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SETTLEMENT IN NOVEL HABITATS INDUCED BY SOCIAL INFORMATION MAY DISRUPT COMMUNITY STRUCTURE

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Abstract. Birds may colonize new habitats because of introduction, changing environmental conditions, and/or altered social or environmental cues. However, aside from introduced (often invasive) species, little is known about the consequences of such colonizations for members of existing communities. If the realized niche is influenced by the presence or absence of heterospecific competitors, then addition of a species to a novel habitat or location could result in extirpation or avoidance if members of the existing community are subdominant. Alternatively, if for some species heterospecific cues are the primary means for collecting information about a site's quality, heterospecific attraction could occur. To test these predictions, we experimentally induced free-living Black-throated Blue Warblers (*Dendroica caerulescens*) to colonize a novel environment within their existing range. We used dynamic occupancy modeling to test for the dynamics of colonization and local extinction as a function of our experimental treatment. We found strong evidence for dynamic occupancy by birds during the breeding season; colonizations and extirpations were common. Although dynamics were not generally well explained by our experimental introduction of Black-throated Blue Warblers, we found some support for the heterospecific-avoidance hypothesis; three of the four species we examined that prefer early seral forests tended to abandon a site once Black-throated Blue Warblers occupied it. We suggest that heterospecific interactions should be considered when species' distributions are projected in relation to climate change. Our results provide a caution that managers broadcasting a species' song to increase its abundance should consider the technique's effects on the broader community.

Key words: Black-throated Blue Warbler, competitive exclusion, *Dendroica caerulescens*, heterospecific attraction and avoidance, no-analog community, realized niche, social information.

El Establecimiento en Ambientes Nuevos Inducido por Información Social podría Perturbar la Estructura de las Comunidades

Resumen. Las aves pueden colonizar nuevos ambientes debido a introducciones, a cambios en las condiciones ambientales y/o a alteraciones en las señales sociales o ambientales. Sin embargo, con excepción del caso de especies introducidas (a menudo invasoras), se conoce poco acerca de las consecuencias de dichas colonizaciones para los miembros de las comunidades existentes. Si el nicho realizado es influenciado por la presencia o ausencia de individuos competidores heteroespecíficos, entonces la adición de una especie a un hábitat o localidad nueva podría conducir a la extinción local o a la evitación si los miembros de la comunidad existente no son dominantes. Por otro lado, si para algunas especies las señales heteroespecíficas son el medio principal para obtener información sobre la calidad de los sitios, podría existir atracción entre individuos heteroespecíficos. Para poner a prueba estas predicciones, inducimos experimentalmente a individuos de la especie *Dendroica caerulescens* a colonizar un ambiente nuevo ubicado en su área de distribución actual. Utilizamos modelos dinámicos de ocupación para evaluar la dinámica de colonización y extinción local como una función de nuestro tratamiento experimental. Encontramos evidencia fuerte de una ocupación dinámica de las localidades por parte de las aves durante la estación reproductiva: las colonizaciones y extinciones locales fueron comunes. Aunque, en general, la dinámica no se explicó bien con base en nuestra introducción experimental de *D. caerulescens*, encontramos algo de evidencia que apoya la hipótesis de la evitación de individuos heteroespecíficos: tres de las cuatro especies estudiadas que prefieren bosques en estadios sucesionales tempranos tendieron a extinguirse localmente una vez que los sitios fueron ocupados por *D. caerulescens*. Sugerimos que deben considerarse las interacciones entre especies cuando sus distribuciones se proyectan en relación con cambios en el clima. Nuestros resultados son un llamado de atención para que los gestores que reproducen el canto de una especie para incrementar su abundancia tengan en cuenta los efectos de esta técnica sobre la comunidad de forma más amplia.

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INTRODUCTION

Birds select potential breeding sites on the basis of structural habitat and/or social cues. A species can settle novel breeding sites when (1) it is a generalist capable of invasion (Shirley and Kark 2009), (2) a habitat's structure has changed, making it more accessible (e.g., range shifts due to climate change; Parmesan and Yohe 2003), and/or (3) social cues indicate, sometimes incorrectly (Giraldeau et al. 2002), that new sites are available. Direct management often centers on manipulating social cues to induce settlement (see review by Ahlering et al. 2010, this issue). Although the dynamics of invasions have been the subject of many previous studies (see review by Sakai et al. 2001), we know little about the community-level consequences of immigration by birds induced to settle new areas by broad-scale habitat change and/or manipulation of social cues for management (Fletcher 2008). Understanding these consequences is particularly important if we are to predict how populations will respond to habitat loss and climate change (Bowler and Benton 2005).

It is becoming increasingly clear that animals respond to climate change in various ways (Parmesan and Yohe 2003). Though some species are capable of shifting their ranges to keep pace with warming temperatures and shifting distributions of prey, others appear to lack either the capacity or the motivation for such behavior (Devictor et al. 2008). These differences in rates of immigration to new regions across elevations and latitudes are predicted to disrupt community composition creating novel communities without analogs (Thomas and Lennon 1999, Williams and Jackson 2007, Stralberg et al. 2009). Predictions about how communities will respond to changes in species composition have frequently been informed by the assumption of "niche conservatism"—the notion that characteristics of a species' niche will be conserved under future conditions (Wiens and Graham 2005). This assumption is predominant in bioclimatic envelope modeling (e.g., Peterson et al. 2002) and underlies many projections of species' response to climate change (Botkin et al. 2007). However, according to Hutchinson (1957), although the fundamental niche comprises all conditions under which an organism is physiologically capable of persisting, the realized niche represents a subset of the fundamental niche where an organism actually persists in the context of competitive interactions. The concept of the realized niche thus supports the potential for the presence of other species to influence an organism's distribution. Under scenarios of management experiments using conspecific attraction, different rates of shifting of birds' ranges, or simply multiple species' asynchronous population fluctuations, the realized niche of a species should therefore be dynamic, rather than "conserved," because competitors' abundances and distributions change over time.

Sympatric heterospecifics are often attracted to each other (Slagsvold 1980), commonly as a means of gathering information on habitat quality by observing others (Mönkkönen et al.

1990, 1996). However, heterospecifics may also avoid one another. For example avoidance could arise when information use is density dependent (e.g., when too few or too many birds indicate poor habitat; Forsman et al. 2008) or to reduce interaction with a particularly aggressive species (Fletcher 2008). It is currently unclear how these seemingly conflicting strategies of attraction and avoidance interact when allopatric species come into contact, such as through manipulation of social cues for management or range shifts. Resources being constant, if a realized niche is governed by the presence of competitors, addition of a new competitor should result in displacement of heterospecifics. Alternatively, if heterospecific cues are the primary means by which a species gets information about a site's quality, either heterospecific attraction or avoidance should occur. Fulfilling of the former of these predictions has been observed with introduced species (Clavero and Garcia 2005). Aside from introductions, however, little is known about the community-level consequences of birds' colonizing novel habitats (Guisan and Thuiller 2005). This is presumably because it has been challenging, or at least ecologically risky, to experimentally supplement species to specific sites in order to observe subsequent effects on the community.

To test our predictions, we experimentally induced free-living Black-throated Blue Warblers (*Dendroica caerulescens*) to colonize a novel environment within their existing range. Black-throated Blue Warblers breed mainly in contiguous tracts of undisturbed deciduous or mixed forest (Holmes et al. 2005); our experiments attracted males to settle in such uncharacteristic habitat as clearcuts regenerating 5–30 years after being logged (Betts et al. 2008a). We used a recently developed statistical approach, dynamic occupancy modeling (MacKenzie et al. 2003), to test for local colonization and extinction dynamics as a function of this experimental treatment. By modeling the changes in the bird communities of early-seral forest before and after the controlled "invasion" of Black-throated Blue Warblers, we are able to test whether other species colonize, remain, or leave as a function of this treatment. Under the heterospecific-avoidance hypothesis, we expected that species typically associated with early seral forest should be displaced by experimentally introduced Black-throated Blue Warblers. Under the heterospecific-attraction hypothesis, if species typically occurring with the Black-throated Blue Warbler use this species as an indicator of site quality, our experimental introduction of this species should induce settlement.

METHODS

STUDY AREA

We conducted our study within the Pemigewasset River valley region of the White Mountain National Forest, New Hampshire. The landscape is dominated by contiguous second-growth forest consisting primarily of sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*) (Doran and Holmes 2005).

SPECIES ADDITION

As part of larger study investigating use of social information in habitat selection (Betts et al. 2008a), we were able to override structural cues and induce Black-throated Blue Warblers to colonize habitats where they would typically not occur. This migratory species is typically strongly associated with mature deciduous forest (Betts et al. 2006). Our experiment attracted the species into recently clear-cut forest (~5–30 years old). It provided us with an unprecedented opportunity to examine the effects of experimentally supplementing a species into a novel habitat. By introducing a species to a novel habitat, where vegetation structure and bird communities are markedly different from those at sites where it typically occurs, we were able to examine how introduction of a new species affects site-level community structure. We established 54 research sites across a vegetation-structure gradient from early seral hardwood forest to mature hardwood and mixed coniferous–deciduous forest. We established three broad categories of sites that represented this gradient: <10 years ($n = 15$; shrub cover $79.0\% \pm 4.3$ SE, tree density $0.1 \text{ ha}^{-1} \pm 0.1$), 10–30 years ($n = 21$; shrub cover $6.4\% \pm 2.5$, tree density $3.1 \text{ ha}^{-1} \pm 2.6$), and >60 years ($n = 18$; shrub cover $52.9\% \pm 6.1$, tree density $104.0 \text{ ha}^{-1} \pm 11.6$). We confirmed that no sites contained Black-throated Blue Warblers during the breeding season of 2006 by passive observation (10-min point counts) followed by playback (for <5 min) of the species' song. We deemed a site acceptable for inclusion in our study only if we detected no Black-throated Blue Warblers within 50 m of the playback. Because in our study area the probability of detecting the Black-throated Blue Warbler within a 10-min count is high ($P > 0.9$; Betts et al. 2008b), we are confident that our sampling periods were sufficient for occupancy to be assessed. We broadcast the male's song from 05:00 to 15:00 for 5 or 6 days during two separate visits (a total of 10–12 days) at each site from 10 July to 30 August 2006 to provide conspecific social cues for Black-throated Blue Warblers. We selected locations of playback ($n = 36$) and controls (no playback, $n = 18$) randomly from our total sample of 54. This randomization resulted in spatial interspersed of treatments. We apportioned our 36 experimental sites between two treatments, (1) male song only ($n = 18$) and (2) male song, female calls, and fledgling begging calls ($n = 18$), to test the hypothesis, as part of a different study, that public information (male, female, fledglings) constitutes information superior to location cues (song only; see Betts et al. 2008a for details). We detected no significant difference between the two treatments in the Black-throated Blue Warbler's settlement response (Betts et al. 2008a), so in the current study we treated these as equivalent. Furthermore, we detected no significant difference between control and playback treatments in shrub cover ($t = 0.04$, $P = 0.96$) or tree density ($t = 0.30$, $P = 0.76$). The following spring, we returned to sites during and after migration to determine warbler settlement. We considered male Black-throated Blue Warblers to have settled at a site if they

behaved territorially (singing, aggression with neighboring males) within 50 m of the speakers broadcasting the song. This experimentally induced settlement resulted in Black-throated Blue Warblers colonizing sites where they did not typically occur (Betts et al. 2008a).

POINT-COUNT METHOD

We visited each point five times between 5 and 25 May 2007 at intervals of 2–4 days. Each 10-min count was divided into three subcounts of 3 min, 20 sec. We treated each subcount as a new sampling period (i.e., one individual would be recorded three times if it sang during all subcounts). Each visit is equivalent conceptually to a "season" of MacKenzie et al (2003). This protocol resulted in a total of 15 samples (5 primary visits each containing 3 secondary subcounts). We conducted counts from 05:30 to 11:00 but not during rain or strong wind ($>15 \text{ km hr}^{-1}$). To reduce the influence of observer bias we randomly assigned observers to count points on the first visit and rotated them among points on each subsequent primary visit; this ensured that during later visits observers were not biased by previous experience at a point. We considered a species present during a count if a male was detected singing within a 100-m radius of the point. We considered a Black-throated Blue Warbler to have colonized a site if a male was present during any of the secondary subcounts within a primary visit. It is unlikely that the Black-throated Blue warblers we observed were migratory transients because (1) they behaved territorially (i.e., sang), (2) we observed Black-throated Blue Warblers on multiple occasions at the majority (69%) of sites where they settled, and (3) sites were occupied well into the breeding season (i.e., late June). Nevertheless, we analyzed results both with and without data from the putative period of migration.

STATISTICAL ANALYSIS

We selected the seven most common species detected at point counts for analysis. Each of the seven occurred at 10% to 70% of the sites. These species also represented a gradient in their association with forest of various ages: three species, the Ovenbird (*Seiurus aurocapilla*), Black-throated Green Warbler (*Dendroica virens*), and Black-and-White Warbler (*Mniotilta varia*), are typically associated with mature forest (Van Horn and Donovan 1994, Sherry and Holmes 1997, Morse and Poole 2005), one, the American Redstart (*Setophaga ruticilla*) is associated with mid-seral forest (Kricher 1995, Betts et al. 2006), and three species, the White-throated Sparrow (*Zonotrichia albicollis*), Chestnut-sided Warbler (*D. pensylvanica*), and Common Yellowthroat (*Geothlypis trichas*) tend to be associated with forest of very early seral stages (Falls and Kopachena 1994, Richardson and Brauning 1995, Betts et al. 2006).

We modeled site occupancy, settlement, avoidance, and probability of detection of these putative competitors with the Black-throated Blue Warbler by the "dynamic occupancy" methods designed for open populations by MacKenzie et al.

(2003). “Settlement” and “avoidance” are equivalent to “colonization” and “local extinction” outlined by MacKenzie et al. (2003). Overall, this approach is analogous to Pollock’s (1982) robust design for estimating survival in that site occupancy may change from one primary visit to the next, but among secondary subcounts occupancy is assumed to be static. In our study, this assumption is reasonable because subcounts within a visit were consecutive within a single 10-min period. We summarized records of bird detection (1) and nondetection (0) into “encounter histories” similar to those of mark-recapture studies (e.g., 001 101 111). A maximum-likelihood modeling procedure then relies on detection-history data to estimate occupancy (ψ), attraction (γ), avoidance (ϵ), and detection probability (p) (MacKenzie et al. 2003). From visit to visit, occupancy changes as a result of immigration (attraction) to a site if it is unoccupied or emigration (avoidance) from a site if it is occupied. In this sense, occupancy of a site is a Markovian process; occupancy at time $t + 1$ is dependent upon occupancy at time t . This approach is appropriate for territorial, site-faithful species (MacKenzie et al. 2006). We used Akaike’s information criterion (AIC) to select models (Akaike 1974) and analyzed occupancy with the program PRESENCE (<http://www.mbr-pwrc.usgs.gov/software/presence.html>).

Our models included two main predictor variables. (1) Settlement of Black-throated Blue Warblers at sites as a function of our experimental treatment in the previous breeding season. This dichotomous variable is a sample covariate (i.e., it varied within sites across primary sampling periods). In a preliminary analysis we also used relative abundance (mean number of warblers detected in point counts) as a measure of Black-throated Blue Warbler settlement. Results were not qualitatively different from those of presence/absence models except that fewer models converged, so we report only presence/absence results here. (2) We also tested for the effects of our initial treatment—song playback or control—on heterospecific attraction and avoidance. Models including this variable test the hypothesis that other species use Black-throated Blue Warbler song in the previous breeding season as a heterospecific cue indicating site quality. In all subsequent models, we tested the influence of both the above variables on heterospecific site occupancy, attraction, avoidance, and probability of detection. As ours was an experimental study, for logistical reasons our sample size was smaller than is typical for studies of site occupancy by songbirds (e.g., Betts et al. 2008b). Therefore, to limit the risk of overfitting the models, we did not test every possible combination. Rather, our set of models included univariate effects of Black-throated Blue Warbler colonization or initial treatment on (1) probability of local avoidance, (2) probability of settlement, and (3) occupancy. These models describe whether observed patterns of local extinction (through avoidance) or settlement might be driven simply by negative or positive associations of each species with the Black-throated Blue Warbler for indirect reasons

such as habitat structure. We also tested the null model that occupancy dynamics could not be explained by either Black-throated Blue Warbler settlement or our initial treatment. Finally, we tested the hypothesis of “population closure” (i.e., no movement within a season) with the global “single-season” (nondynamic) model, which does not include parameters for settlement and avoidance (MacKenzie et al. 2002). If a population is closed, models without colonization and local extinction should explain the data as well or better than models including additional movement parameters (e.g., Betts et al. 2008b, Rota et al. 2009). Where possible, we controlled for the potential influence of the presence of Black-throated Blue Warblers on detection probability. In three instances (i.e., models for Chestnut-sided Warbler, American Redstart, and Black-and-White Warbler), however, models with this additional parameter did not converge, so we assumed detection probability to be constant. In total, this procedure yielded seven models for each species.

RESULTS

We found strong evidence for movement within a season by all species examined; dynamic models of site occupancy tended to be more strongly supported than those that assumed population closure. Values of Δ AIC with respect to the nondynamic model ranged from 52.8 (Common Yellowthroat), to 137.2 (Chestnut-sided Warbler). This result was expected given that our surveys began prior to the arrival of most of our focal species, all of which are migrants (Fig. 1). However, when we used only data collected after post-migration settlement stabilized, after period 3 (20 May; Fig. 1), models containing colonization and extinction terms were still better supported than models assuming site fidelity and population closure; Δ AIC with respect to the nondynamic model ranged from 3.1 (White-throated Sparrow) to 298.2 (Chestnut-sided Warbler).

These occupancy dynamics were not generally well explained by our experimental introduction of Black-throated Blue Warblers. Under the heterospecific-attraction hypothesis, we predicted that settlement rates of species typically associated with the Black-throated Blue Warbler should increase where we introduced this species. At introduction sites, the colonization rates of the three species associated with mature forest associated birds differed very little from those at control sites (Fig. 2). For all species, models containing Black-throated Blue Warbler introduction as a predictor of colonization had AIC values consistently higher than intercept-only models (Fig. 2). Sample size appeared to be insufficient to allow models of the three early-seral species to converge. Nevertheless, the sizes of the colonization effect as a function of Black-throated Blue Warbler introduction were not qualitatively greater for the mature-forest species than for the White-throated Sparrow, a species associated with early-seral forest (Fig. 3).

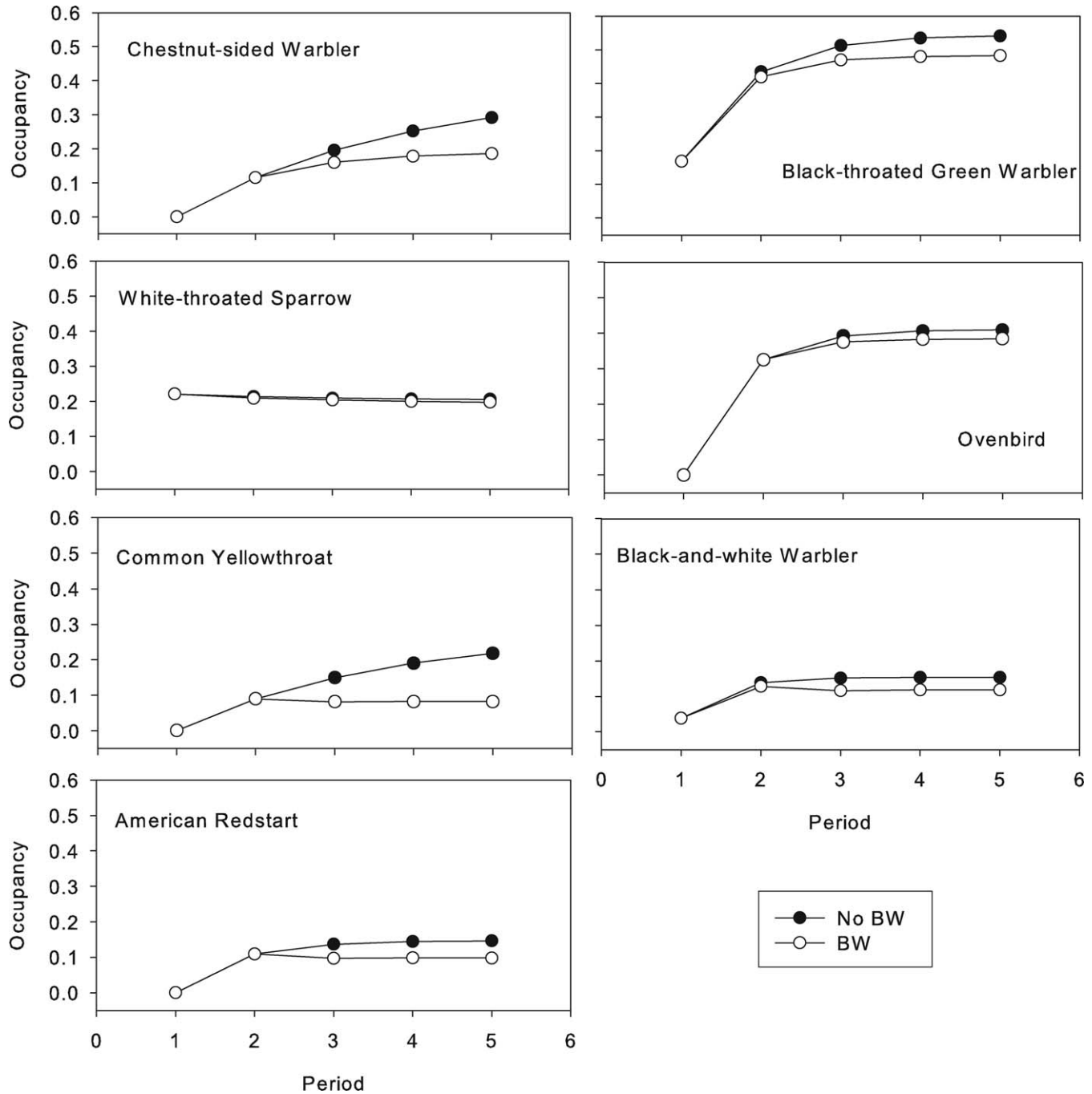


FIGURE 1. Trends in estimated occupancy of seven focal species from 5 to 31 May over five visits as a function of experimental addition of Black-throated Blue Warblers (BW) or no addition (no BW).

Under the heterospecific-avoidance hypothesis, we expected that species typically associated with early-seral forest should have a greater likelihood of being displaced by introduced Black-throated Blue Warblers. Three out of four early- and mid-seral species showed some evidence of avoidance (Figs. 3 and 4), though within ΔAIC of 2, the AIC of models

predicting local emigration as a function of Black-throated Blue Warbler introduction tended to be lower than that of intercept-only models. Though statistical error was substantial, effect sizes were large for two of the three early-seral associates; the likelihood of local emigration as a function of Black-throated Blue Warbler settlement was 1.64, 2.69, and

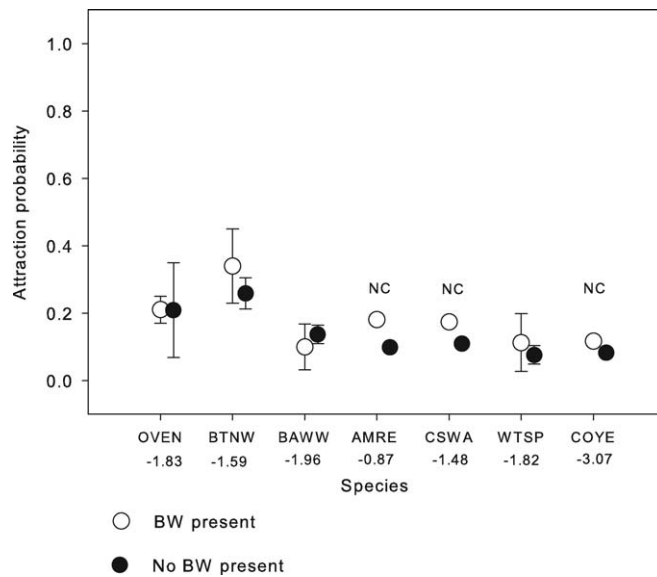


FIGURE 2. Estimated probability of conspecific attraction (\pm SE) as a function of the experimental addition of a Black-throated Blue Warbler to sites where this species would not typically occur. Addition of Black-throated Blue Warblers appears to have little effect on probability of subsequent settlement of the species tested. Numbers below species codes are Δ AIC from a model with settlement as a function of Black-throated Blue Warbler presence to the top-ranked model with no such parameter. NC, model did not converge adequately so SE is not reported. OVEN, Ovenbird; BTNW, Black-throated Green Warbler; BAWW, Black-and-white Warbler; AMRE, American Redstart; CSWA, Chestnut-sided Warbler; WTSP, White-throated Sparrow; COYE, Common Yellowthroat.

4.24 times that of controls for the American Redstart, Chestnut-sided Warbler, and Common Yellowthroat, respectively. In contrast, there was little evidence that species typically associated with the Black-throated Blue Warbler (the Ovenbird, Black-throated Green Warbler, Black-and-White Warbler) were displaced; intercept-only models received substantially more support (Fig. 3), and effect sizes tended to be small.

The potential negative response by heterospecifics that we observed appears to be due to interactions with real Black-throated Blue Warblers that settled at sites rather than our playbacks after the previous breeding season. We found little evidence that playback influenced either attraction or avoidance. Local-emigration models containing this indirect effect of the treatment were ranked consistently lower than models with intercept only or with Black-throated Blue Warbler introduction (Δ AIC with respect to intercept-only model: Common Yellowthroat = 1.33, Chestnut-sided Warbler = 1.37, American Redstart = 1.85, Ovenbird = 1.40, Black-throated Green Warbler = 0.73). Only the White-throated Sparrow showed some weak evidence for a playback effect (Δ AIC with respect to intercept-only model = -1.28); however, the effect size was small (probability of emigration with no playback 0.35 ± 0.10 SE, with playback 0.40 ± 0.33 SE). Similarly, colonization

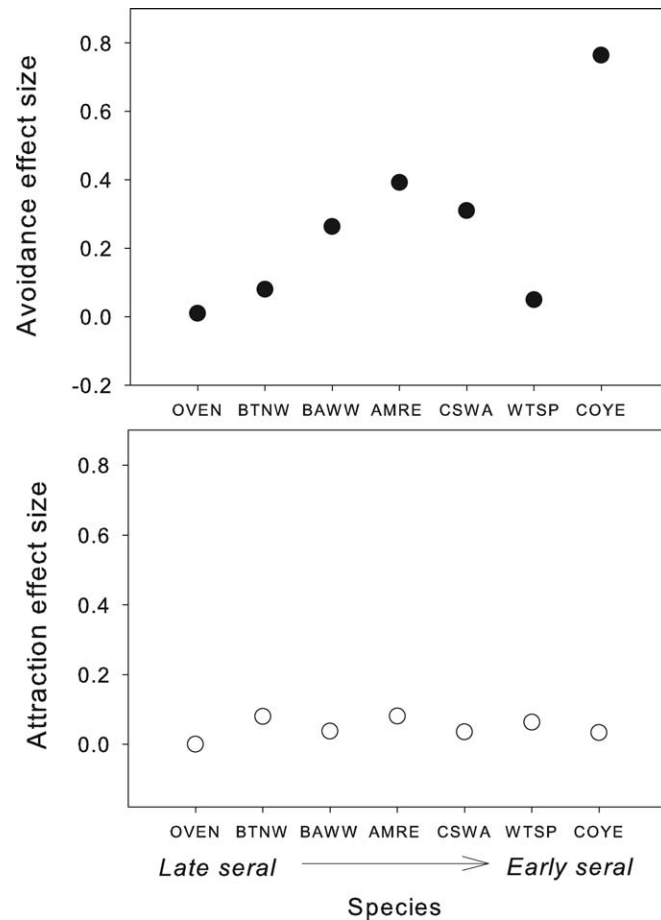


FIGURE 3. Effect size of avoidance or settlement as a function of experimental addition of Black-throated Blue Warblers. Effect size was measured as probability of avoidance or attraction at control sites minus the same probabilities at treatment sites. Note that effect size of avoidance is stronger for species associated with early-seral forest. Effect size for settlement tended to be small and showed no pattern as a function of the bird's association with a seral stage. See Fig. 2 for species codes.

models containing playback treatment were ranked lower than intercept-only models (Δ AIC with respect to intercept-only model >1 for all species).

DISCUSSION

Though avian occupancy dynamics were generally not clearly explained by our experimental introduction of Black-throated Blue Warblers, our results do provide some support for the heterospecific-avoidance hypothesis. Three of the four species we examined that prefer early- to mid-seral forests and do not usually occur with the Black-throated Blue Warbler showed evidence of emigration once Black-throated Blue Warblers occupied a site. In some instances, estimates of vacancy rates at sites with Black-throated Blue Warblers were twice as high as at those without them; the Common Yellowthroat was the

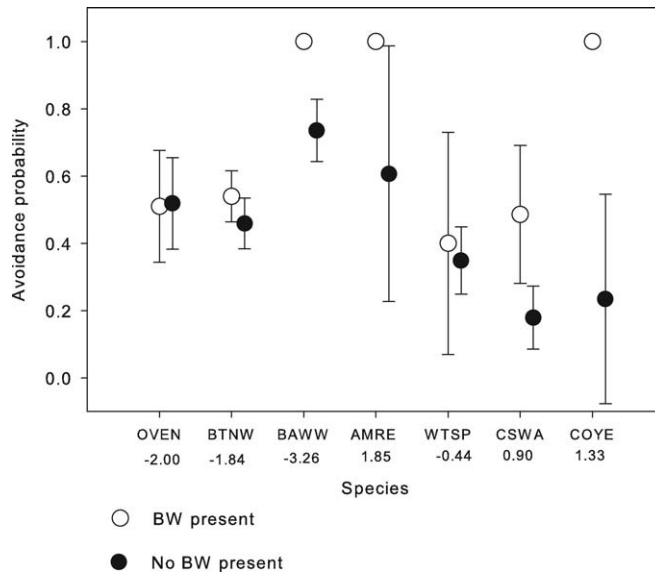


FIGURE 4. Estimated probability of conspecific avoidance as a function of the experimental addition of a Black-throated Blue Warbler to sites where this species would not typically occur. Though statistical error (measured here as SE) was high in most instances, effect sizes for avoidance of several species/associated with early-seral forest (American Redstart, AMRE; Chestnut-sided Warbler, CSWA; Common Yellowthroat, COYE) were positive and quite large. Numerical values below species codes are Δ AIC from a model with avoidance as a function of Black-throated Blue Warbler presence to the top-ranked model with no such parameter. See Fig. 2 for additional species codes.

most prone to emigrate, followed by the Chestnut-sided Warbler and American Redstart. The statistical strength of these relationships is modest, though the results are in the predicted direction. The White-throated Sparrow is a notable exception because it did not seem to be affected by the immigration of Black-throated Blue Warblers, probably because it forages on the ground, supplements its diet with seeds and fruit (Falls and Kopachena 1994), and likely competes little with the Black-throated Blue Warbler for most resources.

Conversely, we found that heterospecifics with life histories and habitat preferences similar to those of the Black-throated Blue Warbler were not attracted to colonize areas with that species. Perhaps the species we assessed do not commonly perceive the Black-throated Blue Warbler as a source of interspecific social information on habitat quality. Additionally, the role of density cannot be discounted; density of competitors may act as a cue to signal habitat quality and facilitate coexistence (Forsman et al. 2008, Parejo et al. 2008). Low densities of competitors may signal poor habitat and fail to attract others, while high densities may be repellent because of intense competition (Mönkkönen et al. 1999, Fletcher 2007). In such cases, heterospecific attraction should occur largely at intermediate densities. We did not observe substantial density gradients (e.g., very high to very low) so were unable to

assess such relationships adequately. However, Forsman et al. (2009) showed that the relationship can be linear for species that use similar resources; if this were the case in our study area we should have detected some attraction toward Black-throated Blue Warblers by the closely associated congeneric Black-throated Green Warbler.

To our knowledge, ours is the first study to experimentally supplement a bird species (a migrant of mature forests) into a novel habitat (regenerating clearcuts) to test the heterospecific-avoidance and attraction hypotheses simultaneously. Our observations of emigration in three species support a growing body of evidence that songbirds might not be as faithful to a site within a breeding season as previously thought (Dale et al. 2006, Betts et al. 2008b, Rota et al. 2009). Future work should elucidate the process that may have led these species to emigrate when faced with immigrant Black-throated Blue Warblers; there are several possible explanations, not mutually exclusive. First, interference by Black-throated Blue Warblers may have instigated the emigration we observed. If so, whether that interference was direct (through despotism or aggression as a dominant competitor) or indirect (through pre-emption) remains to be seen, data on interspecific interference involving the Black-throated Blue Warbler are few. Regardless, the currency that is being disrupted needs to be quantified; preventing access to resources, space, or communication are all possible mechanisms. Second, perhaps birds of early-seral forest avoided the novel areas (clearcuts) colonized by introduced Black-throated Blue Warblers because they are usually associated with mature contiguous forest and could therefore be perceived as indicating poor habitat. Finally, it is possible that the birds of early-seral forest avoided the introduced Black-throated Blue Warblers simply because they were foreign entities in an otherwise favorable place, a response termed “neophobia” (Barnett 1958).

Heterospecific avoidance and attraction play a strong role in the spatial and behavioral structuring of numerous communities (Robinson and Terborgh 1995, Simeonovska-Nikolova 2007, Seppänen et al. 2007, Pope and Haney 2008, Harmssen et al. 2009). As habitats experience broad-scale changes at an ever-increasing rate, their component species are under constant pressure to restructure the faunal community. Novel communities may result not only from the addition of new species capable of shifting ranges (Thomas and Lennon 1999) but also from the deletion of species unable to compete with new community members. Heterospecific attraction by invasive or novel species toward established species is likely to result in increased fitness of immigrants (i.e., by facilitating resource assessment through heterospecific social information; Forsman et al. 2002, Seppänen et al. 2005), at least until competition limits such benefit. Conversely, some established species may avoid invasive species (e.g., Polo-Cavia et al. 2009). This interplay illustrates that heterospecific attraction and avoidance may have indirect cascading effects

on community structure that persists for generations. Therefore, as these situations become more common, more experiments such as ours are needed for the potential dynamics to be described.

Our results have implications for climatic-envelope models (e.g., Peterson et al. 2002, Stralberg et al. 2009), which discount the effects of interspecific interactions in constraining current and future distributions of species. If climate disruption causes species to shift ranges at different rates, novel communities will likely result. However, these novel communities are unlikely to be a predictable function of climate envelopes if heterospecific avoidance is frequent in nature. Until natural or manipulative experiments are conducted, it will be difficult to predict which species will persist and which will be displaced when novel environments are colonized. As empirical evidence grows, climatic-envelope modeling should benefit from the inclusion of quantitative information about the current and projected future distributions of heterospecifics (Ferrier and Guisan 2006) and the role these play in settlement dynamics. Unfortunately, it appears that in order for heterospecific effects to be detected, large samples will be necessary; even with substantial effect sizes and large samples (for an experimental study), our results were not strongly conclusive. Regardless, our results provide a preliminary cautionary note that managers should consider the broader community-wide effects of increasing abundance of a species with conspecific playback. Our results support the concern raised by Fletcher (2008) and Ahlering et al. (2010, this issue) that such approaches may have consequences for other species associated with the target system.

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