

GEOGRAPHIC CLINES OF AGE RATIOS OF BLACK-THROATED BLUE WARBLERS (*DENDROICA CAERULESCENS*)

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Abstract. I investigated the age structure of breeding populations of Black-throated Blue Warblers (*Dendroica caerulescens*) in eastern North America. The proportion of yearling males increases as relative abundance decreases toward the margins of the breeding range. Geographic clines in age structure are hypothesized to correlate with gradients in habitat quality radiating from the Appalachian Mountains, the probable axis of source populations. Data from the southern Appalachians suggest that despotism of older males may impose a ceiling on the proportion of yearlings in saturated high-quality habitats, regardless of local productivity. Populations that exhibit low variance in yearling recruitment and high population densities may fall toward the “source” end of the “source–sink” continuum, and vice versa. It is hypothesized that the regional distribution of source and sink populations of the Black-throated Blue Warbler might closely mirror the prevalence of successful multiple brooding.

Key words: age ratio; Appalachian Mountains; Black-throated Blue Warbler; *Dendroica caerulescens*; despotism; dispersal; geographic clines; multiple brooding; source–sink dynamics.

INTRODUCTION

Long-term studies of avian populations have yielded significant insights as to why species thrive in some locations but not in others, or disperse from one habitat patch to the next (e.g., Kluijver 1951). Extrapolation of findings from local to continental scales has been less successful (see Wiens 1981, 1989). The advent of continent-wide breeding bird censuses (e.g., Robbins et al. 1986) has encouraged large-scale mapping (Price et al. 1995) and analyses (e.g., Bystrak 1981, Hengeveld and Haeck 1982, Brown 1984, Maurer and Brown 1989, Maurer 1994, Brown et al. 1995, Villard and Maurer 1996) that have verified and amplified biogeographic hypotheses in circulation since early in this century (e.g., Grinnell 1917). These studies have revealed that significant density gradients occur within the breeding ranges of avian species. Continental species are relatively abundant only in a few locations within their geographic ranges, and peaks of abundance frequently occur near the centers of geographic ranges, implying that ecological conditions are less favorable near range margins where population densities approach zero.

Abundance gradients ultimately reflect habitat selection on a local and regional scale. Many data suggest that habitat selection in birds is influenced by intraspecific density (e.g., Mayr 1926, Kluijver 1951,

Brown 1969, Orians 1969, Fretwell and Lucas 1970, Krebs 1971, Newton 1992). For avian species with despotic habitat selection, yearlings are often forced to settle in less favorable habitat (see Sutherland and Parker 1985, Parker and Sutherland 1986). Intrinsic natal dispersal, in combination with density-dependent territoriality, may cause young or inexperienced individuals to accumulate in low-quality “sink” habitats (see Lidicker 1975, Van Horne 1983). Clines in age structure may thus occur along spatial gradients that reflect habitat quality. Although a number of studies have demonstrated despotic distributions within local populations (e.g., Goss-Custard et al. 1982), age-structured habitat selection at large spatial scales has not been well established, primarily because the pertinent demographic data (e.g., unbiased population samples) are nearly impossible to obtain. Consequently, we still do not know whether despotic and ideal free processes of habitat selection observed in local populations (Sutherland and Parker 1985, Parker and Sutherland 1986) can result in geographic clines in age structure on a continental scale. Geographic clines in age structure, should they occur, would have important applied and theoretical consequences for the conservation and management of populations.

I offer evidence that geographic clines in age structure are present among breeding populations of a small migratory passerine, the Black-throated Blue Warbler, *Dendroica caerulescens*, in eastern North America. Analysis of geographically dispersed population samples is used to estimate the relationship between age structure, relative abundance, and the geographic position of populations within the breeding range.

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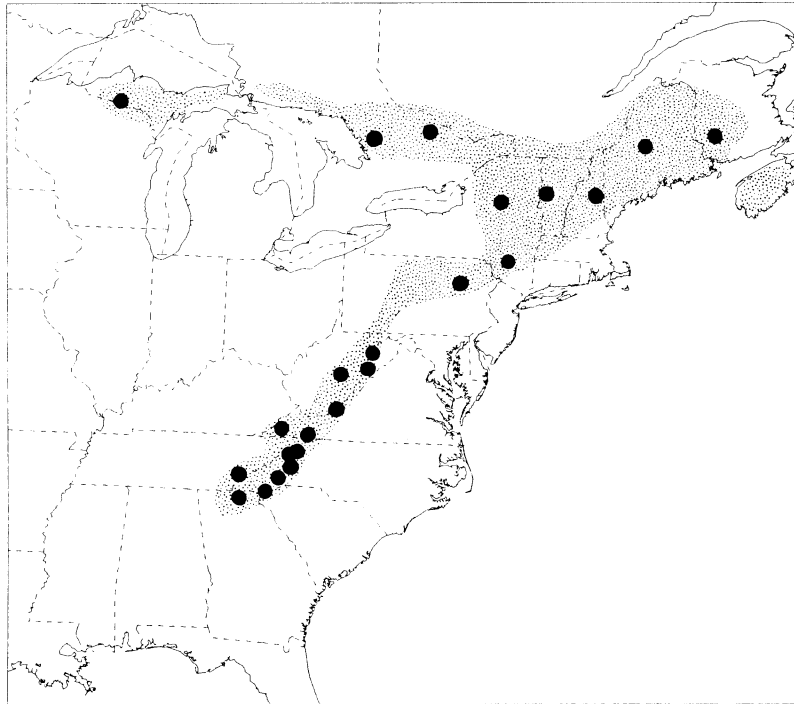


FIG. 1. Distribution of collecting sites (see Table 1) within the core breeding range (stippled) of the Black-throated Blue Warbler (*Dendroica caerulescens*) in eastern North America. Hatched lines represent state and provincial boundaries.

METHODS

The focal species

Black-throated Blue Warblers (Fringillidae, Tribe Parulini; taxonomy of Sibley and Monroe 1990) breed in cool deciduous and mixed deciduous–coniferous forests in eastern North America, and winter in the Caribbean basin (Holmes 1994, Price et al. 1995; Fig. 1). Males returning from their wintering grounds establish territories in mixed deciduous–coniferous or deciduous forests as early as the last week of April at the southern terminus of their breeding range in Georgia, and by the last week of May near the northern margins of the range in Michigan, south-central Ontario, and the Maritime Provinces of Canada (Fig. 1). Older males precede yearling males and females in spring migration by a few days to a week or more (Hubbard 1965, Holmes 1994). Detailed information on the breeding ecology of the species can be found in Holmes et al. (1992, 1996), Rodenhouse and Holmes (1992), and Holmes (1994).

The distribution and abundance of breeding Black-throated Blue Warblers (especially south of 43° N) are strongly influenced by elevation. In the southern Appalachian Mountains where it is one of the most abundant breeding birds (Wilcove 1988), most males establish territories above 750 m (above sea level). The elevational width of the breeding zone varies from 300 to 500 m on spurs and outliers of the southern Appalachians, to >1000 m in the Great Smoky and Black

mountains (35–36° N) of Tennessee and North Carolina.

Population samples

Population samples of breeding males were collected over the course of eight field seasons (1986–1994). The research protocol required discrete population samples, meaning that sampling was limited to areas within the breeding range where Black-throated Blue Warblers were fairly common to abundant, and where a quota of territorial males could be collected quickly in a circumscribed area without significantly diminishing local populations. Dozens of locations near the northern and western margins of the warbler's breeding range were censused and rejected as potential collecting sites (e.g., Minnesota, Ontario, Nova Scotia) because population density was too low. Population samples were obtained from the smallest area possible in large tracts of forest on public lands, usually along trails or old logging roads. Fragmented forest plots were avoided, as were sites near human habitation or agriculture. In the Appalachians, sampling was conducted well above the species' lower elevational limit. Sampling was opportunistic, in that males were collected as they were encountered. No attempt was made to age specimens in the field. Observation of males was necessarily brief, and I could not rule out the possibility that some were nonterritorial or that yearlings were more vocal than older males. However, because the collecting protocol was consistent at all of the collecting sites (i.e., all

TABLE 1. Population samples of male Black-throated Blue Warblers (*Dendroica caerulescens*) collected at breeding localities.

State or province	Date	Locality coordinates†		Yearling	Older male	Relative abundance‡
1) Georgia	10–12 June 1989	34.75	84.03	6	14	3.64
2) South Carolina	5–8 June 1989	35.00	83.10	6	12	2.57
3) North Carolina	17–18 June 1989	35.38	82.67	8	17	3.85
4) Tennessee	13–15 June 1989	35.45	84.08	6	11	5.67
5) North Carolina	25–27 June 1989	35.71	82.18	4	16	5.00
6) Tennessee	19–20 June 1989	36.13	82.33	5	15	2.08
7) Tennessee	22–23 June 1989	36.20	82.13	3	12	5.00
8) Virginia	9–10 June 1988	36.72	81.58	3	16	2.53
9) Virginia	11–12 June 1988	36.88	82.58	4	10	5.80
10) Virginia	12–13 June 1988	37.46	80.52	6	14	2.50
11) West Virginia	6–7 July 1986	38.31	80.50	3	18	2.53
	21 June 1988					
12) West Virginia	19 June 1988	38.68	79.52	8	10	4.00
13) West Virginia	24–25 June 1988	39.13	79.30	6	14	4.30
	12–13 June 1993	9	16	4.30
14) Pennsylvania	9–11 June 1994	41.20	76.23	12	20	2.28
15) New York	18–20 June 1992	41.92	74.50	11	14	1.28
16) New York	23–25 June 1992	43.70	74.72	14	11	2.45
17) Vermont	21–22 June 1992	43.98	73.00	16	9	2.78
18) New Hampshire	27–28 June 1991	44.00	71.32	8	17	3.96
19) Ontario	22–24 June 1990	45.37	79.58	14	21	0.88
20) Maine	23–25 June 1991	45.48	69.52	15	7	0.96
21) Ontario	25–29 June 1990	45.67	77.50	20	20	1.68
22) New Brunswick	14–17 June 1991	45.83	67.00	11	13	0.74
23) Michigan	12–16 June 1990	46.17	88.92	9	11	1.04

† Coordinates, presented as north latitude . . . west longitude, have been converted to decimals for computational purposes.

‡ Total number of specimens collected in a locality divided by the greatest distance between collecting sites *within* a locality (males per kilometer).

observation and collecting was performed by the author), geographical bias owing to differential detectability of yearlings and older males was minimized.

The low elevation of the central Appalachians (seldom >800 m) greatly restricts the breeding distribution of Black-throated Blue Warblers from western Maryland north to the South Branch of the Susquehanna River in north-central Pennsylvania (see Brauning 1992). Most males that occur in this region settle between 500 m and the edge of the plateau (600–800 m) in a narrow elevational zone along the Allegheny front. The elevational zone of breeding populations is thus substantially narrower, and some 150 to 250 m lower in this region than in the southern Appalachians. Populations north of Pennsylvania are more widely and continuously distributed, and warblers may breed near sea level in Maine, Nova Scotia, and New Brunswick (e.g., Erskine 1992).

Age-related plumage characteristics

Two age classes of male Black-throated Blue Warblers can be distinguished by plumage characters in breeding specimens (see Dwight 1900, Holmes 1994, Graves, *in press*): (1) yearlings (first alternate plumage, SY in banding terminology) in their first potential breeding season, and (2) older individuals (definitive alternate plumage, ASY in banding terminology) in their second or later breeding season. The definitive alternate plumage of older males is completed on the

wintering ground after the first potential breeding season. Age-related plumage differences are subtle, and unlikely to result in collecting bias. Neither females nor fledglings were collected. To ensure that neither migrating nor wandering postbreeding birds were collected, I sampled and censused populations during the peak of breeding season, 5 June–7 July (obtaining all but one sample before 30 June).

The brief breeding season and the large size of the breeding range (2000 km from east to west and north to south) precluded a geographically stratified sampling design each year. Instead, I collected population samples within a limited region each field season, beginning in the central Appalachians in the first year, and in subsequent years collecting to the south, northwest, northeast, north-central, etc., until all regions of the breeding range had been sampled. Replicate samples at Locality 13 (Table 1) were obtained 5 yr apart.

Relative abundance

Geographic variation in relative abundance among sampled populations cannot be reliably extrapolated from Breeding Bird Survey (BBS) census data because the Appalachians are insufficiently sampled by BBS routes. Several of my population samples were collected in areas that exhibit near-zero BBS density estimates (see Holmes 1994, Price et al. 1995). I estimated the relative abundance of local populations as the total number of specimens collected in a locality

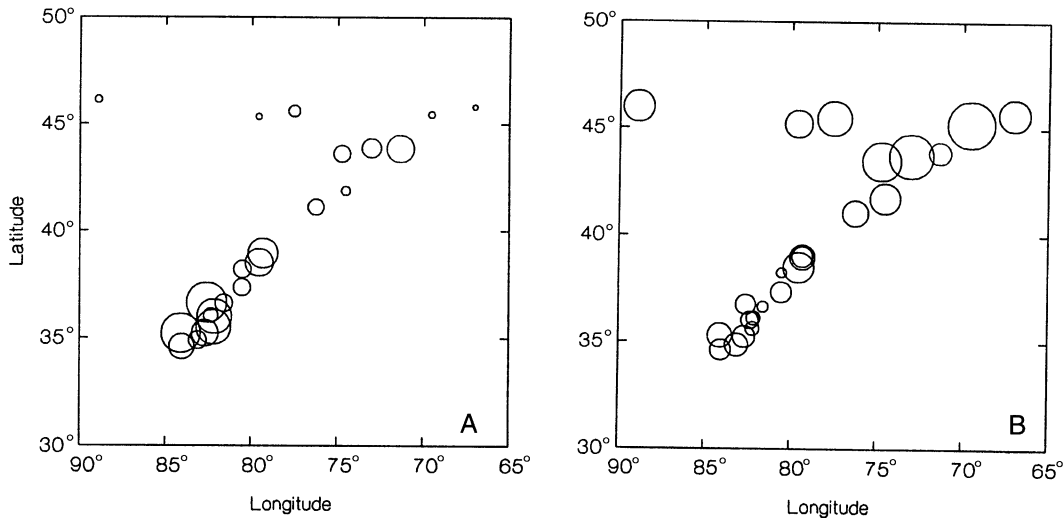


FIG. 2. Relative abundance (A) and percentage of yearling males (B) in breeding population samples of Black-throated Blue Warblers in eastern North America (see Table 1, Fig 1). Diameter of locality circles is proportional to the relative abundance (A) and the percentage of yearlings (B).

divided by the greatest distance between collecting sites *within* the sampling locality (males per kilometer) (Table 1). When relative abundance was high, the sampling quota was quickly obtained over a relatively short distance, and vice versa.

Data analysis

The relationship between yearling percentage, relative abundance, and latitude (for population samples) was examined with Spearman rank correlation coefficients (R_s , two-tailed). The effects of collection year on age structure (arcsine transformed percentage of yearlings) were examined with one-way analysis of

variance (ANOVA). To clarify the spatial and temporal correlates of age structure, I used a regression model that incorporated the percentage of yearling males as the dependent variable, and "year" (categorical) and latitude as independent variables. Chi-square tests of independence were performed on 2×2 contingency tables to test for differences between population samples in the proportion of yearlings and older males. All statistical tests were performed on SYSTAT (Wilkinson 1989).

RESULTS

Relative abundance exhibited a sevenfold difference across the breeding range (Table 1), and was negatively correlated with latitude ($R_s = -0.62$, $P < 0.005$) (Fig. 2). The highest relative abundance of Black-throated Blue Warblers was recorded in the Appalachian Mountains, especially south of 40° N. The percentage of yearling males in population samples was positively correlated with latitude ($R_s = 0.70$, $P < 0.001$; Fig. 2) and negatively correlated with relative abundance ($R_s = -0.51$, $P < 0.02$; Fig. 3). The proportion of yearling male Black-throated Blue Warblers in population samples appears to increase clinally from the Appalachian axis (from Georgia to New Hampshire) outward to the northern and northwestern margins of the species' breeding range. Moreover, the percentage of yearlings was inversely proportional to local relative abundance.

The estimated proportions of yearling males in populations exhibited considerable variation among years (annual averages: 1988, 27%; 1989, 28%; 1990, 45%; 1991, 48%; 1992, 55%; 1993, 36%; 1994, 38%; see Table 1). Year effects were significant (ANOVA, $F_{6,17}$, $P = 0.009$), but much of the variation can be explained by latitude and constraints of the sampling protocol.

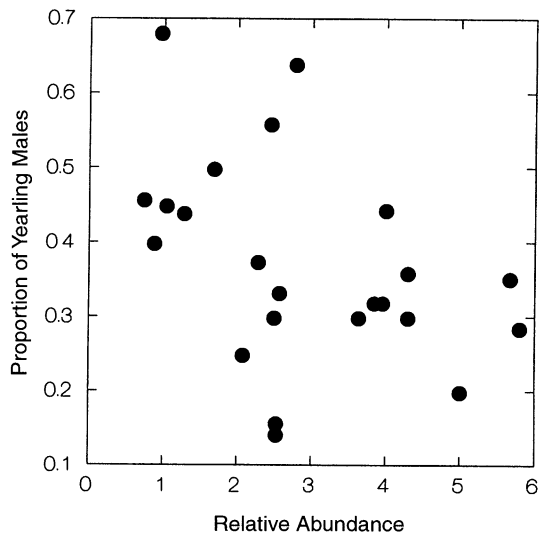


FIG. 3. Bivariate relationship of relative abundance and proportion of yearling males in population samples of Black-throated Blue Warblers.

TABLE 2. Effects of latitude and year on the percentage of yearling males in population samples of Black-throated Blue Warblers (see Table 1).

Source	df	ss	MS	F ratio	P
Latitude	1	0.035	0.035	3.016	0.102
Year†	6	0.080	0.013	1.151	0.379
Error	16	0.186	0.012		

† Entered as a categorical variable.

Sampling localities spanned 11.4° of latitude, but the latitudinal span of population samples within years varied from 0.0° (single localities in 1993 and 1994) to 2.4° (1988). When year and latitude were entered into a multiple regression model, year effects were nonsignificant, whereas latitude explained a larger fraction of the continent-wide variation in age ratios (Table 2).

The relationship between age structure and latitude is clearer when the population samples are partitioned into northern (>40° N) and southern (<40° N) groups. The percentage of yearling males in the northern group (collected 1990, 1991, 1992, and 1994) averaged 47.6%, vs. 28.3% for the southern group (collected in 1988, 1989, and 1993). This difference was significant ($\chi^2 = 21.6$, $df = 1$, $P < 0.001$). The percentage of yearlings in population samples was uncorrelated with the date of collection (median day of year; $R_s = 0.11$, $n = 24$, $P > 0.50$). The percentages of yearling males from population samples taken 5 yr apart at the same site (Table 1, Locality 13) in West Virginia were not significantly different ($\chi^2 = 0.06$, $df = 1$, $P = 0.81$).

DISCUSSION

Large-scale spatial variation in age structure of breeding bird populations has not been studied intensively (see Snow 1956, Greenberg 1980). Rohwer et al. (1980) examined the age structure of breeding American Redstarts (*Setophaga ruticilla*) represented in museum collections, and interpreted the significant difference in the proportion of yearlings collected east and west of the Great Plains as the result of a regional shift in molting chronology. Rohwer et al. (1983) later rejected this hypothesis, and Sherry and Holmes (1991) pointed out that a fixed age ratio was illusory unless replicated over large areas and long time periods. Nevertheless, geographic variation in age differences observed in American Redstarts warrants additional scrutiny.

The specimens examined by Snow (1956), Greenberg (1980), and Rohwer et al. (1980) were collected over a period of many decades, by many field collectors, and may have been systematically biased by factors unknown to the investigators. In the present study, many of the potential biases exhibited in the accumulated series of specimens in museums have been minimized or eliminated because of the standardized sampling protocol.

Hypotheses

I considered four partially overlapping hypotheses that may account for the higher proportion of yearlings in peripheral populations: (1) males in peripheral regions of the breeding range suffer greater mortality, (2) peripheral populations exhibit higher productivity and local recruitment of yearlings, (3) observed differences are caused by sampling methods, and (4) peripheral areas of the breeding range have a higher proportion of lower quality breeding sites that operate as population sinks for dispersing yearlings from source populations along the Appalachian axis.

The first hypothesis does not seem likely as the principal cause of age and abundance clines in male Black-throated Blue Warblers. Assuming that habitat near the northern and western margins of the breeding range is relatively poor, males that settle there may suffer higher mortality than males in the Appalachians, although survivorship data are lacking. However, the higher proportion of yearlings in peripheral populations would not be predicted under the differential mortality hypothesis, because mortality would presumably accrue to locally produced fledglings (hatching year, HY in banding terminology) as well as to breeding males. In fact, annual survivorship of adult passerines is significantly higher than that of hatching-year birds.

The second hypothesis is that the abundance of yearlings in local populations reflects the recruitment of young birds hatched at those locations the previous year (Nolan 1978, Sherry and Holmes 1991, 1992, Holmes et al. 1992). If yearling recruitment is directly linked to local productivity, the fledging rate in geographically peripheral areas (e.g., Michigan, Ontario, Maine, New Brunswick) must be relatively high compared to populations from the Appalachian axis. However, if productivity is elevated in peripheral areas, why is relative abundance so low? This hypothesis would require the unlikely scenario that peripheral populations (but not core populations) were sampled during periods of rapid population growth, yielding an excess of yearlings. However, survivorship and productivity data for the sampled populations are unavailable.

A third possibility is that the observed clines in age structure are an artifact of regional variation in the relative abundance and elevational distribution of the Black-throated Blue Warbler, and the effect of this variation on sampling protocol. As mentioned earlier, sampling of populations in the Appalachians (as elsewhere) was conducted where relative abundance of breeding populations was high enough to permit sampling. I avoided collecting in peripheral habitats where abundance was low, especially near the elevational boundaries of local breeding populations, where yearlings may be more common. If older males tend to aggregate near the center of the warbler's elevational distribution, yearlings will be underrepresented in population samples restricted to the warbler's optimal elevational

zone. However, significant correlations with latitude (percentage of yearlings, $R_s = 0.53$, $P < 0.03$) persist when analyses are limited to Appalachian localities (Table 1, Localities 1–18). In other words, although it is possible that sampling bias accounts for some of the regional differences in age ratios, there is little evidence that the nearly 20% difference in yearling percentages between southern and northern populations can be explained by regional collecting bias (see *Methods*).

A fourth hypothesis is that the higher proportion of yearlings in peripheral areas (presumably in poorer quality habitat) is due to emigration from highly productive areas along the Appalachian axis. This hypothesis is related to “source–sink” theory (e.g., Wiens and Rotenberry 1981, Van Horne 1983, Pulliam 1988, Howe et al. 1991, Pulliam and Danielson 1991, Robinson 1992, Donovan et al. 1995, Brawn and Robinson 1996). “Source” populations are usually defined as those that exhibit no net change in size over several generations, and are net exporters of individuals to other populations. Conversely, “sink” populations are net importers of individuals.

The genesis of habitat segregation on a local scale (e.g., elevational transects) begins in spring when older, socially dominant males arrive early and preempt the most desirable habitat (see Brown 1969, Fretwell and Lucas 1970, Holmes 1994, Holmes et al. 1996). Yearling males establish territories where they can, in the interstices of high-quality habitat and in less optimal patches. I hypothesize that the age-related habitat segregation observed in local habitats (e.g., Holmes et al. 1996; G. R. Graves, *unpublished data*) corresponds to a source–sink spectrum that may be extrapolated to the entire breeding range of the species. Under this interpretation, source populations are distributed primarily along the higher Appalachians, whereas the northern and western frontiers of the breeding range function as population sinks in some or most years.

Although direct evidence of long-distance dispersal in Black-throated Blue Warblers has not been obtained, data from other migratory passerines suggest that natal dispersal is leptokurtic, and that a small fraction of yearlings may settle hundreds of kilometers from their natal site (for references see Pitelka 1974, Greenwood and Harvey 1982, Moore and Dolbeer 1989, Payne 1991). Holmes (1994) reported that only 1 of 800+ nestling Black-throated Blue Warblers banded on the 70-ha Hubbard Brook study site was resighted in subsequent years (a female that nested 2.5 km from her natal site).

The spatial distribution of suitable breeding habitat and the dispersion probability field (Hengeveld 1989) of natal dispersal (from natal area to the site of first reproduction) varies substantially in different parts of the Black-throated Blue Warbler's breeding range. Birds returning to their natal regions or territories in the Appalachians ($<40^\circ$ N) are constrained by elevation

to a corridor of habitat many times longer in one dimension than the other (see Graves 1988). For example, the 700-m contour interval outlines the potential array of settlement sites at the southern terminus of the species' breeding range. If successful long-distance dispersal occurs, vectors must be predominately aligned northeastward. Potential natal dispersal of Black-throated Blue Warblers from northern breeding sites ($43^\circ30'–47^\circ$ N) is more rotationally symmetric, meaning that birds may disperse in any direction and find breeding habitat. The radii of symmetric dispersion fields in much of New England, for example, may be as large as several hundred kilometers.

The relatively uniform percentage of yearlings in population samples from the southern Appalachians suggests a compensatory relationship between the proportion of yearlings and older males in high-quality, saturated habitats. In essence, there may be a ceiling on the number of yearlings recruited into saturated, high-quality habitats, regardless of local productivity. As long as the pool of males is sufficiently large in adjacent suboptimal habitats, annual fluctuations in productivity in optimal habitats may well be masked by immigration (see Wilcove and Terborgh 1984)—i.e., the proportion of yearlings in saturated habitats may decline after poor reproductive years, but may never rise above the ceiling dictated by mortality of older males, even after a season of superior productivity. This situation may arise frequently along steep elevational gradients, where yearlings that settle in peripheral, low-quality territories in one year emigrate to adjacent high-quality habitat (as older males) in a subsequent year. In some instances, most regional reproduction could occur in areas that exhibit low yearling recruitment. Rather than reflecting fluctuations in local productivity, as suggested by Holmes et al. (1992), variance in annual recruitment of yearlings may serve to distinguish source from sink populations (see Winker et al. 1995). Those that exhibit low variance in yearling recruitment and high population densities might be considered to fall toward the source end of the source–sink continuum, and vice versa.

In conclusion, settlement patterns of yearlings and older males in local habitats are likely to result from social dominance and the preemption of high-quality habitat by older males, although this remains to be tested. The question of geographic clines in age structure is more difficult to address with the available correlative data. Subtle changes in sampling procedure associated with elevation may result in minor variation in observed age ratios, but as I have suggested, the bulk of the regional variance may be caused by the dispersal of yearlings from source populations (high relative abundance) along the Appalachian axis to peripheral sink populations (low relative abundance). In any event, the demography of Appalachian and peripheral populations seems to be significantly different.

Multiple brooding and source-sink dynamics

Holmes et al. (1992) concluded that multiple brooding in the Black-throated Blue Warbler accounted for most of the annual variation of young fledged per female. An average of 48% of females at Hubbard Brook initiated second clutches after successfully fledging a first brood. Successful multiple brooding coincided with warm, dry springs, low levels of predation, and an abundance of caterpillars (Holmes et al. 1992, Rodenhouse and Holmes 1992). Egg-laying was delayed by cool, wet weather. Late frosts affected leafing phenology and the appearance of phytophagous insects eaten by warblers. The percentage of clutches in which one or more young died of starvation was negatively correlated with caterpillar abundance and biomass. Growth rates and body masses of nestlings were negatively correlated with precipitation, and positively correlated with daily minimum temperature.

The Hubbard Brook data suggest that the reproductive potential of Black-throated Blue Warblers is linked to the length of the growing season (the period without killing frost). Based on data presented by Holmes et al. (1992), Holmes (1994), and Nolan (1978), I estimated the nesting cycle of the Black-throated Blue Warbler (initiation of nest building to independence of young) to be a minimum of 53 d. Key in this calculation was Nolan's (1978) conclusion that fledgling Prairie Warblers (*Dendroica discolor*) <33 d old (from hatching day) could not survive without parental assistance. This suggests that successful double brooding in the Black-throated Blue Warbler may not be possible in regions with growing seasons of less than ~95–100 d, allowing a week of overlap between first and second broods.

Temperature gradients within the breeding range of the Black-throated Blue Warbler are correlated with latitude, elevation, and proximity to bodies of water, especially the Atlantic Ocean and Great Lakes. For example, the mean frost-free period at Hanover, New Hampshire, on the Connecticut River is 135 d (17 May–30 September), 118 d (24 May–19 September) at Woodstock on the Pemigewasset River some 60 km northeast of Hanover, and only 39 d (8 July–17 August) on Mount Washington, the highest peak in the White Mountains (Koss et al. 1988). In regions near the 100-d growing season isotherm, any nesting failure that occurs >2 wk after the first eggs are laid automatically halves the potential annual reproductive output of a female. These data suggest that on a continental scale, a rapid transition in per capita productivity may occur near the 100-d isotherm, and that the location of source and sink populations of the Black-throated Blue Warbler might correlate with the regional distribution of successful multiple-brooding.

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