SCALE-DEPENDENT MECHANISMS OF HABITAT SELECTION FOR A MIGRATORY PASSERINE: AN EXPERIMENTAL APPROACH

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Abstract.—Habitat selection theory predicts that individuals choose breeding habitats that maximize fitness returns on the basis of indirect environmental cues at multiple spatial scales. We performed a 3-year field experiment to evaluate five alternative hypotheses regarding whether individuals choose breeding territories in heterogeneous landscapes on the basis of (1) shrub cover within a site, (2) forest land-cover pattern surrounding a site, (3) conspecific song cues during prebreeding settlement periods, (4) a combination of these factors, and (5) interactions among these factors. We tested hypotheses with playbacks of conspecific song across a gradient of landscape pattern and shrub density and evaluated changes in territory occupancy patterns in a forest-nesting passerine, the Black-throated Blue Warbler (*Dendroica caerulescens*). Our results support the hypothesis that vegetation structure plays a primary role during presettlement periods in determining occupancy patterns in this species. Further, both occupancy rates and territory turnover were affected by an interaction between local shrub density and amount of forest in the surrounding landscape, but not by interactions between habitat cues and social cues. Although previous studies of this species in unfragmented landscapes found that social postbreeding song cues played a key role in determining territory settlement, our prebreeding playbacks were not associated with territory occupancy or turnover. Our results suggest that in heterogeneous landscapes during spring settlement, vegetation structure may be a more reliable signal of reproductive performance than the physical location of other individuals. *Received 10 September 2009, accepted 27 April 2010.*

Key words: Black-throated Blue Warbler, conspecific attraction, *Dendroica caerulescens,* habitat selection cues, landscape fragmentation, multiseason occupancy models.

Mecanismos de Selección de Hábitat Dependientes de la Escala por parte de un Ave Paserina Migratoria: una Aproximación Experimental

Resumen.—La teoría de selección de hábitat predice que los individuos escogen hábitats que maximizan su adecuación biológica con base en señales ambientales indirectas a múltiples escalas. Realizamos un experimento de campo de tres años para evaluar cinco hipótesis alternativas con relación a si los individuos escogen los territorios de cría en paisajes heterogéneos con base en (1) la cobertura de arbustos dentro de un sitio, (2) los patrones de cobertura de bosque alrededor de un sitio, (3) las señales de canto coespecíficas durante el periodo de asentamiento pre-reproductivo, (4) una combinación de estos factores y (5) interacciones entre estos factores. Probamos estas hipótesis utilizando reproducciones de cantos coespecíficos a través de un gradiente de patrones de paisaje y densidad de arbustos y evaluamos los cambios en los patrones de ocupación de territorios en *Dendroica caerulescens,* un ave paserina que anida en bosques. Nuestros resultados apoyan la hipótesis de que la estructura de la vegetación juega un papel primario en determinar los patrones de ocupación de esta especie durante los periodos que preceden al asentamiento. Además, tanto las tasas de ocupación como el recambio de territorios fueron afectados por una interacción entre la densidad local de arbustos y la cantidad de bosque en el paisaje circundante, pero no por la interacción entre señales de hábitat y señales sociales. A pesar de que estudios anteriores en paisajes no fragmentados en esta especie encontraron que las señales de canto post-reproductivas jugaban un papel importante en determinar el asentamiento en los territorios, nuestros experimentos de reproducciones de canto en la época pre-reproductiva no se relacionaron con la ocupación de territorios o su recambio. Nuestros resultados sugieren que durante el asentamiento en primavera en paisajes heterogéneos, la estructura de la vegetación podría ser una señal más confiable del desempeño reproductivo que la localización física de otros individuos.

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THE PROCESS OF breeding-habitat selection influences individual fitness and can have important consequences for population dynamics and species' responses to human-altered landscapes (Pulliam and Danielson 1991, Fletcher 2006). A fundamental tenet of habitat selection theory is that individuals choose the best available breeding habitats on the basis of indirect cues in their environment. These stimuli are proximate factors that may include the physical features of habitat at multiple spatial scales and social interactions (Hildén 1965, James 1971). How individuals or breeding pairs respond to these stimuli determines the spatial distribution of a population, which may affect breeding success and survival. Thus, habitat selection decisions are adaptive and shaped by evolutionary forces.

Avian studies have played a major role in the development of habitat selection theory (reviewed in Jones 2001). Of these, many illustrate how structural features of vegetation at different spatial scales (e.g., territory, patch, and landscape scales) are of prime importance and may signal ultimate factors that affect survival and reproduction such as food availability (Steele 1992, Burke and Nol 1998, Zanette et al. 2000), nest-site requirements (Rodenhouse and Holmes 1992), and shelter from weather, predation, (Bowman and Harris 1980, Martin and Roper 1988, Holway 1991), and parasitism (Donovan et al. 1995, 1997; Burhans 1997). James (1971) defined the "niche-gestalt" as the subset of a multidimensional space containing the proximate structural features of a bird's environment that act to elicit a settling response and allow a species to thrive over and above those that allow it to persist. In this light, the density and arrangement of vegetation within breeding territories (e.g., shrub density) and in the larger landscape (e.g., amount of forest cover within 5 km) may act synergistically in a complex fashion to attract a bird or breeding population.

In addition to vegetation cues, Hildén (1965) proposed that social interactions with other animals may provide reliable information about the availability of a particular resource (e.g., food, nest sites, mating opportunities, and predation or parasitism pressures) that would permit individuals to quickly assess potential breeding sites without the energy burdens associated with direct assessment. Thus, using social information as an assessment of habitat quality would be evolutionarily advantageous.

The exploration of the importance of proximate cues provided by conspecifics has garnered much attention in recent years (reviewed in Ahlering and Faaborg 2006). There is growing evidence in support of the hypothesis that social cues play an important positive role (i.e., attraction) in shaping songbirds' decisions about where to establish breeding territories (e.g., Muller et al. 1997; Danchin et al. 2004; Ward and Schlossberg 2004; Hahn and Silverman 2006, 2007; Betts et al. 2008; Mukhin et al. 2008; Fletcher 2009). These studies have also indicated that social attraction may be working at multiple times during the habitat selection process, including during migration (Mukhin et al. 2008), prebreeding searching and settlement (Ward and Schlossberg 2004, Fletcher 2009), and postbreeding dispersal (Nocera et al. 2006, Betts et al. 2008).

Despite the recent progress toward understanding habitat selection strategies, much remains to be learned about the relative contribution of different proximate and ultimate factors that individuals use to select breeding locations. For example, conspecific cues and other innate cues of vegetation structure occurring at

multiple spatial extents may work independently, hierarchically as a system of sequential decisions, or synergistically in a complex fashion of gestalt (Hildén 1965, James 1971, Hutto 1985). Further, it is unclear whether the recently observed patterns of the use of conspecifics as positive cues, particularly in territorial forest songbirds (e.g., Betts et al. 2008), will hold in highly heterogeneous landscapes. It is possible that in these landscapes, conspecific presence may play a reduced role compared with vegetation structure, and if territory space is highly limited, conspecific presence could potentially deter settlers (Kluijver and Tinbergen 1953, Fretwell 1972). As humans alter landscapes, birds must learn to respond to new environmental cues, a process that may significantly influence the evolution of habitat selection behavior (Thomas et al. 2001).

We examined the relative effects of vegetation structure and conspecific attraction on site occupancy rates (the probability that a site is occupied) and changes in site occupancy rates (colonization, the probability that a previously vacant site becomes occupied; and extinction, the probability that an occupied site is vacated) in a forest-nesting passerine, the Black-throated Blue Warbler (*Dendroica caerulescens*). Here, a "site" is a 3.14-ha location of interest, defined by the average territory size of a Black-throated Blue Warbler (Holmes et al. 2005). Our experiment tested five alternative hypotheses regarding whether individuals choose breeding territories on the basis of (1) shrub cover within a site, (2) forest land-cover pattern surrounding a site, (3) conspecific song cues during prebreeding settlement periods, (4) a combination of these factors, and (5) interactions among these factors. We predicted that if conspecific cues are a key positive stimulus in breeding-territory selection, then exposure of individuals to simulated song cues would result in birds choosing to settle in breeding territories even if vegetation structure was not ideal. We predicted that if territory space is limited and conspecific song cues are a deterrent, then simulation of the presence of a new individual in a previously occupied area would result in territory extinction. Alternatively, we predicted that if the presence of a conspecific is not a reliable indicator of reproductive success, then vegetation structure at either the site or landscape scale, or both, would be a primary cue driving habitat selection.

METHODS

Study species.—The Black-throated Blue Warbler is a territorial migratory songbird that breeds in parts of the eastern United States and southern Canada and winters in the Greater Antilles (Holmes et al. 2005). During the breeding season, Black-throated Blue Warblers are common to forest patches across many different landscape types throughout Vermont, a quality that facilitates analysis of distribution patterns across the landscape. Males arrive on the breeding grounds in early May, before females, and select and defend breeding territories. Males advertise their presence through song and by responding aggressively to the presence of male conspecifics. Territories range in size from about 1 to 4 ha, depending on habitat, and are smallest where shrub layer is dense (Steele 1992, K. Cornell unpubl. data). Males are easily counted in a variety of field conditions on the basis of vocalizations.

Study areas.—We conducted a field experiment from April to July, 2003–2005, within 10 forested study areas in Chittenden and

Addison counties, Vermont. Study areas were selected to span a wide gradient of forest fragmentation (i.e., highly heterogeneous landscape composition vs. homogeneously forested areas; Cornell and Donovan 2010). Study areas 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 areas in more fragmented landscapes were located in the Champlain Valley, a heterogeneous area 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 had a higher diversity of canopy tree species than the contiguous forests, variable vertical structure, and an understory dominated by American Witchhazel (*Hamamelis virginiana*), *Rubus* spp., Blue Cohosh (*Caulophyllum thalictroides*), and elms (*Ulmus* spp.) rather than Hobblebush.

Experimental design.—Our experiment evaluated three proximate cues that may be important for habitat selection: (1) the amount and arrangement of potential nesting habitat within 5 km of a study area, (2) the amount of shrub cover within each site, and (3) the presence of conspecifics. We surveyed birds in study areas that varied in landscape pattern, shrub cover, and conspecific cues, with the latter being experimentally manipulated in the early portion of the breeding season. Our goal was not only to test the main effect of each factor but to evaluate their combined effects on baseline occupancy probability (ψ, the probability that a site was occupied by a Black-throated Blue Warbler), colonization probability (γ, the probability that a vacant site in year t would be colonized in year $t + 1$), and extinction probability (ε, the probability that an occupied site in year t would go locally extinct in year $t + 1$). We used an information-theoretic analysis approach to evaluate support in the observed data for each hypothesis. Thus, our model set (described in detail below) evaluated (1) the main effects of shrub cover, landscape pattern, and conspecific playback; (2) their additive effects; and (3) interactions among main effects.

In 2002, we randomly selected one Black-throated Warbler territory in each of the 10 study areas. The demography of these focal birds was intensively studied from 2002 to 2005 (Cornell and Donovan 2010). At each of the 10 study areas, we established nine sites at which to monitor patterns of bird occupancy across a gradient of both landscape fragmentation and shrub cover. One site was a randomly chosen location within the focal territory, and the remaining eight sites were established at 250 m and 500 m in cardinal directions from the focal site ($n = 9$ sampling points total per study area). This sampling scheme ensured that baseline occupancy probability (ψ) was $\geq 9/90 = 0.1$ for modeling purposes while attempting to ensure that all nine sites within a study area had similar landscape conditions.

In 2004 and 2005, we played recordings of Black-throated Blue Warbler vocalizations at two sites within each of the 10 study areas (hereafter "treatment sites"). Treatment sites were selected on the basis of counts conducted in 2003. We selected sites with zero Black-throated Blue Warblers within 100 m of a survey point in order to test for colonization, and points with one Black-throated Blue Warbler within 100 m in order to measure site extinction.

Treatment sites were located across a gradient of forested habitat. The rationale for these criteria was that if conspecific cues are an important positive driver of site occupancy, the effect would be most apparent when abundances are initially low and where habitat conditions are less than ideal (i.e., either highly fragmented or with low shrub density; Ward and Schlossberg 2004). Alternatively, if conspecific presence is a negative driver of occupancy, the effect would be apparent where territories were previously occupied and where habitat condition in the area was poor. Because understory shrub density may be an important proximate cue in the territory selection process (Hildén 1965, Holmes et al. 2005), we broadcast Black-throated Blue Warbler vocalizations (treatment points) across a gradient of shrub density in which one treatment point was located in an area with highest shrub cover and one was located in an area of lowest shrub cover within each study area. This allowed us to evaluate their independent effects. The other seven sites within each study area were controls in which no recordings were broadcast (hereafter "control sites").

The conspecific cue: Song playbacks.—At each treatment site, we played prerecorded vocalizations of Black-throated Blue Warblers on portable compact disc players and stereo speakers housed in weatherproof boxes (playback boxes) and powered by 12-volt deep-cycle batteries. Because prospecting males may assess sites at dawn during the dawn chorus (Amrhein et al. 2004), vocalizations were played from 0400 to 1200 hours daily throughout the settlement period and early breeding season from late April to early July in 2004 and 2005. The experimental playbacks were not conducted in 2003 to establish baseline occupancy patterns. The compact disc players repeated all tracks on a 74-min compact disc and included 55 min of Black-throated Blue Warbler song and calls recorded in New York and New Hampshire. To prevent individuals from habituating to the playbacks, the tracks also included 10 min of continuous silence and a continuous 9 min of songs of other species that generally occur in the same bird community with Black-throated Blue Warblers, including the Black-throated Green Warbler (*D. virens*), Ovenbird (*Seiurus aurocapilla*), Red-eyed Vireo (*Vireo olivaceus*), and Wood Thrush (*Hylocichla mustelina*). Vocalizations were not played at control points.

We performed a pilot study of this playback protocol to ensure that it could be an effective conspecific cue for Black-throated Blue Warblers (Cornell 2007). Playback protocols were developed and tested at three study sites in three different study areas (high, low, and medium landscape fragmentation) in 2003. At least two pairs of Black-throated Blue Warblers settled at or directly adjacent to playback-box locations at each of the three experimental locations. All pairs were confirmed to be breeding; at one study site, nests of two different pairs were located within 20 m of a single playback box. Thus, we had an *a priori* expectation that prebreeding conspecific cuing could be an important positive determinant of site occupancy rates.

Occupancy surveys and site monitoring.—To evaluate site occupancy patterns, we conducted two 10-min single-observer point counts in succession at each of the 90 sites from 25 May to 15 July in 2003–2005. Surveys from 2003 at the 90 sites were used as base occupancy levels. The repeated surveys in 2004 and 2005 allowed us to determine changes in site occupancy that were attributable to site colonization (γ) or site extinction (ε). Additionally, this protocol allowed us to evaluate and adjust for detection probability

(*p*, the probability that a Black-throated Blue Warbler would be detected by observers given that it was present at a site) under the assumption of site closure (no changes in site occupancy between surveys). Surveys were conducted on mornings with low wind and no rain, between 0600 and 1100 hours. All surveys were conducted by experienced observers who recorded the number of all Black-throated Blue Warblers heard or seen within 100 m of the sampling point. The raw data from field observations were then processed for statistical analysis (see below).

Quantifying understory shrub cover.—We quantified the understory shrub cover at each of 90 sites using two field methods. First, we measured understory leaf density at each point 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 sampling point. At the distal end of each transect, a ground-level 9-m^2 plane was erected using two 3-m vertical poles set 3 m apart. We counted all leaves of all understory species that intersected this plane and summed them across all four transects for each sampling point. Second, we established three 50-m transects, spaced 50 m apart and running in the north–south cardinal directions, with the center transect bisecting the focal site. At three survey stations spaced evenly along each transect, we estimated the percentage of the ground covered by individual shrub species that Black-throated Blue Warblers may potentially use for nesting, foraging, or perching within a 10-m-radius circle surrounding each survey station. The cover estimates were first summed across species for each survey station and then averaged across survey stations to estimate understory shrub cover for each sampling point.

We used a correlation-based principal component analysis (PCA; Proc Princomp in SAS, version 8.2; SAS Institute, Cary, North Carolina) to condense the two shrub measures into a single metric for each of the 90 sites for our model-selection analyses. This analysis incorporated information from each of the two shrub variables into a single principal component (PC1) that explained 56.9% of the total variation among sampling points. We termed this component "shrub." Sites with high shrub PC1 score had high leaf density and overall high cover of shrubs used by Black-throated Blue Warblers, whereas sites with low shrub PC1 score were less shrubby.

Quantifying landscape pattern.—We characterized the landscape pattern that surrounded each study area using U.S. Geological Survey–Environmental Protection Agency MRLC (Multi-Resolution Land Characteristics Consortium) 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 the 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, version 9.1 (ESRI, Redlands, California), to reduce the original 18 land-use classes to three classes based on perceived biological relevance and ease of interpretation, including (1) open water, (2) deciduous and mixed coniferous forest (potential Black-throated Blue Warbler breeding habitat), and (3) terrestrial or aquatic nonhabitat (urban, agriculture, coniferous forest, wetlands).

We used the quantitative spatial-analysis program FRAGSTATS (McGarigal and Marks 1995) to obtain specific measures of landscape 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 (*Molothrus ater*; Thompson 1994), an important determinant of reproductive success in our system (Cornell and Donovan 2010). We used the percentage of landscape in the deciduous–mixed coniferous forest land-use category as a single landscape-composition metric. Study sites ranged in forest cover from 13% to 85%. Landscape-configuration metrics included percent core deciduous–mixed coniferous forest area (defined as >120 m from edge), mean forest patch area, mean shape index, forest patch density, and edge density. Landscape-composition and -configuration metrics were consistently collinear (Pearson's correlations, *P* < 0.05). To manage this problem, we used a correlation-based PCA (Proc Princomp in SAS) to condense the six landscape metrics into a single landscape measure for each study site (each of the nine sampling points at each site had the same landscape score). This analysis incorporated information from each variable into a single component (PC1) that explained 91.0% of the total variation among study sites. We termed this component "landscape." Sites with high landscape PC1 scores had high percent forest cover in the landscape, high core forest area, large mean patch area, and more irregularly shaped patches, whereas sites with low landscape PC1 scores were more heterogeneous, with a higher density of more isolated forest patches and more edge.

Statistical analyses.—To assess how conspecific cues and habitat features (shrub and landscape pattern) influenced occupancy, colonization, and extinction of Black-throated Blue Warblers at a given site (MacKenzie et al. 2003), we created primary and secondary encounter histories from the observed field data, which consisted of two surveys in each of the 3 years of the study (2003–2005) at each of the sites (*n* = 90 histories). Each history consisted of 0's and 1's, which described whether a Black-throated Blue Warbler was detected on a survey over time. For example, an encounter history of "11 10 00" at a site indicated that at least one Black-throated Blue Warbler was present at the site in the first year of the study and was detected on both surveys; in year 2, at least one Black-throated Blue Warbler was present and detected on the first survey but was not detected in the second; and in year 3, no Black-throated Blue Warblers were detected, either because the site went locally extinct or because observers failed to detect Black-throated Blue Warblers that were present on either survey.

Given the observed encounter histories, we estimated ψ, γ, ε, and *p* in Black-throated Blue Warblers with multiseason occupancy models (MacKenzie et al. 2003) in Program MARK (White and Burnham 1999). We compared 49 linear models, representing our hypotheses that site occupancy probabilities varied by playback treatment, shrub, and landscape, either alone or in combination. For example, the model *p*(detection covariates) ψ(shrub*landscape)γ(treatment)ε(landscape) assessed the likelihood of the field data when detection probability was a function of factors thought to influence an observer's ability to detect Black-throated Blue Warblers at a site (given presence), occupancy was a function of a shrub*landscape interaction, colonization was a function of playback treatment, and extinction probability was a function of landscape. In all models, ψ was modeled as a function of the interaction between shrub and landscape because previous

TABLE 1. Summary of sampling points that went extinct or were colonized in each of the two experiment categories for each of the two periods of our study.

Year	Experiment category	Extinct	Colonized
2003–2004	Treatment	1	2
	Control	9	16
	Total	10	18
2004–2005	Treatment	4	3
	Control	11	8
	Total	15	11

research showed that the interaction between these two habitat levels played an important role in determining Black-throated Blue Warbler abundance in this system (Cornell and Donovan 2010). In all models, p was modeled as a function of four variables known to affect detection of Black-throated Blue Warblers on point counts, including wind intensity, average daily temperature, date of survey, and time of day (Cornell and Donovan 2010). Detection probability was held constant across surveys within a year (secondary sampling occasions) but was allowed to vary between years. Thus, with ψ and p accounted for, we modeled γ and ε as functions of all univariate and additive combinations, and the two-way interactions, of playback treatment, shrub, and landscape

simultaneously. In all models, the logit link option was used to allow linear modeling. We then used information-theoretic approaches to rank and weight each model in the model set (Burnham and Anderson 2002).

RESULTS

We conducted 540 ten-minute point counts from 2003 to 2005 and counted 231 male Black-throated Blue Warblers. Raw counts ranged from 0 to 4 males within 100 m of the survey location per 10-min survey.

Occupancy, extinction, and colonization.—We estimated site occupancy, probability of extinction, and probability of site colonization at each of the 90 sites; 20 points were experimental points, and 70 points were control points. From 2003 to 2004, 10 sites occupied in 2003 went extinct in 2004, and 18 sites that were unoccupied in 2003 were colonized in 2004 (Table 1). One of the sites that went extinct was a treatment point, and 2 sites that were colonized were also treatment points. From 2004 to 2005, 15 sites went extinct and 11 were colonized (Table 1). Of those that went extinct 26% (4 of 15) were treatment points, and of those that were colonized 27% (3 of 11) were treatment points.

Of the 49 alternative models evaluated, 24 models comprised the 95% confidence set, indicating considerable uncertainty as to which model was best supported by the data (Table 2; Burnham

TABLE 2. A 95% confidence set of models of site occupancy (ψ) for Black-throated Blue Warblers in Vermont, number of model parameters (K), deviance, scaled second-order Akaike's information criteria (ΔAIC_c), and AIC_c weights (w_i). Models are ranked in ascending order according to fit (ΔAIC_c). In all models, ψ was modeled as a function of shrub*landscape and capture probability (p) was modeled as a function of the additive effects of wind intensity, average daily temperature, date of survey, and time of day (γ = colonization probability, ε = extinction probability).

| Model	K	Deviance	ΔAIC_c	w_i	Rank
$\varepsilon(.)$, $\gamma(.)$	13	606.89	0	0.14	1
ε(shrub*landscape), $\gamma(.)$	16	598.30	0.08	0.14	2
ε(landscape), $\gamma(.)$	14	604.59	0.51	0.11	3
ε(treatment), $\gamma(.)$	14	605.11	1.03	0.08	4
ε(shrub*landscape), γ(landscape)	17	597.08	1.90	0.05	5
ε(landscape), γ(landscape)	15	603.21	2.02	0.05	6
ε(shrub), $\gamma(.)$	14	606.58	2.51	0.04	7
ε(shrub*landscape), γ(treatment)	17	597.73	2.55	0.04	8
ε(treatment), γ(landscape)	15	603.79	2.60	0.04	9
ε(landscape), γ(treatment)	15	604.01	2.82	0.03	10
ε(treatment), γ(treatment)	15	604.15	2.96	0.03	11
ε(shrub*landscape), γ(shrub)	17	598.3	3.13	0.03	12
ε(landscape), γ(shrub)	15	604.58	3.39	0.03	13
ε(shrub), γ(landscape)	15	604.85	3.66	0.02	14
ε(treatment), γ(shrub)	15	605.11	3.92	0.02	15
ε(landscape*treatment), $\gamma(.)$	16	603.02	4.79	0.01	16
ε(shrub + landscape + treatment), $\gamma(.)$	16	603.06	4.83	0.01	17
ε(shrub), γ(treatment)	15	606.13	4.94	0.01	18
ε(shrub), γ(shrub)	15	606.56	5.37	0.01	19
ε(treatment), γ(shrub*landscape)	17	600.60	5.42	0.01	20
ε(shrub*landscape), γ(shrub*landscape)	19	594.34	5.52	0.01	21
ε(landscape), γ(shrub*landscape)	17	601.15	5.97	0.01	22
ε(landscape*treatment), γ(landscape)	17	601.89	6.71	0	23
ε(shrub + landscape + treatment), γ(landscape)	17	601.99	6.81	0	24
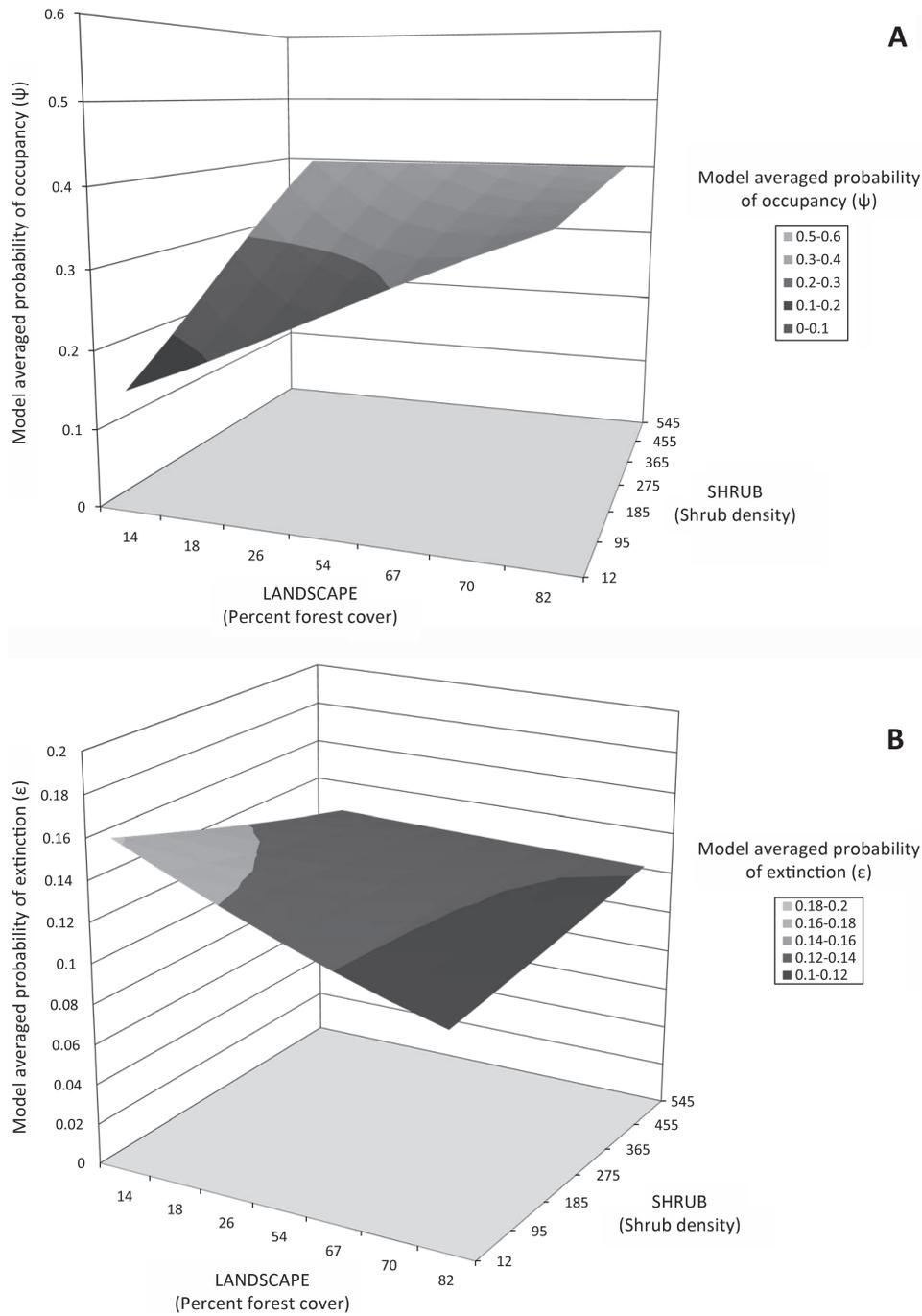
FIG. 1. Surface plots of (A) model-averaged probability of site occupancy as a function of the components "landscape" and "shrub" (see text; higher scores indicate a more contiguous landscape and greater shrub cover) and (B) model-averaged probability of site extinction as a function of landscape and shrub (higher scores indicate a more contiguous landscape and greater shrub cover).

and Anderson 2002). Therefore, we model-averaged to estimate the effect sizes of playback treatment, shrub, and landscape on ψ, γ, and ε. Recall that ψ establishes the baseline occupancy pattern in the first year of surveys and that changes in occupancy status thereafter are determined by γ and ε. The effect of shrub cover varied, depending on landscape pattern. Sites with high shrub cover had the highest probability of being occupied (~0.40), regardless of landscape-level patterns. However, in sites with low shrub cover, the probability that a site was occupied declined from 0.3 in contiguous landscapes to only ~0.1 in fragmented landscapes (Fig. 1A), which suggests that similar levels of shrub cover had a larger negative effect in fragmented landscapes.

There was little evidence that habitat variables or treatment (conspecific song cue) affected colonization probability. The top four ranked models in the model set suggested that colonization rates were constant for all sites, regardless of the treatment or habitat conditions. The fifth and sixth best-supported models, which carried a combined weight of 0.10, included a landscape effect on colonization probability and suggested that the probability that a previously unoccupied site in year t would become colonized in year $t + 1$ was higher if it was located in more contiguous forest habitat (Appendix).

In contrast to colonization probability, there was evidence that habitat variables affected site extinction probability. Model-averaged extinction probabilities ranged between 0.08 and 0.16 (Fig. 1B). Sites with the lowest shrub and most fragmented landscape variables had a 0.16 probability of going locally extinct (Fig. 1B). In the most fragmented study areas, this site extinction probability decreased to 0.13 when shrub was maximized. Site extinction probability was lowest in the most continuously forested landscapes, where the probability of extinction ranged between 0.08 and 0.12 (Fig. 1B). The fourth best-supported model, which carried a model weight of 0.08, included the effect of playback treatment on site extinction probability (Table 2), and the effect was negative, which suggests that conspecific cues might reduce the probability of site extinction.

Discussion

We used an experimental approach to test multiple hypotheses about avian habitat selection, in which structural features of vegetation at multiple spatial extents and the presence of other conspecifics may both be important proximate cues of habitat quality (Hildén 1965). Proximate vegetation cues directly signal ultimate factors such as nest site and food availability, predation pressure, and parasitism pressure. Alternatively, the presence of conspecifics, in addition to the availability of resources mentioned above, may also signal other ultimate factors, including mate availability. Although vegetation cues require direct sampling by individuals, conspecific location may be a more efficient means of site assessment and, in some cases, provide greater detail about habitat quality than vegetation structure alone (e.g., individuals may be informed by private information). Our results supported our hypotheses that (1) territory- and landscape-level vegetation patterns were relatively more important than prebreeding conspecific song cues, either as attractants or deterrents, for determining Black-throated Blue Warbler occupancy patterns; and (2) occupancy and extinction probabilities were affected by an interaction between habitat features at different spatial extents.

We found that site occupancy probability was driven by an interaction between site- and landscape-scale habitat patterns. This interaction suggests that the importance of "shrub" on site-occupancy probability depends on the "landscape" context. In fragmented and contiguous landscapes, occupancy probability was highest at sites with high shrub cover. In contiguous landscapes, occupancy probability remained nearly unchanged as shrub cover declined, but in fragmented landscapes, a decline in shrub cover resulted in lower probability of occupancy compared with high shrub areas in either fragmented or intact landscapes. This interaction is likely the result of the overall distribution of shrubs in our study system, in which forest fragments had higher shrub density overall because of the effects of an ice storm that affected the region in 1998. Therefore, intact forested sites had consistently adequate shrub cover, but it was, on average, lower overall than fragmented sites.

Our experimental approach allowed us to examine changes in site occupancy patterns as they were related to habitat and playback treatment. We found that the probability of site extinction was also influenced by the interaction of understory shrub cover and landscape pattern: sites with low shrub cover in fragmented landscapes were more likely to experience extinction than sites with low shrub cover in intact forests. These findings confirmed the results of a previous study that examined the influence of habitat features at multiple spatial extents on demographic measures (Cornell and Donovan 2010); it appears that Black-throated Blue Warblers use a combination of fine-scale understory shrub cover and landscape pattern as primary cues of territory selection decisions. This result is consistent with James's (1971) theory that individuals may visualize and respond to a holistic suite of proximate factors in the environment that may effect breeding success. However, for Black-throated Blue Warblers, choosing high-shrub areas in fragmented landscapes may result in reduced fitness. We found that Black-throated Blue Warblers breeding in such habitats were typically first-time breeders, had lower pairing success, and had reduced annual fecundity (Cornell and Donovan 2010). Reduced reproductive success in these areas is likely the result of an increased probability of being parasitized by cowbirds, the influence of a more diverse predator community, and, potentially, lower food availability. Thus, birds that selected territories in fragmented landscapes were more likely to fail in their reproductive efforts, potentially triggering them to vacate territories and move to new territories in subsequent years (Greenwood and Harvey 1982). By contrast, birds in contiguous landscape had higher annual productivity, regardless of territorial shrub cover, and the probability that territories went extinct was lower, because either adults were more likely to return or the site was more likely to be colonized by new recruits.

There is strong evidence of associations between bird abundance and vegetation structure (Hildén 1965, James 1971, Hutto 1985, Holmes et al. 1996, Jones 2001, Lichstein et al. 2002). Researchers propose that correlations of individuals of a species with specific habitat features or overall habitat gestalt may suggest that individuals primarily use vegetation cues at multiple spatial scales to select breeding territories (James 1971). Not surprisingly, our results are consistent with these long-standing patterns. However, there is also recent support for the idea that territorial species, in addition to colonial species, may base their choice of breeding-territory location on social cues observed during the presettlement period (Ward and Schlossberg 2004) or on observations of postbreeding locations (public information) or breeding success (private information) (Boulinier and Danchin 1997, Doligez et al. 2002, Danchin et al. 2004, Betts et al. 2008). Given these recent findings, we expected that social cues may also be important for determining territory occupancy in Black-throated Blue Warblers or act in combination with vegetation cues. Our results did not support our hypothesis that prebreeding conspecific song cues act alone, or in combination with habitat cues, to determine breeding-site selection. Further, our results are not consistent with Betts

et al.'s (2008) study conducted on the same species in the same geographic region, which found that postbreeding conspecific cues override vegetation cues for territory selection. Although our field methods differed, there are several additional plausible explanations for discrepancies.

First, it is possible that conspecific cuing plays a role in territory selection in this species at a different time during the annual cycle than when our study was conducted. There is some evidence in the literature to suggest that prebreeding conspecific locations may play a role in territory selection. For example, in a study of the endangered Black-capped Vireo (*V. atricapilla*), Ward and Schlossberg (2004) used experimental simulations of conspecific song played during spring settlement to lure birds to settle in new habitats. However, there is also a large body of evidence from studies in both North America and Europe in support of the hypothesis that birds use private (e.g., successful breeding attempts) or public information (e.g., parents feeding fledglings) in late summer to direct their territory-selection decisions in the following year. Betts et al. (2008) found support for this hypothesis in Black-throated Blue Warblers in an unfragmented forest in New Hampshire. It is possible that Black-throated Blue Warblers may also use postbreeding cues in our heterogeneous study system, but it remains untested. We have observed that adults breeding on fragments tend to leave earlier in the season than adults breeding in contiguously forested landscapes (K. Cornell and T. Donovan unpubl. data). If prospecting indeed happens in the late summer on the basis of private or public information, it suggests that site colonization will be higher in these more forested areas.

Second, it may be that song is not the cue that this species uses in social interactions. The songs that we used were recorded from birds in New York and New Hampshire, and it is possible that dialects differ in Vermont. Additionally, birds may respond more strongly to the physical presence of other birds than to song. Where the playbacks appeared to have triggered settling, we noticed that two or more birds were typically present, such that each bird provided visual and physical stimuli in addition to increased vocal stimuli at the playback-box locations. In many cases, we observed birds prospecting playback-box locations but leaving if there was not another bird there. In addition, Betts et al. (2008) used both song playback and decoys to simulate conspecific presence but did not separate the effects of these different stimuli. Future experiments are needed to tease apart the actual social cue(s) that individuals evaluate.

Third, if the cue used in our experiment was indeed correct and prebreeding song is important, we may have failed to detect an effect because our experiment was designed to test the effect of conspecific cuing under vastly different vegetation structures at both the local and landscape scales. Many of the studies that have demonstrated a positive effect of conspecific cuing were conducted in relatively homogeneous landscapes (comparatively speaking). For instance, in contrast to our study, Betts et al.'s (2008) study took place within the contiguously forested White Mountain National Forest in New Hampshire. Although their test sites varied in forest structure, all of the sites were highly forested, essentially controlling for this variation and lessening the importance of landscape pattern. When viewed across a large gradient of shrub and landscape structure, our results suggest that vegetation structure is a more important determinant of site occupancy

patterns and changes in site occupancy patterns. If playback treatment affected settlement, the signal likely needed to be great in order for our study design to detect it. Thus, given the extent to which humans are altering natural landscapes, additional studies in developed landscapes are needed to determine the extent of the roles of vegetation cues and social information in territory selection. Further, because cues can become disassociated from abundance and reproductive success in altered landscapes (Van Horne 1983, Weldon and Haddad 2005), studies that examine multiple cues and association of cues with fitness parameters (reproduction and survival) are needed to direct conservation practices.

A final possible explanation for our results is that birds may employ a two-step strategy for selecting breeding territories where prospecting Black-throated Blue Warblers are first attracted to the song-playback sites, then inspect and reject those sites that appear to be suboptimal in habitat features. Under this scenario, our results would not imply that acoustic conspecific cues are not used by Black-throated Blue Warblers for territory assessment. Rather, they might suggest that the first step of territory selection involves a rapid assessment based on cues from other birds that are already present in a particular habitat, followed by a more thorough investigation of the potential breeding site (direct sampling). Given the potential high fitness costs of breeding in suboptimal habitat, we would expect birds to invest some time and energy into directly inspecting the habitats at their potential breeding site, rather than relying solely on the location of other individuals. Neither our study nor that of Betts et al. (2008) investigated such a hierarchical process. Evidence suggests that selection decisions may occur in descending order from large to small scales (Hutto 1985), and well-designed experiments are needed to test this across large landscapes.

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Appendix. Coefficients ($\beta \pm SE$) of Black-throated Blue Warbler occupancy (ψ), extinction (ε), and colonization (γ) for the five best-supported models (Table 2).

Model	Parameter	Intercept	Shrub	Landscape	Treatment	Shrub*landscape
$\varepsilon(.)$, $\gamma(.)$	ψ	0.62 ± 0.41	0.19 ± 0.10	0.15 ± 0.06		-0.05 ± 0.02
$\varepsilon(shrub*landscape)$, $\gamma(.)$	ψ	0.61 ± 0.38	0.20 ± 0.11	0.15 ± 0.06		-0.05 ± 0.02
$\varepsilon(landscape)$, $\gamma(.)$	ψ	0.63 ± 0.39	0.19 ± 0.10	0.16 ± 0.06		-0.05 ± 0.02
$\varepsilon(treatment)$, $\gamma(.)$	ψ	0.63 ± 0.39	0.19 ± 0.10	0.16 ± 0.06		-0.05 ± 0.02
$\varepsilon(shrub*landscape)$, $\gamma(landscape)$	ψ	0.47 ± 0.34	0.19 ± 0.10	0.13 ± 0.05		-0.04 ± 0.02
$\varepsilon(.)$, $\gamma(.)$	ε	-1.29 ± 0.26				
$\varepsilon(shrub*landscape)$, $\gamma(.)$	ε	-1.02 ± 0.30	-0.03 ± 0.10	-0.11 ± 0.05		0.04 ± 0.02
$\varepsilon(landscape)$, $\gamma(.)$	ε	-1.15 ± 0.27		-0.05 ± 0.04		
$\varepsilon(treatment)$, $\gamma(.)$	ε	-1.18 ± 0.27			-1.41 ± 1.61	
$\varepsilon(shrub*landscape)$, $\gamma(landscape)$	ε	-1.00 ± 0.29	-0.03 ± 0.10	-0.10 ± 0.05		0.04 ± 0.02
$\varepsilon(.)$, $\gamma(.)$	γ	-0.71 ± 0.34				
$\varepsilon(shrub*landscape)$, $\gamma(.)$	γ	-0.66 ± 0.33				
$\varepsilon(landscape)$, $\gamma(.)$	γ	-0.71 ± 0.34				
$\varepsilon(treatment)$, $\gamma(.)$	γ	-0.74 ± 0.34				
$\varepsilon(shrub*landscape)$, $\gamma(landscape)$	γ	-0.47 ± 0.32		0.05 ± 0.05		