



# Dynamic occupancy models reveal within-breeding season movement up a habitat quality gradient by a migratory songbird

Matthew G. Betts, Nicholas L. Rodenhouse, T. Scott Sillett, Patrick J. Doran and Richard T. Holmes

M.G. Betts, ([matthew.betts@oregonstate.edu](mailto:matthew.betts@oregonstate.edu)), Dept of Forest Science, 312 Richardson Hall, Oregon State Univ., Corvallis, OR 97331, USA – N.L. Rodenhouse, Dept of Biological Sciences, Wellesley College, Wellesley, MA 02481, USA. – T.S. Sillett, Smithsonian Migratory Bird Center, National Zoological Park, Washington, DC 20008, USA. – P.J. Doran, The Nature Conservancy, Michigan Field Office, 101 East Grand River Lansing, MI 48906, USA. – R.T. Holmes, Dept of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA.

The timing of settlement decisions likely influences the quality of breeding site choices, particularly in migratory birds, because the conditions that enhance breeding success are often not apparent upon arrival after migration. A strategy that addresses this problem is to adjust settlement decisions when reliable information becomes available.

We used a new indirect method – dynamic site occupancy modeling – to estimate apparent movement of black-throated blue warblers *Dendroica caerulescens* among sites within a breeding season. Because individuals should disperse to sites that maximize their fitness, we hypothesized that warblers would move up a habitat quality gradient when opportunities arose. For our study species, that would involve moving into sites with greater shrub density and at higher elevation within northern hardwoods forest, as these two features are positively correlated with reproduction and apparent survival in this species.

Although the probability of site occupancy in our study landscape remained consistent throughout the breeding season (range: 0.66–0.69), occupancy models revealed substantial support for apparent movement of individuals within the breeding season. The mean probability of emigration from a point count site was 0.21 ( $\pm 0.03$  SE), and the mean probability of immigration to a site not previously occupied was 0.51 ( $\pm 0.05$  SE). The spatial distribution of this movement was a function of habitat quality. A portion of the black-throated blue warbler population appears to arrive on the breeding grounds and settle initially in sub-optimal habitat, moving subsequently into high quality densely shrubbed habitat at higher elevations. This modeling approach provides a new means to test hypotheses about habitat selection and movement by using presence–non-detection data.

Habitat selection is critical to both individual fitness (reviewed in Rodenhouse et al. 1997, Greene and Stamps 2001) and population dynamics (Pulliam and Danielson 1991, McPeck et al. 2001). Recent research has revealed that for migratory birds habitat selection can occur during either pre-breeding (Hahn and Silverman 2006) or post-breeding periods (Doligez et al. 2002, Nocera et al. 2006), and numerous species shift to higher quality sites when they change territory locations between breeding seasons (Krebs 1971, Rodenhouse et al. 1997). Few studies, however, have tested for within-season adjustments in site selection by breeding birds.

The timing of habitat selection may be important to the quality of settlement decisions. One drawback to selecting territories during the pre-breeding period is that conditions that enhance breeding success may not be apparent upon arrival after migration. For instance, reproductive success of some passerine species is strongly correlated with insect abundance and leaf area (Lack 1954, Martin 1987, Roden-

house et al. 2003), and the appropriate cues for these habitat features may not be available or may be misleading when individuals arrive on breeding grounds in the early spring. A limitation to using information gleaned at the end of the previous breeding season is that site quality may differ among years. Insect abundance or reproductive output of conspecifics in time  $t-1$  may not correlate well with the same variables in time  $t$  (Marshall and Cooper 2004). Even when post-breeding public information is used, unless the correlation between cues and potential territory quality is perfect, non-optimal site selection by some individuals may result (Citta and Lindberg 2007).

A strategy that could overcome some of these limitations is for individuals to adjust site selection as more reliable information becomes available within the first part of the breeding period (Dall et al. 2005). Naïve animals could initially settle at sub-optimal sites and then move towards sites of higher quality once differences in either structural or conspecific cues become perceptible. Reliable information

could also take the form of directly acquired personal information about a site of initial settlement. Individuals have been reported to abandon territories after nest failure (Switzer 1993, Hoover 2003, Klemm 2003), and presumably these animals attempt to re-settle in sites that minimize the future risk of this outcome.

Despite evidence that birds can shift locations during a breeding season (Krebs 1971, Hoover 2003), such shifts have seldom been quantified and reported from intensive demographic studies or from point-count surveys. Studies using point counts, for example, tend to assume that once birds arrive on breeding grounds, territory location is static. This is reflected in methods for summarizing point count data (maximum abundance, presence/absence, mean abundance) (for review see Betts et al. 2005). More recent methods estimate animal occupancy while accounting for detectability (MacKenzie et al. 2002). Such models are based on the assumption of population closure, that is, animals do not emigrate from or immigrate to sample sites during the sampling period. For birds, the sampling period is usually a single breeding season (Kroll et al. 2007).

Here, we examine evidence of intra-season movement (site immigration [hereafter “settlement”] and emigration [hereafter “vacancy”]) during the breeding period by a migrant, forest-dwelling bird species, the black-throated blue warbler *Dendroica caerulescens*. Such movement of small birds has been difficult to examine directly due to low band recovery rates at large spatial scales and the multiple constraints of radio transmitters (Webster et al. 2002, Kendall and Nichols 2004). We used point count data and a new indirect method – dynamic site occupancy models (MacKenzie et al. 2003) – to test for animal movement among sites within a breeding season. Importantly, because our study does not rely on physically marked individuals to determine movement, our results should be considered estimates of movement only; we term these estimates “apparent movement”. These models account for biases in site occupancy and movement caused by imperfect detectability – a feature common in many animal surveys (Zhou and Griffiths 2007, Allredge et al. 2007).

After migration, experienced individuals tend to arrive on the breeding grounds before younger birds, thus preemptively occupying the best sites (Holmes et al. 1996). We hypothesized that some later-arriving younger birds (with imperfect knowledge about habitat quality) would settle initially in sub-optimal sites and then move to higher quality vacant sites as more precise information about habitat quality becomes available. Animals should settle at sites that maximize their fitness (Fretwell and Lucas 1970). Previous research indicates that both reproduction and survival of black-throated blue warblers is greatest a) at higher elevation sites where food becomes more abundant during the breeding season (Rodenhouse et al. 2003) and b) at sites with an abundant shrub layer (Holmes et al. 1996, Rodenhouse et al. 2003, Sillett et al. 2004). We therefore predicted that intra-season black-throated blue warbler apparent movement should be toward sites with these characteristics and away from sites without them.

## Methods

### Study area and species

We conducted this research within the 3160 ha Hubbard Brook Experimental Forest in north-central New Hampshire, USA. The Hubbard Brook valley is covered by contiguous, 90+ yr-old second-growth forest consisting primarily of sugar maple *Acer saccharum*, American beech *Fagus grandifolia* and yellow birch *Betula alleghaniensis* at low elevations. Red spruce *Picea rubens*, balsam fir *Abies balsamea* and white birch *B. papyrifera* predominate at higher elevations (Schwartz et al. 2003).

We focused on black-throated blue warblers because this species is widely distributed and abundant within northern hardwoods forest (Holmes et al. 2005), and the habitat features influencing territory quality and demography are well known (Holmes et al. 1996, Rodenhouse et al. 2003). Arrival of this neotropical migrant spans early May–early June, with laying in first nesting attempts occurring during late May–mid June (Holmes et al. 2005). Features of its breeding biology are typical of such small migrants: laying lasts four days, incubation ca 12 d, and nestlings fledge 8–10 d after hatching. Nest predation is the most frequent cause of nest failure, and re-nesting is frequent particularly following the failure of a first nesting attempt (Holmes et al. 2005).

Points sampled ( $n = 184$ ) followed the systematic design of Schwartz et al. (2003) that includes 15 north-south transects spaced 500 m apart. Along each transect, distance between points alternates between 200 and 300 m. In 2007, we used 10-min fixed-radius point counts (Ralph et al. 1995) to survey relative abundance and occurrence of black-throated blue warblers at each point. All points were visited three times between 2 June and 2 July. Visits to individual points were separated by 6–8 d. Each 10-min count was divided into three, 3-min 20-s sub-counts. We treated each sub-count as a new sampling period (i.e. the presence of an individual bird would be recorded three separate times if the bird sang in all sub-counts). Each visit is equivalent conceptually to a “season” in MacKenzie et al. (2003). This resulted in a total of 9 sampling visits (3 primary visits each containing 3 secondary sub-counts). Counts were conducted from 05:30–10:00 and did not occur during rain or strong wind ( $>15$  kph). To reduce the influence of observer bias we randomly assigned observers to sample points in the first visit and rotated observers among points for each subsequent primary visit; this ensured that observers were not biased in later visits by previous experience at a point. We determined the elevation of each site using a digital elevation model for the Hubbard Brook valley (Schwartz et al. 2003).

Male black-throated blue warblers were considered present in a sampling occasion if they were detected singing within a 100 m radius of the point location. We determined relative warbler abundance by recording observations of simultaneous song (counter-singing) by individual territorial birds within 100 m. Relative abundance consisted of the maximum number of distinct singing individuals within a 10-min count. Though it is possible to use point count data to estimate absolute abundance (Buckland et al. 2001), the reliability of these methods are highly dependent on

accurate estimates of distance between birds and the observer. Such accuracy is difficult in a vertically heterogeneous forest and especially on hilly and often steep terrain. However, relative bird abundance from point counts tends to be correlated with actual abundance (Howell et al. 2004); consequently, abundance should be considered a coarse index of density.

At Hubbard Brook, hobblebush *Viburnum alnifolium* is the dominant understory species, representing >80% of shrub cover (Doran and Holmes 2005), and a key feature influencing habitat quality for *D. caerulescens* (Rodenhouse et al. 2003). Here, we use Doran and Holmes' (2005) data on hobblebush stem density as the value for the shrub's abundance at survey points. Briefly, stem density was counted within a 25 × 2 m strip transect centered on each survey point; every hobblebush stem within the transect was counted if it intersected a horizontal plane 1 m above ground. See Doran and Holmes (2005) for additional detail. Hobblebush abundance was log-transformed to reflect the hypothesis that the strength of bird response to hobblebush diminishes at extremely high stem densities.

## Statistics

We modeled site occupancy, settlement, vacancy, and detection probability using the “dynamic occupancy” methods designed for open populations by MacKenzie et al. (2003). This modeling approach is analogous to Pollock's robust design for estimating survival (Pollock 1982) in that changes in site occupancy may occur among major sampling visits but occupancy is assumed to be static among secondary sub-counts. This is a reasonable assumption in the present study because sub-counts within a visit were consecutive (e.g. within a single 10-min period). We summarized records of bird detection (1) and non-detection (0) into “encounter histories” similar to mark-recapture studies ( $\mathbf{X}_i$ ; e.g. 001 101 111). A maximum likelihood modeling procedure then relies on detection history data to estimate occupancy ( $\psi$ ), settlement ( $\gamma$ ) vacancy ( $\varepsilon$ ) and detection probability ( $p$ ) (MacKenzie et al. 2003):

$$L(\psi, \varepsilon, \gamma, p | \mathbf{X}_1, \dots, \mathbf{X}_n) = \prod_{i=1}^N \Pr(\mathbf{X}_i)$$

where  $\psi$  is a vector of site occupancy probabilities for the first primary sampling period,  $\gamma$  and  $\varepsilon$  are matrices of settlement and vacancy, and  $p$  is a matrix of detection probabilities. Changes in occupancy occur between visits as a result of immigration (settlement) to a site if it is unoccupied or emigration (vacancy) from a site if it is occupied. In this sense, the site occupancy is a Markovian process; occupancy at time  $t+1$  is dependent upon occupancy at time  $t$ . This is an appropriate approach for a territorial, site-faithful species (MacKenzie et al. 2006). We used Akaike's information criterion [AIC] to select models (Burnham and Anderson 2002) and performed all occupancy analysis using the program PRESENCE <<http://www.mbr-pwrc.usgs.gov/software/presence.html>>.

To limit the total number of models considered, we constructed our models using a hierarchical approach (Olson et al. 2005); we held explanatory variables for occupancy and detection probability constant while focusing on our primary objective – to determine factors

influencing apparent movement. First, we built a single global model with the variables most likely to explain occupancy. Because black-throated blue warblers at Hubbard Brook are closely associated with hobblebush and typically occur in higher densities at higher elevations (600–800 m; Rodenhouse et al. 2003, Holmes et al. 2005) we tested for the effects of both variables. At high elevations (>800 m), much of Hubbard Brook valley is characterized by coniferous vegetation, which is generally not occupied by black-throated blue warblers (Doran and Holmes 2005). Thus, we expected a curvilinear response of this species to elevation and modeled occupancy as a function of elevation squared.

Breeding site selection by this species tends to be spatially autocorrelated, even after accounting for environmental variation (Bourque and Desrochers 2006, Betts et al. 2006); hence, we included in all models a spatial autocovariate (Augustin et al. 1996) to account for this potential spatial dependency. This autocovariate was calculated as the probability of observing a species at one sample point conditional on the presence of the same species at neighboring sample points within 500 m (for details see Betts et al. 2006). Presence at the focal sample point was not included in the autocovariate calculation. Because we did not take detectability into account when calculating the autocovariate, this variable should be considered only an index of bird presence at neighboring points. All subsequent models that tested for effects of apparent movement thus predicted occupancy as a function of elevation (and its squared term), hobblebush, and the spatial autocovariate.

Second, we built a single model with variables most likely to explain probability of detection. We expected that birds should sing more frequently in higher quality habitat (Berg et al. 2005), so we included both habitat quality variables (hobblebush abundance, elevation squared) in our models. Because our sub-counts were consecutive within a 10-min point-count, we also expected temporal autocorrelation in detections; the likelihood of a bird singing in time  $t$  could be conditional on it singing in time  $t-1$ . We modeled this effect by including survey-specific covariate equal to the presence of song (a binary variable) in  $t-1$  if  $t-1$  occurred within the same visit. We also built a second model that included the covariates listed above, but tested for time-dependent detection probability; however, as there was little evidence for the importance of time as a predictor of detectability within the breeding season ( $\Delta\text{AIC } 3.62$ ,  $\text{AIC } w_i = 0.14$ ) we did not include time dependency in subsequent model sets.

Using the fixed global model set for occupancy and detection probability (without time dependence), we modeled settlement and vacancy as a function of elevation squared, hobblebush abundance and time of season (i.e. the interval between visits 1 and 2 and between visits 2 and 3). Our *a priori* hypothesis was that probability of settlement should be greatest at sites with the highest abundance of hobblebush and at high elevations. In contrast, probability of vacancy should be greatest at low elevation, hobblebush-poor sites. The prediction that birds should move from low quality to high quality sites is coupled; thus, because we sought to limit the total number of models tested, we did not test for separate individual effects of these variables on settlement or vacancy.

Finally, we tested the hypothesis of “population closure” (i.e. no within-season movement) with the global “single-season” (non-dynamic) model, which does not include parameters for settlement and vacancy (MacKenzie et al. 2002). If population closure exists, we would expect models without apparent movement to explain the data as well or better than models including additional movement parameters. Using this hierarchical approach our total model set comprised nine models (Table 3).

If the spatial extent of sampling does not perfectly match the extent of animal territories (as is usually the case) we expected that the ability to infer immigration and emigration at the territory scale could be biased. This may be a problem regardless of the time-scale of analysis (i.e. within season, among seasons). Though black-throated blue warbler territories are similar in size (1–4 ha; Holmes et al. 2005) to our point count circles (3.14 ha) we could not exclude the possibility that absence from a point count sample was not necessarily equivalent to absence at the territory scale; apparent settlement and vacancy could simply be a function of birds moving within their territories, but into or outside of our point count radii. For instance, if a territory boundary extended beyond the 100-m point count circle it would be possible for movement within a territory but outside of the sample unit to be considered a vacancy event. This possibility would result in an over-estimation of settlement/vacancy events, and it could also overemphasize the importance of habitat quality in influencing these events. High quality habitat is typified by higher densities (Holmes et al. 1996) and smaller territory sizes. With multiple territories per point count circle, the likelihood of an observed vacancy is reduced, because it would only occur if all territories were vacated simultaneously. To account for this hypothesized bias, we built the entire model set described above with relative abundance added as a covariate to predict occupancy, settlement, vacancy and detection probability.

We predicted that if territory size influences apparent movement, vacancy should be a negative function of relative abundance. More importantly, if our other hypothesized relationships (hobblebush, elevation) remained important after controlling for relative abundance, our within season apparent movement results were likely to be robust. This approach is conservative in that even inter-territory movement could be strongly influenced by relative abundance; birds should move to locations with highest density because that is likely where the high-quality habitat exists. Such apparent conspecific attraction has been observed in the study species (Hahn and Silverman 2007). We emphasize that we used this approach to, as conservatively as possible, test for within season apparent movement. Because abundance at a point is necessarily correlated with occupancy these results should be interpreted with caution. The primary emphasis should be placed on analysis where we did not control for abundance in dynamic occupancy models. In the models where we did not control for abundance, results should be interpreted as settlement and vacancy of the sampled 100-m radius point count circle rather than inter-territorial movement per se. Together, these two approaches (i.e. models with versus without relative abundance included as a covariate) can be seen as

upper and lower bounds on the degree of settlement and vacancy occurring in the Hubbard Brook valley.

We used a model averaging approach to address model selection uncertainty in our analyses. Summed AIC weights ( $\sigma w_i$ ) can be interpreted as the relative likelihood of each model fitting the data (Burnham and Anderson 2002, Zabel et al. 2003). In all analyses, variables were z-transformed to standardize means and variances. Predictor variables used in analyses (elevation, hobblebush, spatial autocovariate, warbler abundance) were not highly collinear ( $r < 0.3$ ).

## Results

### Occupancy and detection probability

Occupancy by black-throated blue warblers was positively influenced by abundance of hobblebush (Table 1). Occupancy increased with elevation except for sites above ca 700 m where it decreased. Assuming within-breeding season population closure, black-throated blue warblers occupied 90.3% ( $\psi = 0.903 \pm 0.115$  SE) of the Hubbard Brook Valley. This did not vary considerably from the naïve occupancy estimate of 0.901 because detection probability for 3 min 20 s sub-counts was 0.561 ( $\pm 0.046$  SE) or 99.9% across all 9 sampling occasions (after MacKenzie et al. 2002:  $p = (1 - (1 - 0.56)^9 \times 100)$ ). We found no support for the influence of spatial autocorrelation on occupancy; parameter estimates of autocovariates tended to be small and confidence intervals bounded zero. Detection probability was influenced by the same variables as occupancy and in the same directions, but was also strongly positively influenced by the presence of song in the previous sub-count, which suggests temporal autocorrelation in detectability (Table 1, 2).

Table 1. Parameter estimates and 95% confidence intervals (CI) for the AIC best-ranked model for occupancy ( $\psi$ ), settlement ( $\gamma$ ), vacancy ( $\epsilon$ ) and probability of detection ( $p$ ) for black-throated blue warblers as a function of a spatial autocovariate (autocov), log hobblebush density (hob; *Viburnum alnifolium*), time, elevation (elv), and singing in the previous sample period (song  $p(t-1)$ ).

Variables	$\beta$	LCI	UCI
$\psi$ intercept	0.15	-0.34	0.63
elv	1.16	0.96	1.36
elv <sup>2</sup>	-1.42	-1.62	-1.21
hob	0.57	0.40	0.75
autocov	-0.08	-0.25	0.08
$\gamma$ intercept	1.45	0.90	2.01
elv	4.11	3.32	4.90
elv <sup>2</sup>	-4.67	-5.55	-3.79
hob	0.20	-0.04	0.44
$\epsilon$ intercept	0.30	-0.25	0.85
elv	-0.69	-0.87	-0.52
elv <sup>2</sup>	0.69	0.51	0.87
hob	-0.55	-0.71	-0.39
$p$ intercept	0.72	0.45	0.99
elv	1.26	1.19	1.33
elv <sup>2</sup>	-1.45	-1.53	-1.38
hob	0.12	0.06	0.19
song $p(t-1)$	0.83	0.54	1.11

Table 2. Abundance-corrected, parameter estimates and 95% confidence intervals for the AIC best-ranked model for of settlement ( $\gamma$ ), vacancy ( $\varepsilon$ ) for black-throated blue warblers as a function of a spatial autocovariate (autocov), log hobblesh density (hob; *Viburnum alnifolium*), time, elevation (elv).

Variables	$\beta$	LCI	UCI
$\psi$ intercept	-1.29	-1.93	-0.65
abund	0.62	0.43	0.81
Hob	0.60	0.40	0.80
Elv	-0.83	-1.05	-0.62
elv <sup>2</sup>	0.65	0.44	0.87
Autocov	-0.22	-0.42	-0.03
$\gamma$ intercept	-2.82	-3.65	-1.99
Hob	0.82	0.46	1.17
Abund	0.61	0.32	0.90
$\varepsilon$ intercept	2.48	1.93	3.04
Hob	-0.51	-0.68	-0.35
Abund	-0.80	-0.96	-0.64
$p$ intercept	-1.50	-1.73	-1.26
Elv	0.85	0.77	0.92
elv <sup>2</sup>	-1.11	-1.18	-1.03
Hob	0.00	-0.07	0.06
song $p(t-1)$	0.87	0.59	1.14
Abund	0.88	0.81	0.94

## Apparent movement

Evidence for apparent movement by black-throated blue warblers within the breeding season in our study landscape was substantial. We, therefore, found little support for the population closure hypothesis. Evidence ratios indicated that the non-dynamic model (that would indicate population closure) was 466 times less likely to describe data than the top-ranked dynamic model ( $\Delta AIC = 44.38$ ; Table 3). The mean probability of vacancy from an occupied point count site was 0.21 ( $\pm 0.03$  SE), and the mean probability of settlement to a site not previously occupied was 0.51 ( $\pm 0.05$  SE). Because a greater proportion of sites were occupied than unoccupied, these apparently unequal rates of vacancy and settlement balanced each other (i.e. apparent settlement was approximately equal to apparent vacancy). Thus the valley-wide probability of site occupancy varied little over the breeding season ( $\psi_{\text{visit } 1} = 0.664$ ,  $\psi_{\text{visit } 2} = 0.691$ ,  $\psi_{\text{visit } 3} = 0.677$ ). For example, in the first primary visit 34% of sites (1 – 66%) were unoccupied (ca 63 sites). Of these, 51% (ca 32 sites) became occupied by the second primary visit in relation to 21% of occupied sites

that were vacated (ca 26 sites). Only six additional sites (out 184) were estimated to be occupied in visit 2 than in visit 1 (32–26). Importantly, the spatial location of occupied and unoccupied sites shifted among visits.

The spatial distribution of warbler apparent movement was as predicted; without accounting for abundance, warbler movement was influenced by both elevation and hobblesh density (Table 3, Fig. 1, 2). Settlement was greatest at hobblesh-rich sites occurring at mid- to high elevations. Site vacancy was negatively associated with hobblesh and tended to occur at low and at very high elevations (Table 2).

When we controlled for differences in warbler abundance across sites, the relative importance of movement covariates changed substantially. In the environmental variable-only models, the summed AIC model weights for elevation and hobblesh were 0.82 and 0.93 respectively, indicating strong support for the inclusion of both variables (Table 3). However, when we included warbler abundance as a covariate, elevation received little statistical support ( $\Sigma w_i = 0.13$ ) (Supplementary material, Table S1). Warbler abundance was included in the top five models and was strongly supported ( $\Sigma w_i = 0.95$ ). Even after controlling for the influence of warbler abundance, hobblesh remained a useful predictor of black-throated blue settlement and vacancy ( $\Sigma w_i = 0.90$ ). As in environmental variable-only models, settlement was greatest at hobblesh-rich sites and vacancy was most likely at hobblesh-poor sites (Supplementary material, Table S1).

## Discussion

To our knowledge, our study provides the first estimate of apparent within-season breeding movement for a migrant songbird species. Many habitat selection models assume that animals have the dispersal and cognitive abilities required to find the best site (Fretwell and Lucas 1970, Pulliam and Danielson 1991). However, reliable information about site quality may not always be immediately available (Stamps 2006). Individuals may need to invest time collecting either personal information through experience with sites (Hoover 2003), or gathering social information gleaned from other animals (Doligez et al. 2002, Osborne et al. 2007), thereby creating a “lag” between their initial arrival at a location and settlement on

Table 3. AIC-ranked occupancy models used to describe occupancy ( $\psi$ ), detection probability ( $p$ ), settlement ( $\gamma$ ) and vacancy ( $\varepsilon$ ) by black-throated blue warblers. Settlement and vacancy are best modeled as a non-linear function of elevation (elv<sup>2</sup>) and density of hobblesh (hob). Note that the non-dynamic model (in bold) received no support. Occupancy was modeled as a function of an autocovariate (autocov; see text). Detection probability was modeled as a function of singing in the previous sample period (song  $p(t-1)$ ). The time-dependent model for  $p$  (italics) did not perform as well as the non-time dependent model.

Model	AIC	$\Delta AIC$	$w_i$	K
$\psi$ (elv <sup>2</sup> + hob + autocov), $\gamma$ (elv <sup>2</sup> + hob), $\varepsilon$ (elv <sup>2</sup> + hob), $p$ (elv <sup>2</sup> + hob + song $p(t-1)$ )	1848.17	0	0.69	18
<i><math>\psi</math> (elv<sup>2</sup> + hob + autocov), <math>\gamma</math> (elv<sup>2</sup> + hob), <math>\varepsilon</math> (elv<sup>2</sup> + hob), <math>p</math>(t + elv<sup>2</sup> + hob + song <math>p(t-1)</math>)</i>	1851.79	3.62	0.11	20
$\psi$ (elv <sup>2</sup> + hob + autocov), $\gamma$ (elv <sup>2</sup> + hob + t), $\varepsilon$ (elv <sup>2</sup> + hob + t), $p$ (elv <sup>2</sup> + hob + song $p(t-1)$ )	1851.95	3.78	0.10	20
$\psi$ (elv <sup>2</sup> + hob + autocov), $\gamma$ (hob), $\varepsilon$ (hob), $p$ (elv <sup>2</sup> + hob + song $p(t-1)$ )	1853.06	4.89	0.06	14
$\psi$ (elv <sup>2</sup> + hob + autocov), $\gamma$ (elv <sup>2</sup> ), $\varepsilon$ (elv <sup>2</sup> ), $p$ (elv <sup>2</sup> + hob + song $p(t-1)$ )	1854.49	6.32	0.03	18
$\psi$ (elv <sup>2</sup> + hob + autocov), $\gamma$ (elv <sup>2</sup> + t), $\varepsilon$ (elv <sup>2</sup> + t), $p$ (elv <sup>2</sup> + hob + song $p(t-1)$ )	1854.82	6.65	0.02	18
$\psi$ (elv <sup>2</sup> + hob + autocov), $\gamma$ (hob + t), $\varepsilon$ (hob + t), $p$ (elv <sup>2</sup> + hob + song $p(t-1)$ )	1856.71	8.54	0.01	16
$\psi$ (elv <sup>2</sup> + hob + autocov), $\gamma$ (.), $\varepsilon$ (.), $p$ (elv <sup>2</sup> + hob + song $p(t-1)$ )	1860.46	12.29	0.00	12
<b><math>\psi</math> (elv<sup>2</sup> + hob + autocov), <math>p</math>(elv<sup>2</sup> + hob + song <math>p(t-1)</math>)</b>	<b>1892.55</b>	<b>44.38</b>	<b>0.00</b>	<b>10</b>

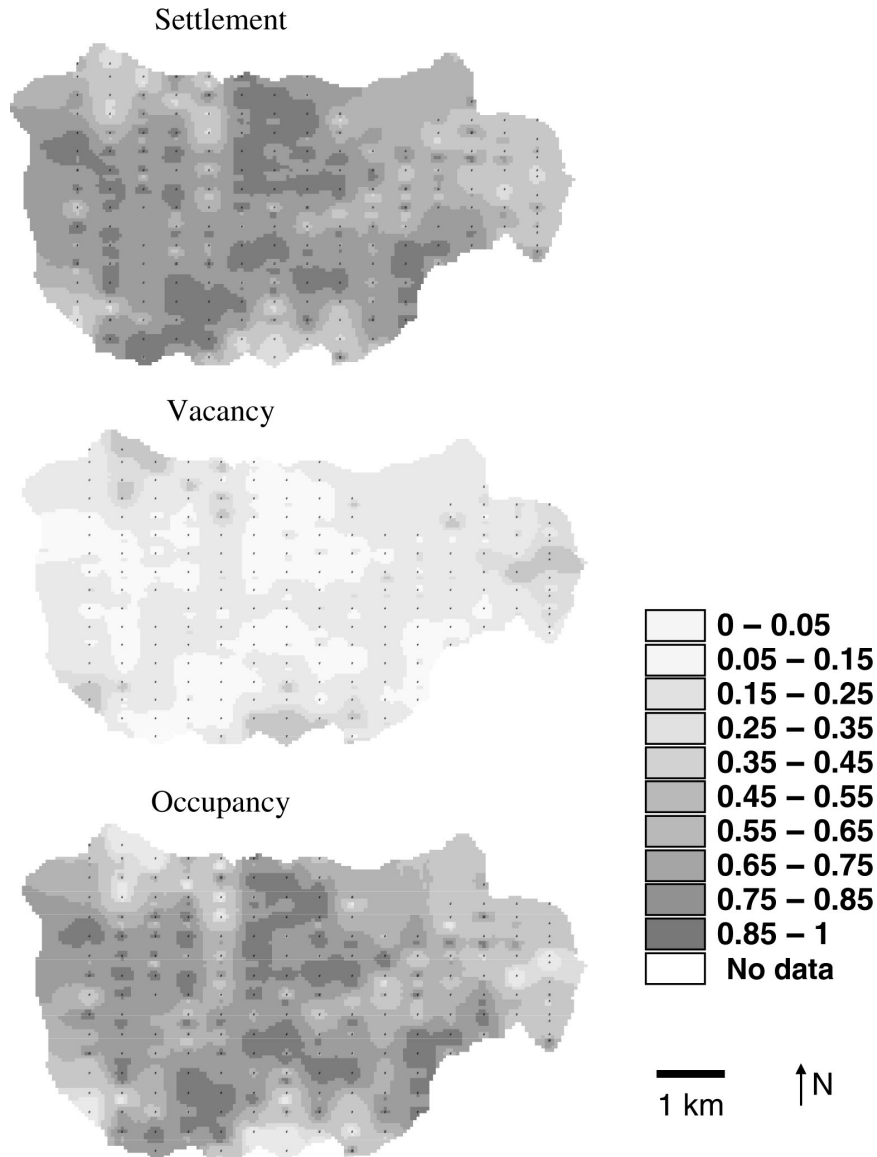


Figure 1. Predicted spatial distribution of the probability of settlement and vacancy events and site occupancy for black-throated blue warbler in the Hubbard Brook Experimental Forest, New Hampshire. Black dots indicate the locations of point-counts. Fitted probabilities beyond sample points were calculated using inverse distance weighting (IDW) spatial interpolation.

a breeding site. In this paper, we use dynamic occupancy models to provide indirect evidence for such lags in breeding site selection. A portion of the black-throated blue warbler population in the Hubbard Brook valley appears to arrive on the breeding grounds and advertise (sing) initially in sub-optimal habitat (low elevation, low shrub cover); some of these individuals subsequently move up a habitat quality gradient into densely shrubbed habitat at moderate-to-high elevations. Such movements seem adaptive because they have the effect of increasing reproductive success (Rodenhouse et al. 2003) and apparent survival (Rodenhouse et al. unpubl.).

Recent experimental evidence also supports the hypothesis that settlement decisions of this species continue to occur over a period of a few weeks after arrival in breeding areas (25 May–8 June; Hahn and Silverman, 2007). Though social information collected by black-throated blue warblers in the post-breeding period may be a more reliable measure of

future site quality (Betts et al. unpubl.), this species also appears to rely on the location of conspecifics in the early breeding season as a cue in site selection. Collection of personal information may also play a role in the apparent movement we observed. Direct assessment of nest predation or risk of predation as indicated by the diurnal activity of nest predators (e.g. *Tamias striatus*, *Tamiasciurus hudsonicus*) could be used as a cue to avoid settlement or to move. Early nesting pairs, typically site-faithful, returning breeders, experience first-nest failures during this time, and birds, whether arriving early or late, may directly assess the risk of nest predation by observing or hearing nest predators. Abundance of nest predators at the time of arrival is a good predictor of their abundance throughout the breeding season (Holmes et al. unpubl.).

Because territory size may be larger than the extent of our sample units, it is possible that within-territory movement could result in some of the apparent vacancies or

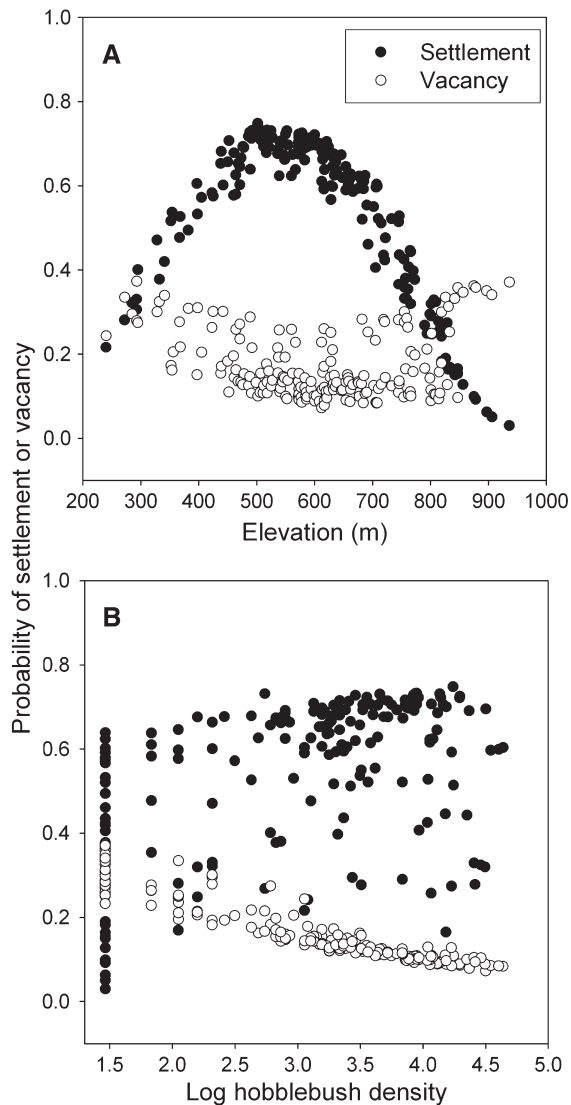


Figure 2. Predicted probability of black-throated blue warbler settlement (black dots) and vacancy (white dots) as a function of elevation after accounting for hobblebush density (A) and hobblebush density after accounting for elevation (B) in the Hubbard Brook Experimental Forest, New Hampshire. All fitted model values account for detection probability.

settlement that we observed. The models we present that do not include warbler abundance reveal the proportion of sites “used” by warblers and detectability should be considered the probability that the species is present at the time of the survey and detected at occupied or used sites (MacKenzie et al. 2006). Alternatively, apparent movement models that included conspecific abundance as a covariate suggest that some of the movement we detected entailed temporary within-territory movement. As expected in this case, sites with low abundance (a proxy for low territory density and large territories) exhibited greater rates of temporary emigration (probability of vacancy). However, it is important to note that our key result, i.e. that shrub density is the most critical factor influencing site choice, did not differ qualitatively among models with or without controlling for conspecific abundance. We included conspecific abundance as a covariate to test, as conservatively as possible, whether

apparent bird movement, independent of local density, could be predicted by environmental variables alone. Though elevation became substantially less important when conspecific abundance was included in the models, hobblebush remained a useful predictor of apparent settlement and vacancy.

As animal density can influence results of dynamic occupancy models, it will be a critical issue to consider explicitly in future studies. Density often varies across habitat quality gradients; thus, within-territory movement could be confounded with “true” extinction or colonization. For instance, metapopulation models that predict greater rates of extinction in small patches may need to control for lower density at these sites (Nol et al. 2005) unless the spatial pattern of sampling matches precisely that of the home range of the species of interest or entire patches are surveyed. More research is needed to reveal the relationships between animal density and occupancy dynamics.

Occupancy dynamics may, to some extent, be influenced by the age structure of the population as well as by habitat quality. Holmes et al. (1996) showed that older experienced birds occupy the best habitat, leaving that of lesser quality for younger, subordinate individuals. Hence age undoubtedly plays a role in predicting likelihood of breeding dispersal, as first year breeders of many species appear more likely to disperse (Alrt and Part 2008), and older birds are typically the most site-faithful (Switzer 1993). However, these findings would seem to work against the movement indicated by the present study, securing older birds in habitat of highest quality. Thus most of the apparent movement reported is probably being undertaken by first-time breeders; unfortunately, the point-count data used in this study cannot be used to distinguish age classes because point count studies rely primarily on auditory detections. Nevertheless, the hypothesis we tested was not contingent on age.

Regardless of the mechanism driving apparent movement patterns, dynamic occupancy modeling provides a means to obtain further information about habitat quality from presence/non-detection data. Animals should a) occur at higher densities in high quality habitat and b) show greater immigration to high-quality sites. Exceptions to this rule occur in ecological traps where high density may not reflect high quality habitat (Schlaepfer et al. 2006). Our indirect observations of movement provide independent support for previous findings that patches with abundant hobblebush and at higher elevations have greater food abundance and fewer nest predators, and therefore, are better quality habitat for black-throated blue warblers (Doran and Holmes 2005, Rodenhouse et al. unpubl.).

We found that both occupancy and probability of detection were influenced strongly by environmental variables. Site occupancy of black-throated blue warblers reflected patterns observed for settlement and was greatest at upper elevations in hobblebush-rich sites. Detectability tended to be influenced by the same variables affecting occupancy. This was likely for two reasons. First, high-quality sites tend to have a greater density of birds which increases the total number of songs per sampled area. Second, at the individual level, birds in good condition have been observed to sing more frequently (Berg et al.

2005). In this respect, if we had not controlled for detection probability, our estimates of occupancy, settlement and vacancy would have been biased (Royle and Kéry 2007).

Accurate measures of avian reproductive success are essential to conservation and management of bird species. Presence-absence and density estimates are not necessarily indicative of reproductive success and, as a result, may be inadequate indicators of habitat quality (van Horne 1983). However, collection of data on reproductive success usually requires intensive nest-searching, season-long observations of individually marked birds, and detailed and accurate accounts of the fates of all nestlings and fledglings (Holmes et al. 1996, Doran et al. 2005). It is thus time-consuming and logistically challenging to directly measure reproductive output, particularly at large spatial scales. Our results indicate that dynamic occupancy models can be used to obtain information about the habitat selection process and habitat quality from presence/ non-detection data. This information is likely to be useful to managers in making conservation decisions.

*Acknowledgements* – We are grateful to M. Cannon, A. S. Hadley, D. I. MacKenzie, J. J. Nocera, P. Osborne and four anonymous reviewers for insightful comments on the manuscript. Thanks are also due to field assistants: B. Griffith, M. Smith, T. Weidman, and E. Whidden and to the staff of the Hubbard Brook Experimental Forest. Financial support was provided by the US National Science Foundation LTER program. The research was conducted under the auspices of the Northern Research Station, Forest Service, US Dept of Agriculture, Newtown Square, PA, and is a contribution of the Hubbard Brook Ecosystem Study. M. G. Betts was partly supported by a post-doctoral fellowship from the Natural Sciences and Engineering Research Council of Canada.

## References

- Allredge, M. W. et al. 2007. Factors affecting aural detections of songbirds. – *Ecol. Appl.* 17: 948–955.
- Alt, D. and Part, T. 2008. Post-breeding information gathering and breeding territory shifts in northern wheatears. – *J. Anim. Ecol.* 77: 211–219.
- Augustin, N. H et al. 1996. An autologistic model for the spatial distribution of wildlife. – *J. Appl. Ecol.* 33: 339–347.
- Berg, M. L. et al. 2005. Singing as a handicap: the effects of food availability and weather on song output in the Australian reed warbler *Acrocephalus australis*. – *J. Avian Biol.* 32: 102–109.
- Betts, M. G. et al. 2005. Point count summary statistics differentially predict reproductive activity in bird-habitat relationship studies. – *J. Ornithol.* 146: 151–159.
- Betts, M. G. et al. 2006. The importance of spatial autocorrelation, extent and resolution in predicting forest bird occurrence. – *Ecol. Model.* 191: 197–224.
- Bourque, J. and Desrochers, A. 2006. Spatial aggregation of forest songbird territories and possible implications for area sensitivity. – *Avian Conserv. Ecol.* 1: 3, <<http://www.ace-eco.org/vol1/iss2/art3/>>.
- Buckland, S. T. et al. 2001. Distance sampling: estimating abundance of biological populations. – Oxford Univ. Press.
- Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference. – Springer.
- Citta, J. J. and Lindberg, M. S. 2007. Nest-site selection of passerines: effects of geographic scale and public and personal information. – *Ecology* 88: 2034–2046.
- Dall, S. R. X. et al. 2005. Information and its use by animals in evolutionary ecology. – *Trends Ecol. Evol.* 20: 187–193.
- Doligez, B. et al. 2002. Public information and breeding habitat selection in a wild bird population. – *Science* 297: 1168–1170.
- Doran, P. J. and Holmes, R. T. 2005. Habitat occupancy patterns of a forest dwelling songbird: causes and consequences. – *Can. J. Zool.* 83: 1297–1305.
- Doran, P. J. et al. 2005. A test of the mobbing playback method as a means to estimate bird reproductive success. – *J. Field Ornithol.* 76: 227–233.
- Fretwell, S. D. and Lucas, H. L. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. – *Acta Biotheor.* 19: 16–36.
- Greene, C. M. and Stamps, J. A. 2001. Habitat selection at low population densities. – *Ecology* 82: 2091–2100.
- Hahn, B. A. and Silverman, E. D. 2006. Social cues facilitate habitat selection: American redstarts establish breeding territories in response to song. – *Biol. Lett.* 2: 337–340.
- Hahn, B. A. and Silverman, E. D. 2007. Managing breeding forest songbirds with conspecific song playbacks. – *Anim. Conserv.* 10: 436–441.
- Holmes, R. T. et al. 1996. Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics. – *J. Anim. Ecol.* 65: 183–195.
- Holmes, R. T. et al. 2005. Black-throated blue warbler (*Dendroica caerulescens*). – In: Poole, A. (ed.), *The birds of North America online*. Cornell Lab of Ornithology, <<http://bna.birds.cornell.edu/review/species/087>>.
- Hoover, J. P. 2003. Decision rules for site fidelity in a migratory bird, the prothonotary warbler. – *Ecology* 84: 416–430.
- Howell, C. A. et al. 2004. Breeding density affects point-count accuracy in Missouri forest birds. – *J. Field Ornithol.* 75: 123–133.
- Kendall, W. L. and Nichols, J. D. 2004. On the estimation of dispersal and movement of birds. – *Condor* 106: 720–731
- Klemp, S. 2003. Altitudinal dispersal within the breeding season in the grey wagtail *Motacilla cinerea*. – *Ibis* 143: 509–511.
- Krebs, J. R. 1971. Territory and breeding density in the great tit, *Parus major* L. – *Ecology* 52: 2–22.
- Kroll, A. J. et al. 2007. Modeling habitat occupancy of orange-crowned warblers in managed forests of Oregon and Washington, USA. – *J. Wildl. Manage.* 71: 1089–1097.
- Lack, D. 1954. Natural regulation of animal populations. – Clarendon Press.
- MacKenzie, D. I. et al. 2002. Estimating site occupancy rates when detection probabilities are less than one. – *Ecology* 83: 2248–2255.
- MacKenzie, D. I. et al. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. – *Ecology* 84: 2200–2207.
- MacKenzie, D. I. et al. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. – Academic Press.
- Marshall, M. R. and Cooper, R. J. 2004. Territory size of a migratory songbird in response to caterpillar density and foliage structure. – *Ecology* 85: 432–445.
- Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. – *Annu. Rev. Ecol. Evol. Syst.* 18: 453–487.
- McPeck, M. A. et al. 2001. A general model of site-dependent population regulation: population-level regulation without individual-level interactions. – *Oikos* 94: 417–424.



- Nocera, J. J. et al. 2006. Inadvertent social information in breeding site selection of natal dispersing birds. – *Proc. R. Soc. B* 273: 349–355.
- Nol, E. et al. 2005. Using distance from putative source woodlots to predict occurrence of forest birds in putative sinks. – *Conserv. Biol.* 19: 836–844.
- Olson, G. S. et al. 2005. Modeling of site occupancy dynamics for northern spotted owls, with emphasis on the effects of barred owls. – *J. Wildl. Manage.* 69: 918–932.
- Osborne, P. E. et al. 2007. Behavioural mechanisms that undermine species envelope models: the causes of patchiness in the distribution of great bustards *Otis tarda* in Spain. – *Ecography* 30: 819–829.
- Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of recapture. – *J. Wildl. Manage.* 46: 752–757.
- Pulliam, H. R. and Danielson, B. J. 1991. Sources, sinks and habitat selection – a landscape perspective on population-dynamics. – *Am. Nat.* 137: S50–S66.
- Ralph et al. 1995. **Please provide further details.**
- Rodenhouse, N. L. et al. 1997. Site-dependent regulation of population size: a new synthesis. – *Ecology* 78: 2025–2042.
- Rodenhouse, N. L. et al. 2003. Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. – *Proc. R. Soc. B.* 270: 2105–2110.
- Royle, A. J. and Kéry, M. 2007. A Bayesian state-space formulation of dynamic occupancy models. – *Ecology* 88:1813–1823.
- Schlaepfer, M. A. et al. 2006. Ecological and evolutionary traps. – *Trends Ecol. Evol.* 17: 474–480.
- Schwartz, P. A. et al. 2003. Factors controlling spatial variation of tree species abundance in a forested landscape. – *Ecology* 84: 1862–1878.
- Sillett, T. S. et al. 2004. Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. – *Ecology* 85: 2467–2477.
- Stamps, J. A. 2006. The silver spoon effect and habitat selection by natal dispersers. – *Ecol. Lett.* 9: 1179–1185.
- Switzer, P. V. 1993. Site fidelity in predictable and unpredictable habitats. – *Evol. Ecol.* 7: 533–555.
- van Horne, B. 1983. Density as a misleading indicator of habitat quality. – *J. Wildl. Manage.* 47: 893–901.
- Webster, M. S. et al. 2002. Links between worlds: unraveling migratory connectivity. – *Trends Ecol. Evol.* 17: 76–83.
- Zabel, C. J. et al. 2003. Northern spotted owl habitat models for research and management application in California (USA). – *Ecol. Appl.* 13: 1027–1040.
- Zhou, S. and Griffiths, S. P. 2007. Estimating abundance from detection-nondetection data for randomly distributed or aggregative elusive populations. – *Ecography* 30: 537–549.

Download the Supplementary material as file E5490 from  
<[www.oikos.ekol.lu.se/appendix](http://www.oikos.ekol.lu.se/appendix)>.