

Effects of spatial habitat heterogeneity on habitat selection and annual fecundity for a migratory forest songbird

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Abstract Understanding how spatial habitat patterns influence abundance and dynamics of animal populations is a primary goal in landscape ecology. We used an information-theoretic approach to investigate the association between habitat patterns at multiple spatial scales and demographic patterns for black-throated blue warblers (*Dendroica caerulescens*) at 20 study sites in west-central Vermont, USA from 2002 to 2005. Sites were characterized by: (1) territory-scale shrub density, (2) patch-scale shrub density occurring within 25 ha of territories, and (3) landscape-scale habitat patterns occurring within 5 km radius extents of territories. We considered multiple population parameters including abundance, age ratios, and annual fecundity. Territory-scale shrub density was most important for determining abundance and age

ratios, but landscape-scale habitat structure strongly influenced reproductive output. Sites with higher territory-scale shrub density had higher abundance, and were more likely to be occupied by older, more experienced individuals compared to sites with lower shrub density. However, annual fecundity was higher on sites located in contiguously forested landscapes where shrub density was lower than the fragmented sites. Further, effects of habitat pattern at one spatial scale depended on habitat conditions at different scales. For example, abundance increased with increasing territory-scale shrub density, but this effect was much stronger in fragmented landscapes than in contiguously forested landscapes. These results suggest that habitat pattern at different spatial scales affect demographic parameters in different ways, and that effects of habitat patterns at one spatial scale depends on habitat conditions at other scales.

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Introduction

A central goal in landscape ecology is to understand how the spatial pattern of habitat influences the abundance and dynamics of natural populations

(Turner 1989). Given the rate at which human-induced changes are altering patterns of biodiversity across the globe, information about the landscape patterns that influence abundance and fitness is crucial for species preservation. Songbirds have long served as model organisms in studies investigating habitat associations and the consequences of changing environments (Ambuel and Temple 1983; Cody 1985). As the result of these studies, we now know that birds, in general, respond to the composition and configuration of habitats (i.e., habitat pattern) at multiple spatial scales (Hildén 1965; Orians and Wittenberger 1991), including territory, patch, and landscape scales (Rolstad 1991). Here, we define these spatial scales as (1) territory-level habitat patterns measured within a 5 ha area, (2) patch-level habitat patterns measured within 25 ha area surrounding a breeding territory, and (3) landscape-level habitat patterns measured within a 5 km radius extent surrounding a breeding territory (based on relevance to our focal species and for small forest breeding migratory passerines; see below).

Numerous studies have examined how habitat features at these scales independently affect the distribution of birds (i.e., pattern; Thompson et al. 2002). At the territory scale, the density and arrangement of vegetation within a home range may influence the availability and selection of nest sites (Walsberg 1981; Rodrigues 1994). At the patch scale, vegetation composition and structure (e.g., the abundance of shrubs or trees) have been shown to influence territory occupancy and density (James 1971; Wiens and Rotenberry 1981; Cody 1985). At the landscape scale, for forest-nesting passerines in particular, population density often declines as the total amount of habitat cover in a landscape declines (Whitcomb et al. 1981), pairing success tends to be lower on small isolated patches (Villard et al. 1993; Bayne and Hobson 2001), and first-year breeders tend to dominate such populations (Richards 1999; Bayne and Hobson 2001). In some cases, the arrangement of habitats within a landscape is an important predictor of abundance, particularly when the amount of habitat cover is low (e.g., Andren 1994; McGarigal and McComb 1995; Trzcinski et al. 1999).

Although the effects of habitat structure on distribution patterns of songbirds are well established, fewer studies have examined how habitat features at different spatial scales influence vital demographic

parameters, such as annual fecundity (i.e., the total number of offspring fledged per adult female per year). Most studies typically investigate demographic parameters at a single spatial scale or in isolation. For example, shrub density within a territory may be positively correlated with food abundance, thus influencing annual fecundity (Rodenhouse et al. 2003). Nest concealment can influence the likelihood of brood parasitism by brown-headed cowbirds (*Molothrus ater*) and nest depredation (e.g., Flaspohler et al. 2000; Budnik et al. 2002), two mechanisms that directly affect annual fecundity of many songbirds. Patch-scale studies also show that nest predation and parasitism rates are influenced by the vegetation structure of a localized area (reviewed in Thompson et al. 2002). For instance, shrub density influences how nest predators move through a localized environment, potentially affecting predation rates within a habitat patch (Bowman and Harris 1980). Finally, landscape-scale investigations in eastern North America have shown that nest survival decreases and brood parasitism levels increase as landscapes become more fragmented (e.g., Donovan et al. 1995; Robinson et al. 1995; Hochachka et al. 1999). Additionally, food resources for nesting songbirds can be lower in fragmented habitats (Burke and Nol 1998; Zanette et al. 2000). From these studies, it is likely that territory-, patch-, and landscape-scale habitat structure are all important factors that shape demographic rates.

Yet, a firm understanding of how habitat patterns at multiple spatial scales affect forest bird population demography has not yet been synthesized. This inability is likely the result of several factors. First, different studies use different methodological approaches and evaluate different spatial scales, making comparisons among studies difficult. Second, local songbird populations are influenced by factors occurring at scales much larger than the patch-scale, where populations can be structured as sources and sinks (Pulliam 1988) or metapopulations (Hanski and Simberloff 1997). Third, the effects of habitat features at one spatial scale may depend on habitat conditions at other scales (Rodenhouse et al. 2003). Studies that examine such interactions among habitat features across scales are lacking (Turner 2005), mainly due to logistical difficulties in acquiring demographic data across multiple scales simultaneously.

To address some of these shortcomings, we evaluated the association between habitat patterns at

territory, patch, and landscape scales and several different demographic parameters for the black-throated blue warbler (*Dendroica caerulescens*) at twenty study sites in west-central Vermont, USA. Our objectives were to: (1) Use an information-theoretic analysis approach to assess and compare twelve models representing univariate, additive, and interactive combinations of territory-, patch-, and landscape-scale habitat patterns for three vital population parameters: abundance, age ratios, and annual fecundity; and (2) identify the most important spatial scale(s) affecting each demographic parameter, and determine how habitat conditions at one scale may affect demography differently depending on habitat conditions at another scale.

Study species

The black-throated blue warbler is common to forest patches across many different landscape types throughout Vermont, which facilitates analysis of abundance and demographic patterns across the landscape. This species is sexually dichromatic and highly territorial; males sing to defend exclusive territories that typically ranging in size from 1 to 4 ha during the breeding season (Holmes et al. 2005). Thus, males are easily counted based on vocalizations, can be captured in mist-nests, and banded for individual identification. Females build nests in understory shrubs, and can therefore be flushed from nests after 6 days of incubation, captured, and banded. Easy access to nests also allows for accurate assessment of annual fecundity. Breeding pairs can successfully raise two broods of young in a single breeding season.

Black-throated blue warbler population demography in a large, unfragmented temperate forest, is well studied (Holmes et al. 1996; Sillett and Holmes 2002; Holmes et al. 2005). Long-term research on this species shows that the most productive breeding territories have high shrub density, low nest predation rates, and high food abundance (Steele 1992; Rodenhouse et al. 2003). Further, annual fecundity rates decline as population size increases due to despotic interactions which force some birds into suboptimal habitats (Sillett et al. 2004; Rodenhouse et al. 1997). Recruitment of first-year breeders into the population each spring is positively correlated with fecundity in the previous year (Sillett et al. 2004). Little is known,

however, about how landscape-scale habitat patterns affect warbler demography, and whether landscape pattern alters the importance of territory and patch habitat features on demography.

Study sites

We conducted field research from May to August 2002–2005 at 20 forested sites in Chittenden and Addison counties, Vermont, USA (Fig. 1). We chose study sites based on accessibility to forest patches that offered potential breeding habitat and the presence of at least one black-throated blue warbler territory (i.e., one singing male) as of 1 June 2002. At each study site, we randomly selected a single breeding pair that actively defended a territory. We referred to each of these as a “focal territory” of intense study. All 20 focal territories were monitored every year of the study. Study sites were at least 1 km apart (average = 4.7 km) in order to increase statistical independence among focal territories, predator communities, and landscape extents.

Study sites were selected to span a wide gradient of forest fragmentation. Sites within contiguously forested landscapes were located in the northern half of Green Mountain National Forest, a relatively homogeneous forest with a canopy dominated by northern hardwoods such as sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and American beech (*Fagus grandifolia*), and an understory dominated by hobblebush (*Viburnum alnifolium*), striped maple (*A. pensylvanicum*), and beech saplings. Study sites in more fragmented landscapes were located in the Champlain Valley, characterized by small forest patches situated in a matrix dominated by agriculture. These lower elevation forests differed from contiguous forests in the region in that they exhibited a higher diversity of canopy tree species, and the understory was dominated by witch hazel (*Hammamelis virginiana*), *Rubus* spp., and blue cohosh (*Caulophyllum thalictroides*), rather than hobblebush.

On January 8, 1998, a destructive ice storm affected approximately 260,000 hectares of Vermont forest land (Kelley 2001). As a result, suitable habitat for black-throated blue warblers was abundant, particularly in the more fragmented Champlain Valley, where newly opened gaps in the canopy allowed understory growth (Faccio 2003).

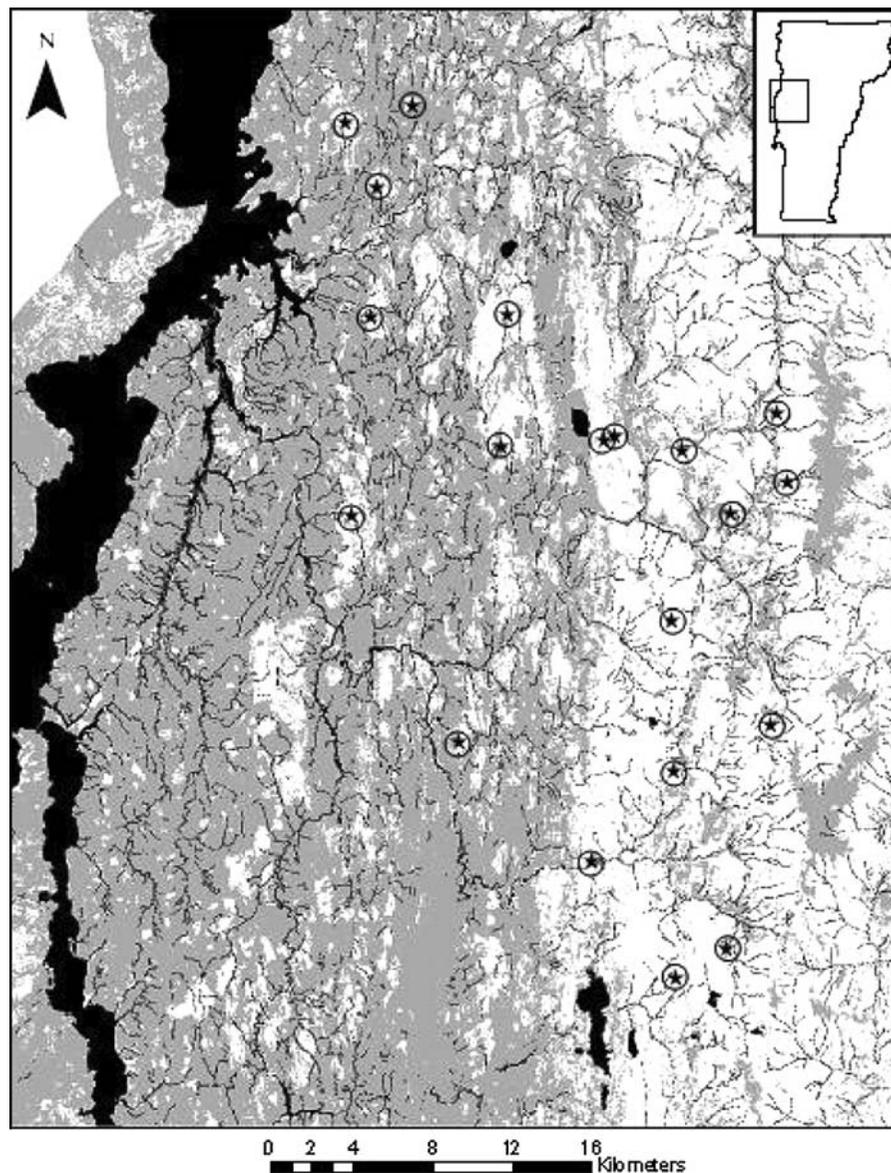


Fig. 1 Graphical locations of twenty study sites in Chittenden and Addison Counties, Vermont, USA. Location of study region in Vermont is indicated on *insert map*. *Black* areas represent water; *gray* areas represent non-habitat (urban,

agriculture, coniferous forest); *white* areas represent mixed-deciduous/coniferous forested habitat potentially used as black-throated blue warbler breeding habitat

Field methods

Point count surveys and abundance estimation

Two, 10-min, single-observer point counts were conducted in succession on a single day at a randomly selected survey point located near the center of each mapped focal territory in all 20 study

sites from 25 May to 15 July in 2002–2005 between 0600 and 1,100 h. All surveys were conducted by experienced observers who recorded the number of all male black-throated blue warblers heard or seen (unlimited distance) and the time at which each warbler was first detected. These methods allowed us to correct our raw point count data for detection bias (Thompson et al. 2002).

To adjust our raw counts, we first used the Huggins closed-capture time removal models (Huggins 1989, 1991) within Program MARK (White and Burnham 1999) to estimate detection probability (P , the probability that a warbler would be detected in a 10-min point count, given it is present). We divided each 10 min count into five, 2-min intervals to create capture histories for each bird on each survey, and used an information-theoretic model selection approach (Burnham and Anderson 2002) to assess how various environmental variables (e.g., time of day, date, year, weather conditions) affected P (Appendix 2; Cornell 2007). Next, we obtained a model-averaged P for each survey conducted in the study (Burnham and Anderson 2002). Finally, raw count data for each survey were divided by the survey-specific model-averaged P to obtain a corrected abundance estimate for statistical analysis.

Demographic characteristics

In each breeding season from 2002 to 2004, we conducted a band-resight and nest-searching study to evaluate annual fecundity and age ratios for each sex. We captured all adults on focal territories, marked each individual with a unique combination of one aluminum and three colored leg bands, and determined age according to plumage characteristics as either SY (second-year; first-year breeder) or ASY (after-second-year; Pyle et al. 1987). We located and documented fates of all nest attempts for each focal female across the entire breeding season. Most nests were found during the building or incubation stage and checked every 2–4 days until fledging or failure.

Quantifying habitat structure at three spatial scales

For each of the 20 focal territories, we measured habitat characteristics within the territory itself (TERRITORY), within a habitat patch surrounding each territory (PATCH), and within a 5-km radius landscape surrounding each territory (LANDSCAPE). Each site had unique TERRITORY, PATCH, and LANDSCAPE characteristics, which were used as explanatory variables in this study. We describe how each of these metrics was estimated below.

TERRITORY described the general understory shrub density within a focal territory. We measured leaf density at all nests attempted by the focal pair, and in which eggs were laid, after fledging or failure, following procedures described by Sillett et al. (2004). Four, 11.2-m transects were delineated in the understory in cardinal directions within plots centered on each nest site. At the distal end of each transect, a vertical 9-m² plane was erected using two 3-m vertical poles set 3-m apart. We counted all deciduous leaves of all understory species that intersected this plane. To avoid bias resulting from measuring only locations near nest sites, we also measured understory leaf density at a single random sampling point within each mapped focal territory using the same methods. TERRITORY was computed for each of the 20 focal territories as the average of leaf counts across all four planes for each nest site and random sampling point. This metric was measured on an annual basis.

PATCH described understory shrub density within a 25 ha area surrounding each focal territory. Eight sampling points were established at 250 and 500 m in cardinal directions and centered at a random sampling point within the focal territory. At each study site in 2002, understory leaf density was measured at each of the eight sampling stations. Leaf counts were conducted using the same methods as described for TERRITORY. PATCH was computed as the average total leaf counts across all four planes for each of the eight sampling points and was assumed to remain relatively constant over the study period.

LANDSCAPE described the composition and configuration of forested areas within 5 km of each focal territory, and was assumed to remain relatively constant over the study period. We characterized landscape pattern surrounding each study site using USGS/EPA MRLC land cover maps derived from a version of the 1992 National Land Cover Dataset (30 m pixel size; Vogelmann et al. 2001) and updated to include extent of developed land in Vermont as of 2002 (Spatial Analysis Lab, University of Vermont). Black-throated blue warblers breed mainly in deciduous or mixed/coniferous forests (Holmes et al. 2005). Thus, we used ArcGIS 9.1 (Esri, Inc) to reduce the original 18 land-use classes to three classes based on perceived biological relevance and ease of interpretation, including (1) water, (2) deciduous and mixed-coniferous forest (potential warbler

breeding habitat), (3) terrestrial non-habitat (urban, agriculture, coniferous forest).

We used FRAGSTATS (McGargal and Marks 1995) to obtain specific measures of forest (land-use category 2) composition and configuration within a 5 km radius area surrounding the center of each study site (Donovan et al. 2000). This scale was selected because it reflects the home range size of brown-headed cowbirds (Thompson 1994), a potentially important determinant of annual fecundity in our system (Coker and Capen 1995). We used the percent of landscape in the deciduous/mixed coniferous forest category as a single landscape composition metric. Landscape configuration metrics included percent core deciduous/mixed coniferous forest area (defined as >120 m from edge), mean forest patch area, mean shape index (a measure of shape complexity compared to a Euclidean square where high scores indicate irregularly shaped patches), and edge density (total edge length of forest divided by the total landscape area). Because landscape composition and configuration metrics were consistently collinear (Pearson's correlations, $P < 0.05$; SAS 1999), we used a Principal Components Analysis (PROC PRINCOMP; SAS 1999) to condense the five landscape composition and configuration metrics into a single measure that explained 91.0% of the total variation

among research sites. We termed this component LANDSCAPE. Sites with high LANDSCAPE PCA scores had high percent forest cover, high core forest area, large mean patch area, and more complex patch shapes, while sites with low PCA score were more heterogeneous with more isolated forest patches and more edge.

Statistical analysis

Model set

Our primary objective was to determine which habitat scale(s) were most strongly associated with the following demographic parameters: 1) abundance, 2) age, and 3) annual fecundity. For each of these three response variables, we evaluated 12 alternative models that depicted the relationship between the response variable and habitat pattern at different spatial scales (Table 1), and compared the results of the 12 models with information theoretic approaches (Burnham and Anderson 2002).

The model set included a territory-scale model containing TERRITORY as the explanatory variable, a patch-scale model with PATCH as the explanatory variable, and a landscape-scale model with

Table 1 Models of mean annual abundance, male and female age ratios, and annual fecundity of black-throated blue warblers as a function of three habitat variables [TERRITORY (T), PATCH (P), LANDSCAPE (L)], number of estimated

parameters (K), scaled deviance ($-2 \log$ likelihood), scaled second-order Akaike's information criteria (ΔAIC_c), and AIC_c weights (w_i)

Model No.	Model name	K	Abundance			Male age ratio			Female age ratio			Annual fecundity		
			$-2(L)$	ΔAIC_c	w_i	$-2(L)$	ΔAIC_c	w_i	$-2(L)$	ΔAIC_c	w_i	$-2(L)$	ΔAIC_c	w_i
1	T	2	46.14	1.60	0.09	65.96	4.90	0.05	77.74	0.00	0.20	187.02	20.24	0.00
2	P	2	47.11	2.56	0.06	70.93	9.87	0.00	80.21	2.46	0.06	187.77	21.00	0.00
3	L	2	45.43	0.89	0.13	73.98	12.92	0.00	81.36	3.62	0.03	167.07	0.29	0.23
4	T + P	3	46.10	3.77	0.03	64.22	5.39	0.04	75.55	0.02	0.20	177.65	13.07	0.00
5	T + L	3	43.52	1.20	0.11	60.81	1.98	0.21	77.43	1.91	0.08	164.58	0.00	0.26
6	P + L	3	45.01	2.68	0.05	69.02	10.18	0.00	79.48	3.96	0.03	167.04	2.45	0.08
7	T + P + L	4	42.83	2.80	0.05	56.54	0.00	0.55	75.52	2.30	0.06	164.14	1.81	0.11
8	T * P	4	45.61	5.58	0.01	63.73	7.19	0.02	75.49	2.28	0.06	169.11	6.78	0.01
9	T * L	4	40.03	0.00	0.20	60.25	3.71	0.09	73.55	0.34	0.17	164.47	2.14	0.09
10	P * L	4	41.62	1.59	0.09	66.17	9.63	0.00	79.26	6.04	0.01	163.55	1.22	0.14
11	Global	7	37.65	5.05	0.02	54.49	5.38	0.04	71.95	6.19	0.01	157.53	2.41	0.08
12	Null	1	47.13	0.44	0.16	74.01	10.81	0.00	81.37	1.48	0.10	195.98	27.08	0.00

Models with $\Delta AIC_c < 2$ were supported in the data and are shown in bold

LANDSCAPE as the explanatory variable (models 1–3). The model set also considered all additive (models 4–7), and two-way interactive combinations of these variables (models 8–10). Finally, a global model with all effects (model 11) and an intercept model that did not include habitat variables (model 12) were evaluated. This model set allowed us to (1) determine how each of the three demographic response variables were associated with habitat features at different spatial scales, (2) directly assess whether the effect of habitat at one spatial scale depended on habitat features at other spatial scales (Turner 2005), and (3) determine which variable was most closely associated with each demographic parameter.

Model assessment and relative variable importance

We modeled corrected warbler abundance, age ratio (SY vs. ASY) for both males and females, and annual fecundity each as linear functions of habitat variables (Table 1) using PROC GENMOD (SAS 8.2, SAS 1999). In each model, we specified the distribution which appropriately described the response variable (Poisson or negative binomial) and accounted for temporal and spatial correlation by designating study site as a repeated factor. Because at least one model in the model set must “fit” the data, we assessed fit of the most saturated model in the set (model 11) for each response variable by evaluating model residuals and the ratio of deviance divided by degrees of freedom. We report parameter estimates and standard errors for all models.

For each demographic analysis, we used model selection procedures (Burnham and Anderson 2002) to determine which of the 12 models was most strongly supported by the field data. Model selection procedures involve calculating an AIC_c score for each model (Akaike’s Information Criterion for small sample sizes—a measure of how well a model fits the observed field data adjusted by the number of parameters estimated). The 12 models were then ranked from best to worst, where the best-fit model had the lowest AIC_c score. Models were compared by calculating the differences in AIC_c scores between each model and the best-fit model (ΔAIC_c); models with $\Delta AIC_c < 2$ were considered to have substantial support, models with ΔAIC_c between 4 and 7 were considered to have considerably less

support, and models with $\Delta AIC_c > 10$ were considered to have no support. Model weights (w_i) were then calculated from the ΔAIC_c scores. These weights can be thought of as the probability that a model is the best Kullback–Leiber model in the model set (Burnham and Anderson 2002). We used these weights to compute a model-averaged effect of TERRITORY, PATCH, and LANDSCAPE for each demographic variable (Burnham and Anderson 2002).

In addition, because each habitat variable was equally represented in the model set, we used variable importance methods to measure the relative importance of each habitat variable (TERRITORY, PATCH, and LANDSCAPE) for each of the three demographic variables (Burnham and Anderson 2002). This procedure involved summing the model weights for all 12 models in which the variable appeared. The predictor variable with the largest sum was estimated to be the most important, while the variable with the smallest sum was estimated to be the least important variable.

Results

Habitat patterns

By design, vegetation structure differed among study sites at all spatial scales (Appendix 1). At a landscape-scale, sites ranged from 13 to 81% deciduous/mixed deciduous forest cover within 5 km of the focal territory. Both PATCH and TERRITORY were correlated with LANDSCAPE (Pearson correlation coefficient $r = -0.32$ and -0.57 respectively; $P < 0.01$ for both). In general, study sites located in more fragmented landscapes had higher shrub density at both the territory and patch scales, due in part to the aforementioned ice storm.

For each of our analyses investigating the association between demographic variables and habitat variables, there was no evidence for lack-of-fit, indicating that the parameter estimates from our models fit the observed field data adequately.

Abundance

We conducted a total of 160 point count surveys. Our ability to detect warblers on point counts, given presence, was high, ranging from 93 to 100%.

Average warbler abundance ranged from 0 to 3.03 singing males per site per year, where 0's indicate territory vacancy. Six models were supported in the data (having $\Delta AICc < 2$; Table 1), but overall territory- and landscape-scale habitat variables were most important for explaining variation in abundance patterns (Fig. 2). Importantly, a model containing only a two-way interaction between these two scales carried the most weight (0.20; Table 1, model 9) suggesting that the effect of TERRITORY on abundance was dependent on the effect of LANDSCAPE. Model-averaged results show that territories with high shrub density and located within unfragmented landscapes had high abundance of black-throated blue warblers (Fig. 3; Appendix 3). However, the highest abundances occurred at territories in fragmented landscapes with high territory-scale shrub density (Fig. 3). Patch level habitat was not consistently related to abundance.

Age

For males, territory-and landscape-scale habitat patterns were most important for explaining variation in age ratios (Table 1, models 5 and 7; Fig. 2). The best supported models contained additive effects of territory and landscape scales, as well as the additive effect of patch-scale shrub density (model 5), but the

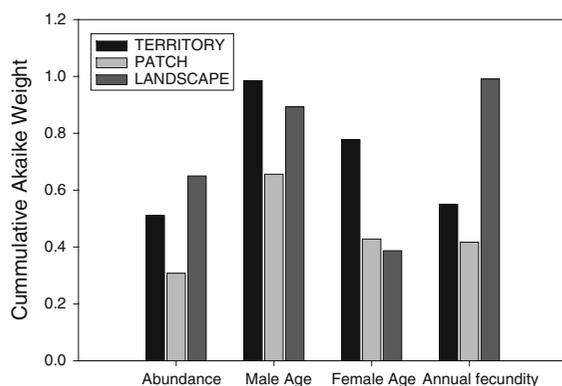


Fig. 2 Variable importance weights (Σw_i) for the three habitat variables that were included in the models for each demographic parameter. Importance of explanatory variables was assessed by summing the Akaike weights of all candidate models that included the variable (Burnham and Anderson 2002). Values closer to 1.00 indicate higher importance compared with other variables in the candidate model set

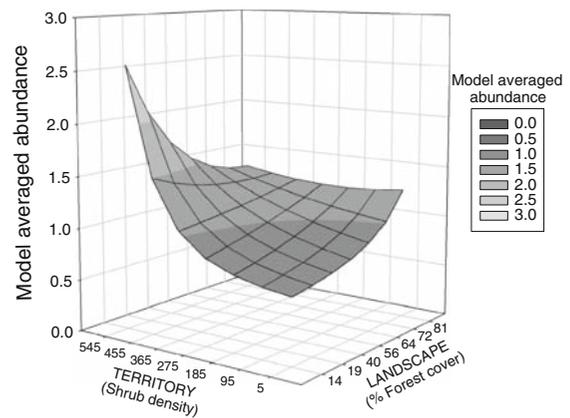


Fig. 3 Surface plot of model averaged abundance as a function of TERRITORY (*shrub density*) and LANDSCAPE, depicted here as percent of deciduous and mixed coniferous forest in 5-km landscape rather than the PCA score used in statistical models, for ease of interpretation

effect of shrub density of the patch was relatively less important than either of the other two variables (Fig. 2, Appendix 4). In general, territories with low shrub density were more likely to support SY males, especially in fragmented landscapes. Territories exhibiting high shrub density always supported ASY males, regardless of landscape pattern (Fig. 4).

The univariate effect of shrub density within a territory provided the best model for explaining variation in female age ratios for black-throated blue warblers (Table 1, model 1) and was present as a significant negative effect in model 1 and three other models supported in the data (Table 1, models 4, 5, and 9; Appendix 5). Variable importance analysis revealed that territory-level shrub density affected female age ratios more than either patch- or landscape-scale variables (Fig. 2). Overall, SY females occupied territories with the lowest shrub density, and this effect was intensified as landscapes became more forested (Fig. 4b, Appendix 5). These results were based on analysis of 61 males and 59 females.

Annual fecundity

Landscape-scale habitat pattern explained the most variation in annual fecundity (Fig. 2). Of the four models supported in the data (Table 1, models 3, 5, 7, 10), all contained significant additive effects of the landscape-scale variable (Appendix 6). Individuals located in more unfragmented landscapes fledged

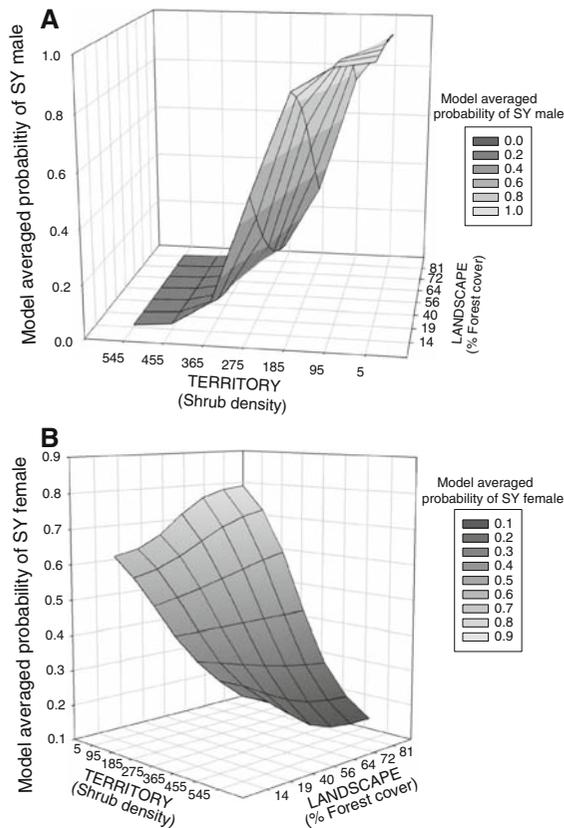


Fig. 4 Surface plots of model averaged probability of SY (first-year breeder) male (a) and female (b) as a function of TERRITORY and LANDSCAPE, depicted here as percent of deciduous and mixed coniferous forest in 5-km landscape rather than the PCA score used in statistical models, for ease of interpretation

more young per year (Fig. 5; Appendix 6). Territory-scale shrub density played a smaller role in explaining annual fecundity (Fig. 2). Annual fecundity was lowest in the most fragmented sites but where territory-scale shrub density was high (Fig. 5).

These results were based on monitoring 65 uniquely banded female warblers for fecundity analyses across the 20 study sites from 2002 to 2004. Annual fecundity ranged from zero to eight warbler young fledged per female across all sites and all years. Annual fecundity averaged 2.5 fledglings per female in 2002, 2.6 fledglings per female in 2003, and 4.2 fledglings per female in 2004. On average, over all years and study sites, 51% of monitored nests were successful, 32% failed due to predation, and 16% failed due to brood parasitism.

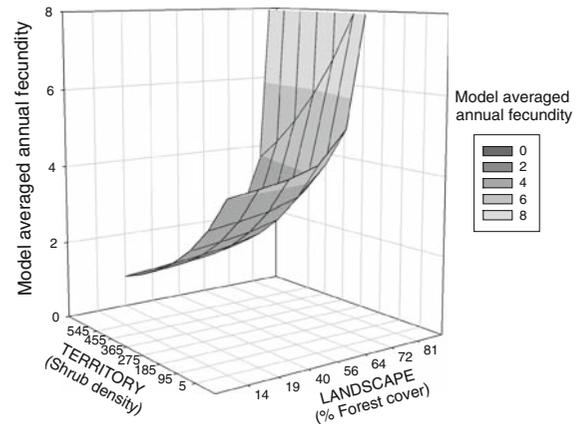


Fig. 5 Surface plot of model averaged annual fecundity as a function of TERRITORY and LANDSCAPE, depicted here as percent of deciduous and mixed coniferous forest in 5-km landscape rather than the PCA score used in statistical models, for ease of interpretation

Discussion

Advancement of the field of landscape ecology calls for studies that consider interactions of patterns and processes across spatial scales because they provide a more comprehensive look at ecological dynamics in heterogeneous landscapes (Turner 2005). In this study, we found evidence that (1) patterns of habitat at different spatial scales affect different aspects of a species' demography, and (2) habitat patterns at one spatial scale can be influenced by habitat patterns at different scales in shaping demographic patterns. In short, territory-level shrub cover strongly influenced distribution and age ratios while landscape pattern most strongly influenced annual fecundity. However, the story is complex because the effect of shrub cover on any of the demographic parameters depended on the surrounding landscape conditions.

Territory-scale shrub density as a proximate cue of territory selection

Our findings that territory-scale shrub cover may serve as a proximate cue for territory selection are consistent with the habitat-specific distribution patterns reported for black-throated blue warblers by (Holmes et al. 1996) in a large (>10,000 ha), unfragmented temperate forest in New Hampshire. In a comparison between high shrub density and low shrub density study plots, they reported that warbler

density was higher and there were proportionately more older (≥ 2 years old) breeders in the high shrub density plot compared to the low shrub density plot. Further, of the small number of males that were unmated, significantly more of them occurred on the low shrub density plot. Lichstein et al. (2002) similarly reported a positive relationship of black-throated blue warbler abundance with the amount of older and more structurally diverse forest in a managed landscape in the southeastern Appalachians, USA, but found that landscape variables explained only a small amount of variation in the counts after controlling for local habitat effects, including elevation.

Ecological effects of landscape pattern on reproductive output

Although the distribution (i.e., the abundance and age ratio patterns) of black-throated blue warblers was largely shaped by territory-scale shrub cover, we found that landscape fragmentation negatively influenced black-throated blue warbler annual fecundity. Three potential mechanisms that affect annual fecundity and are shaped by landscape pattern include nest predation, parasitism by the brown-headed cowbird, and food. Here, we consider how landscape pattern can shape these three factors and could account for the observed patterns of annual fecundity for black-throated blue warblers and potentially other forest passerines in this system.

Predation pressures may play an important role in determining reproductive success in our system. Based on video documentation of nest predators in extensively forested landscapes in the Northeast, the dominant nest predators in our system are likely to be red squirrels (*Tamias hudsonicus*), eastern chipmunks (*Tamias striatus*), blue jays (*Cyanocitta cristata*), crows (*Corvus brachyrhynchos*), and other small mammals (King and DeGraaf 2006). These nest predators may respond to landscape fragmentation in different ways (Kurki et al. 2000; Chalfoun et al. 2002). For example, corvid abundances are often lower in contiguous forests compared to fragmented landscapes (Andren 1992), and predation levels by corvids are also lower in more contiguous landscapes (Donovan et al. 1997). In Montana, nest predation increased with increasing agriculture in the larger landscape, suggesting that generalist predators

associated with agriculture and predators living in small woodlots together can magnify predation rates (Tewksbury et al. 2006). Our fragments in the Champlain Valley are similarly embedded within an agricultural matrix, and nest predation rates may be similarly magnified due to a more diverse predator pool.

Landscape pattern is known to shape the distribution of brown-headed cowbirds, an obligate brood parasite. This is the first study to document the costs of parasitism incurred by black-throated blue warblers. Parasitism was significantly greater on fragmented sites in all years of this study (Cornell 2007). In this study region in Vermont, a single brown-headed cowbird nestling in a black-throated blue warbler nest can cause complete reproductive failure. In some cases, host fledglings are successful, but their condition at fledging is unknown and may be compromised, thereby affecting longer term survival.

In the Midwest, cowbird abundance is significantly greater in fragmented landscapes than contiguous landscapes (Donovan et al. 1997). Whereas contiguous areas have limited feeding areas, fragmented landscapes offer both feeding and breeding opportunities for cowbirds and may maximize cowbird occurrence. For instance, Thompson (1994) radio-collared 84 female cowbirds in the Midwest US, and found that females were located in forest and shrub-sapling habitats during the morning breeding period, but commuted to short-grass, cropland, and feedlot habitats from midmorning to early afternoon. Cowbirds moved an average of 3.6 km between roosting and breeding locations, 1.2 km between breeding and feeding locations, and 2.6 km between feeding and roosting locations, consistent with cowbird habitat use in other portions of their range (Thompson 1994). In our study system, Coker and Capen (1995) found that cowbirds were most consistently detected where there was new suburban development and at locations within 1 km of livestock areas. Thus, landscape pattern is known to influence distribution and abundance of cowbirds in our system, which in turn affected the annual fecundity of breeding black-throated blue warblers.

The negative influence of cowbird parasitism in this system may interact with the frequency of double-brooding to further reduce reproductive output. This could occur in two ways: (1) a female produces a single brood, fledges a cowbird, and does

not offset the loss of the first brood by attempting a second because she is expending all of her energy attending a large fledgling cowbird, or (2) a female produces a first brood, fledges a cowbird, attempts a second brood, and fledges another cowbird. We found that younger, less experienced females are more likely to be found in fragmented sites, and previous studies have shown that younger females are less likely to produce two broods per season than are older birds, even in high shrub density habitats (Holmes and Sherry 1992). Thus, increased reproductive failure in fragmented landscapes may be primarily influenced by brood parasitism in our system.

Food limitation is another possibility explaining reduced reproduction on fragmented sites with high shrub cover. Holmes et al. (1996) found that the factor that accounted for the greatest difference in reproductive output between high and low quality habitats was the frequency of double-brooding which was accomplished most often by older females on high shrub density plots. Nagy and Holmes (2005) conducted controlled food supplementation experiments and demonstrated that the observed frequency of double-brooding is positively related to food resources on a territory. If these patterns apply to our system, we would expect that food resources may drive the patterns of reproductive success in our system as well. Several studies demonstrate that food resources decrease with increasing fragmentation (Burke and Nol 2000; Zanette et al. 2000), suggesting that poor reproduction in fragmented sites could be the result of reduced local food resources on those sites. This remains uncertain in our system. Hughes (2003) found increased diversity and abundance of insect populations in edge habitats versus core habitat in sites located within fragmented sites in west-central Vermont. However, the distribution of insects across the gradient of fragmentation of sites used in this study has not been investigated.

Cross-scale interactions of habitat structure

Multi-scale research problems and investigations of cross-scale interactions have emerged as a dominant research theme in landscape ecology (Peters et al. 2004; Battin and Lawler 2006; Schooley and Branch 2007). Associations between cross-scale interactions and species abundance and habitat use are well

studied (Lichstein et al. 2002; Betts et al. 2006; Mahon et al. 2008; Renfrew and Ribic 2008; Vergara and Armesto 2009). Many of these studies have found support for the hypothesis that interactions among habitat features at different scales are important for explaining distribution patterns (but see Mahon et al. 2008). Battin and Lawler (2006) found evidence that cross-interactions between home range, tree and path scales predict abundance for the red-napped sapsucker (*Sphyrapicus nuchalis*) and the northern flicker (*Colaptes auratus*). In a study of grassland birds, Renfrew and Ribic (2008) found that the direction and strength of the effect of core pasture size on relative abundance changed depending on amount of wooded area in the landscape. Vergara and Armesto (2009) proposed that interactions across scales in fragmented landscapes go further than the simple interaction between forest cover and patch size since different habitat structures within forest stands (e.g., canopy height, tree dbh, understory cover) can interact with landscape configuration or patch features significantly affecting bird abundance. Further, they found that specialist understory species, in particular, responded positively to understory cover depending on forest patch area and percent forest cover in the landscape. Our results are consistent with these studies; we found support for effects of cross-scale interactions on abundance for black-throated blue warblers where the effects of fine-scale understory shrub cover on territory selection were dependent on the amount and arrangement of forest cover in the landscape.

Although investigations about effects of habitat scale interactions on abundance patterns are plentiful, there remains a general dearth of information on how cross-scale interactions may affect reproductive output directly. Several multi-scale studies have investigated effects of habitat pattern on nest success for bird species (e.g., Driscoll et al. 2005; Vander Haegen 2007), but none of these examined effects of cross-scale interactions. Further, while nest success can provide some information on reproductive success, direct measures of productivity, such as annual fecundity of marked individuals, are ideal for predicting population persistence. This study is among the first to report effects of a cross-scale interaction between territory- and landscape-scale habitat features on annual fecundity for a migratory songbird.

Cross-scale interactions such as this can result in “surprises” with severe consequences for species welfare (Peters et al. 2004). For example, we show that birds who select nest sites largely based on innate proximate cues at fine scales may be overwhelmed by interacting processes at larger scales. This result may imply that the negative impact of forest cover loss on bird species cannot always be compensated by improving local habitat quality, such as maintaining large trees and dense understory. As the heterogeneity of breeding habitats used by this and other similar species increases, the complexity of the interactions between spatial habitat patterns and demographic processes will be enhanced. Thus, recognizing the potential for cross-scale interactions is a critical challenge for managers and conservation planners.

Appendices 1–6 for this article are available as supplementary material online.

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References

- Ambuel B, Temple SA (1983) Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* 64:1057–1068
- Andren H (1992) Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology* 73:794–804
- Andren H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat—a review. *Oikos* 71:355–366
- Battin J, Lawler JJ (2006) Cross-scale correlations and the design and analysis of avian habitat selection studies. *Condor* 108:59–70
- Bayne EM, Hobson KA (2001) Effects of habitat fragmentation on pairing success of ovenbirds: importance of male age and floater behavior. *Auk* 118:380–388
- Betts MG, Forbes GJ, Diamon AW, Taylor PD (2006) Independent effects of fragmentation on forest songbirds: an organism based approach. *Ecol Appl* 16:1076–1089
- Bowman GB, Harris LD (1980) Effects of spatial heterogeneity on ground-nest depredation. *J Wildl Manage* 44:806–813
- Budnik JMT, Thompson FR, Ryan MR (2002) Effect of habitat characteristics on the probability of parasitism and predation of Bell’s vireo nests. *J Wildl Manage* 66:232–239
- Burke DM, Nol E (1998) Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. *Auk* 115:96–104
- Burke DM, Nol E (2000) Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. *Ecol Appl* 10:1749–1761
- Burnham KP, Anderson DE (2002) Model inference and multimodel selection. Academic Press, New York
- Chalfoun AD, Thompson FR, Ratnaswamy MJ (2002) Nest predators and fragmentation: a review and meta-analysis. *Conserv Biol* 16:306–318
- Cody ML (1985) Habitat selection in birds. Academic Press, London
- Coker DR, Capen DE (1995) Landscape-level habitat use by brown-headed cowbirds in Vermont. *J Wildl Manage* 59:631–637
- Cornell KL (2007) Scale-dependent mechanisms of habitat selection and demography for a forest songbird in a heterogeneous landscape. Dissertation, University of Vermont
- Donovan TM, Lamberson RH, Kimber A, Thompson FR, Faaborg J (1995) Modeling the effects of habitat fragmentation on source and sink demography of neotropical migrant birds. *Conserv Biol* 9:1396–1407
- Donovan TM, Jones PW, Annand EM, Thompson FR (1997) Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78:2064–2075
- Donovan TM, Thompson FR, Faaborg J (2000) Cowbird distribution at different scales of fragmentation: tradeoffs between breeding and feeding opportunities. In: Cooke T, Robinson SK, Rothstein SI, Sealy SG, Smith JNM (eds) Ecology and management of cowbirds. University of Texas Press, Austin, TX
- Driscoll MJL, Donovan TM, Mickey R, Howard A, Fleming KK (2005) Determinants of wood thrush nest success: a multi-scale, model selection approach. *J Wildl Manage* 69:699–709
- Faccio SD (2003) Effects of ice storm created gaps on forest breeding bird communities in Central Vermont. *For Ecol Manage* 186:133–145
- Flaspohler DJ, Temple SA, Rosenfield RN (2000) Relationship between nest success and concealment in two ground-nesting passerines. *J Field Ornithol* 71:736–747
- Hanski IA, Simberloff D (1997) The metapopulation approach, it’s history, conceptual domain, and application to conservation. In: Hanski IA, Gilpin ME (eds) Metapopulation biology, ecology, genetics, and evolution. Academic Press, San Diego
- Hildén O (1965) Habitat selection in birds: a review. *Ann Zoo Fenn* 2:53–75
- Hochachka WM, Martin TE, Artman V, Smith CR, Hejl SJ, Andersen DE, Curson D, Petit L, Mathews N, Donovan T, Klaas EE, Wood PB, Manolis JC, McFarland KP, Nichols JV, Bednarz JC, Evans DM, Duguay JP, Garner S, Tewksbury J, Purcell KL, Faaborg J, Goguen CB, Rimmer C, Dettmers R, Knutson M, Collazo JA, Garner L,

- Whitehead D, Geupel G (1999) Scale dependence in the effects of forest coverage on parasitization by brown-headed Cowbirds. *Stud Avian Biol* 18:80–88
- Holmes RT, Sherry TW (1992) Site fidelity of migratory warblers in temperate breeding and neotropical wintering areas: implications for population dynamics, habitat selection, and conservation. In: Hagan JM, Johnston DW (eds) *Ecology and conservation of neotropical migrant landbirds*. Smithsonian Institution Press, Washington DC, pp 563–575
- Holmes RT, Marra PP, Sherry TW (1996) Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics. *J Anim Ecol* 65:183–195
- Holmes RT, Rodenhouse NL, Sillett TS (2005) Black-throated blue warbler (*Dendroica caerulescens*). In: Poole A (ed) *The birds of North America*. Cornell Laboratory of Ornithology, Ithaca
- Huggins RM (1989) On the statistical analysis of capture experiments. *Biometrika* 76:133–140
- Huggins RM (1991) Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics* 47:725–732
- Hughes M (2003) Effects of local- and landscape-scale variation on the distribution of three area-sensitive forest songbirds in Vermont. Thesis, University of Vermont
- James FC (1971) Ordinations of habitat relationships among breeding birds. *Wilson Bull* 83:21–236
- Kelley R (2001) The 1998 ice storm: Vermont assessment and response. In *Proceedings of the New York Society of American Foresters Ice Storm symposium*, pp. 91–96. USDA Forest Service Report NA-TP-03-01
- King DI, DeGraaf RM (2006) Predators at bird nests in a northern hardwood forest in New Hampshire. *J Field Ornithol* 77:239–243
- Kurki S, Nikula A, Helle P, Linden H (2000) Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. *Ecology* 81:1985–1997
- Lichstein JW, Simons TR, Franzweb KE (2002) Landscape effects of breeding songbird abundance in managed forests. *Ecol Appl* 12:836–857
- Mahon CL, Martin K, LeMay V (2008) Do cross-scale correlations confound analysis of nest site selection for chestnut-backed chickadees? *Condor* 110:563–568
- McGargal K, Marks B (1995) *Fragstats: spatial pattern analysis program for quantifying landscape structure*. USDA Forest Service
- McGarigal K, McComb WC (1995) Relationships between landscape structure and breeding birds in the Oregon coast range. *Ecol Monogr* 65:235–260
- Nagy LR, Holmes RT (2005) To double-brood or not? Individual variation in the reproductive effort in black-throated blue warblers (*Dendroica caerulescens*). *Auk* 122:902–914
- Orians GH, Wittenberger JF (1991) Spatial and temporal scales in habitat selection. *Am Nat* 137:S29–S49
- Peters DPC, Pielke RA Sr, Bestelmeyer BT, Allen CD, Munson-McGee S, Havstad KM (2004) Cross scale interactions, nonlinearities, and forecasting catastrophic events. *Proc Natl Acad Sci USA* 101:15130–15135
- Pulliam HR (1988) Sources, sinks, and population regulation. *Am Nat* 132:652–661
- Pyle P, Howell SNG, Yundick RP, DeSante DF (1987) *Identification guide to North American passerines*. Slate Creek Press, Bolinas
- Renfrew RB, Ribic CA (2008) Multi-scale models on grassland passerine abundance in a fragmented system in Wisconsin. *Landscape Ecol* 23:181–193
- Richards ZL (1999) The effect of forest isolation on breeding black-throated blue warblers in Vermont. M.S. thesis, University of Vermont, Burlington, Vermont
- Robinson SK, Thompson FR, Donovan TM, Whitehead DR, Faaborg J (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990
- Rodenhouse NL, Sherry TW, Holmes RT (1997) Site-dependent regulation of population size: a new synthesis. *Ecology* 78:2025–2042
- Rodenhouse NL, Sillett TS, Doran PJ, Holmes RT (2003) Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. *Proc R Soc Lond B Biol Sci* 270:2105–2110
- Rodrigues R (1994) Microhabitat variables influencing nest-site selection in tundra birds. *Ecol Appl* 4:110–116
- Rolstad J (1991) Consequences of forest fragmentation for the dynamics of bird populations: conceptual issues and the evidence. *Biol J Linn Soc* 42:149–163
- SAS (1999) *The SAS system for windows*. SAS Institute, Cary
- Schooley RL, Branch LC (2007) Spatial heterogeneity in habitat quality and cross-scale interactions in metapopulations. *Ecosystems* 10:846–853
- Sillett TS, Holmes RT (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. *J Anim Ecol* 71:296–308
- Sillett TS, Rodenhouse NL, Holmes RT (2004) Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. *Ecology* 85:2467–2477
- Steele BB (1992) Habitat selection in breeding black-throated blue warblers at two spatial scales. *Ornis Scand* 23:33–42
- Tewksbury JJ, Garner L, Garner S, Lloyd JD, Saab V, Martin TE (2006) Tests of landscape influence: nest predation and brood parasitism in fragmented ecosystems. *Ecology* 87:759–768
- Thompson FR (1994) Temporal and spatial patterns of breeding brown-headed cowbirds in the midwestern United States. *Auk* 111:979–990
- Thompson FR, Donovan TM, DeGraaf RM, Faaborg J, Robinson SK (2002) A multi-scale perspective of the effects of forest fragmentation on birds in eastern forests. *Stud Avian Biol* 25:8–19
- Trzcinski MK, Fahrig L, Merriam G (1999) Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecol Appl* 9:586–593
- Turner M (1989) Landscape ecology: the effect of pattern on process. *Ann Rev Ecol Syst* 20:171–197
- Turner MG (2005) Landscape ecology: what is the state of the science? *Ann Rev Ecol Syst* 36:319–344
- Vander Haegen WM (2007) Fragmentation by agriculture influences reproductive success of birds in a shrubsteppe landscape. *Ecol Appl* 17:934–937

- Vergara PM, Armesto JJ (2009) Response of Chilean forest birds to anthropogenic habitat fragmentation across spatial scales. *Landscape Ecol* 24:25–38
- Villard MA, Martin P, Drummond C (1993) Habitat fragmentation and pairing success in the ovenbird (*Seiurus aurocapillus*). *Auk* 110:759–768
- Vogelmann JE, Howard SM, Yang L, Larson CR, Wylie BK, Van Driel N (2001) Completion of the 1990s National Land Cover Data Set for the conterminous United States from Landsat Thematic Mapper data and ancillary. *Photogramm Eng Rem S* 67:650–652
- Walsberg G (1981) Nest-site selection and the radiative environment of the warbling vireo. *Condor* 83:86–88
- Whitcomb RF, Robbins CS, Lynch BL, Whitcomb MK, Klimkiewicz MK, Bystrak D (1981) Effects of forest fragmentation on avifauna of the eastern deciduous forest. In: Burgess RL, Sharpe DM (eds) *Forest island dynamics in man-dominated landscapes*. Springer, New York, pp 125–205
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–139
- Wiens JA, Rotenberry JT (1981) Habitat associations and community structure of birds in shrubsteppe environments. *Ecol Monog* 5:21–41
- Zanette L, Doyle P, Tremont S (2000) Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology* 81:1654–1666