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Featured Article

Effects of Early-Successional Shrubland Management on Breeding Wood Thrush Populations

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ABSTRACT In forested landscapes, creation of habitat for early-successional shrubland birds is controversial because of perceived conflicts with the conservation of mature-forest birds. Nonetheless, many mature-forest birds, especially fledglings, readily use early-successional stands during the post-breeding period. This suggests that for mature-forest birds, creating habitat for early-successional birds could involve a tradeoff: reduced abundance and nest survival due to the loss of nesting habitat versus enhanced fledgling survival in early-successional stands. Our research addressed the effects of the creation of early-successional habitat for shrubland birds on wood thrushes (*Hylocichla mustelina*) in western Massachusetts, USA. We compared wood thrush abundance, nest success, fecundity, and post-fledging survival in landscapes with high (~20%) or low (~1%) cover of early-successional stands suitable for shrubland birds. We found no differences in nest success, fecundity, and post-fledging survival between the 2 types of landscapes. Abundance of breeders, however, was significantly greater on the sites with high cover of early-successional habitat. We conclude that in forested landscapes, creation of early-successional habitat at levels recommended for the conservation of shrubland birds is compatible with viable wood thrush populations. © 2018 The Wildlife Society.

KEY WORDS forestry, habitat, *Hylocichla mustelina*, logging, nest, point count, post-fledging, predation, silviculture.

As natural areas are altered, remaining lands are under increasing pressure to provide refuges for plants and animals (Hoekstra et al. 2004, Gaston et al. 2008). When sympatric species have incompatible habitat needs, conflict over management may result. For birds, forested landscapes in eastern North America are a nexus for this type of conflict; numbers of species on both ends of the successional gradient are in decline (Hunter et al. 2001, Link and Sauer 2002, Schlossberg and King 2007, Sauer and Link 2011). Mature-forest birds typically nest in stands with closed canopies and medium- or large-sized trees and are reported to be less abundant or have lower nesting success in small patches and near edges (Robbins et al. 1989, Robinson et al. 1995, Rosenberg et al. 2003). Early-successional shrubland species, by contrast, require forest gaps >1 ha with a developed shrub layer (Hunter et al. 2001, DeGraaf and Yamasaki 2003, Schlossberg and King 2009, Roberts and King 2017).

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With the extent of natural shrublands limited, conservation of shrubland birds may require converting some areas of mature forest to shrublands. Creation of early-successional shrubland habitat is often challenged, however, because of concerns about mature-forest birds (Askins 2001). This has impeded conservation of shrubland birds and has contributed to the continued declines in shrubland bird species to what may be record-low population levels in the eastern United States (King and Schlossberg 2014). Nevertheless, shrubland birds remain a conservation priority, ranking as high as or higher than mature-forest birds in State Wildlife Action Plans or the Partners in Flight Prioritization Scheme (King and Schlossberg 2014). In response to this concern, conservationists recommend maintaining 10–15% of forested landscapes in the seedling and sapling stage for shrubland birds (DeGraaf and Yamasaki 2003, Dettmers 2003). Most parts of the eastern United States fail to meet this recommendation (King and Schlossberg 2014).

Recent research on the post-fledging period suggests a possible resolution to this conflict. After nesting, both adults and young of many mature-forest bird species move into shrubby areas (Marshall et al. 2003, Vitz and Rodewald

2006). For post-breeding birds, this type of dense cover provides abundant fruit and insects and dense foliage for avoiding predators (Vitz and Rodewald 2007, Chandler et al. 2012). Early-successional stands may be especially important for fledglings, whose foraging and flight abilities are still developing (Vega-Rivera et al. 1998, White et al. 2005). Still unknown is whether the creation of early-successional habitat through logging improves survival of fledglings and thereby compensates for potential effects on the abundance and nesting success of mature-forest birds. If these shrublands enhance fledgling survival, creating openings could benefit mature-forest and early-successional birds.

A chief obstacle in resolving this issue is the lack of studies in which access by fledglings to early-successional shrublands is restricted. Most studies of fledgling mature-forest birds have occurred in landscapes where birds are free to choose among early- or later-successional stands (Vega-Rivera et al. 1998, Dellinger 2007, Vitz 2008, Streby and Andersen 2011). Fledglings are mobile and can disperse several kilometers from nest sites to post-fledging areas (Anders et al. 1998, Vitz and Rodewald 2010). Associations between fledging survival and shrubland conditions in forests could be influenced by the presence of different seral stages within the landscape, perhaps as the result of unobserved forays by fledglings into different land cover types or effects of these cover types on adult provisioning. Thus, an appropriate test of management influences on fledglings will require a landscape approach, in which access to early-successional stands varies at scales larger than typical dispersal distances of fledglings. To our knowledge, only 1 study of post-fledging ecology has employed such a landscape approach; Powell et al. (2000) detected no differences in wood thrush (*Hylocichla mustelina*) demography between landscapes in which thinning or burning took place and landscapes in which these practices did not occur.

Clearly, the creation of early-successional habitat through silviculture or other means can impose costs for mature-forest birds. Regenerating clearcuts, for example, are unsuitable for nesting by most mature-forest species, so silviculture can reduce breeding populations by reducing the extent of nesting habitat (Thompson et al. 1992, Lent and Capen 1995, Annand and Thompson 1997). Intensive management where large areas of forest are converted to seedling or sapling stands can result in forest fragmentation (Drapeau et al. 2000, Etheridge et al. 2005). The effect of silvicultural openings like regenerating clearcuts on mature forest birds is sometimes dismissed as a problem because clearcuts appear to have less effect on nest success than fragmentation by agriculture or suburban development (Hanski et al. 1996, Rodewald 2002, Schmiegelow and Mönkkönen 2002). Still, studies have reported that clearcutting can reduce nesting success of birds in adjacent forest (King et al. 1996, Manolis et al. 2000*a*, Flaspohler et al. 2001*a*).

In this study, we investigated the effects of the creation of early-successional habitat through silviculture on the wood thrush, a forest-nesting bird that uses early-successional shrublands during the post-fledging period (Anders et al. 1998, Vega-Rivera et al. 1998) and has declined in population across its breeding range (Sauer et al. 2017). Our objective was to describe how management for early-successional species affected the viability of mature forest birds in an extensively forested landscape.

STUDY AREA

We conducted the study from May through September of 2010 and 2011. The study area has a humid continental climate, with precipitation averaging 114 cm per year and falling in roughly equal amounts by month. Elevation on the study sites averaged 282 m above sea level, and topography was generally hilly. Forests in the study area consisted of transition hardwoods-white pine (*Pinus strobus*) forest (DeGraaf and Yamasaki 2001), which, depending on site conditions, were variously dominated by yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), red maple (*A. rubrum*), beech (*Fagus grandifolia*), northern red oak (*Quercus rubra*), American hemlock (*Tsuga canadensis*), white pine, and shagbark hickory (*Carya ovata*). We classified clearcuts or shelterwoods created within the last 20 years as early-successional because they typically have dense understory vegetation suitable for shrubland birds (Annand and Thompson 1997, King and DeGraaf 2000, Thompson and DeGraaf 2001). From the original dataset, we created 4 composite land covers: forest (forests and forested wetlands), shrubland (logged areas, old fields, and shrub wetlands), agriculture (hayfields, pastures, and row crops), and developed areas (human-built areas, roads, other infrastructure). Potential nest predators observed on video depredating nests in New England forests (King and DeGraaf 2006) included northern goshawk (*Accipiter gentilis*), broad-winged hawk (*Buteo platypterus*), red squirrel (*Tamias hudsonicus*), eastern chipmunk (*Tamias straitus*), blue jay (*Cyanocitta cristata*), and American crow (*Corvus brachyrhyncus*). These same species are suspected to be major predators of fledging birds (King et al. 2006).

Using a geographic information system (GIS), we identified 5 study areas with relatively high or low amounts of early-successional habitat in the landscape (Fig. 1, Table 1). All sites were located on state-owned land, and each study area was approximately 1 km^2. Sites with high early-successional habitat (i.e., managed sites) were in the Quabbin Reservoir watershed and have been managed with clearcuts, shelterwood cuts, and lighter thinning, resulting in a mosaic of mature forest, thinned stands, and regeneration of varying ages. These areas include numerous openings >1 ha in size, which are suitable for most shrubland bird species in our region (Roberts and King 2017). Priority species present in these openings included chestnut-sided warbler (*Setophaga pensylvanica*), eastern towhee (*Pipilo erythrophthalmus*), indigo bunting (*Passerina cyanea*), and prairie warbler (*S. discolor*; Roberts and King 2017). Sites with low early-successional habitat (i.e., unmanaged) were primarily mature forest except for small areas that had been thinned.

METHODS

Field Methods

Our approach was to compare wood thrush abundance, nest success and productivity, fledgling survival, and population

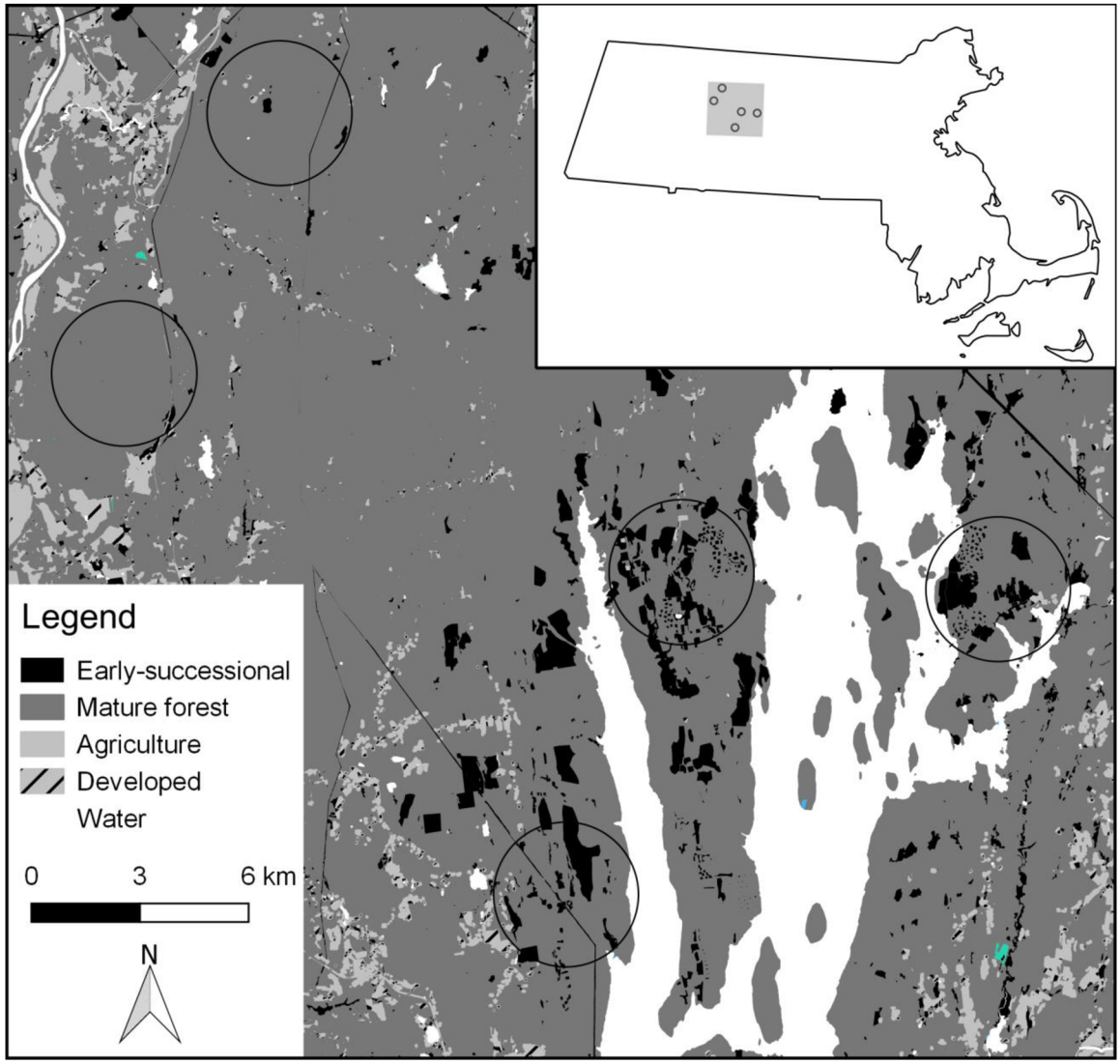

Figure 1. Study landscapes (circled) in western Massachusetts, USA, where we studied wood thrush abundance and demography, 2011 and 2012. Enlarged area is shown on inset.

growth rates between forested landscapes with a level of active management approximating recommended levels of shrubland cover suggested in the literature (DeGraaf and Yamasaki 2003, Dettmers 2003), and forest landscapes without active management and with little or no shrubland cover as a result. We used a GIS to measure cover of early- and late-successional forests in Hampshire, Hampden, Franklin, and Worcester counties in western Massachusetts. The GIS data came from the state's 2005 Land Use coverage based on aerial photography from 2005, with a minimum patch size of 0.4 ha (Massachusetts Office of Geographic Information 2009). Because this dataset misclassified some

Table 1. Land cover (%) within 2 km of study sites in western Massachusetts, USA, where we studied wood thrush abundance and demography, 2011 and 2012.

Name	Early-successional forest	Mature forest	Agriculture	Developed	Other[a]
Managed sites					
Prescott	26.0	68.7	1.1	0.5	0.0
West Quabbin	13.3	82.2	0.0	0.5	4.0
Dana	21.4	75.3	0.9	0.0	2.5
Unmanaged sites					
Montague WMA	1.2	96.7	0.3	0.6	1.2
Mount Toby	0.3	94.8	0.0	1.1	3.4

[a] Primarily freshwater wetlands.

early-successional patches, we used orthophotos from 2008 and 2009 to correct the coverage in potential study areas. Although this time did not correspond directly to years in which we carried out fieldwork, the towns where sites were located experienced the lowest rates of land conversion in Massachusetts ($\leq$0.2%/yr; Lautzenheiser et al. 2014). Additionally, we were able to ground-truth our GIS coverage during field work. Thus, the orthophotos from 2008 and 2009 should be a good representation of the land cover during our study.

To locate study sites, we placed a 70 × 70-m grid over the entire study region and measured the area of our 4 land-use categories in a 2-km radius around each grid cell. We used 2 km as a radius because the mean dispersal distance reported for wood thrush fledglings leaving their natal territories is <2 km (Anders et al. 1998, Vega-Rivera et al. 1998, Dellinger 2007). Development and agriculture can reduce avian nest success (Rodewald et al. 2001, Phillips et al. 2005), so we eliminated sites where the combined cover of agriculture and development in the 2-km buffer zone was $\geq$2% of the land area.

We conducted field research from May through September of 2011 and 2012. We searched for nests from May through early August in closed-canopy forest and selectively harvested stands where trees had been removed singly, in groups of 2–3 trees, or in shelterwoods with more open tree canopy over regenerating saplings or small trees. To locate nests, we followed adults that were carrying food or nest material and observed them as they returned to their nests or visually searched the area where they disappeared from view (Martin and Geupel 1993). We monitored nests every 2 to 4 days and recorded nest status and contents. We attempted to capture nestlings for radio-marking 8–10 days after hatching. For nests that were low enough to reach with a ladder (<~4 m high), we temporarily removed the nestlings from the nest. Additionally, some nestlings force-fledged during nest checks, and we captured these birds by hand. We weighed each nestling to the nearest 0.5 g, and measured wing chord to the nearest mm with a ruler and bill length to the nearest 0.01 mm with calipers. We banded nestlings with a metal band from the United States Geological Survey (USGS) Bird Banding Laboratory on 1 leg and a plastic color band on the other. Each bird in a brood received a different color to facilitate visual identification. Because our supply of radio-transmitters was limited, we attached transmitters to $\leq$3 nestlings/nest; remaining birds were only banded. We attached radio-transmitters using a 57-mm-long leg-loop harness of thin elastic. Transmitters weighed 1.5 g and had a 153-mm antenna. All banded birds appeared to behave normally with the transmitter attached. These practices were authorized under the University of Massachusetts Institutional Animal Care and Use Committee protocol number 2011-0026.

After banding, if the nest was reachable, we returned birds to their nests. In some cases, birds that were replaced in the nest refused to stay and jumped to the ground. These birds were replaced a second time, and if they left the nest again, they were placed on a branch or log below the nest. For birds whose nests could not be reached, we also left the birds below the nest.

Transmitters had a battery life of 6–7 weeks and were detectable from up to 1 km away. We relocated fledglings on foot every 2–3 days with 2- or 3-element yagi antennas and portable receivers. When we resighted a bird, we recorded whether it was alive or dead and used a global positioning system (GPS) to record its location.

In 2012, we conducted point counts to estimate abundance of wood thrushes on our study sites. On each site, we established a route with 8–10 sampling points spaced 250 m apart in the area where nest searching and monitoring were being conducted. Each route began at an arbitrarily selected road or trail intersection and followed trails or closed roads that traversed our study sites. Prior work suggests forest songbird abundance is unaffected by proximity to hiking trails (DeLuca and King 2014) or forest roads (King and DeGraaf 2002). Furthermore, sample points in managed and unmanaged sites were located on roads and trails. Thus, we assumed that locating sample points in this way did not affect our comparison between managed and unmanaged sites. We distributed point counts within habitats in which we encountered nesting wood thrushes. We conducted 3 rounds of counts on each site between late May and early July, with rounds separated by approximately 2 weeks. Counts took place in the first 3 hours after sunrise, and we varied the order of counts within and between sites from round to round. Each count lasted 10 minutes, and we recorded all birds detected within a 100-m radius.

Statistical Analysis

Nest success and productivity.—We used the logistic-exposure model to determine effects of management on wood thrush nest survival (Shaffer 2004). We followed Manolis et al. (2000*b*) to determine which observations to exclude and the treatment of fledging and failure dates. We identified 5 variables that could potentially affect nest survival: date (linear), date (quadratic), study site, year, and management (managed vs. unmanaged). We were also interested in nest height, but this measure was not recorded for 8 nests. Thus, we could not analyze nest height with the other variables. Nonetheless, for nests where height was recorded, nest height had no effect on nest survival ($P = 0.99$ for the nest-height parameter). Furthermore, we did not quantify distance from edge, because in many instances nests were adjacent to edges of varying age or type that were not always discernable, and for the unmanaged sites there was no distance from edge, which would have made a comparison impractical. Regardless, if management affected nest predation through edge effects or some other mechanism, we were confident we would be able to detect it via the management effect.

We assessed nest-survival models using Akaike's Information Criterion corrected for small sample size (AIC_c). Because our models were overdispersed, we used quasi-AIC_c ($QAIC_c$) values calculated with the overdispersion parameter from a global model with all variables (Burnham and Anderson 2002). We used a 2-stage process to select models

and make inferences about model parameters. First, we pre-screened variables individually to see if they improved the $QAIC_c$ of a constant-only model. Besides the 5 variables listed above, we also pre-screened a year by management interaction because this could be important even if year and management were not good predictors individually. Second, for variables that passed the pre-screening, we created a final model set including all possible combinations of those variables. We made inferences based on models with $\Delta QAIC_c \leq 2$. We used the delta method, which uses a Taylor series expansion to derive the variance of a function of asymptotically normal random variables with known variance (Powell 2007), to calculate standard errors of back-transformed estimates of daily survival from the top model(s).

The number of fledglings/successful nest could indicate differences in food availability or parental quality. Thus, we used a pooled-variance *t*-test to compare the number of fledged young for successful nests between managed and unmanaged sites.

Fledgling survival.—Fledgling wood thrushes typically disperse up to several kilometers away from their parents and siblings 3–4 weeks after fledging (Anders et al. 1998, Vega-Rivera et al. 1998, Lang et al. 2002). We located most dispersed birds on the managed sites but very few on the unmanaged sites. To avoid confounding management and dispersal status, we restricted our dataset to the time after young fledged from the nest but before they dispersed from the natal territory (Cox et al. 2014). Thus, for each radio-tracked fledgling, we used only observations within 30 days of fledging, and we censored data after the first time a bird moved $\geq$1 km from its previous location because this would likely indicate dispersal. One bird lost its transmitter 1 day after fledging but was resighted afterwards via its color band, so we included this bird in analyses.

As with nests, we used the logistic-exposure model to determine whether fledgling survival differed between managed and unmanaged landscapes. We suspected that force-fledging would negatively affect post-fledging survival (Streby et al. 2013). Thus, we modeled the survival of force-fledged wood thrushes as a linear-logistic function of age but survival of fledglings that remained in the nest and fledged normally was considered constant over time. This model, with an age by force-fledging interaction, received the strongest support in a large set of candidate models (Akaike weight $= 0.92$) and fit the data well (Hosmer-Lemeshow test: $P = 0.49$; Supporting Data S1, available online in Supporting Information). Exploratory analyses revealed that other model formulations, without the age by force-fledging interaction, had $\Delta AIC_c > 10$ and fit the data poorly (Supporting Data S1). As a result, we used this model as the starting point for our analysis of management effects on post-fledging survival. To ensure that including force-fledged birds did not affect our results, we also conducted a separate analysis of management effects using only birds that were not force-fledged and obtained the same qualitative results.

We considered 3 possible ways that management could affect post-fledging survival: a simple additive affect, an interaction with year (separate management parameters for each year), and an interaction with force-fledging (separate management parameters for normal and force-fledged birds). Because fledglings from the same nest experience similar environments and may move together, their fates are not independent. Consequently, we included a random effect of nest in all models. We used AIC_c to compare the above 3 models with the baseline age by force-fledging model. We made inferences from models with $\Delta AIC_c \leq 2$, but we excluded models that had 1 more parameter than the top model but a larger AIC_c. The additional parameter in such models is uninformative (Burnham and Anderson 2002, Arnold 2010).

The purpose of our study design was to ensure that fledglings in managed landscapes used early-successional habitat, whereas birds in unmanaged landscapes used mature forest. To determine if our design was successful, we quantified coarse-scale habitat usage by fledglings. Using the GIS maps of the study sites, we determined the land cover for each fledgling resighting. Over 99% of observations were in mature forest or early-successional forest. For each fledgling, we determined the proportion of its resightings in early-successional forest, and we compared this value between managed and unmanaged sites with a 2-group *t*-test weighted by the number of observations/bird.

Abundance.—We used N-mixture models to estimate abundance of wood thrush at our point-count sites while correcting for imperfect detection (Royle 2004). Although the validity of using N-mixture models for generating abundance estimates from point count data has been questioned (Barker et al. 2018), N-mixture models do appear to yield valid comparisons of relative abundance (Barker et al. 2018), and are thus sufficient to accomplish our objective of contrasting wood thrush abundance between managed and unmanaged landscapes. These models incorporate separate covariates on abundance and detectability, making them apt for hypothesis testing. Our models used a Poisson distribution for abundance and a logit link for detectability. As above, we used a 2-stage process to select models. First, we used AIC_c to test predictors individually against a constant-only model. For detectability, we had 3 predictors: date (linear), date (quadratic), and observer (there were 2 observers). For abundance, management was our only predictor. Second, for variables that passed the pre-screening, we ran models with all possible combinations of those variables. Because our goal was to make inferences about management, we used model averaging to estimate the unconditional mean and standard error of the management parameter.

Population growth rates.—We used our estimates of nest success and post-fledging survival to estimate population growth rates (λ) for wood thrush on managed and unmanaged sites. We pooled nest success and post-fledging survival estimates across years because of the lack of support for year effects in the candidate models for both measures. We estimated λ as:

$$\lambda = S_{ad} + S_{jp} \times S_{jw} \times f$$

where s_{ad} is adult annual survival, s_{jp} is post-fledging survival to 30 days, s_{jw} is survival of fledglings from 31 days

post-fledging until they return to the breeding grounds as yearlings, and f is seasonal productivity, measured as female fledglings/female. We took s_{jp} from our data. We estimated s_{ad} and its standard error as the mean of 3 values from the literature (Savidge and Davis 1974, Powell et al. 2000, Evans et al. 2011). Because no estimates are available for s_{jw}, we estimated λ as a function of possible values of s_{jw}. We estimated f via a day-by-day simulation of reproductive behavior and nest survival for a population of 1,000 pairs, similar to that of Powell et al. (1999). We took estimates of fecundity and nest success from our data, and we obtained estimates of other breeding parameters from the literature (Powell et al. 1999, DeCecco et al. 2000, Powell and Knutson 2006, Evans et al. 2011). Where we found >1 published estimate for a parameter, we used the mean, but we made an exception for the probability of double-brooding. Available estimates of rates of double brooding cited in Evans et al. (2011) were derived from studies in Ontario, Canada and Pennsylvania, USA, which are at a similar latitude to our study site, and Delaware, USA, which is farther south. To account for potential geographic variation, we ran our model with 3 different levels (0, 0.45, and 0.9) for the probability of beginning a new brood after fledging a first brood, encompassing the range of reported values (Evans et al. 2011). For each double-brooding value, we ran the model 900 times and used the mean and standard deviation of the distribution of f values in our λ analysis. We estimated standard errors for λ with standard formulas for the variance of the sum or product of random variables. We report all results as mean ± 1 standard error.

RESULTS

We monitored 58 nests for 818.5 exposure days on unmanaged sites and 53 nests for 858 exposure days on managed sites. In pre-screening variables predicting nest survival, no individual variable, including management, improved the $QAIC_c$ of a constant-only model (Supporting Data S2). Moreover, the parameter estimate for the management effect was not significantly different from zero. As a result, we conclude that nest success did not differ between managed and unmanaged sites. For all nests, daily nest survival was 0.980 ± 0.003 using the top model; this translates to interval survival of 0.57 ± 0.06 for the nesting period. The number of fledglings/successful nest did not differ between managed (3.11 ± 0.15 fledglings, $n = 28$) and unmanaged sites (2.95 ± 0.21 fledglings, $n = 21$; $t_{47} = 0.62$, $P = 0.54$).

We radio-tracked 97 fledglings, 64 from managed sites and 33 from unmanaged sites. We found no evidence that management affected post-fledging survival. The baseline age by force-fledging model was the top model, with weight = 0.81, implying strong support (Table 2). The model with an additive effect of management had $\Delta AIC_c = 1.73$, which indicates that the management parameter was uninformative. Also, parameters for management effects were not significantly different from zero in any model. For birds that fledged normally, estimated daily survival was 0.995 ± 0.003, and survival to 30 days after fledging was 0.85 ± 0.05. For force-fledged birds, estimated survival to 30 days was 0.64 ± 0.10. On managed sites, 50.0 ± 4.2% of resighting locations were in early-successional habitat, versus 4.2 ± 1.8% on unmanaged sites ($t_{88} = 6.83$, $P < 0.001$).

We conducted 129 point counts at 43 points. In the N-mixture models, all variables passed the pre-screening. In the final set of models, 2 of the top 3 models included an effect of management (Table 3). Based on model averaging, wood thrush abundance was greater on managed sites than on unmanaged sites (parameter estimate = 0.53, 95% CI = 0.20–0.86). Estimated abundance was 1.71 ± 0.35 birds/ha on managed sites and 1.01 ± 0.17 birds/ha on unmanaged sites.

Estimated population growth rates were nearly identical between managed and unmanaged sites (Fig. 2). For given values of overwinter survival and double-brooding frequency, the mean difference between managed and unmanaged sites was 0.02, but the mean standard error of λ was 0.15. As expected, λ increased with juvenile overwinter survival (s_{jw}) and the probability of double-brooding. For most values of s_{jw}, λ estimates were >1, indicating that both managed and unmanaged sites were sources unless juvenile survival is extremely low.

DISCUSSION

Contrary to reports that wood thrushes are negatively affected by edges and canopy openings in more fragmented landscapes (Robbins et al. 1989, Robinson et al. 1995, Rosenberg et al. 2003), the creation of early-successional habitat via forestry did not affect nest survival, fecundity, or post-fledging survival of wood thrushes in our extensively forested landscapes. Some studies of forest birds reported

Table 2. Results for models predicting post-fledging survival of wood thrushes studied on managed and unmanaged landscapes in western Massachusetts, USA, 2011–2012. All models had a force-fledging by age interaction (FF × age).

Model	Log likelihood	K[a]	AIC_c[b]	ΔAIC_c	χ^2	P[c]
FF × age	−77.90	4	163.85	0.00	7.41	0.49
FF × age + management[d]	−77.75	5	165.57	1.73		
FF × age × management	−77.63	6	167.37	3.52	13.01	0.11
FF × age + management × year	−77.59	7	169.33	5.48	15.00	0.06

[a] Number of parameters in the model.
[b] Akaike's Information Criterion corrected for small sample size.
[c] χ^2 and P value are from the Hosmer-Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1980).
[d] We did not evaluate the model because the management parameter was uninformative.

Table 3. Results for N-mixture models of wood thrush abundance from point count data collected on managed and unmanaged landscapes in western Massachusetts, USA, 2011 and 2012.

Parameters in model							Management effect	
Abundance	Detection	Log likelihood	AIC_c[a]	K[b]	ΔAIC_c	w_i[c]	Estimate	SE
Management	Day (quadratic) + observer	−137.04	288.41	6	0.00	0.29	0.48	0.05
Constant	Day (quadratic) + observer	−138.52	288.65	5	0.24	0.25		
Management	Day (linear) + observer	−139.19	290.01	5	1.60	0.13	0.48	0.15
Constant	Day (linear) + observer	−140.73	290.52	4	2.10	0.10		
Management	Day (linear)	−140.97	290.99	4	2.58	0.08	0.71	0.02
Management	Day (quadratic)	−139.94	291.51	5	3.09	0.06	0.75	0.31
Constant	Observer	−142.61	291.84	3	3.43	0.05		
Management	Observer	−141.79	292.64	4	4.22	0.03	0.35	0.01
Constant	Day (linear)	−145.50	297.61	3	9.19	0.00		
Constant	Day (quadratic)	−144.85	298.75	4	10.34	0.00		
Constant	Constant	−149.08	302.46	2	14.05	0.00		

[a] Akaike's Information Criterion corrected for small sample size.
[b] Number of parameters in the model.
[c] Akaike weight indicating relative support for the model.

that nest success was lower in forest adjacent to silvicultural openings (King et al. 1996, 1998; Flaspohler et al. 2001*b*; Manolis et al. 2002). Similarly, fledglings of many species, including wood thrushes, select dense habitat such as shrubland created by silviculture (Anders et al. 1998, Vega-Rivera et al. 1998), and the use of shrubland habitat has been reported to increase fledgling survival in some studies (King et al. 2006).

Our finding that the creation of silvicultural openings did not elevate nest predation rates in our managed landscapes is consistent with some previous studies reporting that clearcut borders have little effect on nest success in adjacent mature forests (Hanski et al. 1996, Schmiegelow and Mönkkönen 2002, Gram et al. 2003). Edge-related nest predation may be less pronounced in extensively forested landscapes such as those in our study (Driscoll and Donovan 2004). Nevertheless, a number of studies have reported that nest success of forest birds is lower in forest adjacent to regenerating clearcuts (Manolis et al. 2000*a*). Most studies reporting edge-related nest predation near clearcuts were studies of ground-nesting birds; however, nest success of above-ground nesting species like wood thrushes has generally been unaffected by proximity to clearcut borders (King et al. 1996, Flaspohler et al. 2001*a*, Manolis et al. 2002). Even in cases where nest survival of ground nesting birds is affected by clearcut borders, in extensively forested landscapes the effects on overall productivity is low because they renest readily (King et al. 1996) or compensate with larger clutches (Flaspohler et al 2001*b*).

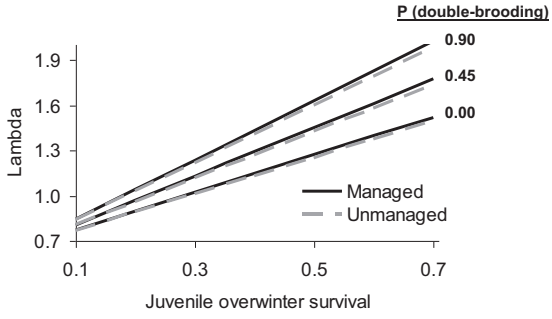

Figure 2. Estimated wood thrush population growth rates (lambda), generated from data collected during 2011 and 2012 on managed and unmanaged sites in western Massachusetts, USA, as a function of juvenile overwinter survival and the probability (P) of double-brooding. Standard errors are not shown for clarity but averaged 0.15, exceeding the difference between managed and unmanaged sites for each value of double-brooding.

Our estimate of daily nest survival (0.980) is among the highest values ever reported for wood thrush (Evans et al. 2011). Similarly, our estimates of seasonal fecundity, from 1.5 to 2.3 fledgling females/pair, are also near the upper limits for this species, though there is uncertainty in the rate of double-brooding (Evans et al. 2011). One factor contributing to high productivity in our study is that a mean of 96% of the land cover within 2 km of study sites was forest. For mature-forest birds, nest success tends to increase with the amount of forest in the surrounding landscape (Robinson et al. 1995, Driscoll et al. 2005). Additionally, cover of developed areas and agriculture each averaged 0.5% around our study sites. These types of land cover can reduce nest success in forest-breeding birds (Porneluzi and Faaborg 1999, Rodewald et al. 2001).

Several past studies have reported that, as on our managed sites, mature-forest birds move into early-successional habitats soon after fledging (Marshall et al. 2003, Vitz and Rodewald 2006, Streby and Andersen 2013). Protection from predators is widely cited as a reason for fledgling birds to select shrubland habitats (Anders et al. 1998, Vitz and Rodewald 2011). Nonetheless, the evidence for a link between use of shrublands and fledgling survival is equivocal. For wood thrushes, Dellinger (2007) reported that survival rates of fledglings did not differ between mature forest, regenerating clearcuts, and thinned stands. On the other hand, King et al. (2006) reported that understory structure was positively associated with the survival of fledgling ovenbirds (*Seiurus aurocapilla*). On our unmanaged sites, fledglings tended to use areas with relatively high foliage densities (S. R. Schlossberg, University of Massachusetts,

unpublished data). Thus, fledgling wood thrushes may have a flexible strategy that allow them to have relatively high survival rates in forests of varying ages.

Predators were responsible for all nest failures and all but 2 fledgling mortalities in our study. Point-count results indicated that abundances of potential nest predators such as corvids and chipmunks (*Tamias* spp.) were not different between managed and unmanaged sites (S. R. Schlossberg, unpublished data). Unlike agriculture or suburban development, silvicultural openings do not appear to provide resource subsidies that lead to increased predator populations (Porneluzi and Faaborg 1999, Rodewald et al. 2001). In forested landscapes, most tests of fragmentation effects on predator abundance or activity have produced negative results (Chalfoun et al. 2002). Thus, creation of early-successional habitat on our study sites appeared to have little effect on predators of wood thrush nests or fledglings, which may largely explain our results.

For wood thrushes in our study, the only observed difference between managed and unmanaged sites was that density estimates were significantly higher in potential wood thrush nesting habitat on managed sites. We acknowledge that managed landscapes have on average 20% less nesting habitat than unmanaged sites (Table 1). Even after accounting for this difference, estimated abundance is still 36% higher on managed sites, suggesting the difference we reported is not merely an artifact of lower abundance of nesting sites on managed sites. Other studies comparing forested landscapes with and without even-aged forest management also report that wood thrushes were more abundant (although not significantly so) in managed landscapes (Thompson et al. 1992, Welsh and Healy 1993). Wood thrushes typically nest in tall shrubs and saplings in the forest mid-story, features stimulated by increased light penetration into forest adjacent to clearcuts and shelterwoods and found within openings themselves as they regenerate. Thus, increased availability of nest sites may have led to increased abundance of wood thrushes on our managed sites.

These results suggest that in extensively forested landscapes, management for early-successional and mature-forest birds is compatible at the levels of management that characterized our study sites. This is consistent with the findings by Powell et al. (2000), who reported that thinning and burning forest understory for red-cockaded woodpecker (*Picoides borealis*) is compatible with viable populations of wood thrush. Similarly, Hamel et al. (2005) suggested that the creation of forest openings for golden-winged warblers (*Vermivora chrysoptera*) could increase canopy diversity to favor cerulean warblers (*Setophaga cerulea*), a mature forest species, within the same stands. Likewise, multi-species studies have reported modest differences in the abundance of mature-forest birds between and unmanaged landscapes and forested landscapes with levels of shrubland habitat similar to ours (~20%; Thompson et al. 1992, Welsh and Healy 1993), with most species exhibiting higher abundance in managed landscapes. Most species that were less abundant in managed landscapes in these studies remained relatively common and no species present in unmanaged landscapes was absent from managed landscapes (Thompson et al. 1992, Welsh and Healy 1993).

MANAGEMENT IMPLICATIONS

Our finding that wood thrushes in managed and unmanaged landscapes had similar levels of reproductive success provides some resolution to the perceived conflict between management of mature-forest birds, which nest in closed-canopy forests, and shrubland species that require habitat with little or no canopy cover. In extensively forested landscapes, such as those that we studied, our results suggest that maintaining target levels of 10–15% of the landscape in the seedling and sapling stages does not significantly harm forest birds. Care should be taken, however, in extrapolating these findings from our extensively forested landscapes to less forested regions with substantial agriculture or development. Driscoll and Donovan (2004) reported lower wood thrush nesting success than we report in landscapes that were still 76% forested but contained extensive agricultural cover. Finally, although we only studied wood thrushes, previous research suggests similar levels of management do not significantly affect abundance or reproductive success of other forest species. Thus, it is likely these findings apply to other forest bird species as well.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.