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CORRELATES AND CONSEQUENCES OF BREEDING DISPERSAL IN A MIGRATORY SONGBIRD

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ABSTRACT.—Knowledge of breeding dispersal, defined as shifts in territory location between two successive breeding seasons, remains limited for migratory passerines. We investigated the relationship between two ecological factors, habitat structure and reproductive success, and 499 breeding dispersal events in a Nearctic–Neotropic migratory songbird, the Black-throated Blue Warbler (*Setophaga caerulescens*) breeding at the Hubbard Brook Experimental Forest, New Hampshire, from 1998 to 2008. Male dispersal distance was correlated with both individual age and habitat structure, with older males moving shorter distances than younger males, and males on the high-shrub-density plot (i.e., higher quality) moving shorter distances than males on the plot with lower shrub density. Female dispersal distance was also correlated with habitat structure; individuals on the higher-quality plot moved shorter distances than those on the lower-quality plot. In contrast to that of males, female dispersal distance was independent of age, but correlated with reproductive success: females that fledged relatively few offspring in a year subsequently dispersed farther than those that experienced high reproductive success. Mean (\pm SE) breeding dispersal distance for females (245 ± 20 m) was greater than that of males (163 ± 11 m). We also examined reproductive consequences of breeding dispersal and found that males that moved shorter distances fledged more offspring after dispersal than those that moved longer distances; no trend was found for females. These differences in dispersal patterns and outcomes suggest sex-specific selective pressures and life-history strategies. Received 27 December 2012, accepted 20 September 2013.

Key words: Black-throated Blue Warbler, breeding dispersal, habitat structure, migratory passerine, movement, reproductive success, *Setophaga caerulescens*.

Correlatos y Consecuencias de la Dispersión Reproductiva en un Ave Canora Migratoria

RESUMEN.—El conocimiento de la dispersión reproductiva, definida como el cambio en la ubicación del territorio entre dos temporadas reproductivas consecutivas, es limitado en paserinos migratorios. Investigamos la relación entre dos factores ecológicos, la estructura del hábitat y el éxito reproductivo, y 499 eventos de dispersión reproductiva sucedidos entre 1998 y 2008 en el bosque experimental Hubbard Brook, New Hampshire, en *Setophaga caerulescens*, un ave canora que migra entre el Neártico y el Neotrópico. La distancia de dispersión de los machos se correlacionó con la edad individual y la estructura del hábitat, de tal forma los machos más viejos se movieron distancias más cortas que los jóvenes, y los machos en la parcela de alta densidad de arbustos (i.e. mayor calidad) se movieron distancias menores que los de la parcela con baja densidad de arbustos. La distancia de dispersión de las hembras también estuvo correlacionada con la estructura del hábitat; los individuos en la parcela de mayor calidad se movieron distancias más cortas que los de la parcela de menor calidad. En contraste con los machos, la distancia de dispersión de las hembras fue independiente de la edad, pero estuvo correlacionada con el éxito reproductivo: las hembras que produjeron relativamente menos progenie en un año se dispersaron más lejos que aquellas que experimentaron un alto éxito reproductivo. La media (\pm EE) de la distancia de dispersión reproductiva en hembras (245 ± 20 m) fue mayor que la de los machos (163 ± 11 m). También examinamos las consecuencias reproductivas de la dispersión reproductiva y encontramos que los machos que se movieron distancias más cortas produjeron más progenie luego de la dispersión que aquellos que se movieron distancias mayores; no se encontró ninguna tendencia en las hembras. Estas diferencias en los patrones de dispersión y en sus consecuencias sugieren presiones selectivas y estrategias de historia de vida específicas para cada sexo.

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BREEDING DISPERSAL, BROADLY defined as the movement between two successive breeding areas or social groups, is one of the most important but little known processes in population dynamics (Clobert et al. 2001, Bowler and Benton 2005). An individual's decision to disperse between breeding seasons is influenced, presumably, by the relative benefits and costs associated with such movements (Greenwood 1980, Forero et al. 1999, Daniels and Walters 2000, Yoder et al. 2004). A key benefit is the acquisition of a higher-quality breeding site or mate, which increases the probability of reproductive success (Stacey and Ligon 1987) or survival (Pärt and Gustafsson 1989). Potential costs of dispersal include the challenges associated with locating and establishing a new breeding territory (Pärt and Gustafsson 1989). Such costs may include an increased mortality risk (Strickland 1991) and a risk of lower reproductive success due to poor knowledge of the new breeding site (Saunders et al. 2012). Familiarity with a previously occupied site can help establish dominance during territory formation (Greenwood and Harvey 1976) and reduce predation risk (Yoder et al. 2004). The benefits and costs associated with breeding dispersal are likely not fixed and can vary according to life history strategy (Paradis et al. 1998), age (Baker 1978, Lindberg and Sedinger 1997), and individual condition (Clobert et al. 2009).

Our understanding of breeding dispersal remains especially poor for small migratory animals (Holmes et al. 1996, Dieckmann et al. 1999, Nathan 2001, Fajardo et al. 2009). Few empirical studies have examined how breeding dispersal patterns of such species are shaped by environmental features of the breeding area, age and sex, or an individual's previous breeding experience (Forero et al. 1999, Pasinelli et al. 2007, Schaub and von Hirschheydt 2009). We also know little about the fitness consequences of dispersal (Pärt and Gustafsson 1989) and, hence, how and when dispersal can be adaptive (McPeck and Holt 1992, Bowler and Benton 2005).

Breeding dispersal patterns of migratory birds are thought to be influenced by both intrinsic (e.g., sex and experience) and extrinsic (e.g., food availability and habitat quality) factors (Greenwood and Harvey 1982, Harvey et al. 1984, Reed and Oring 1993, Haas 1998, Bötsch et al. 2012). Females generally disperse longer distances than males, and breeding dispersal distance typically decreases with age and as breeding-habitat quality increases. Birds that reproduce successfully are more likely to be site faithful, although exceptions exist (Paton and Edwards 1996, Bernard et al. 2011). Dispersal behavior can also be affected by conspecific densities (Matthysen 2005) and by the reproductive success of neighbors (Doligez et al. 1999, Travis et al. 1999), as well as by nest predators and parasites (Greig-Smith 1982, Stanback and Dervan 2001).

We studied the correlates and reproductive consequences of annual breeding dispersal in the Black-throated Blue Warbler (*Setophaga caerulescens*), a territorial, Nearctic–Neotropic migrant songbird. The breeding ecology of this species has been studied extensively (for an overview, see Holmes 2011), and we know that adults exhibit breeding-site fidelity (Holmes and Sherry 1992, Sillett and Holmes 2002), but previous research has not investigated how individual characteristics and environmental conditions are related to adult dispersal patterns. We hypothesized that variation in adult breeding dispersal in Black-throated Blue Warblers would be associated with sex, age, reproductive success, and habitat quality. On the basis of theoretical and empirical investigations of avian dispersal, we predicted that (1) breeding

dispersal distance would be greater for females than for males, (2) younger birds would disperse greater distances than older birds, (3) individuals that experienced greater reproductive success would subsequently disperse shorter distances than individuals that were less successful, and (4) individuals occupying areas of lower-quality habitat would disperse greater distances than individuals occupying areas of higher-quality habitat. Finally, we predicted that dispersal would be correlated with greater reproductive output in future breeding attempts.

METHODS

Study species and system.—Black-throated Blue Warblers breed in mature northern hardwood forest areas in eastern North America and winter primarily in the Greater Antilles. This species is sexually dichromatic; females build nests in the shrub layer and incubate eggs, and both sexes feed nestlings and fledglings (Holmes et al. 2005). During the breeding season, Black-throated Blue Warblers feed primarily on lepidopteran larvae gleaned from understory leaves (Holmes et al. 2005). Females can renest following nest failure, and a variable number of females, ranging from zero to 87% per year (Nagy and Holmes 2005), initiate a second nest after a successful first attempt (i.e., double brood). In New Hampshire, the breeding season extends from early May into August at Hubbard Brook (Holmes et al. 2005), and territories are typically 2 to 4 ha (Sillett et al. 2004). Apparent annual survival probabilities range from 0.45 to 0.58 for males and from 0.33 to 0.49 for females (Sillett and Holmes 2002). When both members of a pair return to the breeding area in a subsequent year, repairing is common (Holmes et al. 2005).

Data were collected annually from early May through mid-August, 1998 to 2008, within the 3,160-ha Hubbard Brook Experimental Forest, Woodstock, New Hampshire (43°56'N, 71°45'W), as part of a long-term avian research project (for details, see Holmes 2011). The northern hardwood forest at Hubbard Brook was dominated by American Beech (*Fagus grandifolia*), Sugar Maple (*Acer saccharum*), and Yellow Birch (*Betula alleghaniensis*). Red Spruce (*Picea rubens*), Balsam Fir (*Abies balsamea*), and White Birch (*B. papyrifera* var. *cordifolia*) increased in abundance at higher elevations. Dominant understory plants included Hobblebush (*Viburnum alnifolium*) and Striped Maple (*Acer pensylvanicum*). The Hubbard Brook valley has not been logged since the early 1900s.

Field methods.—We worked on three study plots: a 65-ha middle-elevation site at 600 m a.s.l. during 1998–2008; and during 2001–2008, an 85-ha low-elevation site at 250–400 m a.s.l. and a 35-ha high-elevation site at 700–850 m a.s.l. All three plots were demarcated into 50 × 50 m grids with flagging tape to facilitate territory mapping and tracking of birds. Adults were captured with mist nets and marked with a unique combination of a numbered federal band and two or three colored plastic leg bands. Birds were aged using plumage characteristics (Pyle 1997) as either yearlings in their first breeding season (i.e., second-year [SY] individuals) or older adults (after-second-year [ASY] individuals). Warbler territories were visited every 2 days to resight individuals and to monitor breeding activity; territories were mapped at least twice per week. We located nests by following females during the nest-building or incubation periods; over 80% of nests were found during the building stage. When a nest was located, its status was checked every other day until fledging or failure. After a nest fledged or

failed, we continued to monitor territories to confirm successful fledging and to discover re-nests after failure or second broods after fledging.

Territory quality for the Black-throated Blue Warbler is determined in part by understory structure, with high-quality habitats at Hubbard Brook characterized by a dense, heterogeneous shrub layer of Hobblebush and saplings of canopy trees (Steele 1993, Holmes et al. 1996); higher understory leaf density is correlated with a greater abundance of lepidopteran larvae (Holmes et al. 1996). To quantify territory quality, vegetation measurements were taken late in the breeding season, after leaves fully emerged, using the methods in Sillett et al. (2004). Briefly, from 1997 to 2001, vegetation measurements were taken within 11.2-m-radius circles placed at a random subset of plot grid intersections (see above); vegetation survey locations were ≥ 50 m apart. We assumed that these measurements were representative of understory vegetation on our study plots, all of which were in undisturbed, century-old forest, over the 10 years of the data set. Basal area was measured for all trees >7 cm diameter at breast height, and the numbers of leaves and stems of the dominant, deciduous understory species (Hobblebush, American Beech, and Striped Maple) were measured using four 3×3 m vertical plane transects per survey circle. Within each circle, vertical planes were oriented in each of the four cardinal directions, with one end at the circumference of the circle and the other end directed toward the center. All leaves that intersected each vertical plane were counted. These leaf data were used to calculate plot-level estimates of understory vegetation density and spatially explicit estimates of vegetation density at Black-throated Blue Warbler territory centers, which we used as measures of habitat quality at coarse and fine scales, respectively. We only used vegetation surveys from the middle-elevation ($n = 641$) and high-elevation ($n = 103$) plots because the population density of Black-throated Blue Warblers and the number of between-year returns by individuals were sparse on the low-elevation plot.

Data analysis.—Breeding dispersal distances were calculated by comparing the location of an individual's center of activity for breeding season y with that for breeding season $y + 1$. The center of activity was considered the location of the nest for individuals that had only one nest in a breeding season. If an individual had more than one nest per breeding season, the center of activity was the spatial average of all nest locations on the plot grid. If no nests were located for an individual, the center of activity was defined as the center of the bird's territory as mapped through direct observation of male activities. A subset of individuals ($n = 122$) returned more than once, and each return was considered in the analyses as a separate dispersal event.

Our analytical approach did not account for imperfect detection of returning individuals. Some marked birds that returned to our study plots undoubtedly went undetected, whereas others dispersed to locations outside our plots and were thus unavailable for recapture or resighting. However, the probability of detecting a returning marked individual on our plots in any year was high: mean (\pm SE) detection probabilities were 0.93 ± 0.03 and 0.87 ± 0.06 for males and females, respectively (Sillett and Holmes 2002), and the percentage of returning birds that dispersed beyond our plot boundaries was likely to be small (see below). Detection of returning marked individuals could also have differed between our middle- and high-elevation plots because differences in plot

area biased the observed dispersal distances. To test for such bias, we restricted the larger, middle-elevation plot to a random 35-ha area and used a one-tailed t -test to compare the dispersal distances within this restricted area to the dispersal distances on the high-elevation plot. Differences in plot area between the middle- and high-elevation plots did not appear to bias our observed dispersal distances: the one-tailed t -test indicated that dispersal distances were significantly greater on a random 35-ha subunit of the middle-elevation plot than on the high-elevation plot (mean for middle elevation = 107 ± 1 m, mean for high elevation = 85 ± 1 m; $t = 1.96$, $df = 176$, $P = 0.02$). We therefore assumed that any biases due to imperfect detection were low for the inferences presented here, and included birds from the entire 65-ha middle-elevation plot in our modeling of dispersal distances and reproductive consequences of dispersal.

Study plot was considered a coarse-scale indicator of habitat quality for our analyses because understory vegetation density (Table 1), Black-throated Blue Warbler population density, and reproductive success increased with elevation at Hubbard Brook (Fig. 1). Plot-wide average leaf and stem density of all deciduous understory species sampled increased with elevation, though not significantly (leaves: $t = 1.05$, $df = 133$, $P < 0.15$; stems: $t = 0.93$, $df = 143$, $P < 0.18$; Table 1). Leaf and stem density of Hobblebush, the primary nest substrate for Black-throated Blue Warblers at our study sites, increased significantly with plot elevation (leaves: $t = 2.60$, $df = 132$, $P < 0.01$; stems: $t = 4.12$, $df = 128$, $P < 0.01$; Table 1). Additionally, both density ($F = 82.48$, $df = 2$, $P < 0.01$) and fecundity ($F = 3.99$, $df = 2$, $P = 0.03$) of Black-throated Blue Warblers increased significantly with plot elevation (Fig. 1).

Leaf count data, our fine-scale index of Black-throated Blue Warbler territory quality, were processed with ARCGIS, version 9.3 (ESRI, Redlands, California), using an ordinary kriging geostatistical procedure. The semivariogram generated by this procedure was examined to determine spatial autocorrelation of leaf density. We fit a spherical model to this semivariogram because it most accurately approximated the nature of spatial autocorrelation in leaf density. Interpolated kriging maps were created from this model to estimate plot-scale understory leaf density. The closest 12 vegetation survey points, approximately the area of a Black-throated Blue Warbler territory (~ 100 -m radius circle), were used to derive the interpolated prediction of leaf

TABLE 1. Plot-level differences in understory habitat structure at the Hubbard Brook Experimental Forest, New Hampshire. Mean (\pm SE) total deciduous leaf and stem densities are shown. Leaf and stem densities of *Viburnum alnifolium*, the main nest substrate used by Black-throated Blue Warblers at Hubbard Brook, are also shown.

Habitat characteristic	Elevation	Density
Total deciduous leaves	Middle	117.51 ± 2.10
	High	123.72 ± 5.52
Total deciduous stems	Middle	17.54 ± 0.51
	High	18.73 ± 1.18
<i>V. alnifolium</i> leaves	Middle	24.29 ± 0.92
	High	31.18 ± 2.48
<i>V. alnifolium</i> stems	Middle	8.42 ± 0.40
	High	13.50 ± 1.16

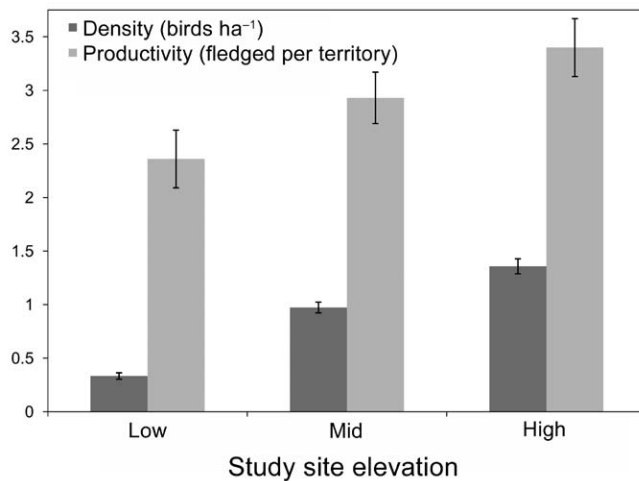


FIG. 1. Plot-level differences in population density and productivity of Black-throated Blue Warblers at the Hubbard Brook Experimental Forest, New Hampshire, 1998–2008. Both density (mean \pm SE) individuals ha⁻¹) and productivity (mean \pm SE) offspring fledged territory⁻¹) increased with elevation.

density for each output cell. In this way, we incorporated spatial variability in territory leaf density that was biologically meaningful for the Black-throated Blue Warbler. The final vegetation variable used in our analyses was the interpolated estimate of total number of deciduous understory leaves within a 5-m-radius circle around each bird's center of activity (see above). A 5-m-radius buffer was selected because it approximated the spatial resolution of our GPS data and allowed for inclusion of birds near the periphery of our study plots in our analyses.

Modeling dispersal distance.—We compared dispersal distances between males and females from all three study plots (low, middle, and high elevation) with a two-tailed *t*-test, then used an information-theoretic approach to determine which of our predictor variables were most important in explaining between-year dispersal distances for Black-throated Blue Warblers. Based on our *a priori* hypothesis that male and female dispersal distances would differ, two identical sets of candidate models were constructed, one set for each sex. Individual (i.e., band combination) was included as a random effect in every model because some individuals underwent multiple dispersal movements and all movements were included in the analyses. Additionally, we included year as a random effect in all models because we expected dispersal distance to vary by year, but this was not of primary interest in our study. Explanatory variables used in model construction were age class (SY or ASY), plot (middle and high elevation), habitat quality (estimated number of deciduous leaves near a bird's center of activity), and reproductive success as a continuous variable (number of young fledged in the year prior to movement). To address our *a priori* hypotheses and limit the number of candidate models, we considered only two interaction terms: age*offspring fledged to test whether possible effects of reproductive success on breeding dispersal distance were consistent between age classes, and age*plot to examine whether age affected dispersal distance differently between plots. Both model

sets included models corresponding to every combination of additive effects and the two interactive effects. Thus, each candidate set contained 26 models, including a null model and a fully parameterized, or global, model. We ranked models with Akaike's information criterion corrected for small sample size (AIC_c) and used model averaging to calculate parameter estimates using the AIC_c-weighted average of all candidate models (Burnham and Anderson 2002).

Aside from kriging, all statistical analyses were conducted using R, version 2.15.3 (R Foundation for Statistical Computing, Vienna). Dispersal distances were log₁₀ transformed to meet model assumptions. We fit linear mixed models via package "lme4" and conducted model selection and averaging with package "AICcmoavg." Correlations between explanatory variables were examined with a heterogeneous correlation matrix using the "polycor" package. All coefficients were <0.4, indicating low correlation.

We tested for a relationship between the change in number of offspring fledged from year *y* to *y* + 1 (hereafter "Δfledged") and dispersal distance from year *y* to *y* + 1 with sex-specific, linear mixed models with a Poisson error structure. Individual identity and year were included as random effects. This approach tested whether reproductive success was correlated with dispersal distance in Black-throated Blue Warblers.

RESULTS

Correlates of dispersal distance.—Female Black-throated Blue Warblers dispersed greater distances (245 ± 20 m) between years than males (163 ± 11 m; $t = 3.93$, $df = 497$, $P < 0.01$). The mean (\pm SE) breeding dispersal distance for all individuals from the three study plots was 193 ± 10 m (median = 121 ± 10 m, maximum = 2,250 m; $n = 499$ breeding dispersal events for 196 males and 147 females). Overall, 66% of males and 46% of females returned to within 150 m of the center of their previous year's territory (Fig. 2).

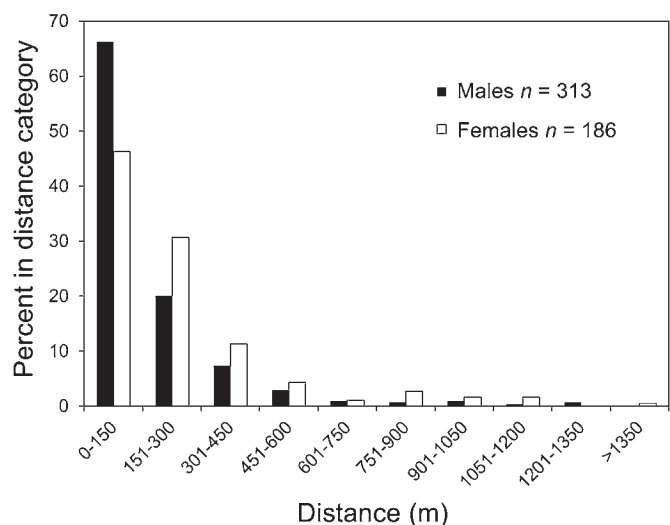


FIG. 2. Dispersal distances of female and male Black-throated Blue Warblers at the Hubbard Brook Experimental Forest, New Hampshire, 1998–2008.

Movement patterns also varied according to age, study plot, and reproductive success, though these effects differed by sex. Our analyses indicated support for two models of male dispersal. The top-ranked model included the effects of age class and plot (Table 2). Also supported was a model including only age class ($\Delta AIC_c < 2$). Model-averaged dispersal distance was shorter, on average, for older males than for younger males and on the high- than on the middle-elevation plot (Table 3).

Study plot, a surrogate for coarse-scale habitat structure and quality in our system (Table 1 and Fig. 1), was the most important predictor of female dispersal distance, but reproductive success also received statistical support (Table 4). An additive model including the effects of plot and reproductive success was the second-ranked model and within two ΔAIC_c units of the top model, which suggests that reproductive success was an uninformative parameter in the second-ranked model (see Burnham and Anderson 2002, Arnold 2010). However, the confidence interval surrounding the reproductive-success parameter estimate did not include zero, so its inclusion was justified in the model set. Model-averaged dispersal distances for females were shorter on the high-elevation plot (Table 3). Additionally, model-averaged dispersal distances for females that fledged more offspring were shorter than distances of females that fledged fewer offspring (Fig. 3).

Consequences of dispersal.—The reproductive consequences of breeding dispersal differed between sexes, but not in the direction we predicted. Males that dispersed shorter distances between years y and $y + 1$ were more likely to have higher reproductive success in year $y + 1$ (β estimate = -1.17 ± 0.55 , 95% confidence interval [CI]: -0.09 to -2.25 ; Fig. 4). Female breeding dispersal distance was not strongly associated with Δ fledged (β estimate = -0.31 ± 0.52 , 95% CI: 0.71 to -1.32).

DISCUSSION

Sex shaped breeding dispersal patterns in Black-throated Blue Warblers, a result consistent with other avian studies (reviewed by Greenwood 1980, Clarke et al. 1997). Female Black-throated Blue Warblers dispersed longer distances than males, and our results

TABLE 2. Model selection results for breeding dispersal distance of male Black-throated Blue Warblers during 1998–2008: model structure, estimated number of parameters (K), difference in adjusted Akaike's information criterion of the current and best model (ΔAIC_c), AIC weight (w_i), and model deviance. Models are ordered according to ΔAIC_c score, with the best-fit model first. Only models with $\Delta AIC_c < 10$ are shown. Predictor variables used in model construction were age class (second-year or after-second-year), plot (middle or high elevation), leaves (territory leaf density), and offspring (number of offspring fledged in the year before dispersal). Model notation: + = additive effect, * = interactive effect.

Model	K	ΔAIC_c	w_i	Deviance
Age + plot	6	0.00	0.55	234.98
Age	5	1.13	0.31	230.48
Age * plot	7	3.32	0.11	241.91
Leaves + age	6	7.94	0.01	207.91
Leaves + age + plot	7	8.04	0.01	235.14
Age + offspring + plot	7	9.43	0.00	212.62

TABLE 3. Model-averaged parameter estimates (\pm SE [unconditional]), and 85% confidence intervals (CI) of \log_{10} breeding dispersal distances (year y to $y + 1$) for Black-throated Blue Warblers at Hubbard Brook Experimental Forest, New Hampshire. Younger males dispersed farther than older males; females that fledged fewer offspring dispersed longer distances than those that fledged more offspring; and both males and females dispersed longer distances on the middle-elevation plot than on the high-elevation plot.

Sex	Parameter	Estimate	85% CI
Male	Age	0.27 ± 0.05	0.20 to 0.33
	Plot	0.14 ± 0.05	0.06 to 0.21
Female	Offspring	-0.05 ± 0.02	-0.07 to -0.02
	Plot	0.26 ± 0.07	0.16 to 0.37

indicate that the effects of experience on dispersal distance varied by sex. Age was important in explaining male dispersal distance, with younger males moving longer distances than older males. By contrast, age was not an important correlate of female dispersal distance. Our prediction that prior reproductive success would influence dispersal distance was supported for females only: females that fledged more offspring tended to disperse shorter distances.

Sex-biased dispersal.—Traditional hypotheses explaining sex-biased dispersal within species include competition for resources, competition for mates, and inbreeding avoidance as forces that shape the evolution of dispersal patterns (reviewed by Dobson 2013). Sexual variation in dispersal distance is likely related to a species' mating system, with polygynous mate-defense mating systems favoring male-biased dispersal and socially monogamous mating systems favoring female-biased dispersal (Greenwood 1980). The "resource defense hypothesis" of Greenwood (1980) is most relevant to our study because Black-throated Blue Warblers are socially monogamous and males defend exclusive breeding territories. Our results indicate that breeding dispersal in Black-throated Blue Warblers is indeed female biased.

TABLE 4. Model selection results for breeding dispersal distance of female Black-throated Blue Warblers during 1998–2008: model structure, estimated number of parameters (K), difference in adjusted Akaike's information criterion of the current and best model (ΔAIC_c), AIC weight (w_i), and model deviance. Models are ordered according to ΔAIC_c score, with the best-fit model first. Only models with $\Delta AIC_c < 10$ are shown. Predictor variables used in model construction were age class (second-year or after-second-year), plot (middle or high elevation), leaves (territory leaf density), and offspring (number of offspring fledged the year before dispersal). Model notation: + = additive effect, * = interactive effect.

Model	K	ΔAIC_c	w_i	Deviance
Plot	5	0.00	0.52	154.18
Offspring + plot	6	1.04	0.31	144.51
Age + plot	6	4.37	0.06	151.19
Age + offspring + plot	7	4.49	0.06	157.31
Offspring	5	6.68	0.02	163.81
Null	4	7.52	0.01	166.57
Offspring + age * plot	8	8.70	0.01	160.98
Age * plot	7	8.70	0.01	154.42

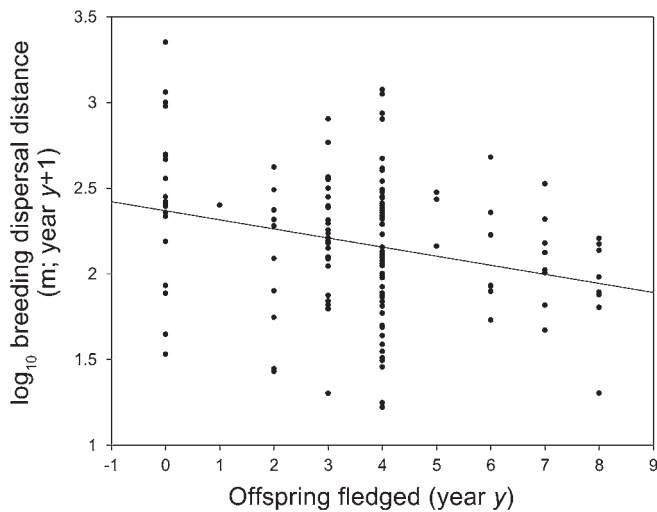


FIG. 3. Dispersal distances of female Black-throated Blue Warblers between years y and $y + 1$ at the Hubbard Brook Experimental Forest, New Hampshire, in relation to the number of young that fledged in year y ($n = 147$ dispersal events).

Unmated males are rare in our system (Holmes et al. 2005), providing more support for the resource defense hypothesis.

Recent hypotheses for sex-biased dispersal focus on the influence of local kin competition and phylogeny (Dobson 2013, Mabry et al. 2013). Black-throated Blue Warbler young hatched on our study sites rarely return to breed at these same sites—natal dispersal generally occurs at a larger scale than breeding dispersal at Hubbard Brook (Holmes et al. 2005). Thus, kin competition

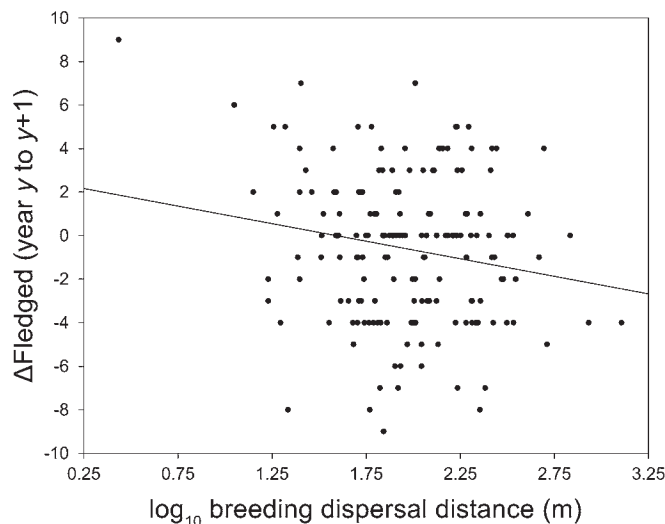


FIG. 4. Change in reproductive success of male Black-throated Blue Warblers between years y and $y + 1$ at the Hubbard Brook Experimental Forest, New Hampshire, in relation to dispersal distance between years; males that fledged relatively more offspring in year $y + 1$ (negative values) dispersed longer distances ($n = 196$ dispersal events). The 95% confidence interval (-0.09 to -2.25) surrounding the β estimate for slope (-1.17) did not include zero.

and inbreeding avoidance are likely mitigated through the process of natal dispersal (e.g., Gandon 1999, Szulkin and Sheldon 2008, Nelson-Flower et al. 2012). We cannot address the importance of phylogeny in shaping the sex-biased dispersal patterns observed in Black-throated Blue Warblers.

Female Black-throated Blue Warblers have higher annual mortality rates and, hence, fewer breeding opportunities than males at Hubbard Brook (Sillett and Holmes 2002). This could increase the relative benefit for females of dispersing away from areas where reproductive success was low. The limited area of our study plots and imperfect detection of returning females could bias inferences about female dispersal patterns, but recapture probability for marked females was relatively high (0.87 ± 0.06 ; Sillett and Holmes 2002). Therefore, our results suggest that the tradeoff between survival and reproduction may more strongly influence the dispersal decisions of female Black-throated Blue Warblers than of males.

Plot-level differences in dispersal.—Habitat quality, measured at the plot scale, was correlated with breeding dispersal distances for both sexes: Black-throated Blue Warblers breeding at our high-elevation plot dispersed shorter distances between years than those breeding at lower elevations. Habitat quality for Black-throated Blue Warblers increases with elevation at Hubbard Brook (Table 1 and Fig. 1), and our results suggest that birds breeding at higher elevations did not have to disperse as far to find suitable territories or mates compared with those breeding at lower elevations. Birds may also have been more likely to return to their territory sites on the high-elevation plot because conspecific reproductive success was high (e.g., Betts et al. 2008), but our study was not designed to determine the relative strengths of habitat versus social cues. Additionally, differences in competition intensity and survival between study plots have the potential to influence population density of Black-throated Blue Warblers and to shape observed patterns in dispersal distances (Waser 1985, Matthysen 2005). Investigating these effects on dispersal was beyond the scope of our study.

Male dispersal patterns.—Study plot and age were the most important factors explaining dispersal distance for males. Males on the middle-elevation plot, with lower deciduous leaf and stem density in the shrub layer (Table 1 and Fig. 1), dispersed greater distances between breeding seasons than males on the high-elevation plot. The abundance of lepidopteran larvae, a main food source for Black-throated Blue Warblers during the breeding season, is greater in areas of high understory leaf density at Hubbard Brook (Rodenhouse et al. 2003). In addition, a dense shrub layer provides other benefits, such as cover from nest predators and nesting substrate (Steele 1993).

Younger Black-throated Blue Warblers generally occupy territories of poor-quality habitat (Holmes et al. 1996). We found that they were more likely to move from these areas and disperse longer distances in subsequent years than older males, a result consistent with studies of other bird species (Forslund and Pärt 1995, Sutherland 1996, Paradis et al. 1998, Clark et al. 2004, Andreu and Barba 2006). Behavioral dominance by ASY males to exclude SY males from high-quality territory sites (Holmes et al. 1996) likely contributed to this pattern.

The lack of a relationship between male dispersal distances and the number of young fledged per territory could be related to

the importance of extrapair offspring to male fitness in this species (Chuang et al. 1999). Webster et al. (2001) found that extrapair fertilizations contribute significantly to the variance in male reproductive success at our study area. For our study, however, offspring resulting from a monitored nest were assigned to the social pair. Thus, we do not have a complete picture of realized male reproductive success. High-shrub-density areas support high population density of Black-throated Blue Warblers (Holmes et al. 1996), and the availability of multiple females in close proximity in these areas may increase the opportunities for males to sire extrapair offspring and, thereby, increase fitness (Webster et al. 2001). The reproductive success of males is most often limited by the number of females with which they can mate (e.g., Bateman 1948). Therefore, returning to territory locations where both shrub and female density are high, regardless of past reproductive success, might be advantageous for male Black-throated Blue Warblers.

Female dispersal patterns.—Female breeding dispersal distance was best explained by plot-level habitat quality (Table 4). Our analyses also indicated an additive effect of plot and number of offspring fledged on female breeding dispersal distance, with females that fledged relatively more young in year y dispersing shorter distances in year $y + 1$. Similar patterns have been documented in other bird species (e.g., Switzer 1997, Haas 1998). Females typically invest more energy per offspring than males (Bateman 1948, Queller 1997), and the number of eggs that females can produce limits the number of offspring they can fledge. Such investments and limitations likely shape female Black-throated Blue Warbler dispersal behavior. Female Black-throated Blue Warblers do not lay eggs in each other's nests (Chuang et al. 1999); thus, they should return to areas where they experienced high reproductive success in the previous breeding season. Our results suggest that after a season of poor reproductive success, female Black-throated Blue Warblers may improve their fitness by dispersing to a site with a higher-quality male or where they have access to extrapair mates.

Reproductive consequences of breeding dispersal.—Males that dispersed shorter distances generally improved their reproductive success in the following breeding season, whereas males that dispersed longer distances generally had poorer reproductive success the next year; no such pattern was found for females. Generally, males that dispersed shorter distances were older individuals that had previously occupied territory sites with relatively high understory leaf density, whereas males that dispersed longer distances tended to be younger birds moving from territory locations with relatively low understory leaf density. This negative correlation between male dispersal distance and Δ fledged might reflect a cost associated with dispersal movement: lack of familiarity with the new territory site (Greenwood and Harvey 1976, Pärt 1995). However, we did not account for extrapair young in our estimates of annual fecundity of males.

Our results for females did not support the hypothesis that dispersal would be correlated with greater reproductive output in future breeding attempts, as has been found for some other species (Newton 2001, Calabuig et al. 2008, García-Navas and Sanz 2011, Gutiérrez et al. 2011). However, numerous studies have concluded that dispersal is unrelated to subsequent reproductive

success (e.g., Danchin and Cam 2002, Shutler and Clark 2003, Schaub and von Hirschheydt 2009). The difficulty in determining the adaptive significance of dispersal has led to a general conclusion that the fitness consequences of dispersal are poorly understood (Öst et al. 2011). In our study, a potential explanation for the lack of a relationship between dispersal and reproductive success is that lower survival and longer-distance dispersal in females reduced our power to detect a statistically significant relationship between dispersal distance and fecundity. Alternatively, dispersal by female Black-throated Blue Warblers may be more closely associated with acquiring a higher-quality mate (Daniels and Walters 2000, Green et al. 2004) or territory (Bollinger and Gavin 1989, García-Navas and Sanz 2011) than with number of young fledged. Ongoing research at Hubbard Brook is investigating these hypotheses.

The broader context of our research.—Our results are similar to those of previous studies of adult dispersal in the Parulidae (Table 5). Investigations of within-year breeding dispersal (Jackson et al. 1989, Howlett and Stutchbury 1997) found that these movements were influenced by both predators and reproductive success, factors that were directly or indirectly related to between-year dispersal in the Black-throated Blue Warbler. Site-fidelity studies (Nolan 1978, Hoover 2003, Howlett and Stutchbury 2003) examined the propensity of birds to return to previously occupied breeding locations and, like our study, found that male Black-throated Blue Warblers were generally more site-faithful than females. Studies that indirectly inferred dispersal distances from feather isotope ratios (Hobson et al. 2004), age-ratios (Rohwer 2004), or genetics (Veit et al. 2005) revealed that some individuals can disperse hundreds or even thousands of kilometers, but those studies were not designed to examine how reproductive and fine-scale habitat variables influenced dispersal. Nolan (1978) directly measured the breeding dispersal of 14 female Prairie Warblers and documented a positive correlation between reproductive success in year y and return rate in year $y + 1$, a result that parallels our findings in female Black-throated Blue Warblers. Similarly, Bernard et al. (2011) concluded that prior reproductive success in male Ovenbirds did not affect male dispersal (Table 5).

Adult dispersal patterns of Black-throated Blue Warblers were consistent with those found in other avian families (e.g., Payne and Payne 1993, Pasinelli et al. 2007, Schaub and von Hirschheydt 2009, García-Navas and Sanz 2011, Botsch et al. 2012): females generally dispersed longer distances than males; individuals that did not successfully reproduce tended to disperse farther between years; and birds occupying poor-quality habitat dispersed longer distances. Avian dispersal can also be influenced by conspecific densities (Matthysen 2005, Molina-Morales et al. 2012) and reproductive success of neighbors (Boulinier et al. 2008, Redmond et al. 2009). Although eggs of brood parasites have never been recorded in nests of Black-throated Blue Warblers at Hubbard Brook (Holmes et al. 2005), brood parasitism can influence avian dispersal (Clobert et al. 2001). We found that dispersal distances were shortest on the high-elevation plot, where Black-throated Blue Warbler densities and reproductive success are highest (Rodenhouse et al. 2003), although we cannot discount the influence of high-quality habitat at this site.

TABLE 5. A summary of dispersal-related research in adult Parulidae. Scientific names and taxonomic order follow the American Ornithologists' Union (1998) and supplements. NA refers to not applicable because no data were provided in the reference.

Species	Investigators	Method for investigating dispersal	Factors influencing dispersal
Ovenbird (<i>Seiurus aurocapilla</i>)	Hobson et al. 2004 Bernard et al. 2011	Inference from isotope signatures Direct measurement of between-season movement	NA Age and prior reproductive success did not affect dispersal
Prothonotary Warbler (<i>Protonotaria citrea</i>)	Hoover 2003	Site fidelity	Prior reproductive success and sex
Hooded Warbler (<i>Setophaga citrina</i>)	Howlett and Stutchbury 1997 Howlett and Stutchbury 2003	Direct measurement of within-season movement Site fidelity	Predators and reproductive success Sex
American Redstart (<i>S. ruticilla</i>)	Hobson et al. 2004	Inference from isotope signatures	NA
Cerulean Warbler (<i>S. cerulea</i>)	Veit et al. 2005	Inference from genetic samples	NA
Yellow Warbler (<i>S. petechia</i>)	Cilimburg et al. 2002	Direct measurement of between-season movement	Sex and year
Prairie Warbler (<i>S. discolor</i>)	Nolan 1978 Jackson et al. 1989	Site fidelity and direct measurement of between-season movement Direct measurement of within-season movement	Prior reproductive success and sex Predators
Townsend's Warbler (<i>S. townsendi</i>)	Rohwer 2004	Inference from age ratios	NA
Hermit Warbler (<i>S. occidentalis</i>)	Rohwer 2004	Inference from age ratios	NA
Golden-cheeked Warbler (<i>S. chrysoparia</i>)	Jetté et al. 1998	Direct measurement of between season movement	Sex

Directions for future research.—We know that avian dispersal is shaped by both individual characteristics and environmental effects (Clobert et al. 2012), yet many gaps remain in our understanding of the causes and adaptive nature of breeding dispersal. Future studies that examine how individual condition and behavior drive breeding dispersal patterns would be especially valuable. For migratory species, we also know little about how events during migration and on winter quarters affect whether an individual remains site faithful or disperses. Finally, we need additional studies of how conspecific social information and pair bonds influence movement decisions. Continued research on avian breeding dispersal will add to our knowledge about the factors that determine immigration and emigration rates and, hence, the dynamics of populations.

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