

# Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics

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## Summary

1. The distribution of individuals among habitats and their relative success in those habitats can have important consequences for population dynamics. To examine these processes for a long-distance migratory bird species, we studied the population structure, age-specific reproductive output, and local survival of black-throated blue warblers (*Dendroica caerulescens*, Gmelin) in two breeding habitats differing in shrub density within northern hardwoods forests in New Hampshire, USA.

2. On forest plots with dense shrubs, warblers occurred at higher densities, and fledged significantly more young per capita per season than those occupying areas with lower shrub density. This differential productivity was due to higher reproductive output, mainly through double-brooding, of older ( $\geq 2$  years of age) individuals, which were disproportionately more abundant in high shrub density sites.

3. Clutch initiation dates, clutch sizes, and predation rates at individual nests did not differ significantly between habitats. Mean body mass of nestlings on day 6 following hatching were higher on average on plots with high shrub density, but differences were not significant.

4. Annual return rates, as indices of local survival, did not differ between habitats for older males or for females. Yearling males, however, returned in subsequent years at a significantly lower rate to low shrub density plots, a result of either lower survival or, more likely, dispersal to more suitable habitat in their second year of breeding.

5. Parental age and habitat suitability interact in that older individuals, through their experience and/or dominance, acquire sites of higher quality, which results in higher reproductive output and probably higher survival. These differences between habitats in density, reproductive performance and local survival are consistent with an ideal-despotic/preemptive distribution of individuals, and suggest that this population could be regulated by the availability, distribution, and extent of high and low quality breeding habitats.

*Key-words:* avian reproductive success, habitat quality, ideal-despotic distribution, neotropical migrant songbirds, source-sink dynamics.

*Journal of Animal Ecology* (1996), **65**, 183–195

## Introduction

The distribution of individuals among habitats and their reproductive output and survivorship in those habitats are crucial for understanding population dynamics and regulation (Brown 1969; Bernstein, Krebs & Kacelnik 1991; Bowers 1994). Fretwell & Lucas (1970; Fretwell 1972) proposed models of com-

petition-based, 'ideal' distributions of animals among habitats. 'Ideal-free' distributions occur where individuals settle optimally in habitats essentially unconstrained by other individuals already present, and 'ideal-despotic' distributions form when some individuals are kept by others from settling in some habitats, e.g. by territorial behaviour, thus limiting bird density. More recently, Pulliam & Danielson (1991)

proposed the term 'ideal-preemptive' habitat selection to include a broader class of phenomena, in which some individuals obtain resources by whatever means, not just despotism, that make those resources unavailable to other individuals.

A critical prediction of the ideal-despotic/preemptive hypothesis, but not the ideal free, is that individuals' fitness will differ among habitats (Fretwell 1972; Sutherland & Parker 1985; Pulliam & Danielson 1991). Differential fitness among habitats, in turn, is important to population dynamics and regulation on a landscape scale, because it affects how different habitats might contribute to overall productivity, survival, and subsequent recruitment of individuals into the available mix of habitats (Lomnicki 1980; Bernstein *et al.* 1991; Sherry & Holmes 1995). When reproductive output or survival differs among habitats, certain habitats may act as net sources where reproduction exceeds local mortality, while other habitats act as sinks where populations are maintained by net immigration (Pulliam 1988).

For bird populations, fitness differences among habitats that conform to the ideal-despotic/preemptive model have been reported for a variety of species, mostly raptors (e.g. Newton 1986) and passerines. For the latter, most studies have concerned temperate zone-resident species such as parids (e.g. Krebs 1971; van Balen 1973; Minot 1981; van Balen & Potting 1990; Dhondt, Kempenaers & Adriaensen 1992; but see Lemel 1989) and corvids (e.g. Andr n 1990; Goodburn 1991). Breeding populations of long-distance migratory species also experience fitness-related differences among habitats, e.g. in pairing success (Carey & Nolan 1975; Probst & Hayes 1987; Gibbs & Faaborg 1990), fledging rates (Lundberg *et al.* 1981; Alatalo, Lundberg & Ulfstrand 1985; Kallander *et al.* 1987; Tye 1992; Porneluzi *et al.* 1993), and site fidelity (Lanyon & Thompson 1986; Payne & Payne 1993). However, few detailed assessments of the effects of habitat quality on annual reproductive output and survival are available for such populations, except for the cavity-nesting pied flycatcher (*Ficedula hypoleuca*, Gezelius *et al.* 1984; Kallander *et al.* 1987; Jarvinen 1993; see Lundberg & Alatalo 1992). Such demographic information is critically lacking for open cup-nesting, migratory species, which comprise the majority of passerine birds nesting in north temperate forests (MacArthur 1959; Herrera 1978) and for which there has been much concern about recent population declines (Terborgh 1989; Askins, Lynch & Greenberg 1990; Crick 1992).

In this study, we examined the demographic characteristics of the forest-dwelling migratory black-throated blue warbler (*Dendroica caerulescens*, Emberizidae: Parulinae) in two habitat types within northern hardwoods forests that differed principally in density of the shrub layer. Previous research had shown that the abundance of this species, which nests exclusively and often feeds in low shrubs (Steele 1993;

Holmes 1994), varied positively with the density of shrub-level vegetation (Steele 1992). It had not been ascertained, however, whether individuals in these sites differed in reproductive output, local survival, or other demographic features, which in turn might influence local population dynamics and regional abundances of this species. Our objectives in this study were therefore to compare the population parameters of black-throated blue warblers on high and low shrub density sites, and to test the hypothesis that occupancy of particular habitats affects individual fitness and ultimately population dynamics. Because despotism could lead to differential settlement of age classes among habitats, we also examined the effects of bird age on the performance of birds in each habitat.

## Methods

### STUDY SITES

The study was conducted on six sites in northern hardwoods forests in north central New Hampshire USA. Three were located within the Hubbard Brook Experimental Forest (see Holmes & Sturges 1975; Holmes, Sherry & Sturges 1986), while the remainder were in surrounding areas of the White Mountain National Forest, all within 20 km of Hubbard Brook. Plots were situated within large tracts (>10 000 ha) of continuous forest at approximately the same elevation (450–600 m above sea level) and aspect (south). All contained relatively mature forests that had regrown from selective cutting that occurred between 1900 and 1910. The forest vegetation on all six sites consisted of American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*), with occasional white ash (*Fraxinus americana*), red spruce (*Picea rubra*), and eastern hemlock (*Tsuga canadensis*). Relative basal areas of these dominant tree species (based on trees >7.5 cm diameter at 1.5 m height, using methods of James & Shugart 1970) did not differ among plots ( $\chi^2 = 1.36$ , d.f. = 4,  $P = 0.85$ ; R.T. Holmes, unpublished data). Thus, the species composition, relative abundances, and sizes of canopy trees were similar among sites.

Vegetation in the shrub stratum of these forests (0.2–3 m) consisted mostly of a low-growing (<1.5 m) shrub, hobblebush (*Viburnum alnifolium*), and seedlings and saplings of the dominant tree species, especially American beech and sugar maple, along with occasional striped maple (*A. pensylvanicum*), mountain maple (*A. spicatum*), and saplings of red spruce. This shrub stratum varied in density, depending on local environmental conditions (e.g. soil types and topography) and disturbance history, both natural (hurricane, insect damage) and human-caused (logging). In some places, the shrub layer was relatively dense over large areas (>20 ha), while in others, it consisted of more widely scattered shrubs and saplings, with only occasional dense patches, usually

occurring in tree fall gaps. The shrub layer is thus patchily distributed within relatively continuous northern hardwoods forest.

For this study, three study sites were chosen with relatively uniformly dense shrub layers (referred to hereafter as high shrub density plots or HSDPs) and three with more open understoreys (= low shrub density plots or LSDPs). The areas surrounding each plot were similar, i.e. each was embedded within a large patch of either high or low shrub density, respectively. For the study plots chosen, the densities of small woody stems (those <5 cm diameter, see James & Shugart 1970) averaged  $1176.2 \pm 450.4$  (SD)  $\text{ha}^{-1}$  in the three HSDPs and  $546.6 \pm 357.0$   $\text{ha}^{-1}$  in the LSDPs ( $t = 11.7$ , d.f. = 298,  $P < 0.001$ ). In an attempt to provide approximately the same number of breeding pairs for study in both habitats, the HSDPs were 10 ha in area, while LSDPs were 20 ha.

#### FIELD MEASUREMENTS

Black-throated blue warblers were studied intensively in the summers of 1990–92, with some additional information (e.g. on return rates) gathered in 1993. Most individuals (>95%) occupying each plot in each year were colour-ringed, and thus identifiable. They were captured by use of a playback-mist netting technique (Holmes, Sherry & Reitsma 1989), given a unique combination of plastic colour rings. They were aged when in the hand by visual inspection of plumage characteristics described by US Fish & Wildlife Service (1977) and Pyle *et al.* (1987) and verified by us through recaptures of birds of known ages (R.T. Holmes, unpublished data). For both males and females, we could distinguish individuals that hatched the previous summer and were in their first potential breeding season (hereafter 'yearlings') from those in their second or later breeding season (hereafter 'older birds').

To determine abundances of males, we mapped their territorial activities, including their movement patterns, singing centres, and especially their countersinging and boundary disputes with neighbouring conspecifics. The presence or absence of females was determined by searching each territory extensively throughout each summer. Densities are expressed as total individuals (males plus females) per 10 ha, and were adjusted for territories that fell partially outside the plot boundaries (see Holmes *et al.* 1986).

For data on reproductive success, we located nests by intensive searching, including re-nests (after nest failure) and second nests (after successfully fledging the first), on each plot, and determined their fates. First clutches were considered to be those initiated on or before 6 June. Nests were checked every second or third day during incubation (females were not disturbed if incubating), or more often if laying date and thus hatching date were not known. Nestlings were weighed (to 0.1 g) between 09.00 h and 15.00 h on day

6 (hatch day = day 0), the last day they could be handled without risking premature fledging. Nestling weights were adjusted to that at 12.00 h, assuming that gain in mass during the day was linear, following procedures of Rodenhouse & Holmes (1992). Nests were checked on days 8 or 9 to confirm that fledging had occurred. Nesting success was assessed as the probability of nest survival from egg-laying until fledging, using the methods of Mayfield (1961, 1975; as modified by Hensler & Nichols 1981). Nesting success was estimated as the daily survival rate raised to the exponent of the duration of the nesting cycle (Hensler & Nichols 1981), which for black-throated blue warblers was considered to be 21.6 days (13-days incubation period, 8.6-days nestling period, Holmes 1994). Nests abandoned prior to the laying of the first egg were not included in these calculations.

We also determined the proportion (%) of nests failing because of predation. A nest was considered to have been depredated if either eggs or young disappeared between nest checks, or if the nest or its contents had been destroyed. Brood parasitism by cowbirds (*Molothrus ater* Boddaert) did not occur in the unfragmented forests in which this study was conducted, and therefore did not affect nesting success in this population.

Annual reproductive output was calculated as the total number of young fledged per pair per season, taking into account all nesting attempts. To consider the effects of parental age on reproductive parameters, the data were expressed in two ways: (i) by age of the female parent, and (ii) by age of the male within whose territory the nest(s) were located and who usually fed and cared for the offspring (the presumed male parent).

Site fidelity or local survivorship was determined from the returns of ringed individuals from one summer to the next. Intensive searches for returning birds were made throughout each plot and within about 100 m of plot boundaries. Thus, individuals returning but dispersing further may not have been detected (Holmes & Sherry 1992). No quantitative data were obtained on post-fledging survival, due to the difficulty of following broods in these forests once they have left the nest, nor on return rates of nestlings in subsequent years, due apparently to very high natal dispersal (Holmes 1994).

#### STATISTICAL ANALYSES

Data from the three sets of plots within each habitat were treated as replicates whenever possible, but were pooled when sample sizes were small. We used Student's *t*-tests to evaluate differences among group means (e.g. bird densities, clutch initiation dates, nestling body mass), and  $\chi^2$ -tests for analysing categorical data (e.g. age distributions, mating patterns, nesting success, annual return rates). Differences in clutch size by habitat, age of female and time of season were

analysed in a three-way analysis of variance (ANOVA). Patterns in annual reproductive output among years, habitats, and parental age groups was also examined by ANOVA. For these analyses, because bird age and habitat were strongly correlated (i.e. older individuals were concentrated in high shrub density habitats, etc.; see Results), we grouped data on reproductive output by parental age-habitat combinations (e.g. for older individuals on HSDPs, for yearlings on LSDPs, etc.), and used this age-habitat variable as one main effect. This was necessary because type III sums of squares (SS), which are appropriate for analysing unbalanced data, can be invalid if ANOVA main effects are highly correlated or not independent (Shaw & Mitchell-Olds 1993). Because sample sizes were small for reproductive output in 1990, ANOVAs were applied only to data from 1991 and 1992. Analyses were performed separately for data based on ages of the female parents and of the male parents ANOVAs and pair-wise comparisons of least square means were performed with a General Linear Model (GLM) procedure for unbalanced designs, using SAS (SAS Institute 1990). Least square means were used as estimators of the subclass means that would have been expected if the design had been balanced (SAS Institute 1990).

## Results

### POPULATION STRUCTURE

#### *Density and age composition*

Black-throated blue warblers were consistently and significantly more abundant on HSDPs than on LSDPs in all 3 years of study, with numbers decreasing slightly in both habitats (Table 1). Over the 3 years, densities averaged 15.1 and 6.6 individuals 10 ha<sup>-1</sup>, respectively, a significant difference ( $t = 7.12$ , d.f. = 4,  $P < 0.002$ ).

Age structure of the population occupying these

two habitats also differed. On HSDPs, an average of 68% of males and 71% of females were 2 years old or older, while on LSDPs only 35% and 36% of the males and females, respectively, were in these older age classes, the majority being yearlings (Table 1). These patterns were consistent on all three plots within each habitat type across all three seasons (unpublished data). These differences between habitats in the proportions of the two age groups were highly significant for both males and females ( $\chi^2 = 16.88$  and 14.40, respectively, with d.f. = 1 and  $P < 0.0001$  in both cases).

#### *Pairing success and polygny*

Most males in both habitats types were mated (to one or more females, Table 1). Of the relatively small number that remained unmated, however, significantly more occurred on LSDPs (12.7%,  $n = 63$ ) than on HSDPs (1.3%,  $n = 76$ ;  $\chi^2 = 6.43$ , d.f. = 2,  $P = 0.01$ ). There were more unmated males on LSDPs, with a particularly high rate (27.3%) in 1990 (Table 1). Five of the six unmated males for which we knew ages were yearlings. The one unmated older male occurred on a LSDP.

Most males in both habitats were mated monogamously. Only 2.6% ( $n = 76$ ) and 3.6% ( $n = 63$ ) of males had two mates (i.e., were bigamous) on HSDPs and LSDPs, respectively, a non-significant difference ( $\chi^2 = 0.034$ , d.f. = 1,  $P = 0.85$ ). Three of four bigamous males were older individuals, two on HSDPs and one on a LSDP. The one bigamous yearling male occupied a territory on a LSDP.

### REPRODUCTIVE PERFORMANCE

We tested for differences between habitats in reproductive activities by comparing the timing of breeding, clutch sizes, nesting success, annual reproductive

**Table 1.** Demographic characteristics of black-throated blue warbler populations on high shrub density plots (HSDP) and low shrub density plots (LSDP), 1990–92

	1990	1991	1992	1990–92
Bird density (numbers per 10 ha, mean $\pm$ SE)*				
HSDP	17.3 $\pm$ 1.1	14.5 $\pm$ 1.3	13.5 $\pm$ 0.8	15.1 $\pm$ 1.2
LSDP	7.2 $\pm$ 0.5	6.7 $\pm$ 0.7	6.0 $\pm$ 1.3	6.6 $\pm$ 0.4
Age composition				
Male age ratio: % older males ( $n$ )				
HSDP	75% (36)	79% (28)	50% (36)	68% (100)
LSDP	25% (28)	26% (19)	54% (24)	35% (71)
Female age ratio: % older females ( $n$ )				
HSDP	75% (28)	71% (28)	67% (30)	71% (86)
LSDP	33% (3)	29% (17)	42% (24)	36% (44)
Mating patterns				
% males unmated ( $n$ )				
HSDP	4.2% (24)	0% (25)	0% (27)	1.3% (76)
LSDP	27.3% (22)	4.8% (21)	5.0% (20)	12.7% (63)

\*  $n = 3$  plots/habitat.

output, and growth rates of nestlings of black-throated blue warblers on HSDPs and LSDPs. Because the age distributions of parents differed between habitats, we also examined the effect of parental age on these reproductive parameters.

#### *Initiation of first clutches*

Initiation of the first clutch (laying of the first egg in the first nest of the season) occurred almost synchronously among sites each year on or about 20 May. Mean dates of clutch initiation (day 0 = 20 May) were day  $10.0 \pm 0.6$  (SE,  $n = 62$ ) on HSDPs and day  $10.6 \pm 0.7$  ( $n = 38$ ) on LSDPs. These means did not differ significantly ( $t = -0.60$ , d.f. = 98,  $P = 0.55$ ).

Older females initiated clutches slightly earlier than did yearling females within each habitat, but not significantly so. On HSDPs, the mean dates of first egg-laying for older and yearling females were day  $9.0 \pm 0.7$  (SE,  $n = 39$ ) and day  $11.1 (\pm 1.1, n = 14)$ , respectively ( $t = -1.56$ , d.f. = 51,  $P = 0.12$ ). On LSDPs, the comparable values were day  $8.0 \pm 0.9$  ( $n = 13$ ) for older females and day  $11.0 \pm 1.2$  ( $n = 16$ ) for yearling females ( $t = -1.95$ , d.f. = 27,  $P = 0.06$ ). There were also no significant differences in mean clutch initiation dates between HSDPs and LSDPs for either older ( $t = -0.74$ , d.f. = 50,  $P = 0.46$ ) or yearling females ( $t = -0.12$ , d.f. = 28,  $P = 0.90$ ).

#### *Clutch size*

Clutches of black-throated blue warblers ranged in size from two to five eggs, with both the median and mode being four. Only three two-egg and three five-egg clutches ( $n = 131$ ) were recorded during the study. Clutch sizes for older females averaged  $3.9 \pm 0.6$  (SE,  $n = 59$ ) on HSDPs and  $3.9 \pm 0.2$  ( $n = 21$ ) on LSDPs. Comparable values for yearling females were  $3.9 \pm 0.3$  ( $n = 29$ ) and  $3.8 \pm 0.5$  ( $n = 16$ ). In a three-way ANOVA comparing clutch size by habitat type, age of female, and time of season (early vs. late), only time of season was significant ( $F = 7.96$ , d.f. = 3, 1,  $P = 0.005$ ). This was due to more larger clutches early in the season (mostly those with four eggs, but including three with five eggs, laid prior to 14 June), and more smaller clutches later in the season (more three-egg clutches, together with two two-egg clutches). Thus, clutch size decreased with time of season, but was unaffected by habitat occupied or age of female.

#### *Nesting success*

Nest survival probabilities, based on the Mayfield (1961, 1975) method of estimating nesting success which takes into account the fate of all nests found (and lost to all causes) at different stages of the nesting cycle, tended to be higher on HSDPs, although the differences between habitats were not significant.

When analysed by age of the female parent, nest

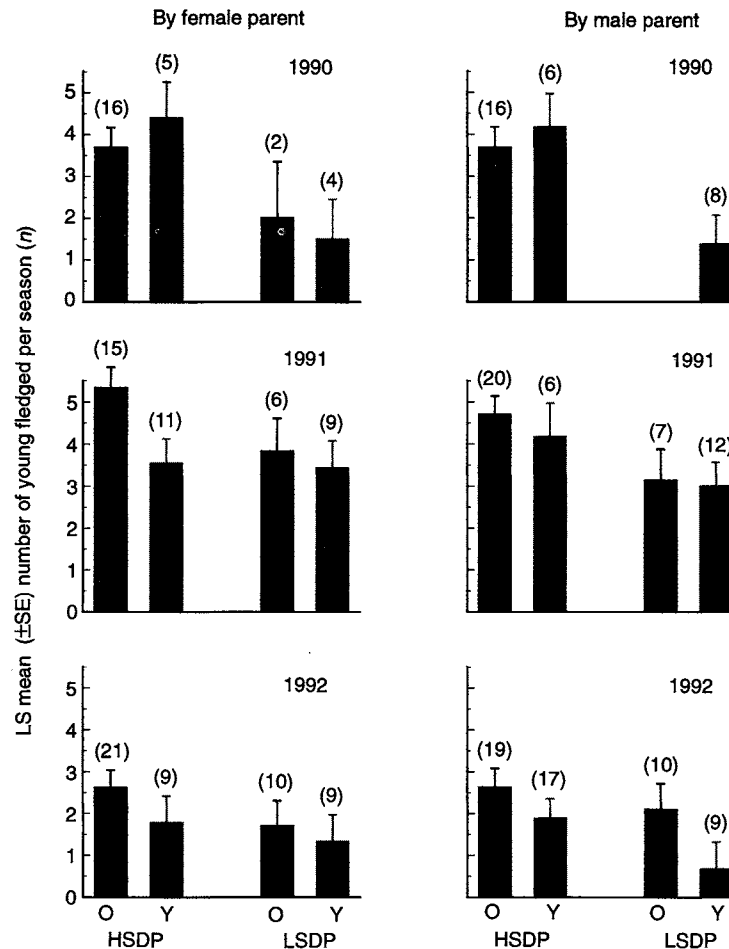
survival probabilities on HSDPs and LSDPs averaged 0.61 and 0.45, respectively, for older females ( $\chi^2 = 1.96$ , d.f. = 1,  $P = 0.16$ ) and 0.45 and 0.55 for yearling females ( $\chi^2 = 0.74$ , d.f. = 1,  $P = 0.39$ ). The comparable values by age of male parent were 0.59 and 0.44 ( $\chi^2 = 1.61$ , d.f. = 1,  $P = 0.20$ ) for older individuals and 0.55 and 0.45 ( $\chi^2 = 0.72$ ,  $n = 1$ ,  $P = 0.40$ ) for yearling males.

Because predation is the major factor causing nest failure for black-throated blue warblers at Hubbard Brook (Holmes *et al.* 1992), we also examined the proportions of nests in the two habitats that were lost just to predation (as opposed to the effects of weather, starvation, etc.; see Holmes *et al.* 1992). Predation losses on HSDPs were 28% ( $n = 36$ ), 14% ( $n = 43$ ) and 45.8% ( $n = 48$ ) in 1990–1992, respectively; the comparable estimates for LSDPs were 42% ( $n = 13$ ), 23% ( $n = 27$ ), and 51.3% ( $n = 39$ ). Thus, more nests were lost to predation on LSDPs in each year relative to those on HSDPs, but the differences were not statistically significant in comparisons within years ( $\chi^2$ ,  $P$ -values  $> 0.30$ ) or for the 3 years combined (30%,  $n = 127$ , on HSDP vs. 41%,  $n = 79$ , on LSDP:  $\chi^2 = 2.43$ , d.f. = 1,  $P = 0.12$ ).

#### *Annual reproductive output*

The number of young fledged per pair of black-throated blue warblers per breeding season ranged from 0 to 9. More young were fledged per season by birds on HSDPs compared to LSDPs, the pattern varying among years and with parental age (Fig. 1). In the ANOVAs that compared data from 1991 and 1992 (see Methods) performed separately for the female and for the male parent, both main effects (year and age–habitat categories) were found to be significant, while the interactions between year and age–habitat categories were not (Table 2). The between-year differences were due largely to more young fledged per pair in 1991 ( $4.04 \pm 0.31$  SE,  $n = 41$ ) compared to 1992 ( $1.86 \pm 0.29$ ,  $n = 49$ ), which was related to the difference in predation on nests in both habitats in the two seasons (see above; R.T. Holmes, unpublished data).

To analyse further patterns underlying the significant parental age–habitat effect, we used the SAS GLM procedure to compare least square means of the annual reproductive output between habitats. These tests demonstrated that older females on HSDPs fledged significantly more young than did older females on LSDPs and than yearling females in either habitat (Table 3, see Fig. 1). In contrast, older females on LSDPs did not differ significantly in numbers of young produced from those of yearlings on either HSDPs or LSDPs (Table 3). Considering males, older individuals on HSDPs fledged significantly more young than did yearling males on LSDPs (Table 3). Furthermore, there was a nearly significant trend for more young to be fledged per season on HSDPs vs.



**Fig. 1.** Annual reproductive output of black-throated blue warblers on high (HSDP) and low (LSDP) shrub density habitats at Hubbard Brook in three summers, 1990–92. Data are LS means ( $\pm$ SE) of the number of young fledged per pair per season, expressed in terms of ages of the female parent and of the male parent (O = older individuals  $\geq 2$  years of age; Y = yearlings, see text).

LSDPs within each age class of males (i.e.  $P$ -values of 0.07 and 0.06 for interhabitat comparisons for older and yearling males, respectively, Table 3).

The fact that some pairs fledged more than four young per season, coupled with the normal clutch size

of 3–4 in this species (see clutch size above; Holmes 1994), suggests the occurrence of double brooding in this population. Indeed, during the 3 years of this study, 17 of 86 individually marked females (24.6%) on HSDPs fledged a second clutch after successfully

**Table 2.** Results of ANOVA comparing numbers of young fledged per season by year (1991, 1992) and by parental age–habitat combinations (four categories based on age of parent and habitat, i.e. older parent on HSDPs and LSDPs; yearling parent on HSDPs and LSDPs). The combination of these two variables was necessitated by the non-independence of parental age and habitat type (see Methods). Data were analysed separately for the female parent and for the male parent

	d.f.	Type III SS	MS	$F$	$P$
By female parent					
Model	7	149.2	21.3	6.0	0.0001
Year	1	94.6	94.6	26.8	0.0001
Age–habitat	3	41.2	13.7	3.9	0.0118
Year by age–habitat	3	3.2	1.1	0.3	0.8268
Error	82	289.7	3.5		
By male parent					
Model	7	145.1	20.7	5.4	0.0001
Year	1	78.0	78.0	20.5	0.0001
Age–habitat	3	47.5	15.8	4.2	0.0083
Year by age–habitat	3	4.7	1.6	0.4	0.7430
Error	92	351.0	3.8		

**Table 3.** Results (*P*-values) of pairwise comparisons of annual reproductive output between parental age-habitat categories (see Table 2). Tests were performed on least square means of the number of young fledged per season by individuals in each category. (see Methods)

Parental age-habitat category	Older-HSDP	Yearling-HSDP	Older-LSDP	Yearling-LSDP
By female parent				
Older-HSDP	–	0.015	0.040	0.005
Yearling-HSDP		–	0.870	0.657
Older-LSDP			–	0.567
Yearling-LSDP				–
By male parent				
Older-HSDP	–	0.255	0.072	0.001
Yearling-HSDP		–	0.548	0.063
Older-LSDP			–	0.223
Yearling-LSDP				–

Older parent =  $\geq 2$  years of age; yearling = first breeding season, 1 year following hatching.  
HSDP = high shrub density plot; LSDP = low shrub density plot.

completing a first, while only 3 of 57 (5.6%) did so on LSDPs ( $\chi^2 = 6.00$ , d.f. = 1,  $P = 0.01$ ). Double brooding was more frequent among older females (16/43) than among yearlings (4/47), a statistically significant difference ( $\chi^2 = 6.82$ , d.f. = 1,  $P = 0.009$ ). Thus, the higher production of young on HSDPs was due largely to the greater frequency of double-brooding by older individuals, which predominated on those plots.

#### Nestling growth

As an index to nestling growth conditions in the two habitats, we measured body masses of black-throated blue warbler nestlings on day 6 following hatching. At nests of older females, mean nestling mass (g) on day 6 on HSDPs was  $7.82 \pm 0.96$  (SE,  $n = 140$  nestlings in 39 nests) compared to  $7.27 \pm 1.35$  ( $n = 36$  nestlings in 11 nests) on LSDPs ( $t = 1.53$ , d.f. = 48,  $P = 0.13$  [d.f. based on the number of nests sampled]). Similarly, in other comparisons based on parental age categories, nestlings consistently averaged 6–8% heavier on HSDPs compared to LSDPs in comparisons based on either female or male age, but

differences were not statistically significant (*t*-tests, *P*-values  $> 0.13$ ).

#### SITE FIDELITY AND LOCAL SURVIVAL

As another indicator of local habitat suitability, we examined the rates at which males and females returned to the two habitat types in succeeding years. Such return rates are a function of both survival between years and commitment to a particular site. When return rates between habitat types were compared, we found that yearling males returned to HSDPs at a significantly higher rate than to LSDPs, while the returns of older males did not differ significantly between habitats (Table 4). Comparisons within habitats show that older and yearling males returned at approximately the same rate on HSDPs (45 vs. 47%, respectively, Table 4;  $\chi^2 = 0.038$ , d.f. = 1,  $P = 0.85$ ). On LSDPs, significantly fewer yearling males returned compared to older males (21% vs. 61%, Table 4;  $\chi^2 = 9.30$ , d.f. = 1,  $P = 0.0003$ ).

For females, there were no significant differences in

**Table 4.** Year-to-year returns of colour-banded male and female black-throated blue warblers to high shrub density plots (HSDP) and to low shrub density plots (LSDP), 1990–92

	% returning ( <i>n</i> )			
	HSDP	LSDP	$\chi^2$	<i>P</i>
Males				
Banded as older individual*	47% (79)	61% (18)	1.20†	0.27
Banded as yearling	45% (51)	21% (43)	6.07	0.01
All males combined	46% (130)	33% (61)	3.05	0.08
Females				
Banded as older individual*	36% (59)	36% (11)	0.002	0.96
Banded as yearling	18% (33)	18% (43)	0.002	0.96
All females combined	29% (92)	22% (54)	0.88	0.35

\* Individuals in their second or later breeding season.

† Chi-square probabilities comparing numbers of each class returning vs. not returning in subsequent years (d.f. = 1 for each comparison).

return rates between habitats either when ages were pooled or separate (Table 4). However, older females returned about twice as often as did yearling females in both habitats (for HSDPs:  $\chi^2 = 3.094$ , d.f. = 1,  $P = 0.07$ ; for LSDPs:  $\chi^2 = 1.60$ , d.f. = 1,  $P = 0.21$ ; Table 4).

These differences in return rates suggest that some black-throated blue warblers, particularly yearling males, might shift locations in subsequent breeding seasons. If this were true, then more new (unbanded) older individuals should appear on the HSDPs compared to LSDPs. To test this, we examined data from 1991 to 1993 (data for 1990; the first year of this study, were excluded because many birds had not been ringed previously; data for 1993 were available as part of an on-going study; R. T. Holmes, unpublished data.). On HSDPs, 25 of 55 (45%) new, i.e. unmarked, males were older individuals, compared to 12 of 46 (26%) on LSDPs ( $\chi^2 = 4.05$ , d.f. = 1,  $P = 0.04$ ). For females, there were 27 older individuals among the 57 unmarked females observed on HSDPs (47%) vs. 17 of 46 (37%) on LSDPs ( $\chi^2 = 2.52$ , d.f. = 1,  $P = 0.11$ ). Thus, older males and possibly some females do change locations and colonize new sites in their second or subsequent breeding seasons.

## Discussion

Differences in reproductive success, local survival, and other fitness correlates among habitats have been reported for a variety of bird species (see Introduction). In most cases, these studies have compared populations in strongly contrasting habitats (e.g. between coniferous and deciduous forests), and the effects of bird age have rarely been taken into account. In this study, we found habitat-specific patterns of demography of an open-cup nesting passerine inhabiting northern hardwoods forests that differed primarily in density of the shrub stratum. Specifically, black-throated blue warbler density was higher, there were proportionately more older ( $\geq 2$  years old) breeders in the high shrub density habitats, and these individuals fledged significantly more young per season and returned to these sites at higher rates from year to year than those (mostly yearlings) occupying forests with a more open shrub layer. In this discussion, we consider the factors that could account for the observed fitness-related differences between these subtly different habitats and their possible consequences for population dynamics of this long-distance migratory species.

### EFFECTS OF PARENTAL AGE VS. HABITAT QUALITY

Among vertebrates, older individuals are often more successful reproductively than younger ones (Curio 1983; Clutton-Brock 1984; Saether 1990). This has been documented for a variety of passerine birds (e.g.

Ralph & Pearson 1971; Nolan 1978; Loman 1984; Perrins & Cleery 1985; Desrochers & Magrath 1993), although most studies have not considered the potential effect of habitat quality along with that of parental age. In other words, are older individuals more successful simply because they are older and presumably more experienced, or because they preempt and occupy higher quality habitats?

For black-throated blue warblers, we found that older birds consistently fledged more offspring per season than did yearlings (Fig. 1). This was particularly evident on HSDPs, where older females fledged significantly more offspring than did yearling females (Table 3). Much of this increased reproductive performance was a result of older females producing a second brood significantly more often than yearling females, and this occurred primarily in high shrub density habitats. How widespread and important this is throughout the range of habitats occupied by black-throated warblers, however, is unknown. The frequency of double-brooding may not only vary with habitat, but also with latitude (and elevation), since it ought to be affected by length of favourable season. In areas to the north of Hubbard Brook (or at higher elevations), the season may be too short for any pairs to raise two broods, and presumably, to the south (or lower), more should be able to do so. At this point, however, there is no information on the breeding productivity of this species in any other parts of its breeding range. Nevertheless, within our study region, double-brooding, which is age-related, is at least one important factor influencing reproductive success of black-throated blue warblers.

The habitat occupied also influenced the reproductive output of black-throated blue warblers in our study. Comparisons between habitats indicated that more young were fledged per capita per season on HSDPs than on LSDPs within sex/age groupings (Fig. 1, Table 3). Thus, older birds raised more young in sites with dense shrubs compared to older birds in low shrub density habitats, and similar patterns occurred even for yearlings. In other words, there were habitat differences even among birds of similar age groupings. Furthermore, nestlings raised on HSDPs were slightly heavier at 6 days of age compared to those on LSDPs, suggesting differences in growth conditions (e.g. food availability), which in turn could influence their subsequent survival. The latter result, however, could be confounded by parental age, in that older, presumably more experienced adults were feeding those nestlings on HSDPs. Likewise, there were more unmated males on LSDPs and these were mostly yearlings, suggesting the effects of both habitat quality and bird age.

Additional support for differences in quality between high and low shrub density habitats comes from data on local survival. Older male black-throated blue warblers returned at similar rates in both habitats, suggesting that once an individual has



bred in a site in at least its second breeding season, it tends to return there in subsequent years. Likewise, on HSDPs, yearling males returned at rates similar to those of older birds, but on LSDPs, they returned significantly less often than did yearlings on HSDPs. Thus, yearling males on LSDPs either experienced higher mortality, or they dispersed in subsequent breeding seasons to more suitable habitats. The latter hypothesis is supported by the higher number of unbanded older males colonizing HSDPs plots each year than LSDPs. Such shifting of breeding locations accounts at least in part for the disproportionate occurrence of more older individuals in high shrub density habitats.

The lack of strong differences in reproductive output among age/sex groupings on LSDPs may be a result of considerable local heterogeneity in habitat quality even within those habitats. Thus, site-faithful, older males may occupy higher quality patches within each habitat, which results in their being more successful in reproducing, compared to new individuals, particularly yearlings, which might be relegated to the poorer sites. Observations at Hubbard Brook indicate that older males usually occurred in areas with densest shrubs within both HSDPs and LSDPs (P.P. Marra & R.T. Holmes, unpublished data). Thus, differential habitat selection may occur at a variety of scales, ranging from that of individual territory to the landscape level.

In summary, parental age and habitat suitability appear to interact in black-throated blue warblers, in that older individuals, through their presumed experience and/or dominance, occupy sites of higher quality, which results in their higher reproductive output and local survival.

#### ECOLOGICAL DETERMINANTS OF HABITAT QUALITY

What determines habitat suitability for breeding black-throated blue warblers and other forest passerines? The most important factors seem to be those that influence reproductive success, of which nest predation/parasitism and food limitation are probably the most likely (Martin 1992).

Predation is the most important factor causing nesting failure in this population of black-throated blue warblers (Holmes *et al.* 1992). Although survival probabilities for individual nests tended to be higher and predation rates lower on HSDPs relative to LSDPs, the differences were not statistically significant. Thus, differences in nest predation did not seem to be a major contributor to the observed habitat-specific demographic patterns. Furthermore, brood parasitism by cowbirds, which can influence habitat quality and demography of small passerine birds (Brittingham & Temple 1983; Robinson *et al.* 1995), did not occur in these study areas in New Hampshire,

and therefore was not a factor affecting demographic differences.

The factor that accounted for the greatest difference in reproductive output of black-throated blue warblers between habitats was frequency of double-brooding, which was accomplished most often by older females on HSDPs. Previous studies have also shown that older black-throated blue warblers are more likely to produce two broods per season than are yearlings, even within high shrub density habitats (Holmes *et al.* 1992). More importantly, the frequency of double-brooding across years is positively correlated with the abundance of food, mainly Lepidoptera larvae (Holmes, Sherry & Sturges 1991; Rodenhouse & Holmes 1992). During the present study, Lepidoptera larvae occurred at low population levels (R.T. Holmes, unpublished data), and double-brooding was relatively infrequent, even on HSDPs. In comparison, 48% of black-throated blue warbler pairs double-brooded in 1986–89 on one large HSDP (Holmes *et al.* 1992) compared to 24.6% in this study. Despite their generally low abundances during the present study, lepidopteran larvae were 10–50% more abundant per unit leaf area on HSDPs compared to LSDPs (R.T. Holmes, unpublished data). Coupled with the greater number of leaves in areas of high shrub density, this higher food abundance on HSDPs could alone account for both the higher warbler densities and their significantly higher level of double-brooding there. The possibility of better feeding conditions on high shrub density areas is also suggested by the slightly heavier weights of nestlings just prior to fledging compared to those reared on LSDPs. Because clutch sizes and clutch initiation times were similar between habitats, it seems unlikely that there were any important differences in early season food availabilities (see Tye 1992) that might have influenced birds in these two habitats.

Thus, the presence of more older, experienced adult birds, coupled with higher food abundance and possibly safer nesting sites, may explain why the reproductive performance and local philopatry of black-throated blue warblers were greater in high shrub density areas. The higher food levels may be the ultimate reason why older individuals selected these high shrub density areas from within the forest matrix. Other studies have shown that food is particularly important in affecting breeding success for passerine birds (Lack 1954; Martin 1987; Holmes *et al.* 1992), and this has been confirmed experimentally in a few cases (e.g. Hogstedt 1981; Simons & Martin 1990; Rodenhouse & Holmes 1992).

#### IMPLICATIONS FOR POPULATION DYNAMICS

The differences we report in black-throated blue warbler density, age structure, local survival, and annual reproductive output between high and low shrub density habitats are consistent with the ideal-des-

otic/preemptive model of habitat distribution (Fretwell & Lucas 1970). These habitat-specific patterns of demography suggest intraspecific competition for the more suitable (high shrub density) habitats, which in turn may have population consequences. For instance, to replace adults lost annually to mortality, assuming an annual survival probability of 50–60%, c. 3–4 young would need to be fledged per pair to maintain a steady population level (Holmes *et al.* 1992; Sherry & Holmes 1995). During this study, black-throated blue warblers exceeded this level of production in high shrub density habitats (mean  $\pm$  SE =  $3.6 \pm 0.3$ ,  $n = 77$ , young fledged per female) but not in areas of low shrub density ( $2.5 \pm 0.3$ ,  $n = 37$ ). The former thus represents a source habitat, while the latter can be considered a sink (i.e. one that is maintained at least in part by immigration from elsewhere, Pulliam 1988).

The mechanisms producing these differential patterns of habitat occupancy are despotism or some other form of preemption. Despotism in this and many forest-dwelling passerine species is suggested by the territorial and agonistic behaviour of breeding males (Morse 1980; Newton 1992; Holmes *et al.* 1992; Holmes 1994), which results in their overdispersion within breeding habitats (Sherry & Holmes 1985). Behavioural dominance by older males leading to age-specific patterns of habitat distribution has been reported for American redstarts (*Setophaga ruticilla*, L.) at Hubbard Brook (Sherry & Holmes 1989) and for other species (see Newton 1992). Similar patterns, however, may develop by differential arrival on the breeding grounds. In black-throated blue warblers and many other migratory passerines, older males arrive in breeding areas first and settle before most yearlings appear (R.T. Holmes, unpublished data; see Francis & Cooke 1986; Lundberg & Alatalo 1992), thus preempting the most suitable sites. Earlier arrival by older female black-throated blue warblers may also account for their predominance in high shrub density areas, although aggression among females also occurs during the arrival and settlement period (Holmes 1994), which could influence their age-related habitat distribution patterns.

Despotic/preemptive distributions of individuals in multiple habitat landscapes provides a potential mechanism for population regulation (Lomnicki 1980; O'Connor 1985; Dhondt *et al.* 1992; Newton 1992; Bowers 1994; Sherry & Holmes 1995). Populations will tend to be stabilized when proportionately more individuals are forced to occupy poor habitats at higher population densities and when individuals reproduce and/or survive less well in those poorer sites. This effect was demonstrated by Dhondt *et al.* (1992), who showed that density-dependent fecundity in tits was a function of more poor-quality sites being occupied with increasing density, and not because of any density-dependent differences in clutch size within a habitat. Viewed in a slightly different way, less pre-

ferred areas provide a refuge for younger or less competitive individuals, thus serving as buffer zones that can stabilize populations occupying the better habitats (Bernstein *et al.* 1991). In the long term, bird densities should be more constant in the preferred high shrub density sites and fluctuate more widely in the less preferred areas. Our study was too short to test for this latter effect, however.

The results of our study support the idea that habitat quantity and quality in the breeding season, and how it influences reproductive success, are critical for maintaining population levels of migratory songbirds (Sherry & Holmes 1992, 1995). This conflicts with the often-cited and perhaps prevailing notion that populations of long-distance migratory birds are affected mostly by mortality occurring during the non-breeding period (Lack 1968; Morse 1980; Alerstam & Hogstedt 1982; Fretwell 1986; Wiens 1989; Baillie & Peach 1992; Morton 1992; Rappole & MacDonald 1944; see Sherry & Holmes, in press, for a review). A resolution of this controversy, however, is suggested by the hypothesis that migratory bird populations may be regulated by habitat availability in both summer and winter (see Sherry & Holmes 1995), which implies that one must consider reproductive output (and survival) in summer and survival in winter in order to assess fully population dynamics for these species. The present study of habitat distribution and demography of black-throated blue warblers in the breeding season thus represents only one phase in the annual cycle of this migratory species, albeit a potentially important one.

In conclusion, further understanding of the population dynamics and regulation in black-throated blue warblers and other long-distance migratory species will require more detailed knowledge of (i) the distributions of habitats across landscapes and of individuals among habitats in both breeding and wintering quarters, (ii) the inherent suitabilities of those habitats; and (iii) the dispersal process by which birds find and settle into new habitats. Dispersal, in particular, is poorly known for most, if not all, migrant passerines (Payne 1990; Newton 1991). Longer-term studies on large spatial scales, including breeding, wintering and migratory stopover periods, are needed to assess more completely the dynamics of habitat distribution patterns and their impact on the year-round population dynamics of long distance migrant species.

#### Acknowledgements

This research was supported by grants from the US National Science Foundation to Dartmouth College and Tulane University. Permission to conduct our studies in the White Mountains was granted by the Northeast Forest Experiment Station, US Department of Agriculture, Forest Service, Radnor, PA, and by the White Mountain National Forest, Plymouth

and Laconia, NH. M.P. Ayres and especially T.S. Sillett kindly helped in the data analysis. We thank D.T. Bolger, P. Hunt, T.S. Sillett and J.N.M. Smith for their constructive comments on the manuscript. Finally, many field assistants helped us locate BWs, identify their colour bands, find their nests, and follow them through the season. Without their persistence and hard work, this study would not have been possible.

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Received 7 December 1994; revision received 26 May 1995