

## Stochasticity as an alternative to deterministic explanations for patterns of habitat use by birds

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**Abstract.** Stochasticity is rarely explicitly investigated as a determinant of patterns of habitat use, even though evidence of its influence would undermine support for deterministic models of habitat selection. To assess the role of stochasticity in generating patterns in habitat use, we compared observed patterns of year-to-year variation in habitat use of 20 bird species over five years with patterns randomly generated from null models with different biological constraints (i.e., abundance, territoriality, exclusion of unused habitat, site fidelity, and habitat preference). We were able to recreate patterns of variability in spatial distributions with one or more null models for 18 species, suggesting an important role of stochasticity. Although year-to-year variability could be modeled as a purely stochastic process for only four species, null models in which random variability was constrained by the influences of vegetation or site fidelity collectively matched the observed patterns of variability of all 18 species. Support for these two models suggested that factors that increase the likelihood of returning to a previously used area and thus limit the spatial extent of random territory placement can generate patterns similar to those we observed. Greater support for models with preference constraints (i.e., models that included bird–vegetation associations) over models with avoidance constraints (i.e., models that excluded areas that were never occupied) indicated that preference was the primary mode of habitat selection. Stochastic patterns in habitat use may have resulted from a weak relationship between habitat selection and habitat quality, influence of non-vegetation habitat features (e.g., climatic fluctuations), nonequilibrium conditions, and a greater influence of stochastic variation at small spatial and temporal scales. Alternatively, responses to environmental cues may have been deterministic, but in summation, these responses may have created variability in spatial distribution patterns that was indistinguishable from random variation. In such cases, we suggest that it may be easier to model variation in habitat use as a random process rather than using deterministic models that account for a multitude of environmental factors influencing habitat selection of birds. Regardless, stochasticity may play a larger role in generating patterns of habitat use than is often considered, and it deserves wider attention.

**Key words:** *Arrowsic Island, Kennebec River, Maine, USA; avoidance constraints; birds; frequency landscapes; habitat use; null models; preference constraints; spatiotemporal variation; stochasticity.*

### INTRODUCTION

The core assumption of habitat selection research is that organisms choose to settle in environments that enhance their fitness (Klopfer and Ganzhorn 1985, Rosenzweig 1991, Garshelis 2000, McLoughlin et al. 2006). A necessary corollary of this assumption is that the decision to settle is a deterministic response to environmental cues, which serve as indicators of a habitat's fitness potential. Accordingly, deterministic models that include these cues should be able to describe

the spatial and temporal variation in distribution patterns.

While deterministic models have been the prevailing means to account for variation in patterns of habitat use, their paradigmatic acceptance may have precluded both the thorough testing of their underlying theoretical framework and consideration of alternative approaches to modeling habitat use. For example, well-known examples of deterministic models such as Fretwell-Lucas models (Fretwell and Lucas 1969) have played key roles in shaping our thinking on habitat selection, population dynamics, and community organization (O'Connor 1987, Rosenzweig 1987), but they have not been fully evaluated. Tests of Fretwell-Lucas models have examined only a few specific predictions at a time (e.g., O'Connor 1986, 1987, Clark and Weatherhead 1987, Eckert and Weatherhead 1987, Calsbeek and Sinervo 2002), rather than simultaneously addressing all aspects of the model, i.e., settling patterns, population density,

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habitat suitability, and fitness (Petit and Petit 1996). If simultaneous tests of multiple predictions produced conflicting results, they would undermine support for the model. Similarly, much work has gone into the development of deterministic models that quantitatively link animal distributions to habitat features (Boyce and McDonald 1999, Pearce and Ferrier 2001, Nielsen et al. 2005). Implicit to the construction of these deterministic models is the existence of a functional relationship between habitat selection and habitat quality. However, few empirical studies have directly tested this relationship, despite concerns that a correlation between animal density and habitat quality might apply only to a narrow range of conditions (Van Horne 1983, Hobbs and Hanley 1990, Garshelis 2000, Nielsen et al. 2005). Furthermore, because the tests of deterministic explanations for habitat selection emphasize verification rather than testing among alternative hypotheses (Wiens 1984), it does not necessarily follow that the proposed processes are, in fact, generating the observed patterns. Ecological processes are sufficiently complex that often there are multiple explanations for an observed phenomenon (Peters 1991), and thus it is often possible to obtain the “right” pattern for the “wrong” reasons (Dayton 1973). Given the potential shortcomings in deterministic approaches, it remains an open question as to whether patterns of habitat use can be largely explained by deterministic processes.

Stochasticity may represent a viable alternative for accounting for year-to-year changes in patterns of habitat occupancy for a number of reasons, yet this is rarely tested for directly (Haila et al. 1996, Virkkala and Rajasärkkä 2006). First, recent studies have suggested that distribution and abundance can vary independently of habitat quality (Hobbs and Hanley 1990, Garshelis 2000, Railsback et al. 2003, Johnson and Seip 2008), and this lack of dependence may allow a role for stochasticity. Second, even if deterministic models are valid, they are generally equilibrium-based theories. If populations are nonequilibrium and are influenced by a wide array of underlying processes with a substantial stochastic component, dynamics in habitat use can appear random (Wiens 1984). Third, if multiple structural cues are used to assess habitat quality and these cues are uncorrelated or negatively correlated (e.g., good cover from predators but poor foraging opportunities), even habitat selection that is strongly related to habitat quality can create variation resembling stochasticity because of trade-offs among responses to conflicting cues. Similarly, nonstructural factors such as climatic fluctuations, food availability, regional population fluctuations, distributions of competitors and predators, and individual variability in how animals evaluate their environment influence occupancy patterns (Morin 1999); the summation of the responses to these influences can create variability in spatial distribution patterns that is indistinguishable from random variation (Haila et al. 1996). Finally, researchers rarely test for the

absence of a deterministic mechanism (i.e., a null model). If a particular pattern can be produced without the hypothesized mechanism (e.g., by stochastic processes alone), parsimony dictates that there would be no need to invoke the mechanism because it adds unnecessary complexity (Gotelli and Graves 1996).

In this paper we investigate stochasticity as an alternative to strictly deterministic processes for explaining variation in the patterns of habitat occupancy in birds. We address this issue using a five-year data set of bird locations collected as part of a long-term (27 years to date) ecosystem study of a pine–oak forest at the Holt Research Forest in Arrowsic, Maine (Witham et al. 1993). Specifically, we compare distribution patterns derived from these empirical data with distribution patterns generated by null models that incorporate biological constraints relevant to bird biology (e.g., territoriality, site fidelity, and habitat preference) but are otherwise random. As such, we are not necessarily investigating “absolute” or “pure” stochasticity (i.e., completely random variation), but rather stochasticity relative to a particular biological constraint (e.g., we assume the existence of territoriality and allow for the random placement of territories). The re-creation of empirical patterns of variation with null models would provide support for the notion that stochasticity can account for year-to-year changes in patterns of habitat selection. Additionally, comparison among the models can identify which biological constraints are fundamental to the creation of observed distribution patterns.

## METHODS

### *Study area*

The Holt Research Forest is a 120-ha tract of forest located near the center of Arrowsic Island in the Kennebec River of Maine ( $43^{\circ}52' N$ ,  $69^{\circ}46' W$ ; see Plate 1). It occurs within the transition zone between oak–pine forest to the west and south and coastal spruce–fir to the east and north (McMahon 1990). The principal tree species, in decreasing order of trees per hectare and basal area, are eastern white pine (*Pinus strobus*), red maple (*Acer rubrum*), northern red oak (*Quercus rubra*), red spruce (*Picea rubens*), and balsam fir (*Abies balsamea*) (Kimball et al. 1995). The forest is a result of secondary succession following the abandonment of agricultural land 70–110 years ago (Moore and Witham 1996).

The study area comprises 40 ha and is buffered by an average of 90 m (range: 17–185 m) of forest from adjacent forests, a public road, and an estuarine river. The study area is demarcated on the ground by a hierarchical grid system with 40 1-ha ( $100 \times 100$  m) blocks, 160 50 × 50 m quadrats, and 640 25 × 25 m subquadrats. When the data were collected in 1983–1987, the most common vegetation cover types (based primarily on dominant tree species in the stand and secondarily on moisture conditions; Witham et al. 1993) were mixed-mesic, coniferous, and pine-dominated

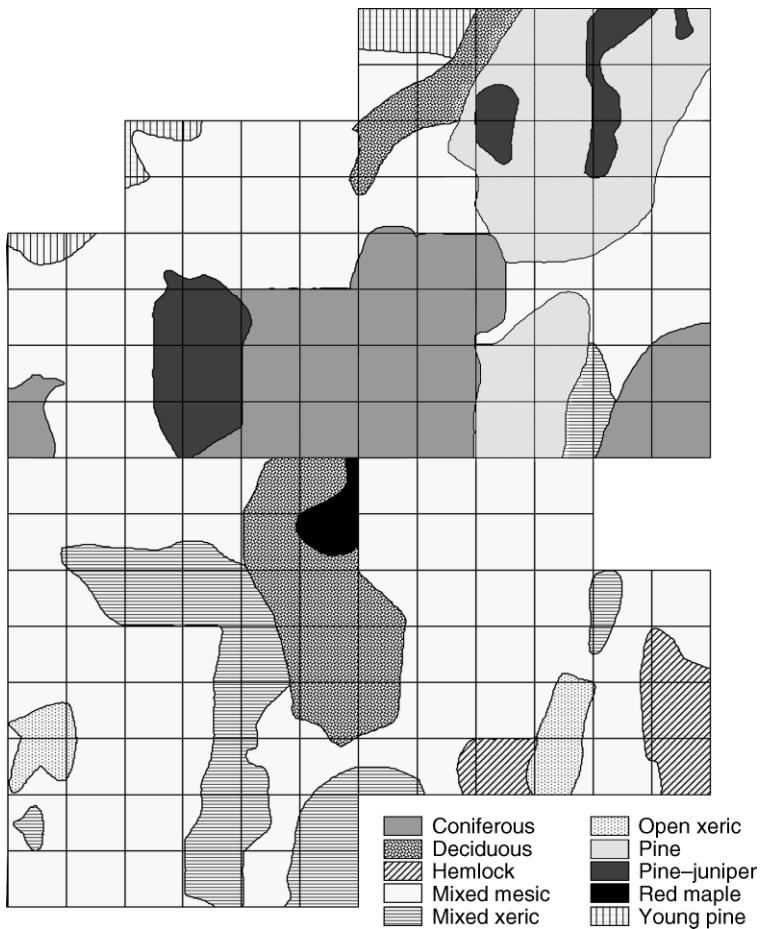


FIG. 1. Distribution of vegetation cover types at the Holt Research Forest, Arrowsic, Maine, USA. Each grid cell is a 50 × 50 m quad. Cover types are described in Witham et al. (1993).

stands, which covered 51%, 12%, and 10% of the study area, respectively (Fig. 1).

#### *Conceptual approach*

We examined variation in habitat use among years with “frequency landscapes” (sensu Haila et al. 1989). A frequency landscape is an area divided into a grid in which each grid cell contains a value representing the number of years the cell was occupied. Here, we use the quadrats (hereafter quads) of our study area as the grid cells.

We generated null frequency landscapes for each species with null models and then we compared these to the observed frequency landscapes. If null models generated patterns of variability similar to the observed patterns, we concluded that variability was predominantly stochastic. Otherwise, we concluded that variability was deterministic.

As with any model, confidence in the acceptance or rejection of our null models depends on their careful construction. If models are “too null” and do not incorporate realistic biological constraints, they can

generate patterns that are very different from patterns seen in real communities (Gotelli and Graves 1996), making their rejection trivial or false. For example, a completely random model of quad occupancy is probably unrealistic, given the variation that exists in the vegetation of quads and the ecology of the birds (e.g., habitat preferences, abundance, territoriality, and site fidelity). Therefore, we incorporated various constraints to make the null models more realistic.

#### *Data collection*

*Bird location and territory data.*—The locations at which birds were seen or heard were collected as part of the territory mapping methodology (IBBC 1969, Witham et al. 1993) used to estimate the number of territories of each species. The data were collected in 16 visits during the breeding season (late May through early July) each year. In each visit, the entire length of all north–south transects through block centers or all north–south transects along the block edges were sampled between 04:30 and 10:30 hours. One observer (J. W. Witham) collected the data for all years. Locations were digitized



PLATE 1. Aerial view of the Holt Research Forest, a 120-ha pine–oak forest located on Arrowsic Island in the Kennebec River in coastal Maine, USA. The research forest is bordered by the Back River, a branch of the Kennebec River (foreground), Sewell Pond (middle right), salt marsh and old field (lower right), and forest (left). Photo credit: M. L. Hunter, Jr.

into a geographic information system (Witham and Kimball 1996) and were compiled to generate composite maps for each species in each year.

Territory numbers were determined from the maps in all years by J. W. Witham. A minimum of five registrations was required to denote a territory, and an emphasis was placed on observations of countersinging males. Territories that straddled the boundary of the study area were counted if a majority of their points fell within the study area.

Although data have been collected since 1983, we limit our consideration to the first five years of the study, because in the winter of 1987–1988 we partially harvested the western half of the study area. The loss of forest led to strong shifts in the distributions of birds (S. P. Campbell, J. W. Witham, and M. L. Hunter, *unpublished data*), which probably overwhelmed the year-to-year variation in habitat use of interest here. Furthermore, we excluded from analysis those bird species that did not establish territories in two or more years and were not reliably counted by territory mapping (e.g., Pileated Woodpecker [*Dryocopus pileatus*], Cedar Waxwing [*Bombycilla cedrorum*], Blue Jay [*Cyanocitta cristata*], and Great Crested Flycatcher [*Myiarchus crinitus*]).

**Vegetation data.**—Vegetation data were collected using timber inventories and relevés (Witham et al. 1993). A complete timber inventory was conducted in every quad in 1984, which generated data on the species, diameter at breast height (dbh), and condition (e.g.,

living or dead) of every tree with dbh > 9.5 cm. For each quad we calculated the total number of trees, total basal area of all trees, and the basal area of all coniferous trees, deciduous trees, oaks (red and white [*Quercus alba*]), eastern white pine, birches (paper [*Betula papyrifera*], yellow [*Betula alleghaniensis*], and gray [*Betula populifolia*]), red maple, hemlock (*Tsuga canadensis*), balsam fir, and red spruce. These 10 species comprise 98% of the trees and 99% of the basal area.

Relevé date were collected in every subquad in 1985 and consisted of the estimated percent cover of each plant species in five strata (<0.25 m, 0.25–1 m, 1–5 m, 5–10 m, >10 m), categorized into one of eight coverage classes: absent, rare, <1%, 1–5%, 5–25%, 25–50%, 50–75%, 75–100% (parameterized as 0%, 0.0025%, 0.25% and midpoints of ranges, respectively). We focused our analysis on the same tree species and species groups of the timber inventory and on the three highest strata. Because the timber inventory data restricted our analysis of frequency landscapes to the quad level, we scaled relevé data to this level by averaging the percent coverages of each subquad. Using the relevé data, we also determined total species richness of ferns and herbs, trees and shrubs, and all plants in each quad.

#### Data analysis

**Generating frequency landscapes.**—We determined the occupancy status of all 160 quads for each species in each year and then summed over the five years to obtain an observed frequency landscape. Similarly, we gener-

ated null frequency landscapes by occupying quads in each year according to the rules (i.e., constraints) of the particular null model and summing the occupancy status over the five years. A description of each constraint and the means by which we operationalized it follow.

1) Yearly sum: To account for variability in abundance within and among species, all the null models were constrained by the yearly sum of occupied quads for each species. Functionally, this meant that the number of randomly occupied quads in a year equaled the observed number of occupied quads in that year.

2) Occupancy: Quads that were unoccupied in all five years were likely to be non-habitat for a species. Thus, we limited the available quads to those that were occupied in at least one of the five years.

3) Spatial autocorrelation: Because birds are territorial and have territories larger than the  $50 \times 50$  m quads, we incorporated spatial autocorrelation. First, we randomly seeded the landscape with the same number of quads as there were territories for a species in a year. These quads acted as nuclei around which we grew territories, using two accretion methods: regular and irregular. The regular method filled the quads surrounding each nucleus in an ordered sequence generating territories that were approximately disk or square shaped. The irregular method filled a randomly selected unoccupied quad that was adjacent to a randomly selected occupied quad within the territory, thus producing irregularly shaped territories. In both of these methods, each territory was grown one quad at a time until reaching the number of quads occupied in that year, and territories were not allowed to expand into a quad that was already occupied.

4) Dispersion: Accounting for spatial autocorrelation based on territoriality did not account for the repelling influence of territorial males. The dispersion constraint prevented territory nuclei from being randomly seeded next to each other by requiring that at least one unoccupied quad occur between territory nuclei. For species with more territories in a year than could be fit under these constraints, territories were seeded according to the rules until the landscape was full, and then the remaining nuclei were randomly seeded into any empty quad.

5) Temporal autocorrelation: The assumption that individuals freely chose their territory locations in each year was probably not valid because site fidelity increased the probability of occupying the same quad(s) in successive years. To incorporate temporal autocorrelation, we filled the landscape with territories in the first year according to the rules of the spatial autocorrelation constraints just described. In subsequent years, we drew a uniform random number for each territory and compared it to  $s$ , a measure of the strength of site fidelity ( $0 \leq s \leq 1$ ). If the random number was less than or equal to  $s$ , the territory nucleus was seeded either in the quad containing the territory nucleus from the previous year or in an adjacent quad, and the territories were grown around the nucleus. If the number was

greater than  $s$ , the territory nucleus was seeded in a random location. Thus, when  $s = 0$ , territory placement is completely random; when  $s = 1$ , all territories are placed at the sites occupied in the previous year. To determine the degree of site fidelity that minimized the difference between observed and null frequency landscapes for the most species, we repeated this procedure for six different levels of  $s$ : 0, 0.2, 0.4, 0.6, 0.8, and 1.0.

6) Habitat: We incorporated species-specific habitat constraints into null models using a two-step process. First, we used multiple logistic regression to build statistical models that related vegetative characteristics of quads (independent variables) to the frequency of quad occupation, which was modeled as the proportion of years in which a quad was occupied (dependent variable). Using these models, we generated frequency landscapes from the fitted frequencies of quad occupation. Next, in each year we drew a uniform random number for each quad and occupied a quad only if the random number was less than or equal to the fitted value of the quad.

Prior to model-building, we removed coverage variables that never exceeded 1% and variables that were highly correlated ( $r > 0.8$ ) with other variables, leaving 30 variables for inclusion (Table 1). Because of the large number of variables and species for which models are being fit, we automated the model-fitting process with the approach proposed by Shtatland et al. (2001). First, we performed stepwise logistic regression with probabilities for entry and removal from the model equal to one; these probabilities allowed all variables to be sequentially entered into the model and prevented their removal once they were in the model. The result was a stepwise sequence of models that ranged in size from one variable to all 30 variables. We used information criteria to determine which model in the stepwise sequence was optimally sized. The model with the lowest information criterion value was of optimal size ( $k$ ), and models that contained  $k \pm 1$  and  $k \pm 2$  variables were of suboptimal size. Because we were interested in developing models that identified vegetation features that explained the observed distribution of bird species, we used Schwarz information criterion (SIC). SIC penalizes models with more parameters more severely than does AIC (Burnham and Anderson 2002), so it tends to select simpler models that are more useful for description and interpretation (Shtatland et al. 2001).

Next we conducted best-subset selection procedures to obtain the best 20 models of each optimal and suboptimal size, in which the best were those that had the highest likelihood score (chi-square) statistic for all possible models of that size (SAS Institute 2003). We ranked all the models for each species according to their values of SIC and considered models with  $\Delta\text{SIC} < 2$  to be candidates for the best model (Burnham and Anderson 2002). We performed model averaging on the candidate models to obtain parameter estimates for the coefficients of the relevant vegetation variables and

TABLE 1. Names and descriptions of 30 vegetation variables used to describe the observed occupancy patterns of quads by birds breeding in the Holt Research Forest, Arrowsic, Maine, USA, in 1983–1987.

Variable†	Description
tree_density	number of trees with dbh > 9.5 cm
tot_ts_spp	number of tree and shrub species
tot_h_spp	number of herbaceous species
ba_###	basal area of all tree species (all), deciduous tree species (dec), oak species (oak), white pine (wp), birch species (brch), red maple (rm), hemlock (hem), balsam fir (bf), and red spruce (rs)
avg_cov_###_3	average coverage of all tree species (all), deciduous tree species (dec), oak species (oak), and white pine (wp) in the 1–5 m stratum
avg_cov_###_4	average coverage of all tree species (all), deciduous tree species (dec), oak species (oak), white pine (wp), birch species (brch), red maple (rm), balsam fir (bf), and red spruce (rs) in the 5–10 m stratum
avg_cov_###_5	average coverage of all tree species (all), coniferous tree species (con), deciduous tree species (dec), oak species (oak), white pine (wp), and red maple (rm) in the >10 m strata

*Notes:* Average coverage variables represent the midpoint of the coverage class of each subquad averaged over all subquads in a quad. Also, variables for some species or species groups are absent from some strata because they were highly correlated with another variable.

† Inclusion of ### in the variable represents a particular species or species group listed parenthetically under the variable description (e.g., ba\_all, avg\_cov\_wp\_3).

their corresponding unconditional standard errors. If a parameter estimate did not exist in one of the models being averaged, it was considered to be present but equal to zero (Burnham and Anderson 2002). With these parameter estimates, we determined the fitted frequencies for each quad.

*Comparing observed and null frequency landscapes.*—We generated 100 frequency landscapes for each species from null models containing one or more of the constraints previously outlined (Table 2). For each frequency landscape of the simulation, we represented the variability in quad use with the frequency distribution of occupied quads (i.e., the number of quads that were occupied in 0, 1, . . . , 5 years), and then averaged the number in each frequency category over the 100 iterations.

We considered a null model to fit the observed data if its resulting average frequency distribution matched the

observed frequency distribution. We could not assess goodness of fit between the two frequency distributions using chi-square tests, because few quads occurred in the 0 and 5 frequency classes of many species. Instead, we used 5000 iterations of a Monte Carlo simulation to generate a distribution of an analogous test statistic:  $\sum_{i=0}^5 |O_i - E_i|$ , where  $E_i$  was the number of quads occurring in the  $i$ th class of the average frequency distribution and  $O_i$  was the number of quads randomly assigned to frequency class  $i$  based on the proportion of quads occurring in that class. We compared the test statistic based on our actual data to this distribution and assessed its statistical significance at  $\alpha = 0.05$ .

## RESULTS

Twenty species met the criteria for inclusion in the analyses, of which the Ovenbird, Black-throated Green

TABLE 2. Names and defining constraints of null models that are used to simulate habitat use in birds breeding at the Holt Research Forest, 1983–1987.

Model name	Constraints					
	Yearly sum	Occupancy	Spatial autocorrelation	Dispersion	Temporal autocorrelation	Habitat
Free	X					
Occupied free	X	X				
Regular	X		X			
Occupied regular	X	X	X			
Irregular	X		X			
Occupied irregular	X	X	X			
Dispersed regular	X		X	X		
Site fidelity	X		X		X	
Habitat	X					X

*Notes:* The free model is the least constrained; the number of quads randomly occupied in a year was equal to the observed number of occupied quads in that year. Other models: occupied free, same as the free model, but randomly occupied quads were limited to those occupied in at least one year; regular and irregular, randomly occupied quads clumped into as many disk- and irregularly-shaped patterns, respectively, as there were territories in a year to account for spatial autocorrelation of quad use (i.e., territoriality); occupied regular and irregular, same as regular and irregular models, but quads that were never occupied were excluded; dispersed regular, same as regular model, but territories were spaced farther apart; site fidelity, same as regular model, but territory locations among years are temporally autocorrelated; habitat, random occupation of quads in a year is based on probabilities that reflect species-specific habitat suitability of the quad. See *Methods: Data analysis: Generating frequency landscapes* for additional details.

TABLE 3. Numbers of occupied quads (Quad), territories (Terr), and occupied quads per territory (Quads/Terr) for 20 bird species at the Holt Research Forest, 1983–1987.

Bird species	Level	Years					Quads/Terr	
		1983	1984	1985	1986	1987	$\bar{X}$	SD
Hairy Woodpecker ( <i>Picoides villosus</i> )	Quad	14	16	14	10	10	10.4	4.62
	Terr	1	1	2	1	2		
Eastern Wood-Pewee ( <i>Contopus virens</i> )	Quad	29	41	58	18	29	8.1	3.58
	Terr	3	3	9	3	6		
Black-capped Chickadee ( <i>Poecile atricapilla</i> )	Quad	80	74	97	87	101	10.6	2.33
	Terr	6	6	11	8	13		
Brown Creeper ( <i>Certhia americana</i> )	Quad	53	85	84	66	60	11.5	2.11
	Terr	5	6	9	5	6		
Red-breasted Nuthatch ( <i>Sitta canadensis</i> )	Quad	14	35	69	46	32	10.3	4.58
	Terr	4	4	6	4	2		
Golden-crowned Kinglet ( <i>Regulus satrapa</i> )	Quad	16	4	23	22	45	6.5	1.64
	Terr	2	1	4	3	6		
Veery ( <i>Catharus fuscescens</i> )	Quad	44	50	31	42	27	8.8	0.83
	Terr	5	5	4	5	3		
Hermit Thrush ( <i>Catharus guttatus</i> )	Quad	55	55	69	65	67	8.9	0.68
	Terr	7	6	8	7	7		
Nashville Warbler ( <i>Vermivora ruficapilla</i> )	Quad	70	49	39	4	25	8.2	1.53
	Terr	8	8	4	0	3		
Yellow-rumped Warbler ( <i>Dendroica coronata</i> )	Quad	57	74	87	85	89	9.2	1.83
	Terr	7	6	10	11	10		
Black-and-white Warbler ( <i>Mniotilla varia</i> )	Quad	76	56	56	48	27	9.1	0.65
	Terr	8	6	7	5	3		
Blackburnian Warbler ( <i>Dendroica fusca</i> )	Quad	58	69	73	73	87	6.4	0.35
	Terr	9	11	11	11	15		
Black-throated Green Warbler ( <i>Dendroica virens</i> )	Quad	141	149	136	117	123	4.7	0.28
	Terr	31	35	28	24	25		
Pine Warbler ( <i>Dendroica pinus</i> )	Quad	27	11	7	11	6	9.7	3.11
	Terr	2	1	1	1	1		
Canada Warbler ( <i>Wilsonia canadensis</i> )	Quad	17	11	19	13	7	11.5	3.77
	Terr	1	1	2	1	1		
Ovenbird ( <i>Seiurus aurocapillus</i> )	Quad	142	143	127	137	137	4.5	0.49
	Terr	29	39	27	29	31		
Common Yellowthroat ( <i>Geothlypis trichas</i> )	Quad	52	44	29	25	30	5.17	2.41
	Terr	8	5	9	7	8		
Scarlet Tanager ( <i>Piranga olivacea</i> )	Quad	36	37	28	30	41	11.3	2.24
	Terr	3	3	2	3	5		
White-throated Sparrow ( <i>Zonotrichia albicollis</i> )	Quad	50	54	41	13	24	6.3	2.25
	Terr	9	6	7	4	3		
Purple Finch ( <i>Carpodacus purpureus</i> )	Quad	22	21	24	18	44	14.7	5.07
	Terr	2	2	2	1	2		

Warbler, and Blackburnian Warbler were the most abundant species, comprising an average of 21%, 19%, and 8% of the territories, respectively (Table 3). All species except one (Nashville Warbler) were present in the study area in every year.

#### Relationship between quad use and abundance

Species with a higher number of territories typically occupied more quads ( $r > 0.65$  for 17 species,  $n = 5$  years), suggesting some level of exclusivity in habitat use. However, only 8 species were significantly correlated ( $r > 0.95$ ,  $P < 0.02$ ) because of the small number of years. When all species were combined, the correlation was also significant ( $r = 0.91$ ,  $P < 0.0001$ ,  $n = 100$  [20 species  $\times$  5 years]). In contrast, territory size and abundance were inversely related when all species were examined collectively ( $r = -0.51$ ,  $P < 0.0001$ ,  $n = 99$ ). When examined individually, the relationship remained negative for 17 of the 20 species, 8 of which had  $r < -0.70$ . Although the relationships were statistically

significant ( $r < -0.91$ ,  $P < 0.03$ ) for only four species (Black-capped Chickadee, Black-throated Green Warbler, Ovenbird, and Scarlet Tanager), the general trend confirms that birds tend to exclude each other from their territories.

#### Patterns of frequency landscapes

Variability in habitat use among the 20 species followed three general patterns (Fig. 2, Appendix A). Highly abundant species that exhibited widespread use of the study area had frequency landscapes that were characterized by a scarcity of unoccupied quads and a high frequency of use for most quads. Two species exhibited this pattern: Ovenbird and Black-throated Green Warbler (Fig. 2A, B) occupied 59% and 52% of the quads in all five years, respectively. Species such as the Black-capped Chickadee and Hermit Thrush also showed widespread use, but were of intermediate abundance (Fig. 2C, D), leading to frequency landscapes with very few quads that were never occupied or

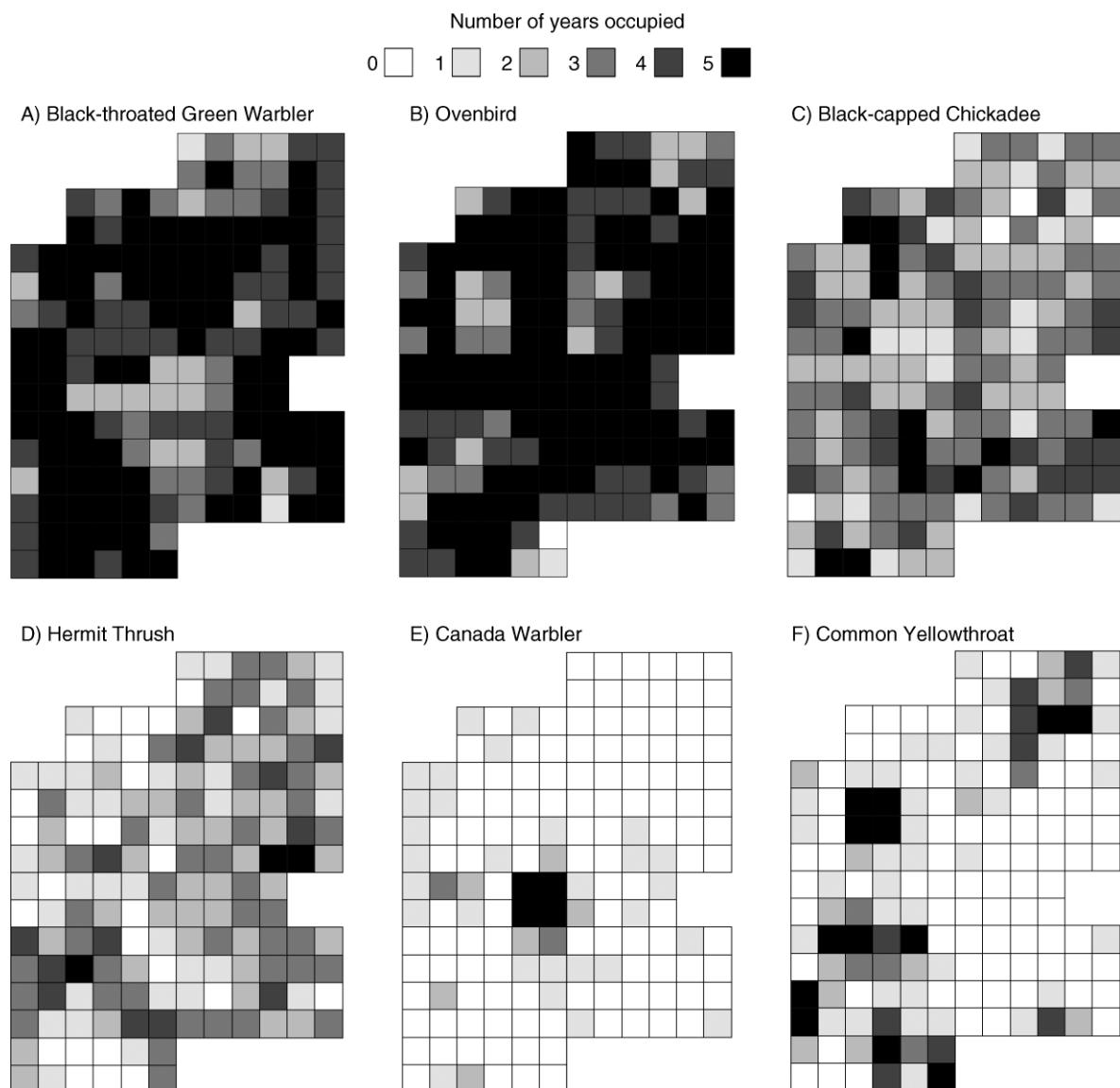


FIG. 2. Observed frequency landscapes for six bird species breeding at the Holt Research Forest, 1983–1987. Each grid cell is a 50 × 50 m quad. See Appendix A for remaining species.

occupied in all years and with most quads occupied in 1–3 years. Thirdly, some species had low to intermediate abundance and were more stenotopic in their use of the study area; their frequency landscapes had many quads that were rarely or never occupied and very few quads that were occupied four or five years (Fig. 2E, F). These patterns were typical of the Canada Warbler, which returned to the red maple swamp near the middle of the study area in all five years (Figs. 1 and 2E), and the Common Yellowthroat, which occurred in the more open areas that were coincident with exposed rock ledges (Figs. 1 and 2F). The differences in types of frequency landscapes were also reflected in the shapes of their observed frequency distribution of occupied quads (Fig. 3, Appendix B).

#### *Fit between observed and null frequency distributions*

We were able to recreate the patterns of variability in spatial distributions with one or more null models for 18 of 20 species. Free models showed a poor fit to observed frequency distributions for all but four species: Hairy Woodpecker, Black-capped Chickadee, Brown Creeper, and Purple Finch (Table 4). Incorporation of the occupancy constraint greatly improved the fit for most species (Fig. 3, Appendix B), but only the frequency distributions for the Hermit Thrush and Pine Warbler improved enough to match the observed data.

Models including spatial autocorrelation to account for territoriality performed nearly the same as the free models (Table 4). There were few, if any, differences in the frequency distributions between the models with

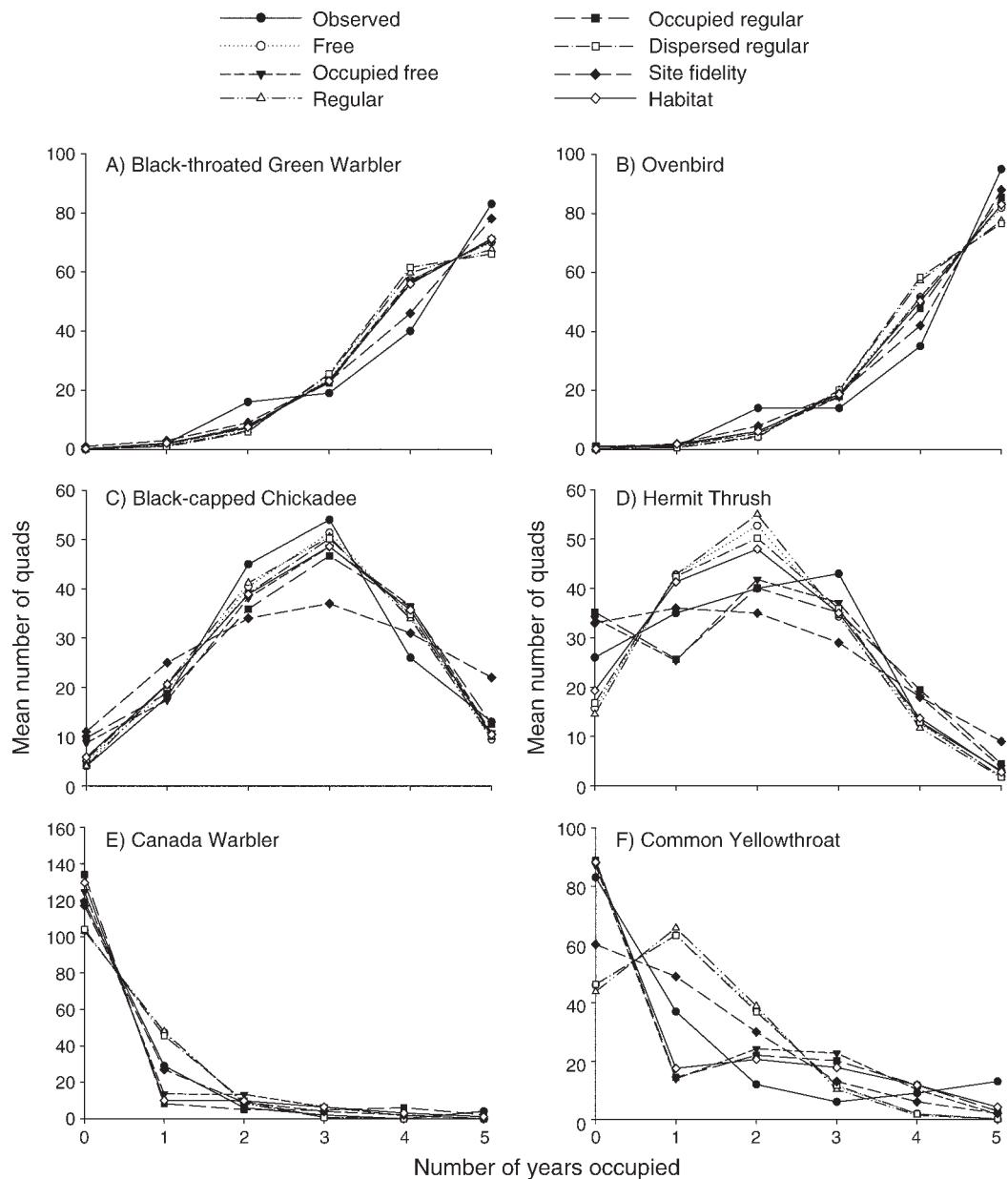


FIG. 3. Frequency distributions of occupied quads based on observed data and various null models for six bird species breeding at the Holt Research Forest, 1983–1987. See *Methods: Data analysis: Generating frequency landscapes* and Table 2 for model descriptions.

regular- and irregular-shaped territories (Appendix B), so we only presented results for models using regular-shaped territories. Constraining the territorial models further with the occupancy and dispersion constraints generally did not improve the fit (Appendix B) over their unconstrained counterpart.

Site fidelity models with a strength of site fidelity ( $s$ ) equal to 0.6 maximized the number of species for which the observed and null frequency distributions matched (Appendix C). At this level of site fidelity, 13 species exhibited fits (Table 4); five were not fit by any other model. When  $s$  was reduced to 0.4 and 0.2, the null and

observed frequency distributions still matched for 9 and 7 species, respectively (Appendix C). When  $s$  was increased to 0.8 and 1.0, the number of species fit decreased to 10 and 4, respectively (Appendix C).

The statistical habitat models varied considerably among species in both the number and identity of constituent variables, indicating that species were idiosyncratic in their responses to vegetation structure and composition (Appendix D). Variables that were consistently important among the species included basal area of all trees combined and basal area of white pine, both of which occurred in models of 8 of the 20 bird

TABLE 4. Results ( $P$  values) of goodness-of-fit tests between average frequency distributions of quad occupancy generated by the null models and the frequency distribution based on the observed data.

Bird species	Free	Occupied free	Regular	Occupied regular	Dispersed regular	Site fidelity	Habitat
Hairy Woodpecker	<b>0.877</b>	0.000	<b>0.880</b>	0.000	<b>0.863</b>	0.008	0.000
Eastern Wood-Pewee	0.000	0.024	0.000	0.003	0.000	0.026	<b>0.555</b>
Black-capped Chickadee	<b>0.402</b>	<b>0.124</b>	<b>0.455</b>	<b>0.057</b>	<b>0.262</b>	0.000	<b>0.225</b>
Brown Creeper	<b>0.081</b>	<b>0.457</b>	<b>0.076</b>	<b>0.378</b>	<b>0.145</b>	<b>0.284</b>	<b>0.698</b>
Red-breasted Nuthatch	0.005	0.000	0.003	0.000	0.002	<b>0.475</b>	<b>0.502</b>
Golden-crowned Kinglet	0.000	0.004	0.000	0.002	0.000	<b>0.248</b>	0.001
Veery	0.000	0.001	0.000	0.001	0.000	<b>0.558</b>	<b>0.358</b>
Hermit Thrush	0.009	<b>0.097</b>	0.003	<b>0.054</b>	0.036	0.022	<b>0.090</b>
Nashville Warbler	0.000	0.001	0.000	0.001	0.000	<b>0.539</b>	<b>0.389</b>
Yellow-rumped Warbler	0.004	0.025	0.002	0.042	0.031	<b>0.337</b>	<b>0.165</b>
Black-and-white Warbler	0.003	0.005	0.001	0.009	0.012	<b>0.693</b>	<b>0.281</b>
Blackburnian Warbler	0.000	0.001	0.000	0.002	0.000	0.044	0.010
Black-throated Green Warbler	0.002	0.002	0.000	0.005	0.000	<b>0.192</b>	0.005
Pine Warbler	0.000	<b>0.195</b>	0.000	<b>0.076</b>	0.000	<b>0.112</b>	<b>0.188</b>
Canada Warbler	0.001	0.000	0.001	0.000	0.001	<b>0.381</b>	0.000
Ovenbird	0.001	0.002	0.000	0.019	0.000	<b>0.076</b>	0.006
Common Yellowthroat	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Scarlet Tanager	0.000	0.041	0.000	0.002	0.001	<b>0.405</b>	0.048
White-throated Sparrow	0.000	0.000	0.000	0.001	0.000	<b>0.470</b>	<b>0.293</b>
Purple Finch	<b>0.304</b>	0.001	<b>0.758</b>	0.000	<b>0.432</b>	0.025	<b>0.318</b>

*Notes:* Here, nonsignificant ( $\alpha = 0.05$ )  $P$  values (in boldface) are important because they indicate frequency distributions that are not significantly different; that is, those with a good fit. See *Methods: Data analysis: Generating frequency landscapes* and Table 2 for model descriptions.

species, and basal area of deciduous trees, which occurred in the models of 7 species (Appendix D).

The fitted frequency landscapes from the single best model and from the average of models with  $\Delta\text{SIC} \leq 2$  were nearly identical and were generally consistent with the observed frequency landscapes (compare Figs. 2 and 4, and see Appendices A and E). For example, the correspondence was high for both abundant, widespread species and stenotopic species (A, B, E, F of Figs. 2 and 4), but tended to be lower for widespread species of intermediate abundance (C, D of Figs. 2 and 4). When null frequency landscapes were generated from the fitted frequency landscapes, 12 of the 20 species had frequency distributions that were not significantly different from the observed distributions; only one of these species (Eastern Wood-Pewee) was fit exclusively by the habitat model.

The Common Yellowthroat and Blackburnian Warbler were the only species whose frequency distributions could not be matched by that of a null model (Table 4). The Common Yellowthroat, had an almost bimodal frequency distribution (Fig. 3), indicating the repeated use of isolated and spatially distinct canopy openings and, thus, a low degree of stochastic variation. The frequency distribution of the Blackburnian Warbler was unique in that it was nearly uniform (Appendix B). Its distribution could only be matched by models with high levels of site fidelity ( $s > 0.8$ ; Appendix C), which is also suggestive of a low degree of stochasticity.

## DISCUSSION

Our results show a substantial role for stochasticity in generating patterns of habitat use. Specifically, we were able to recreate the patterns of variability with one or

more null models for all but two of the 20 bird species that we examined. These findings corroborate those of Haila et al. (1996), who found that the territory locations of 11 of 17 forest bird species varied stochastically from year to year, and those of Virkkala and Rajasärkkä (2006), who found that 8 of 10 bird species were randomly distributed within areas of old-growth forest in northern Finland.

Stochasticity is rarely explicitly investigated as a determinant of patterns of habitat use, yet when it is, as in these studies, it may challenge the primacy of deterministic explanations in habitat selection studies and may suggest that strict reliance on deterministic models could overlook the contribution of stochastic processes. Given the importance of understanding patterns of species occurrence and abundance for ecology and management, it is essential that we comprehend the role of stochasticity in habitat selection research as well as the influence of biological constraints on stochasticity.

### Implications of stochasticity for habitat selection research

Our ability to recreate the year-to-year variation in distribution patterns independent of a paradigm of deterministic habitat selection indicates that the mechanisms underlying habitat selection need to be thoroughly tested. Habitat selection theory provides possible mechanisms that can give rise to a range of patterns (e.g., Brown 1969, Fretwell and Lucas 1969), but simply demonstrating that a specific mechanism can generate the observed patterns is not proof that the mechanisms are indeed responsible for those patterns (Levin 1992). When considering the problem of pattern formation in ecology, mechanisms need to be tested and alternatives

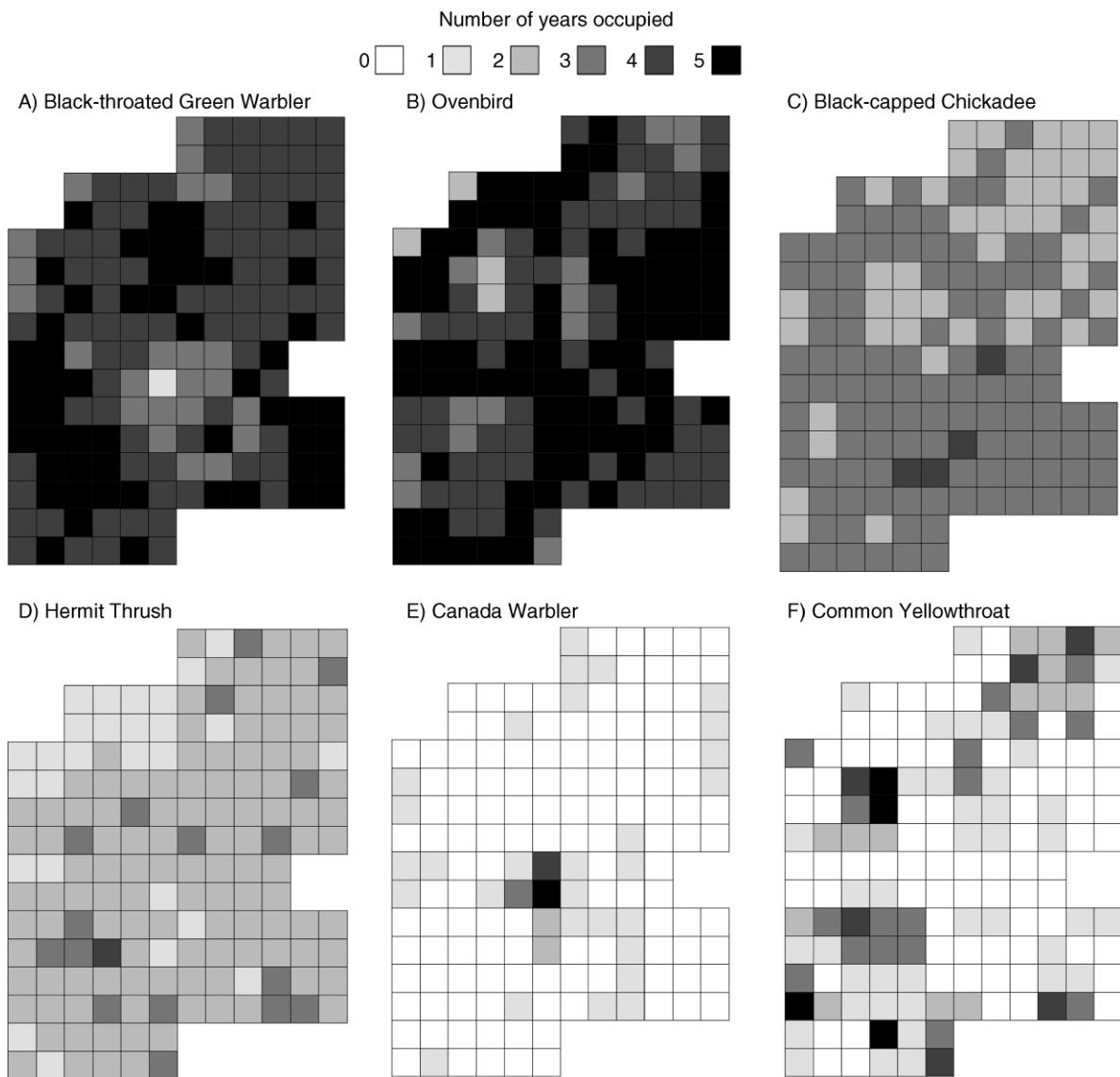


FIG. 4. Frequency landscapes fit by the logistic regression models for six bird species breeding at the Holt Research Forest, 1983–1987. Each grid cell is a 50 × 50 m quad. See Appendix E for remaining species.

considered, especially those outside the prevailing paradigm. Our results suggest that stochasticity is an alternative that merits further consideration.

Although we found that empirical distribution patterns can be recreated with stochasticity, we were unable to distinguish between the influences of “actual” stochasticity (i.e., when an animal’s decision to settle is completely independent from environmental cues and therefore implicitly unpredictable) and “apparent” stochasticity (i.e., when deterministic responses to multiple environmental cues collectively lead to distribution patterns that appear random). From a phenomenological (i.e., pattern) perspective, whether the variation is random or appears random is irrelevant because the resulting distribution patterns are indistin-

guishable. In other words, this finer detail is not relevant for producing the observed patterns (Levin 1992). In contrast, the distinction has clear implications from a mechanistic (i.e., process) perspective: apparent stochasticity can be predicted if the manifold relationships between habitat selection and environmental cues are accounted for, whereas actual stochasticity can not. Although both types of stochastic processes are likely to play a role, demonstration of a disproportionate influence of actual stochasticity would challenge the underlying theoretical framework of habitat selection studies that assumes a strong relationship between habitat selection and habitat quality. Nevertheless, if apparent stochasticity is dominant, the use of stochastic models that incorporate minimal biological constraints

may be preferable to deterministic models that attempt to account for the many factors that influence habitat selection. Such deterministic models can be very complex, which can make them extremely sensitive to parameter estimation, prone to error propagation, and difficult for understanding dynamics and elucidating critical processes (Pascual and Levin 1999).

The scale of sampling is likely to be particularly important in our evaluation of the influences of deterministic and stochastic processes. For example, at an evolutionary timescale, habitat selection must be deterministically tied to environmental cues that increase fitness, while at ecological timescales (i.e., year-to-year variation) other, more dynamic and less rigid, forces (e.g., fluctuations in climate, predator density, and resource abundance) may be at work (Chesson and Case 1986, Johnson and Seip 2008). Similarly, patterns of habitat selection will appear deterministic at coarse spatial scales where differences in environmental conditions (e.g., forest vs. grassland) are greatest (Glas 1960, O'Connor 1986, 1987, Petit and Petit 1996). However, at fine spatial scales, similarity in conditions increases and the influence of deterministic processes (i.e., inherent habitat preference) is likely to be surpassed by stochastic processes (e.g., variation in individual behavior) (Chesson and Case 1986, Milinski and Parker 1991, Levin 1992). Thus, the stochastic variation in habitat occupancy in our study may have occurred because the spatial and temporal extents of our study were relatively small and the habitats relatively homogeneous. Such variation may frequently be overlooked because researchers tend to work at larger spatial and temporal scales or with groupings where statistical behaviors are regular enough for generalizations to be made (Levin 1992, Pascual and Levin 1999). More work is needed to establish the boundary conditions between stochastic and deterministic habitat dynamics both in terms of differences in habitats and spatial and temporal scales at which the dynamics are investigated.

Even at a given spatial and temporal scale, differentiating between patterns resulting from stochastic and deterministic processes is not necessarily straightforward. For example, Ellwood et al. (2009) used null models to examine the relative importance of stochastic and deterministic processes for structuring communities of arthropod decomposers in tropical epiphytic ferns. When ferns were sampled without regard to their environment and history, the arthropod communities appeared to be structured according to niche theory (Chesson and Case 1986, Condit et al. 2006), but when the sampled ferns were of similar size and from a small area, their results were consistent with neutral theory (Bell 2001, Hubbell 2001). Similarly, it is important that the scale at which habitat selection is measured matches the scale at which it is actually occurring (Addicott et al. 1987, Orians and Wittenberger 1991, Garshelis 2000, Deppe and Rotenberry 2008). In our study, we measured presence and absence in 50 × 50 m quads

largely for analytical reasons. If the spatial scale of territories was considerably larger than that of the quads, quad occupancy may appear random within a deterministically located territory (Haila et al. 1996). This may explain why the four bird species that were best fit by a completely random model (Table 4) had some of the largest territories (Table 3). These types of disparities can confound attempts to understand the patterns in natural assemblages and indicate that a detailed knowledge of the system is required to define the spatial and temporal resolution at which to test mechanisms of habitat selection and community structure (Ellwood et al. 2009).

Another important consideration when evaluating mechanisms determining spatial distribution is whether populations are at equilibrium. For example, deterministic models such as those of Fretwell and Lucas (1969) are equilibrium-based theories that assume habitats are saturated, resources are limited, and populations are competitively structured. If habitats are not fully saturated with individuals, populations may be non-equilibrium, in which case “patterns” that are detected using equilibrium-based methods are probably spurious (Wiens 1984). Even deterministic processes such as site fidelity can create inconsistent distribution patterns in nonequilibrium populations. For example, if the population declines, and high-quality habitat becomes available, site fidelity can tie individuals to low-quality habitat even though theory predicts that individuals should move to better habitat.

For many species, our habitat models identified many “suitable” but unoccupied sites, suggesting that habitats were not saturated, and thus providing a possible reason why stochastic dynamics prevailed (Figs. 2 and 4, Appendices A and E). Haila et al. (1996) also found this pattern, predominantly in scarce species. On the other hand, habitats were probably saturated for some species. For example, Ovenbirds and Black-throated Green Warblers had a significantly negative relationship between territory size (number of quads per territory) and the number of territories in a given year, which is consistent with crowding and territorial compression. However, it is also possible that the years of high abundance and smaller territories were years in which habitat quality was high enough that their needs could be met with smaller territories (Calsbeek and Sinervo 2002).

Finally, an elevated importance for stochasticity will probably have implications for applied habitat selection research, especially given that the role of stochasticity is likely to be most prominent at the smaller spatial and temporal scales at which land managers usually operate. For example, deterministic habitat models tend to yield management prescriptions that seek to provide a particular suite of factors in the right combination to create “optimal” conditions for a population. However, if there is a large element of stochasticity in an animal’s decision to use an area, it may be more prudent to

simply manage for general vegetation types (e.g., mature pine–oak forest) instead of trying to optimize specific habitat features that animals may or may not use. Nevertheless, there may also be a role for stochasticity in addressing large-scale issues. The complex interactions between large-scale forces such as climate change and range shifts of competitors and predators may also generate distribution patterns with a substantial stochastic component that are difficult to explain with deterministic models. For example, as animals try to extend their geographic ranges into new areas, the resulting patterns of habitat use and community reassembly are likely to be contingent on stochastic events. High heterogeneity in regional temperature changes (Walther et al. 2002) will further complicate predictions of these ecological responses and potentially lead to dynamics that appear stochastic.

#### *Influences of biological constraints on patterns of avian habitat use*

Comparison of the performances of different null models allowed us to evaluate the influence of different biological constraints inherent to avian habitat selection (e.g., abundance, territoriality, and habitat preference) on distribution patterns. For example, when the only constraint was the number of quads occupied in a year (i.e., abundance), year-to-year variability in distribution patterns only matched for four species. Models that grouped occupied quads into randomly placed territories each year probably better simulated distribution patterns within a year, but they did not perform any better when all years were combined, because the randomization of territory locations in each year disrupted the spatial autocorrelation of occupied quads in the frequency landscape. However, when the random placement of territories was constrained in subsequent years by site fidelity, the performance of the null models improved considerably (Table 4), demonstrating that territoriality per se is not enough to recreate observed distribution patterns; territoriality must work in conjunction with site fidelity.

Comparisons among the null models revealed that site fidelity had a strong influence on year-to-year variability in patterns of habitat use; site fidelity models fit the distributions of 13 of 20 species. The conclusions from these models were based on a probability of 0.6 that territories would occur at or very near to their previous location. The number of species fit by the site fidelity model decreased as this probability increased or decreased from 0.6 (Appendix C). Thus, moderate levels of site fidelity were able to create observed distribution patterns by limiting the variability in random territory placement over time. Site fidelity that was too weak or too strong suggested that completely random territory placement or highly deterministic habitat selection, respectively, were unrealistic for most species. For example, if we assumed that site fidelity were absolute ( $s=1$ ) (i.e., no stochasticity) and that there were at least

as many birds in a year as there were previously occupied sites, then a previously occupied site would be occupied in every subsequent year by the same bird or a different bird replacing one that died and left a vacant territory. Consequently, lack of fit by null models with site fidelity greater than 0.6 suggests that highly stable habitat use due to the inherent suitability of a site is unlikely.

The site fidelity null model may appear superficially to be invalid because it implicitly incorporated the mechanism we were trying to assess, i.e., deterministic tracking of habitat variation (Gilpin and Diamond 1984, Gotelli and Graves 1996). However, the increased probability of quad use in a year occurred strictly as a consequence of the presence in the previous year. Our model assumed nothing about habitat quality when choosing or returning to a site. The initial locations were random and when site fidelity was not a factor (e.g., when a new individual replaced a territory holder in the population), new territories were established in randomly selected locations. These model conditions may not be that different from reality. Site fidelity has presumably evolved because knowledge of a particular territory confers a higher probability of survival and reproduction. If this knowledge confers a great enough advantage, site fidelity can actually inhibit transfers to vacant territories in intrinsically better habitat (Fretwell 1968, O'Connor 1985). Nevertheless, if an individual returns to a site and fails to successfully reproduce, then an individual will be less likely to return to the same place in the following year (Greenwood and Harvey 1982, Haas 1998, Clark and Shutler 1999, Hoover 2003, Fisher and Wiebe 2006). Thus, site fidelity can decouple habitat selection from habitat quality and, at best, site fidelity may allow birds to track habitat conditions with a one-year time lag.

In addition to the site fidelity models, habitat models also performed well, matching the distributions of 12 of the 20 species. This result suggests that the associations of birds with vegetation were not strongly deterministic, as is often assumed. As previously discussed, this may have occurred because the vegetation may have been relatively homogenous in comparison to the scale of habitat selection. Alternatively, it may suggest that birds are able to cope with heterogeneity within broad vegetation types. Another possibility for the role of stochasticity within the habitat constraints is that the habitat models only incorporate vegetation structure and composition. Although vegetation is often assumed to be the primary proximate factor determining habitat use by birds (Deppe and Rotenberry 2008), other important habitat factors include quantity, quality and distribution of food, mate availability, distribution and abundance of competitors and predators, and weather. These factors, acting individually or together, can overwhelm the influence of vegetation, making otherwise suitable habitats unavailable to birds (Block and Brennan 1993) and thus creating distribution patterns

that appear random with respect to the bird–vegetation associations established in our models.

In contrast to site fidelity models, habitat models were more likely to be invalid because they were based on the observed patterns of habitat use, which included site fidelity and territoriality. Thus, support for habitat models may have occurred because of their implicit incorporation of site fidelity and not because they accounted for an area's vegetation features. This may also explain the high overlap in species fit by both models. Empirically, we were unable to distinguish between site fidelity and habitat quality as reasons for returning to an area. Because we did not mark birds, the degree to which areas of high occupancy resulted from individual site fidelity or different individuals responding to the inherent favorability of a site was unknown. Although five years is probably long enough to ensure that there was turnover in the populations of most species, a longer time series would help to distinguish between these processes.

Importantly, the models that incorporated habitat constraints and those that included occupancy constraints (i.e., exclusion of unoccupied quads) allowed us to distinguish between two modes of habitat selection: preference and avoidance, respectively. Preference and avoidance are not symmetrical alternatives (Haila et al. 1996). Preference implies that individuals seek to find an optimal habitat, whereas avoidance allows individual to settle anywhere other than avoided areas. Consequently, preference implies some degree of determinism in habitat use, whereas avoidance of a particular habitat allows variability in the use of the remaining habitats (Haila et al. 1996). Given the much larger number of species that were better fit by habitat models (12 species) than models with the occupancy constraint (four species), habitat selection appeared to be a result of preference in our study, in contrast to the results of Haila et al. (1996).

#### CONCLUSIONS

Only two of 20 species exhibited variability in distribution patterns that could not be matched with a null model. In contrast, year-to-year variability in bird distribution patterns could be modeled as a purely stochastic process for four species. For most species, random variability only had to be constrained by some of the salient biological features of avian habitat selection to allow the patterns of variability in the observed data to be matched by null models. Specifically, null models that incorporated vegetation and site fidelity fit the distribution patterns of 12 and 13 species, respectively. The strong performance of habitat models suggested that random use, coupled with general vegetation associations, was able to recreate the observed patterns of variability. In contrast, the site fidelity models, in which site-tenacious territorial birds were using habitat randomly, indicated that these patterns could be reproduced independent of vegetation.

Regardless of the specific mechanism, it is clear that any factor that increases the likelihood of returning to a previously used area, and thus limits the spatial extent of random territory placement, can generate patterns similar to those observed in our five-year data set.

Stochasticity may play a larger role in generating distribution patterns than is often considered. If the relationship between habitat selection and habitat quality is not as strong as is typically assumed, then distribution patterns may result from truly stochastic processes. Alternatively, stochasticity can act as surrogate for the deterministic response to a complex suite of environmental cues that collectively create patterns that are indistinguishable from randomness. If so, we suggest that, from a practical standpoint, it may be easier to model variation in habitat using random processes rather than trying to use more complex deterministic models to account for the multitude of environmental factors that influence the habitat selection of birds. Of course, the relative influence of these types of stochastic processes is likely to be scale dependent, so it is important that we understand the dynamics of natural communities at the scale at which we sample when developing models of habitat selection. Regardless of these issues, the influence of stochastic processes in habitat selection is understudied and deserves wider attention.

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#### APPENDIX A

Observed frequency landscapes for 14 bird species breeding at the Holt Research Forest, Arrowsic, Maine, USA, 1983–1987 (*Ecological Archives* M080-010-A1).

#### APPENDIX B

Frequency distributions of occupied quads based on observed data and various null models and *P* values from goodness-of-fit tests comparing each distribution to the observed distribution (*Ecological Archives* M080-010-A2).

#### APPENDIX C

Results of goodness-of-fit tests between average frequency distributions of quad occupancy generated by site fidelity models with varying strengths of site fidelity and the frequency distributions based on the observed data (*Ecological Archives* M080-010-A3).

#### APPENDIX D

Model-averaged parameter estimates of vegetation variables and their associated unconditional standard errors (SE) and relative variable importance (RVI) for habitat models of 20 bird species breeding at the Holt Research Forest, 1983–1987 (*Ecological Archives* M080-010-A4).

#### APPENDIX E

Frequency landscapes fit by the logistic regression models for 14 bird species breeding at the Holt Research Forest, 1983–1987 (*Ecological Archives* M080-010-A5).