year movements of wood thrushes in or out of PNWR. Lang (1998) and Powell (1998) reported that within-year emigration probabilities from PNWR compartments are large and movement distances are landscape scale. Therefore, population growth rates predicted from annual density estimates may be more descriptive of the regional population and should not be used to determine local habitat effects on demographic parameters.

MANAGEMENT IMPLICATIONS

The PNWR may manage its forests differently than nearby private and public land managers, but thinning and prescribed burning are common methods of forest management. Because the wood thrush population on PNWR appears to be stable while the population is declining state-wide, PNWR's silviculture practices may be a model worthy of replication throughout the region. Although our experimental design provided temporal and spatial controls, this was a relatively short-term study. During our 4-year study, the population growth model predicted differences in population growth rates as large as 11% on control compartments. Our estimates of apparent annual survival and breeding season survival and our tests for an effect of red-cockaded woodpecker silviculture on survival also showed considerable uncertainty. We suggest that long-term monitoring of population responses to management is needed to fully understand and manage these systems (Walters 1986).

The survival of juveniles is critical to maintaining songbird populations, and juvenile habitat requirements should be a high priority during habitat management decisions. Female survival during the nesting period may also be improved through habitat management. Therefore, continued use of the current management regime at PNWR should result in adequate habitat for wood thrushes and similar songbirds, while providing new colony sites for red-cockaded woodpeckers.

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