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DETERMINANTS OF WOOD THRUSH NEST SUCCESS: A MULTI-SCALE, MODEL SELECTION APPROACH

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Abstract: We collected data on 212 wood thrush (*Hylocichla mustelina*) nests in central New York from 1998 to 2000 to determine the factors that most strongly influence nest success. We used an information–theoretic approach to assess and rank 9 models that examined the relationship between nest success (i.e., the probability that a nest would successfully fledge at least 1 wood thrush offspring) and habitat conditions at different spatial scales. We found that 4 variables were significant predictors of nesting success for wood thrushes: (1) total core habitat within 5 km of a study site, (2) distance to forest–field edge, (3) total forest cover within 5 km of the study site, and (4) density and variation in diameter of trees and shrubs surrounding the nest. The coefficients of these predictors were all positive. Of the 9 models evaluated, amount of core habitat in the 5-km landscape was the best-fit model, but the vegetation structure model (i.e., the density of trees and stems surrounding a nest) was also supported by the data. Based on AIC weights, enhancement of core area is likely to be a more effective management option than any other habitat-management options explored in this study. Bootstrap analysis generally confirmed these results; core and vegetation structure models were ranked 1, 2, or 3 in over 50% of 1,000 bootstrap trials. However, bootstrap results did not point to a decisive model, which suggests that multiple habitat factors are influencing wood thrush nesting success. Due to model uncertainty, we used a model averaging approach to predict the success or failure of each nest in our dataset. This averaged model was able to correctly predict 61.1% of nest outcomes.

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Key words: *Hylocichla mustelina*, information–theoretic approach, nest success, New York, statistical modeling, wood thrush.

Nest success is a key component of management strategies for a variety of bird species. The success or failure of a nest to fledge genetic offspring (nest success) has been linked to factors that could be controlled by vegetation management such as local and stand-level habitat features (Barber et al. 2001, Rodewald and Yahner 2001) and landscape habitat features (Donovan et al. 1995*b*, Robinson et al. 1995). Nest success also may be influenced by factors such as food resources (Duguay et al. 2000), water levels (Beissinger and Snyder 2002), predator population sizes (Schmidt and Ostfeld 2003), parasite levels (Trine 2000), exotic species (Gazda et al. 2002), conspecific density (Barber et al. 2001, Sillett and Holmes 2005), spatial arrangement of conspecific nests (Seymour et al. 2003) and heterospecific nests (Roos 2002), and parental behavior (Ford 1999). From a management perspective, a key goal is to identify those factors that enhance habitat quality through management activities.

We compared 9 models of nesting success for a passerine that nests in the U.S. eastern deciduous forest, the wood thrush (*Hylocichla mustelina*). Although multiple factors are known to influence nesting success, we focused on habitat features that may be directly controlled by natural resource managers. Our approach was non-experimental and correlative in nature, and although it identified those habitat features that best described the success or failure of nests, it did not identify the underlying mechanisms responsible for nest success.

Wood thrushes have been widely studied throughout their breeding range (Roth et al. 1996), and the literature provides a rich source of information on natural history that allows researchers to derive meaningful hypotheses regarding nesting success. Because wood thrushes have undergone significant long-term declines rangewide since 1966 (–1.8% ± 0.4% per yr; Sauer et al. 2003), they have become the focus of conservation and management plans for many forested areas (Carter et al. 2000).

Our first 4 models focused on habitat features at or immediately surrounding a nest. Model 1 eval-

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uated the relationship between nesting success and nest concealment (Hoover and Brittingham 1998, Farnsworth and Simons 1999, Flaspohler et al. 2000). Model 2 evaluated the relationship between nest success and the vegetation structure surrounding a nest site (Fauth 2000). Model 3 evaluated whether nest success was higher for nests placed in native species compared to exotic species, as well as evaluating the diversity of tree species surrounding a nest site (Martin 1993, Rotella and Hansen 1998, Schmidt and Whelan 1999*a*). Model 4 focused on properties of the nest site once a nesting tree or shrub was selected and considered factors such as nest height, number of branches used to support the nest, and distance of the nest from the main trunk (Schmidt and Whelan 1999*a*, Rodewald and Yahner 2001).

Our last 5 models focused on landscape-level characteristics surrounding a nest. These models evaluated either the position of the nest in relation to other features (e.g., forest edge habitat) or amounts and arrangements of the forest habitats that surround the nest at a landscape scale. Model 5 evaluated total forest cover surrounding a nest within a 5-km radius (Donovan et al. 1995a, Robinson et al. 1995, Donovan et al. 1997, Dijak and Thompson 2000, Rodewald and Yahner 2001). Model 6 evaluated the importance of core habitat for nesting success. This model did not consider whether a nest was in core habitat, nor did it consider the distance a nest was from core habitat, but instead it evaluated the amount of core habitat within a 5-km radius surrounding a nest, which emphasized total amount and arrangement of forest habitat within the landscape (i.e., the distribution of total forest into edge and core habitat categories). Model 7 built on models 5 and 6 and tested Andren's (1995) hypothesis that the importance of habitat arrangement varies depending on the amount of total habitat in the landscape (Rosenberg et al. 1999, Villard et al. 1999). Model 8 evaluated the relationship between nest success and the linear (unidimensional) distance between a nest and an agricultural edge (Paton 1994, Dijak and Thompson 2000, Lahti 2001, Chalfoun et al. 2002). Finally, model 9 tested an interaction between distance to edge and landscape type, as experimental and meta-analysis studies demonstrated that agricultural–forest edge effects occur more frequently in landscapes with low levels of forest cover than in landscapes with high levels of forest cover (Andren 1995, Donovan et al. 1997, Hartley and Hunter 1998, Driscoll and Donovan 2004).

For many of the studies cited above, researchers examined local scale and landscape scale variables separately, thus they did not utilize all of the available information to build models. In cases where multiple models were evaluated, few researchers analyzed the data in a manner that allowed them to compare the relative strengths of competing models, which made it difficult to determine the importance of each model when compared to others. Comparing relative strengths of competing models is needed from a management perspective because such analyses allow managers to weigh how limited management funds can be allocated to produce the most benefit to breeding wood thrushes.

Our primary objective was, therefore, to follow a model selection protocol to develop and compare 9 statistical models that predict the probability that a wood thrush nest will fledge offspring (Burnham and Anderson 2002). The analysis allowed us to rank and compare models of wood thrush nesting success and to identify habitat variables that could be manipulated to benefit breeding wood thrush populations. Our second objective was to evaluate model selection uncertainty through a bootstrap analysis, which revealed the degree of confidence we could assume for any given model. Our final objective was to use model averaging across the 9 different models to predict the success or failure of a given nest and to assess model error rates.

METHODS

Study Area

We conducted our study from 1998 to 2000 across a 5-county region in central New York (Driscoll and Donovan 2004). The study area consisted of 53% deciduous and mixed deciduous–coniferous forest with varying degrees of fragmentation surrounding forest patches. Agricultural land, parks, and lawns comprised 43% of the land cover with the remaining 4% classified as developed. To select potential study sites we analyzed the National Land Cover Dataset (NLCD; Vogelmann et al. 2001), a spatial database of land cover of the conterminous United States with a 30-m^2 resolution and in which forest pixels are classified as either deciduous, mixed deciduous–coniferous, or coniferous. We resampled the NLCD to a 90-m^2 resolution and reclassified all forest types into a single forest category. We used ArcView to conduct a moving window analysis in which the percent forest cover within 5 km was

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evaluated for each forested pixel in the study area. We selected a 5-km buffer size because a meta-analysis revealed a significant relationship between daily predation rates and forest cover at this scale (Hartley and Hunter 1998). We stratified forested pixels into low (<50%) and high (>65%) percent forest cover classes to ensure coverage of divergent fragmentation levels. Pixels were randomly selected within each stratum for study under the following constraints: they were publicly owned lands on which we were allowed to conduct research and were separated by a minimum of 8 km from other selected pixels. We selected 16 pixels that met our sampling conditions, and study sites were established in areas that surrounded selected pixels.

Sites ranged from 38% to 86% forest cover within a 5-km radius (Driscoll and Donovan 2004). The 16 sites were deciduous and mixed deciduous–coniferous stands comprised predominantly of ashes (*Fraxinus* spp.), hickories (*Carya* spp.), and maples (*Acer* spp.), and they were bounded on at least 1 side by a hard forest–field edge that was often an agricultural edge. Study sites had similar basal area and stem density (Driscoll and Donovan 2004), although these metrics varied around nest locations within a site. Two sites were eliminated from the analysis due to a small number of located nests.

Nest Success

Our dependent variable was nest success, a binary variable that was scored zero if the nest failed and 1 if it fledged 1 or more genetic offspring. In 1998, we searched for nests on 7 of the 16 study sites. In 1999, we located and monitored nests on all 16 study sites, and in 2000, we searched for nests on 6 of the 16 study sites. Three sites were studied for all 3 breeding seasons. Four people searched for nests from early May until late July each year and primarily conducted intensive area searches and utilized behavioral cues (Martin and Geupel 1993). We monitored all nests and recorded detailed descriptions of nest contents every 3 to 4 days until nest fate could be determined. A nest was considered successful if at least 1 wood thrush nestling fledged. If nest fate was uncertain, we followed Trine's (1998) nest decision rules to determine whether the nest succeeded or failed. We located 251 nests for which we could determine nest outcome (i.e., fledged at least 1 young or failed). When possible we assigned a cause of failure (i.e., nest predation, weather, cowbird parasitism) to each failed nest.

Habitat Variables

We measured vegetation directly at the nest and in a 0.04-ha circle centered on each nest site following a modified James and Shugart (1970) method as described by Martin et al. (1996) (Appendix 1). Additional vegetation variables were measured according to BBIRD field protocols for forest systems (Martin et al. 1996). We attempted to collect vegetation data that would be consistent with data collected by other avian ecologists and that might be important for wood thrushes.

Landscape Variables

To assess landscape predictor variables for wood thrush nesting success (models 5, 6, 7, 8, 9), we analyzed the NLCD at its original 30-m^2 resolution. We combined land-cover classes into 1 of the following 7 categories: (1) water (water classification from the original NLCD), (2) lawn (parks, lawns, and low-intensity residential from the original NLCD), (3) developed (high-intensity residential and commercial/industrial/transportation), (4) barren (bare rock and quarry), (5) deciduous (deciduous forest, mixed forest, and woody wetland), (6) evergreen (coniferous forest), and (7) agriculture (pasture, row crop, and emergent herbaceous wetlands). Combining land-cover classes reduced the complexity of the fragmentation analyses and produced a map that we assumed was more reflective of wood thrush breeding habitat. For example, coniferous forest was not combined with other forest types because wood thrushes prefer mixed or deciduous forests for nesting (Roth et al. 1996, Dettmers et al. 2002).

For each of the 16 sites, we used FRAGSTATS (McGarigal and Marks 1995) within the ArcGIS environment (Environmental Systems Research Institute, Redlands, California, USA) to calculate metrics for each land-cover class for a 5-km radius landscape centered on each study site. Although FRAGSTATS can produce a variety of metrics that describe the spatial pattern of pixels within an area, we focused on 2 metrics hypothesized to be important for predicting wood thrush nesting success: total forest area (CA_41; model 5) and total core forest area (TCA_41; model 6). Total forest area included only deciduous and mixed forest types within the landscape in which wood thrushes readily nest. Total core area was the total amount of deciduous and mixed forest >200 m from any habitat boundary, which is a distance determined to be significantly related to wood thrush nesting success in central New York (Driscoll 2000). To evaluate interactions between

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total core area and landscape type (model 7) and interactions between distance to edge and landscape type (model 9), we classified sites into 2 categories based on forest cover metrics, where fragmented sites had ≤50% forest cover in the landscape and contiguous sites had >65% forest cover in the landscape. No sites had forest cover between 51 and 65% (Driscoll and Donovan 2004). Distance to the closest nonforest edge was measured remotely on the GIS map for nests >100 m from an edge. These nests had a ±30-m error due to the limited resolution of the land-cover data. For nests within 100 m of an edge, distance to the nearest edge was measured by pacing.

Statistical Analysis

We followed the information–theoretic approach outlined by Burnham and Anderson (2002) to build and evaluate the 9 nest-success models. This approach estimates the Kullback and Leibler (1951) distance between reality (f) and each of the 9 nest-success models. Although the true model (f) is unknown, the distance a given model is from the true model can be estimated through Akaike's information criterion (AIC), where models with lower AIC scores are closer to the true model (Akaike 1973).

We built 9 statistical models that corresponded to the 9 models identified previously, where the dependent variable was the success or failure of a nest, and the predictor variables included habitat conditions for each nest. For each model, we first identified all predictor variables that might be important in predicting wood thrush nest success (Appendix 1). We eliminated nests with missing data for any of these variables from the analysis, which reduced our sample size to 212 nests. We evaluated correlations among the potential predictor variables within a model and dropped those that were highly correlated with other variables or combined them with others as suggested by Burnham and Anderson (2002).

Once a final set of predictor variables was determined for each of the 9 models (Appendix 1), we used likelihood-ratio chi-square tests to assess goodness-of-fit on a global model that included all predictor variables across the 9 models where the dependent variable was dichotomous (i.e., fledged or failed). We used the GENMOD procedure in SAS (1999) because it allowed analysis of clustered data such as nests located within the same study site. This approach was necessary because conventional logit models assume that observations (i.e., nests) are independent, and failure to take correlations among observations into account can lead to biased standard errors and test statistics (Allison 1999). Our clustered nest data clearly violated this assumption, and at the time of analysis we were unaware of other statistical methods which handled non-independence of nests. Therefore, we invoked the generalized estimating equations method within GENMOD to account for clustered nests within a site.

A potential bias in estimating nest success may occur, however, if nests fail at different rates depending on the number of days in which nests are observed (Mayfield 1961), or if nest failure is a function of covariates such as date of initiation (Dinsmore et al. 2002). However, the proportion of successful nests in a study site (estimated as total success divided by total nests) was consistent with the nest-success rates computed from Mayfield exposure models (χ^2 = 15.3, 14 df, P = 0.35). Weighted regression analysis of the 2 different nest-success measures indicated that the proportion of successful nest estimates was, on average, ~0.14 higher than the Mayfield nest-success estimates, but the slope of the regression line was not different from 1 (t = –0.4, 12 df, P = 0.69, 95% confidence intervals for slope = 0.85–1.11). Although new methods are needed to assess more thoroughly non-independent observations, these results suggest that this potential bias was relatively small.

The goodness-of-fit analysis for the global model indicated that the data fit the model well (deviance for full model = 272.96, deviance for null model = 293.42 yielding a likelihood-ratio chi-square of 20.46 that was statistically significant at the α = 0.05 level). We also ran diagnostic tests on the full model to examine residuals and influential data points. No remedial actions were required, and the data were not overdispersed (Pearson chi-square/df = 1.05), suggesting that the deviance was about 5% larger than the degrees of freedom, which is a statistically nonsignificant result.

We then evaluated each of the 9 models separately with the same GENMOD procedure. For each model evaluated, we used AIC (with a correction for small sample sizes, AIC_c) to approximate the Kullback–Leibler distance. The model for which AIC_c was minimal was selected as the most parsimonious model of the 9 models evaluated. AIC_c scores for each model were rescaled (Δ_i) by computing the difference in the AIC_c score between a model of interest, and the best-fit model such that the best-fit model had Δ_i = 0. Models with Δ_i < 2 were interpreted as having substantial support, models with Δ_i within 3–7 units of the best model were interpreted to have less

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support, and models with $\Delta_i > 10$ were considered to have little support. We then computed the weight of evidence for each model by normalizing the rescaled AIC_c scores (Δ_i) such that the weights added to 1. These weights were interpreted as probabilities. For example, we interpreted a model with a normalized weight of 0.65 to have a 65% chance of being the best Kullback–Leibler model among the 9 models considered.

To evaluate model selection certainty, we used a bootstrap analysis to randomly sample 212 nests with replacement from the original data of 212 nests and repeated the model selection analysis as follows: we computed AIC_c scores for each of the 9 models, ranked the models, and computed AIC weights for each model. We repeated this analysis 1,000 times and then recorded the AIC_c rankings of each model for each trial (Burnham and Anderson 2002). This allowed us to determine, for example, if a particular model was always selected, or if it was selected only in a portion of bootstrap samples. The bootstrap analysis also allowed us to compute 95% confidence intervals for the parameter estimates of each model.

We then used the model averaging approach advocated by Burnham and Anderson (2002) to determine a predicted probability of fledging for each nest. First, we computed the predicted probability of successfully fledging young for each nest for each of the 9 models. Second, we weighted each model's probability by its corresponding bootstrap frequency (i.e., the frequency in which a model was ranked first in the 1,000 bootstrap trials). Third, we summed the weighted probabilities across the 9 models to produce the model averaged probability for each nest in the dataset. The model averaged probability for each nest was then categorized as either predicted to fledge or predicted to fail based on a given cut-point probability above which nests were predicted to fledge and below which nests were predicted to fail. These predictions, which were derived from bootstrap weights, were then compared to the actual data. We tallied true positives (nests predicted to succeed that actually succeeded), true negatives, commission errors (nests predicted to succeed that actually failed), and omission errors (nests predicted to fail that actually succeeded). We examined 29 different cut-points and selected the cut-point value in which classification errors were minimized.

RESULTS

Slightly more than half of the 212 nests monitored failed (111; 52%). The remaining 48% fledged. Most (89%) of the unsuccessful nests were depredated. The best-supported model of the 9 considered was model 6, which evaluated the total forest core habitat within 5 km of a nest (Table 1, primary analysis). This model had an $AIC_c = 292.73$ and an AIC weight of 0.34, indicating that this model had a 34% chance of being the best K–L model of the 9 models analyzed. The 95% confidence interval for the core area (TCA_41) parameter was above zero, and the model indicated that increasing core habitat by 100 ha increased the probability that a nest will successfully fledge young (Table 1, bootstrap averages) by approximately 0.02.

Models 8, 2, and 5 were ~2.00 AIC_c units from model 6 and had AIC weights between 0.12 and 0.16, which suggested support for these models as well (Table 1, primary analysis). Parameter estimates from model 8 supported the hypothesis that nests farther from forest–field edges were more likely to fledge offspring. Parameter estimates from model 2 suggested that nests surrounded by trees with a variety of diameter classes were more likely to fledge offspring. Parameter estimates from model 5 suggested that increasing forest cover in the landscape by 100 hectares increased the probability of nest success by about 0.004.

Models 7 and 9 had the lowest deviance score of all models, suggesting they fit the data well. However, both models had the greatest number of parameters to estimate ($k = 4$) due to the need to estimate slope and intercepts for fragmented and contiguous sites, which increased their AIC_c scores because of the 2k penalty in the AIC_c computation (Akaike 1973). However, confidence intervals for both of these interaction terms included zero, suggesting that the main effect of core habitat and main effect of distance to edge were driving the model results. The remaining models had less support ($\Delta_i > 2.9$ and AIC weights < 0.10). Thus, 4 variables were significant predictors of nesting success for wood thrushes: (1) total core area within 5 km of a study site, (2) distance from nest to forest–field edge, (3) total forest area within 5 km of the study site, and (4) density and variation in diameter of trees and shrubs surrounding the nest.

Bootstrap Results

Bootstrap results suggested much uncertainty in the model rankings, but they generally mimicked the rankings from the original analysis with a few notable exceptions. Model 6 (core area) was ranked the best model in 23.9% of the bootstrap

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Table 1. Model selection results of wood thrush nesting success in relation to various habitat features, central New York, USA, 1998–2000. Columns under primary analysis are results of original data analysis of 212 nests. Columns under bootstrap analysis give the average results based on 1,000 bootstrap trials.

		Primary analysis								Bootstrap analysis						
Model	Predictors	Parameter	LCI	UCI	*k*	Deviance	AIC_c	Δ_i	Rank	Weight	Parameter	LCI	UCI	Deviance	AIC_c	Δ_i	Rank	Weight
1	Intercept	−0.4925	−0.9655	−0.0194	2	291.57	295.63	2.90	5	0.08	−0.4675	−0.9955	0.0726	265.67	269.72	2.98	7	0.06
	Conceal	0.0084	−0.0014	0.0182							0.0074	−0.0025	0.0164					
2	Intercept	−0.9613	−1.9686	0.0460	3	288.61	294.73	2.00	3	0.13	−0.9858	−1.7101	−0.2425	261.85	267.96	1.22	2	0.15
	Trees	0.0223	−0.0086	0.0532							0.0220	−0.0001	0.0434					
	DBH Std Trees	0.0120	0.0017	0.0224							0.0125	−0.0014	0.0294					
3	Intercept	−0.6666	−1.6121	0.2789	3	290.69	296.81	4.08	8	0.04	−0.6719	−1.3474	−0.0254	263.71	269.82	3.08	8	0.06
	Substrate	0.2481	−0.4984	0.9947							0.1985	−0.7261	1.1105					
	Treerich	0.0431	−0.0202	0.1064							0.0418	−0.0027	0.0857					
4	Intercept	−0.0033	−0.3414	0.3348	3	292.16	298.27	5.54	9	0.02	0.0213	−0.4472	0.5466	265.37	271.49	4.75	9	0.02
	NestHt	−0.0168	−0.0374	0.0038							−0.0262	−0.1688	0.1088					
	Main	−0.0001	−0.0013	0.0011							−0.0001	−0.0023	0.0023					
5	Intercept	−1.0377	−2.1571	0.0818	2	290.72	294.77	2.04	4	0.12	−1.0763	−2.0724	−0.0902	264.63	268.68	1.94	5	0.10
	CA_41	0.0002	0.0000	0.0004							0.0002	0.0000	0.0005					
6	Intercept	−0.4573	−0.9217	0.0071	2	288.67	292.73	0.00	1	0.34	−0.4655	−0.8513	−0.0862	262.68	266.74	0.00	1	0.27
	TCA_41	0.0007	0.0002	0.0011							0.0007	0.0002	0.0012					
7	Intercept	−0.7386	−1.7781	0.3008	4	288.23	296.43	3.70	6	0.05	−0.7625	−1.7343	0.1606	260.20	268.39	1.65	4	0.12
	TCA_41*Land	0.0005	−0.0051	0.0060							0.0002	−0.0041	0.0046					
8	Intercept	−0.3000	−0.6485	0.0485	2	290.18	294.23	1.50	2	0.16	−0.3336	−0.6300	0.0114	264.03	268.08	1.34	3	0.14
	Edge	0.0007	0.0001	0.0013							0.0108	0.0102	0.0114					
9	Intercept	−0.1000	−0.5609	0.3592	4	288.61	296.80	4.07	7	0.04	−0.0966	−0.6347	0.4683	260.84	269.04	2.30	6	0.09
	Edge*Land	0.0017	−0.0011	0.0046							0.0016	−0.0010	0.0041					

trials, and ranked either first, second, third, or fourth in 78.6% of the bootstrap trials (Table 2). Model 2 (vegetation structure) was ranked the best model in 23.3% of the bootstrap trials, and was ranked first–fourth in 52% of the bootstrap trials. Model 8 (distance to edge) was ranked first in 12% of the trials and was most commonly ranked fourth across trials. Model 5 (total forest), which appeared to be supported by the original analysis, was ranked first in only 2.7% of the bootstrap trials and was most frequently ranked fifth across trials. The remaining models (nest concealment, exotic substrate, nest-site characteristics, and the 2 interaction models) were most frequently ranked eighth or ninth, suggesting they had little influence on the probability of nest success.

Model Averaging

Due to model uncertainty, we used model averaged estimates to predict the success or failure of a given nest. This procedure generated a probability that a nest would succeed based on information from all models. We used a cut-point of 0.47. This cut-point was selected because it balanced omission and commission errors. Nests with a model averaged probability of fledging >0.47 were predicted to successfully fledge, and nests with a model averaged probability of fledging <0.47 were predicted to fail. With this cut-point, the averaged model was able to correctly predict 61.1% of nest outcomes: 29.2% of nests predicted to fledge offspring did so, 32.1% of nests predicted to fail did so, 18.4% of nests predicted to succeed actually failed, and 20.3% of nests predicted to fail actually succeeded.

DISCUSSION

Core habitat was the most parsimonious model of the model set we considered. Because nest predation was the most common cause of nest failure, this result suggests that core habitat is in some way correlated with predator abundance or behavior.

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Table 2. Results of rankings of wood thrush nest success models based on 1,000 bootstrap trials, central New York, USA, 1998–2000. Numbers are percentages of trials in which each model was ranked 1 through 9. For example, the forest core model (model 6) was ranked first in 23.9% of the bootstrap trials.

	Model								
	Conceal	Structure	Substrate	Nest Site	Forest	Core	Core*Land	Edge	Edge*Land
Rank	1	2	3	4	5	6	7	8	9
1	12.7	23.3	7.0	3.0	2.7	23.9	9.2	12.0	6.2
2	6.2	13.5	11.4	3.8	7.3	21.3	11.8	13.2	11.5
3	8.2	8.2	6.8	4.3	15.7	19.4	13.4	13.9	10.1
4	9.3	7.7	8.4	4.3	18.1	14.0	12.1	15.9	10.2
5	11.1	7.7	7.1	5.1	20.9	9.4	11.7	15.4	11.6
6	13.4	11.1	9.9	10.3	15.1	7.2	7.9	14.4	10.7
7	13.2	12.0	14.2	14.6	13.3	3.5	8.9	10.6	9.7
8	16.8	10.1	17.9	22.7	5.6	1.1	11.0	3.8	10.9
9	9.1	6.4	17.3	31.8	1.2	0.2	14.0	0.8	19.1

The evidence ratios of the next 3 most supported models, measured by examining the ratios of AIC weights, were >2, suggesting that the core model was over 2 times more likely to be the best K-L model when compared to other models. This result is not new, but our results highlight its importance for nest success in comparison to alternative habitat features. Core habitat has been thought to be a consideration when managing for viable populations of area-sensitive species (Temple and Cary 1988, Donovan and Lamberson 2001), and several empirical studies found correlations between nest success and the amount of core habitat at a landscape scale (Donovan et al. 1995*b*, Robinson et al. 1995). However, because landscape metrics such as amount of core habitat are often highly correlated with other metrics (Bissonette 1997), it is difficult to determine whether the arrangement of forest habitat into core and edge can be a mechanism that strongly influences predator abundance or behavior or if it is a correlate of another mechanism. Some studies suggest that the total amount of forest cover in a landscape mediates the abundance of nest predators, such that mammalian predators like raccoons (*Procyon lotor*), skunks (*Mephitis mephitis*), and Virginia opossums (*Didelphis virginiana*), and avian predators like the American crow (*Corvus brachyrhynchos*) and blue jay (*Cyanocitta cristata*) are more abundant in landscapes with low forest cover (Burke and Nol 1998, Dijak and Thompson 2000). However, for a given amount of forest cover, the influence of core habitat on these predator abundances is still unclear.

The primary results suggest edge effects were operating in our system with nests further from a forest–field edge exhibiting higher probabilities of succeeding. Additionally, the deviance score for the edge by landscape interaction model was among the lowest in the model set, suggesting that edge effects are magnified in fragmented landscapes compared to more forested landscapes (Driscoll and Donovan 2004). We also found some evidence that increasing the density of trees and stems surrounding a nest can increase the probability of successful fledging, a result that was generally confirmed by other investigators (Hoover and Brittingham 1998, Farnsworth and Simons 1999, Fauth 2000, Artman and Downhower 2003). Structural properties of a habitat are known to influence movements of predators. For example, Bowman and Harris (1980) experimentally demonstrated that structural complexity of vegetation influences predation rates by raccoons where nests within more diverse and heterogeneous habitats experienced lower predation rates compared to nests within less diverse and spatially homogeneous habitats.

Although our analyses suggest core habitat, distance to edge, and vegetation structure are important habitat correlates of nest success, 3 caveats are important to consider. First, by definition, the model selection process we used ranked the 9 habitat models we hypothesized as being important for wood thrush nest success. Models not in the candidate set, such as density of other wood thrushes or other open-cup nesters, food abundance, and parental experience and behavior were not considered or ranked.

Second, our methods evaluate the probability that a given nest will fail or fledge wood thrush offspring. Nest failure does not indicate a per capita birth rate of zero; birds can renest after a failure (Pease and Grzybowski 1995, Schmidt and Whelan 1999*b*) and can initiate second or third broods if previous nests are successful. Color-banding studies of wood thrushes show that birds can have up to 4 nest attempts per reproductive

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season (Fauth 2000) and can raise up to 3 broods in ideal circumstances (Roth et al. 1996, Friesen et al. 2001). Thus, the failure of a particular nest may not influence the final number of offspring produced per breeding season unless high nest failure rates are persistent across the season.

Third, in addition to birth and death rates, a PVA analysis requires information on the distribution of birds among habitats that vary in quality (Donovan and Thompson 2001, Donovan and Flather 2002), which we did not assess. From an evolutionary perspective, Murray (2000) points out that even differences in annual reproductive success do not necessarily translate into evolutionary success. The bottom line is that our results suggest that core habitat and heterogeneous forest structure should improve wood thrush nesting success and must be considered in light of other demographic variables for long-term population maintenance.

MANAGEMENT IMPLICATIONS

Our results suggest that wood thrushes will fare better in landscapes with more core habitat and that managers should focus on core habitat more than simply forest cover. Increasing the amount of forest core area by 100 hectares would increase nest success by 0.02 in our system, whereas increasing forest cover by 100 hectares in the landscape would increase nest success by only 0.004. Based on AIC weights, enhancement of core area is likely to be a more effective management option than any other habitat-management options we explored. However, the bootstrap results suggest that the success or failure of a nest may be due to a complex variety of habitat factors as well as factors that were not explored in this study. Management of core habitat may serve as a coarse-filter approach (Hunter 1996) to maintaining or enhancing wood thrush nest success, and presumably the nest success of other forest nesting passerines, in the northeastern United States.

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Appendix 1. List of wood thrush nest-site, habitat, and landscape predictor variables and description of field methodology, central New York, USA, 1998–2000.

Model no.	Model name	Predictor variables	Predictor variable description	How measured	Protocol reference	Fate of variable
1	conceal	over	overhead concealment of nests	% cover in 1-m circle 1 m above nest	Martin et al. 1996	used in metric called "conceal"
1	conceal	avgnest	avg. side concealment of nests	average % cover in 1-m circle 1 m in each of cardinal directions of nest	Martin et al. 1996	used in metric called "conceal"
1	conceal	conceal	avg. total concealment	conceal = (over+avgnest)/2		used in final model
2	structure	denall	density of rooted stems (#/ha) 0–10 cm dbh	transects		used in metric called "trees"
2	structure	tottree	total number of trees surrounding nest	trees selected with a 10 factor prism at nest location	Donovan et al. 1997	used in metric called "trees"
2	structure	dbhmean	avg. dbh of trees surrounding nest	trees selected with a 10 factor prism at nest location	Donovan et al. 1997	dropped due to significant correlations with other model variables
2	structure	dbhstd	avg. standard deviation of trees surrounding nest	trees selected with a 10 factor prism at nest	Donovan et al. 1997	used in final model
2	structure	allcancv	canopy coverage of forest surrounding nest	avg. of 4 densiometer readings taken at nest site location	Martin et al. 1996	dropped due to lack of variation among nests
2	structure	trees	avg. total trees regardless of size	harmonic mean of denall and tottree		used in final model
3	substrate	substrate	exotic or native status of the nesting substrate	categorical: nest trees identified to species and classified as native or exotic	Schmidt and Whelan 1999	used in final model
3	substrate	stemsi	diversity of rooted stems surrounding nest	stems intercepted in 4 5*2m transects from nest center		dropped due to significant correlation with treerich
3	substrate	treerich	diversity of trees surrounding a nest	Shannon-Weiner diversity index of all trees selected with a 10 factor prism at nest location		used in final model
4	character	nstht	nest height	height of nest from ground in meters	Martin et al. 1996	used in final model
4	character	pltht	plant height	height of nest substrate from ground in meters	Martin et al. 1996	dropped due to low variation among nests
4	character	brch	no. of branches supporting nest	no. of branches supporting a nest	Martin et al. 1996	dropped due to low variation among nests
4	character	main	distance in m from the main stem of nest tree	distance from main stem of nest substrate to nest	Martin et al. 1996	used in final model

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Appendix 1. continued.

Model no.	Model name	Predictor variables	Predictor variable description	How measured	Protocol reference	Fate of variable
5	total forest	ca_41	total forest cover	amount of deciduous and mixed deciduous forest within 5-km radius of study site		used in final model
6	core	tca_41	total forest core area	amount of deciduous and mixed deciduous forest beyond 200 m of an edge, measured within a 5-km radius of a study site		used in final model
7	land*core	land	landscape type: fragmented or contiguous	based on total forest cover		used in final model
7	land*core	tca_41	total forest core area			used in final model
8	distance edge	aerial	linear distance to forest field edge	distance to nearest field as measured on ArcView or by pacing		used in final model
9	land*edge	land	landscape type: fragmented or contiguous	based on total forest cover		used in final model
9	land*edge	edge	linear distance to edge	distance to nearest field as measured on ArcView or by pacing		used in final model

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