

# Long-Term Demographic Trends, Limiting Factors, and the Strength of Density Dependence in a Breeding Population of a Migratory Songbird

**E**FFECTIVE CONSERVATION AND MANAGEMENT of migratory bird species requires an understanding of when and how their populations are limited and regulated. From 1986 to 1999, we studied the processes that determine the abundance of a temperate-tropical migrant passerine, the Black-throated Blue Warbler (*Dendroica caerulescens*), during the breeding portion of its annual cycle. We found that young fledged per territory, fledgling mass, and yearling recruitment were negatively correlated with adult density, whereas the proportion of nests depredated per year was not correlated with density. Annual fecundity was also negatively correlated with density-independent nest predation and fluctuated with variation in weather and food supply associated with the El Niño Southern Oscillation. Using matrix population models, we discovered that local abundance of Black-throated Blue Warblers could be regulated by the negative feedback on annual fecundity generated by the density of breeding adults. Taken together, these results indicate that warbler abundance is determined in part by a complex interaction between biotic and abiotic factors during the breeding season and provide the first assessment of the strength of density dependence in a temperate-tropical migrant passerine.

## INTRODUCTION

The processes that limit and regulate bird abundance remain poorly known (Sinclair 1989; Murdoch 1994). Limiting factors affect the average fecundity, survival, and thus

the size of a population (Sinclair 1989). The effects of limiting factors, such as weather and food supply, are not related to population size; that is, they are density independent. Regulatory processes, however, involve density-dependent mechanisms. These mediate local interactions among individuals, their natural enemies, and food supply to cause demographic rates (e.g., fecundity, survival) to decline when population density increases, and vice versa (Begon et al. 1996). Regulation, which requires density dependence, implies that there is a mean population size, or an equilibrium, around which the population fluctuates and that the variance of population size is bounded (Royama 1977; Turchin 1995; Hixon et al. 2002). The influence of a density-dependent process, however, could be masked in some years by a density-independent factor like climate variation. Thus, simply because a process operates in a density-dependent manner does not mean that it is consistently regulatory. The regulatory nature of a process can be assessed more precisely through the use of simulation models that can verify whether a density-dependent process can regulate abundance within the bounds actually observed in nature (Pennycuik 1969; Klomp 1980; Ekman 1984; Arcese et al. 1992; McCallum et al. 2000). The identification of limiting and regulatory processes is a key element for understanding population dynamics and is likewise necessary for the parameterization of models that can aid management and conservation efforts (Lebreton and Clobert 1991; Murdoch 1994; Runge and Johnson 2002).

The importance of knowing what factors affect the size of bird populations is underscored by recent declines in abundances of many species, especially temperate-tropical migratory passerines (Robbins et al. 1989; Terborgh 1989; Askins et al. 1990; Baillie and Peach 1992; Peterjohn et al. 1995; Peach et al. 1998). Documenting when and how populations of migratory songbirds are limited and regulated is complicated by the fact that these birds inhabit a variety of temperate and tropical habitats during their annual cycle. Furthermore, despite mixing of breeding populations on winter quarters (Chamberlain et al. 1997; Kimura et al. 2002; Rubenstein et al. 2002), events in one season can affect population dynamics in subsequent seasons (Baillie and Peach 1992; Marra et al. 1998; Sillett et al. 2000). However, the long-term demographic data required to determine the relative contribution of the breeding, migratory, and overwinter seasons to year-round population dynamics are lacking for most migratory bird species (Rappole and McDonald 1994; Sherry and Holmes 1995, 1996; Latta and Baltz 1997; Askins 2000).

Since 1986, we have been studying the year-round ecology of a migratory songbird, the Black-throated Blue Warbler (*Dendroica caerulescens*) in both its breeding and wintering areas (Holmes et al. 1989; Rodenhouse and Holmes 1992; Holmes et al. 1992, 1996; Sillett et al. 2000; Sillett and Holmes 2002). Recently, we have shown that multiple density-dependent mechanisms operate during the breeding period (Rodenhouse et al. in review[AQ1]) at our study site in New Hampshire, where the warbler population has been

stable for at least the past 30 years (Holmes and Sherry 2001). In this chapter, we examine in detail the demography of this breeding population from 1986 to 1999 to elucidate the factors that determine its local abundance. Our objectives are twofold. First, we analyze long-term data on reproductive ecology to identify which abiotic and biotic processes limit the warbler population during the breeding period and which function in a density-dependent manner. Second, we use a stochastic simulation model, parameterized with field data, to assess whether the density dependence measured in our study population can regulate local abundance within the range observed from 1986 to 1999. We use these results to consider the relative importance of breeding-season events to songbird population dynamics.

## METHODS

### Study Site and Species

We conducted our field research in the 3100-ha Hubbard Brook Experimental Forest in Woodstock and Thornton, New Hampshire, from May to August, 1986–1999. The Hubbard Brook valley, which was extensively logged in the early 1900s, is contiguous with the much larger White Mountain National Forest. Vegetation on our study plot was dominated by hardwoods 20–25 m tall, primarily American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*). The dense understory consisted mainly of hobblebush (*Viburnum alnifolium*), as well as striped maple (*A. pensylvanicum*) and seedlings and saplings of canopy trees. Further details on habitat can be found in Bormann and Likens (1979), Holmes and Sturges (1975), and Holmes (1990).

Our study site at Hubbard Brook represents high-quality habitat for the Black-throated Blue Warbler (Holmes et al. 1992, 1996), one of the most common breeding birds in hardwood forests in northern New England (Holmes 1994). Black-throated Blue Warblers are sexually dichromatic and insectivorous, and they breed in the understory of mature forests in northeastern North America (Holmes 1994). This open-cup-nesting species is territorial during the breeding season and adults have strong fidelity to territory sites from year to year. At Hubbard Brook, Black-throated Blue Warblers are typically socially monogamous breeders, although a few males (5–10%) are bigamous each year (Holmes et al. 1992; authors' unpubl. data). Clutch size is relatively invariant, ranging from three to five for first broods and from two to four for second broods, with a mean and modal clutch size of four (Holmes 1994). Pairs can successfully raise two broods of young per summer. Both parents share in feeding nestlings and fledglings, but only females build nests and incubate eggs. Natal dispersal for our population is high: none of over 2,500 young fledged from our study plot have returned to the plot as adults, although a very small number (<10) have been resighted as breeders within the larger Hubbard Brook valley. New breeders, or yearlings, however, dis-

perse from other areas and settle on the study plot each year. The number of these yearling recruits is strongly and positively correlated with annual fecundity on the study site in the previous year (Sillett et al. 2000), indicating that our study population reflects Black-throated Blue Warbler population dynamics occurring at a broader, regional scale.

## Field Methods

Reproductive ecology of Black-throated Blue Warblers was studied on a 64-ha plot at Hubbard Brook. This study plot was gridded into 25-m quadrats to facilitate daily territory mapping and locating nests. Territories were delineated by using the minimum convex polygon method (Ford and Myers 1981). Annual warbler density on the 64-ha plot ( $44.6 \pm 2.4$  adults) was determined by counting the number of whole or fractional territories within the plot, taking into account the pairing status of each territorial male (e.g., unpaired, monogamous, bigamous). A small number of territorial males (0–2) were unmated each year, and no unmated females were detected. Birds were captured in mist-nets and individually marked with a unique combination of one U.S. Fish and Wildlife Service aluminum leg band and two colored plastic leg bands. Individuals were aged as yearlings or older, by using plumage characters (Pyle et al. 1987).

We searched for nests of all Black-throated Blue Warblers breeding within the 64-ha plot, and found most nests during nest building. Nests were checked every 2 days until fledging or failure. In nearly all cases we determined cause of failure from the condition of failed nests (e.g., egg fragments or missing eggs indicated nest predation). Nestlings were weighed and banded on day 6 of the 8-day nestling period (hatching = day 0), the last day to safely handle young without causing premature fledging. Nestling mass on day 6 was used as an estimate of mass at fledging. Identity of males belonging to nests was verified by observing males and recording their leg band combinations when they came to nests to feed nestlings. Successful fledging was confirmed by noting parents feeding fledglings. Adults were monitored closely after a first brood fledged to ensure that we discovered if pairs attempted a second brood. In total, we collected data from 386 nests, not counting those abandoned during nest building.

Availability of the Black-throated Blue Warbler's primary food in summer, lepidopteran larvae, was quantified each year on four biweekly surveys beginning in late May. A survey entailed visually inspecting understory sugar maple and American beech leaves on transects through the study plot and recording the length of each caterpillar present (Rodenhouse and Holmes 1992). A total of 4,000 leaves per tree species were examined on each survey. Caterpillar lengths were converted to biomass using length-mass regressions (Rodenhouse 1986). Black-throated Blue Warblers usually forage in the understory (Robinson and Holmes 1982), and caterpillar biomass is not strongly stratified by height at our study site (Holmes and Schultz 1988).

## Analysis of Long-Term Demographic Data

Linear regression was used to analyze the correlations between annual warbler density and several variables related to annual fecundity: young fledged, mean clutch size, proportion of females attempting second broods, mean fledgling mass, proportion of bigamous males, yearling recruitment, and annual variation in fledging success. Young fledged equaled the mean number of young fledged per territory per year. Mean fledgling mass was computed by first averaging mass on a per nest basis, then averaging means for all nests per territory per year. Yearling recruitment was defined as the number of whole and fractional territories of yearling males on the 64-ha plot in year  $t+1$ . Annual variation in fledging success was represented by the standardized coefficient of variation (Sokal and Rohlf 1995) in number of young fledged per territory per year. The Durbin-Watson test for independence was used to test for first-order temporal autocorrelations in regression model residuals. All statistical analyses were performed with the JMP computer program (SAS Institute 2000).

We also used linear regression to examine the correlations between annual warbler density and two external variables that affect reproductive success: food availability and nest predation rate. Food availability was defined as total biomass of all lepidopteran larvae recorded in each of the four surveys described above. Nest predation rate was defined as the mean proportion of nests that were depredated per territory per year.

To test for an effect of warbler density on annual adult survival ( $\phi$ ) and recapture ( $p$ ) probabilities, we used Cormack-Jolly-Seber (CJS) models (Pollock et al. 1990; Lebreton et al. 1992) and the MARK computer program (White and Burnham 1999). The data set for this analysis came from the color-banded population breeding on our 64-ha study plot and was composed of capture histories of 171 females and 165 males. Black-throated Blue Warbler survival and recapture probabilities at Hubbard Brook differed between females and males (model notation:  $[\phi_{\text{sex}} p_{\text{sex}}]$ ), but not by bird age (Sillett and Holmes 2002). We therefore chose a set of candidate models (see Results) in which  $\phi$  and  $p$  were always functions of sex. Adult density was included in models as a covariate; additive models were not considered because annual variation in  $\phi$  differed by sex (Sillett and Holmes 2002). Model selection methods based on Akaike's Information Criterion (AIC) were used to assess the statistical evidence for an effect of adult density on  $\phi$  and  $p$  (Burnham and Anderson 1998). Following Burnham and Anderson (1998), models were ranked by second-order AIC differences ( $AIC_c$ ) and the relative likelihood of each model was estimated with AIC weights ( $w_i$ ).

Multiple regression was used to examine the relative effects of biotic and abiotic limiting factors, as well as adult density, on two measures of annual warbler fecundity: number of young fledged and fledgling mass. The latter has been shown to be a predictor of fledgling survival in many bird species (Newton 1998). Because fecundity of Black-

throated Blue Warblers can be strongly affected by nest predation (Holmes et al. 1992), nest predation rate was included in the two multiple regression models. Fecundity of this species is also limited by food availability and climatic variation (Rodenhouse 1992; Rodenhouse and Holmes 1992; Sillett et al. 2000). The El Niño Southern Oscillation, or ENSO, is one source of climatic variation in New England (Ropelewski and Halpert 1986; Montroy et al. 1998). At Hubbard Brook, warbler fecundity and the availability of the birds' primary food source, lepidopteran larvae, were significantly correlated with mean monthly values of the Southern Oscillation Index or SOI (Sillett et al. 2000), a standardized measure of ENSO phase (Kiladis and Diaz 1989). Strongly negative values of SOI indicate El Niño conditions, and strongly positive values indicate La Niña conditions. Between 1986 and 1998, warbler fecundity and caterpillar abundance were low in El Niño years and high in La Niña years (Sillett et al. 2000). SOI was not correlated with adult density ( $r = 0.19, p = 0.51$ ) or with nest predation rate ( $r = 0.16, p = 0.59$ ) from 1986 to 1999. We thus used SOI to represent variation in both climate and warbler food supply in the multiple regression models. Significance tests for model effects were depicted graphically with partial regression leverage plots (Rawlings 1988; Sall 1990).

### Simulation Model

We constructed a stochastic Leslie matrix model (Caswell 2001) to test whether density-dependent fecundity (see Results) was sufficient to regulate local warbler abundance within the levels observed on our study area. Model output was compared with the actual number of males recorded on the 64-ha plot from 1986 to 1999. The two stages in the matrix were "yearling" and "adult" males. Matrix elements were yearlings per yearling (i.e., the number of yearlings recruited in year  $i+1$  per yearling breeder in year  $i$ ), yearlings per adult, yearling survival, and adult survival.

We parameterized the model with estimates of survivorship and fecundity from the Black-throated Blue Warbler population at Hubbard Brook (table 32.1). Stage-specific

survival estimates were taken from Sillett and Holmes (2002). Data on survival of Black-throated Blue Warblers from fledgling until their first breeding season were not available, but survival probabilities of small passerines during this interval typically ranges from 0.1 to 0.3 (Anders et al. 1997). We used 0.3 as our estimate of fledgling survival because values less than this resulted in a population growth rate ( $\phi$ ) of less than 1 in a deterministic model without density-dependent fecundity. Stage-specific fecundity values in the stochastic model were linear functions of population size produced by regressing annual male density on the 64-ha plot against (mean number of fledglings per year/2) for both yearlings and adults. Survivorship and the intercepts of the fecundity functions in the stochastic model were set as random variables, where survival probability was drawn from a beta distribution and fecundity was drawn from a log-normal distribution (Hilborn and Mangel 1997). Estimates of process variance (i.e., environmental stochasticity) in survival rates were taken from Sillett and Holmes (2002). For males, this process variance was close to 0. We chose a value of 0.01 for the model. The estimate of process variance in female survival rate (0.04 [see Sillett and Holmes 2002]) was used for fledglings. Initial population size for both models was one male. Matrices were projected for 50 years; this process was repeated 1,000 times for the stochastic model. All model calculations were performed in Excel (Microsoft Corporation 1999) with PopTools (Hood 2000).

## RESULTS

### Long-Term Demographic Patterns

Several variables related to warbler reproductive success were correlated with adult density. Mean number of young fledged per year, mean annual fledgling mass, and recruitment of yearlings in year  $i+1$  were all significantly negatively correlated with density (fig. 32.1). Likewise, the proportion of females attempting second broods each year was

**Table 32.1** Parameter values for a projection matrix model of the Black-throated Blue Warbler population breeding at Hubbard Brook Experimental Forest, New Hampshire

Model[AQ6]	Parameter	Value
	Adult, yearling survival	0.51 ± 0.01 <sup>a</sup>
	Fledgling survival	0.30 ± 0.04 <sup>b</sup>
	Yearling fecundity	[(1.47 ± 0.65) <sup>c</sup> - 0.01[AQ7]*(no. males)]*fledgling survival
	Adult fecundity	[(4.04 ± 0.66) <sup>c</sup> - 0.09*(no. males)]*fledgling survival

Note: Estimates of adult survival are from Sillett and Holmes (2002). See Methods for parameter details.

<sup>a</sup>Mean ± 1 SD; drawn from a beta distribution.

<sup>b</sup>Drawn from a beta distribution; covaried with adult and yearling survival.

<sup>c</sup>Drawn from a log-normal distribution.

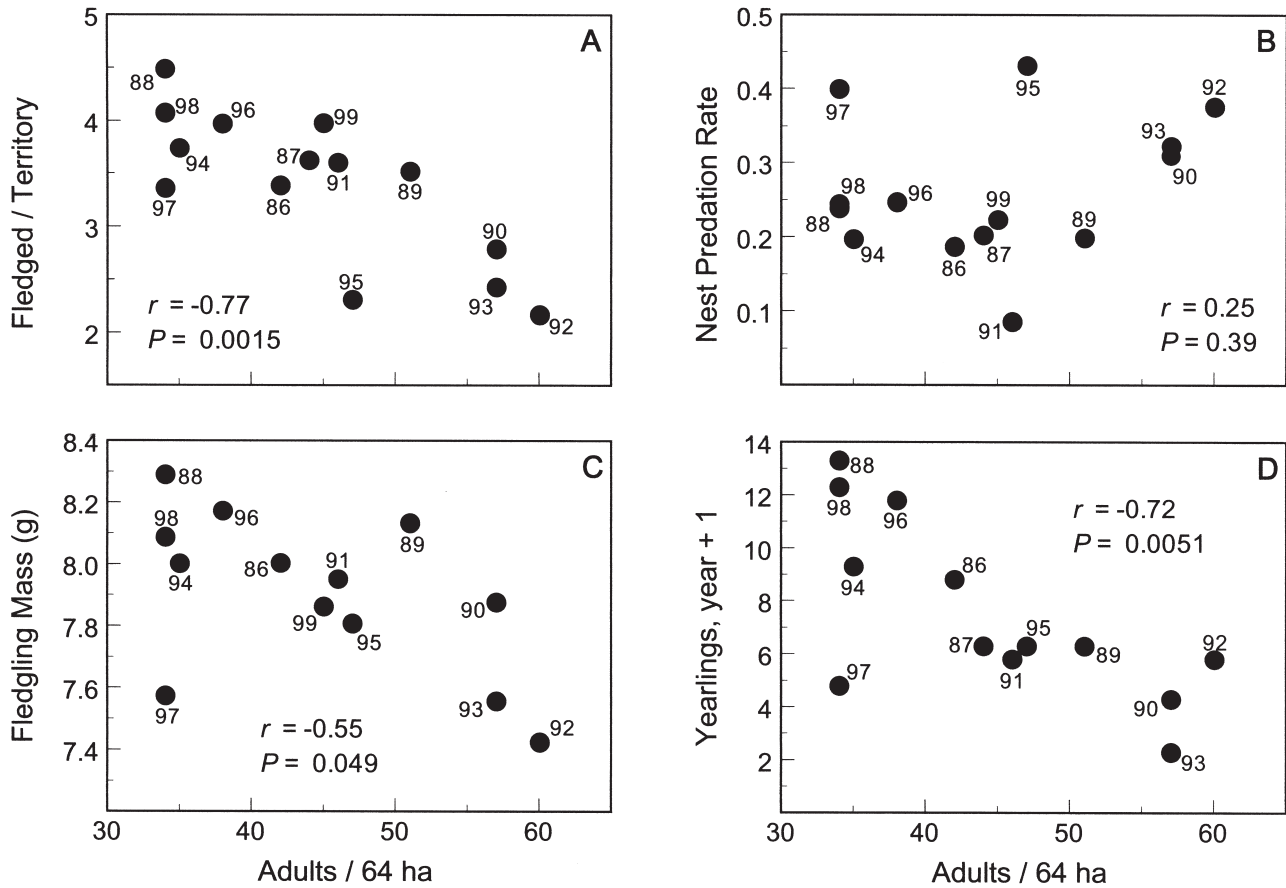


Fig. 32.1. Density of Black-throated Blue Warblers on a 64-ha plot at Hubbard Brook Experimental Forest, New Hampshire, 1986–1999, versus four variables related to reproductive success: mean number of young fledged annually per territory (from Rodenhouse et al., submitted[AQ3]) (A), mean nest predation rate per territory per year (B), mean annual fledgling mass (C), and number of yearling male recruits in year  $t+1$  (D). Numbers by points indicate year. Fledgling mass data were lacking for 1987. First-order temporal autocorrelation in model residuals was not significant in any of the four regressions (Durbin-Watson  $d > 1.61$ ,  $p > 0.19$ ).

strongly density-dependent ( $r = -0.78$ ,  $p = 0.001$ ). In contrast, mean clutch size for both first and second brood nests was not density-dependent (first broods:  $r = -0.39$ ,  $p = 0.17$ ; second broods:  $r = -0.38$ ,  $p = 0.19$ ), nor was the proportion of bigamous males per year ( $r = -0.14$ ,  $p = 0.63$ ). Similarly, variance in fledging success of Black-throated Blue Warblers did not increase with warbler density (fig. 32.4). Adult density was also not significantly correlated with either annual nest predation rate (fig. 32.1B) or with caterpillar biomass (for each of four counts,  $|r| < 0.15$ ,  $p > 0.61$ ).

Population density did not have a strong effect on CJS estimates of annual survival and recapture probabilities (table 32.2). According to  $\sigma w_p$ , simple sex-specific survival (table 32.2: models 1, 3) was 4.7 times more likely to be the best fit to our data than density-dependent survival (33. 2: models 2, 4). Similarly, sex-specific recapture probabilities (table 32.2: models 1, 2) were 6.5 times more likely than density-dependent recapture probabilities (table 32.2: models 3, 4), given our data.

Multiple regression models (table 32.3) indicate that adult density, nest predation rate, and ENSO phase explained the

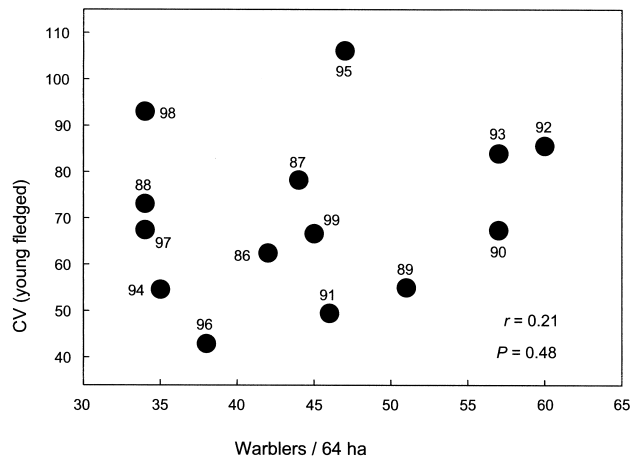


Fig. 32.2. Density of Black-throated Blue Warblers was not correlated with the unbiased coefficient of variation (CV) in mean number of young fledged per territory. Data are from a 64-ha plot at Hubbard Brook Experimental Forest, New Hampshire, 1986–1999. The unbiased CV was calculated as  $(\text{standard deviation}_{\text{young fledged}} * 100[\text{AQ4}] / \text{mean}_{\text{young fledged}}) * (1 + 1/4n[\text{AQ5}])$ , where  $n$  = sample size (Sokal and Rohlf 1995).

**Table 32.2** Models of annual survival ( $\phi$ ) and recapture ( $p$ ) probabilities for Black-throated Blue Warblers at Hubbard Brook Experimental Forest, New Hampshire

Model	$K$	$AIC_c$	$\Delta_i$	$w_i$
1. $\phi_{sex}, p_{sex}$	4	768.84	0.00	0.71
2. $\phi_{sex \times density}, p_{sex}$	6	771.88	3.05	0.16
3. $\phi_{sex}, p_{sex \times density}$	6	772.55	3.72	0.11
4. $\phi_{sex \times density}, p_{sex \times density}$	8	775.85	7.02	0.02
5. $\phi_{sex \times year}, p_{sex \times year}$	39	811.02	42.18	0.00

Note: Columns give model notation, number of estimable parameters ( $K$ ), second-order Akaike's information criterion values ( $AIC_c$ ),  $AIC_c$  differences ( $\Delta_i$ ), and  $AIC_c$  weights ( $w_i$ ). Subscripts describe parameterizations of  $\phi$  and  $p$ : "sex" = parameters different between females and males; "density" = parameter a function of adult density; "year" = parameter varies annually. Subscripts joined by a \* indicate a factorial model. All models were fit by using a logit link function. The program RELEASE (Burnham et al. 1987) indicates that the global model ( $\phi_{sex \times year}, p_{sex \times year}$ ) provided a good fit to the data ( $\chi^2_{38} = 19.37, p = 0.99$ ).

great majority of variation in both mean number of young fledged per year ( $R^2 = 0.91, p < 0.0001$ ) and mean annual fledgling mass ( $R^2 = 0.80, p = 0.002$ ). Number fledged decreased as both adult density and nest predation rate increased and increased with increasing values of SOI, indicating that more young were fledged in La Niña years (fig. 32.3A–C). Mean nestling mass was also negatively affected by increasing adult density and nest predation rate (fig. 32.3D–E), and was low in El Niño years and high in La Niña years (fig. 32.3F). Number fledged was most strongly correlated with adult density, followed by nest predation rate, then ENSO phase (table 32.3). Fledgling mass was most

strongly correlated with ENSO phase, then with nest predation rate, and was only marginally correlated with adult density (table 32.3). Thus, two biotic factors—density-independent nest predation and density-dependent resource competition—the latter in combination with climatically affected food abundance, appear to be the most critical variables influencing warbler fecundity.

### Simulation Model

The Leslie matrix model indicated that local warbler abundance can be tightly regulated by density-dependent fecundity observed in the field study (fig. 32.4). Size of simulated populations typically reached an asymptote after 20 years. Mean population size from the 1,000 model iterations was similar to the mean number of males recorded on the study plot from 1969 to 1999 (fig. 32.4). Furthermore, the 95% confidence interval from the 1,000 model iterations closely bracketed observed variation in warbler abundance (fig. 32.4).

## DISCUSSION

Our results demonstrate that local abundance of Black-throated Blue Warblers at Hubbard Brook can be explained by a complex interaction of abiotic and biotic factors operating on breeding grounds. Fledging success, and to a lesser extent, fledgling mass, were correlated with nest predation rates and with fluctuations in climate and food supply associated with ENSO. However, nest predation, climatic variation, and food availability must be considered limiting fac-

**Table 32.3** Analysis of variance and parameter estimates from two multiple regression models testing the effects of population density, nest predation rate, and ENSO phase on mean number of young fledged per year and fledgling mass from 1986 to 1999

Dependent Variable	Source	d.f.	Estimate $\pm 1$ SE	Mean Square	$F$	$p$
Young fledged <sup>a</sup>	Adult density	1	-0.04 $\pm$ 0.008	1.96	34.14	0.0002
	Nest predation rate	1	-3.34 $\pm$ 0.73	1.22	21.19	0.001
	SOI	1	0.28 $\pm$ 0.09	0.59	10.35	0.009
	Error <sup>b</sup>	10		0.06		
Fledgling mass <sup>c</sup>	Adult density	1	-0.009 $\pm$ 0.004	0.09	4.86	0.06
	Nest predation rate	1	-1.13 $\pm$ 0.41	0.13	7.39	0.02
	SOI	1	0.17 $\pm$ 0.05	0.19	10.75	0.009
	Error <sup>d</sup>	9		0.02		

Note: Fledgling mass data were lacking for 1987. See Methods for description of independent variables.

<sup>a</sup>Intercept = 6.24  $\pm$  0.35

<sup>b</sup>Durbin-Watson  $d = 2.14, p = 0.57$

<sup>c</sup>Intercept = 8.64  $\pm$  0.19

<sup>d</sup>Durbin-Watson  $d = 1.57, p = 0.17$

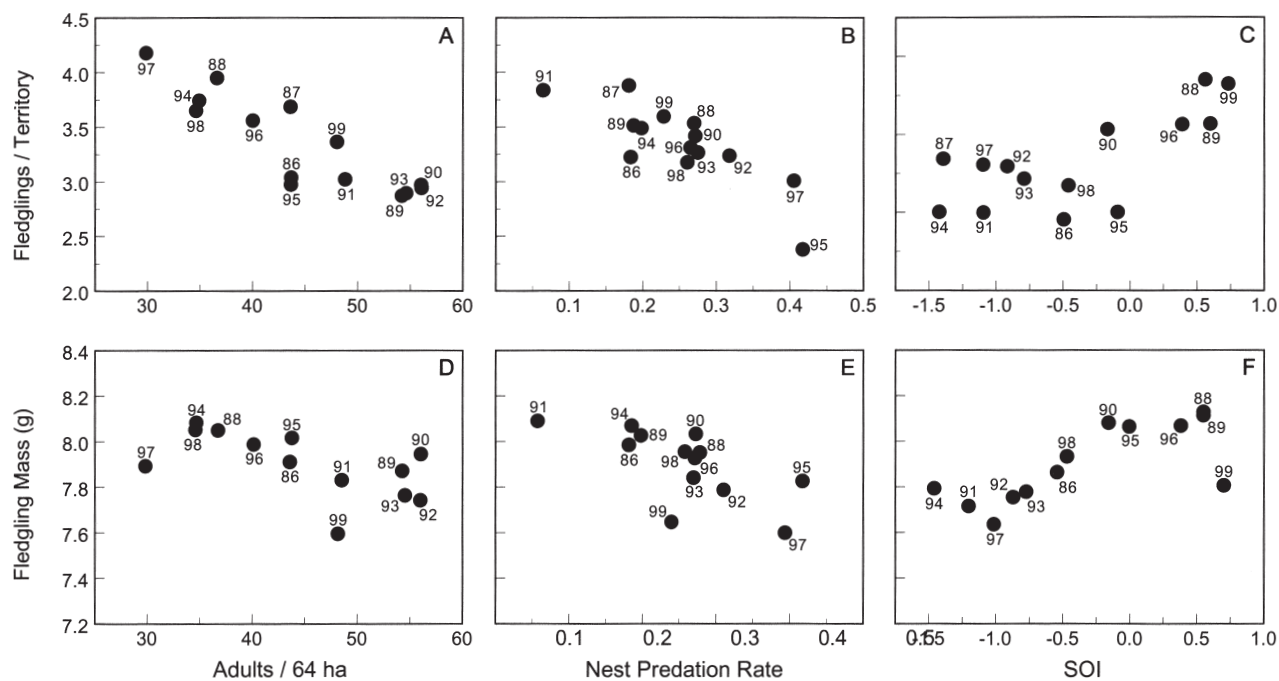


Fig. 32.3. Warbler density, nest predation rate, and ENSO phase explained 91% of the variation in mean number of Black-throated Blue Warbler young fledged per territory from 1986 to 1999 (partial regression leverage plots: A–C) and 80% of the variation in mean annual fledgling mass (partial regression leverage plots: D–F). ENSO phase for each year is represented by annual mean monthly values of the Southern Oscillation Index, or SOI (see Methods). Numbers by points indicate year. Fledgling mass data were lacking for 1987. Test statistics and parameter estimates for the two multiple regression models are given in table 33.3.

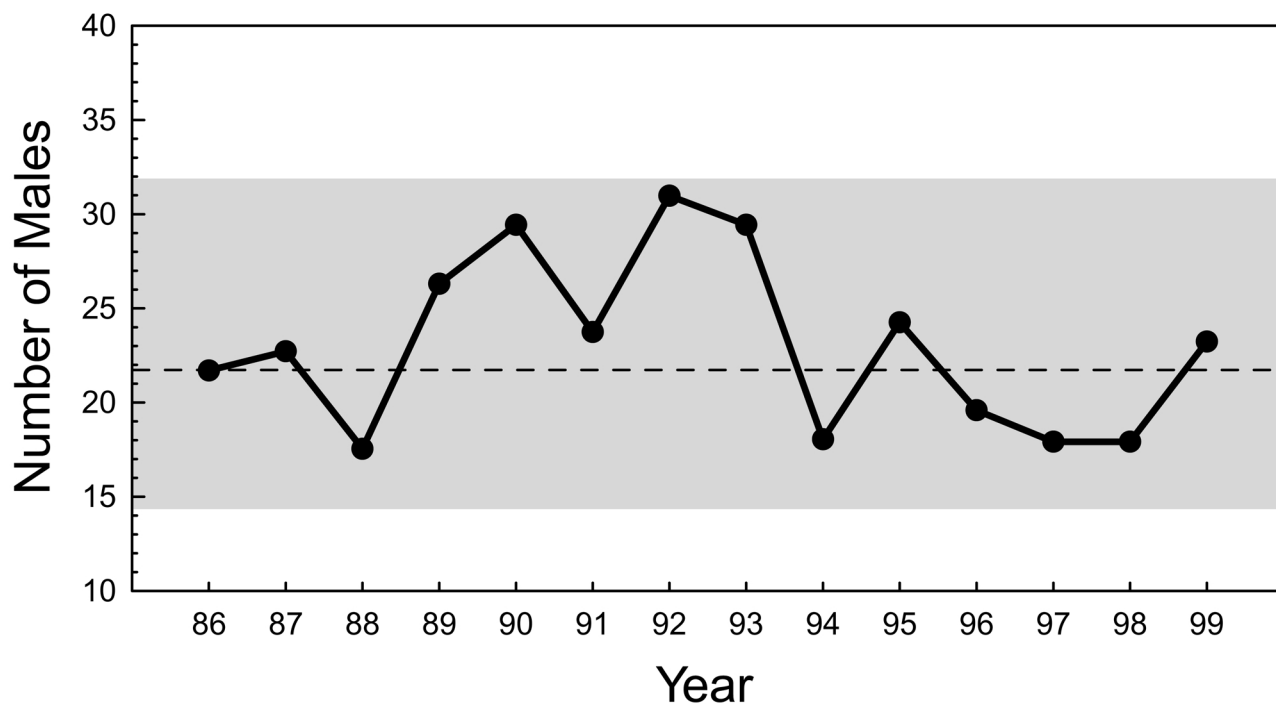


Fig. 32.4. Number of male Black-throated Blue Warblers recorded on a 64-ha plot at Hubbard Brook Experimental Forest, New Hampshire from 1986 to 1999 (solid line with • symbols) compared with output generated by a single sex; stochastic Leslie matrix model parameterized with estimates in table 33.1. The gray region indicates the 95% confidence interval for the model population at year 50. The dashed line gives mean population size from 1,000 model iterations. See Results for further details.

tors because their impact on fecundity was not related to warbler density. Similarly, the factors that determine annual survival rates of adults on our study plot were not density-dependent. Warbler abundance was regulated by the effect of breeding season population density on fledgling success and possibly by the effect of population density on fledgling mass. Recruitment of yearling breeders each May, and hence local population size, was in turn correlated with both fecundity (Sillett et al. 2000) and warbler density in the preceding summer (fig. 32.1D). Multiple regression indicates that the fecundity of this population was strongly affected by density-dependent and density-independent processes. Adult density appeared to have the greatest effect on warbler fledgling success, whereas fledgling mass was most influenced by density-independent factors.

Density-dependent fecundity is a result of multiple demographic processes that determine the quantity and quality of offspring produced. Several factors could result in more young being produced at low density, such as larger clutch sizes (reviewed by Newton 1998), increased levels of bigamy, and higher frequency of double brooding (Kluyver 1971; Both 1998a). Fledgling quality (e.g., as indicated by fledgling mass) is thought to be negatively associated with density because of competition for limited food (Gaston 1985; Both 1998a; Both et al. 1999). For Black-throated Blue Warblers, density-dependent fledgling production was probably related to a declining probability of double brooding as density increased (see Results). Double brooding has a major effect on the seasonal fecundity of this warbler population (Nagy 2002). Fledgling mass in Black-throated Blue Warblers may be limited in part by food (Rodenhouse and Holmes 1992), but we found no direct correlation between warbler density and caterpillar abundance in this study.

Although many studies have documented density dependence in passerine birds (Sinclair 1989; Newton 1998; Paradis et al. 2002), few have examined whether the density-dependent processes measured can actually regulate abundance within meaningful boundaries. Model results given here show that density-dependent fledgling success can regulate local abundance of Black-throated Blue Warblers within observed levels of variation observed in our study area. Density-dependent fecundity has also been shown to regulate populations of Great Tits (*Parus major*) and Song Sparrows (*Melospiza melodia*), although density-dependent juvenile survival and recruitment were of equal or greater importance for these populations (Pennycuick 1969; Klomp 1980; Arcese et al. 1992). For Willow Tits (*Parus montanus*) breeding in Sweden, density-dependent survival of yearlings was the only feedback mechanism capable of regulating population size (Ekman 1984). McCallum et al. (2000) used a simulation model to show that abundance of a tropical resident species, the Gray-breasted Silveryeye (*Zosterops lateralis*) on Heron Island in Australia, is regulated by a density-dependent process, possibly juvenile survival. Estimating juvenile survival for migratory passerines is difficult and has only been done in a few studies (e.g., Anders et al. 1997). Although we lack such data for Black-throated Blue War-

blers, we suspect that the Hubbard Brook population could also be weakly regulated by density-dependent juvenile survival, because fledgling mass is density-dependent (fig. 32.3D, table 32.2), and because fledgling mass is often correlated with first-year survival (Newton 1998).

Variance in fledgling success of Black-throated Blue Warblers did not vary with density (see fig. 32.2) on our study plot. This implies that all individuals on the plot were affected equally by population density (Ferrer and Donazar 1996; Both 1998b). Furthermore, this result suggests that a crowding mechanism (Newton 1998; Rodenhouse et al. 1999) based on intraspecific resource competition may be the primary factor regulating fecundity, and thus local abundance, in areas of relatively homogeneous habitat.

Natural enemies are another factor that can limit bird populations, and many studies have demonstrated density-dependent rates of nest predation (Martin 1996; Newton 1998), brood parasitism (Arcese et al. 1992; Soler et al. 1998), and disease (Moss et al. 1990; Hochachka and Dhondt 2000). Our analysis of long-term demographic data indicate that nest predation is not density-dependent, and is thus not likely to be an important regulatory mechanism for the Black-throated Blue Warbler population at Hubbard Brook. This conclusion is further supported by Reitsma (1992), who found no evidence for density-dependent depredation of artificial nests in the shrub layer at Hubbard Brook. Brown-headed Cowbird (*Molothrus ater*) eggs have never been recorded in nests at Hubbard Brook, indicating that brood parasitism is not a factor affecting our study population. We have no data on parasitism by invertebrates such as *Protocalliphora* flies or on infection by disease organisms.

The results from this study demonstrate that the abundance of Black-throated Blue Warblers can be regulated by breeding-ground events. However, we do not contend that events during other phases of the annual cycle are unimportant to population dynamics. Abundance of migratory birds is certainly determined in part by density-dependent processes during the nonbreeding season. In particular, physical condition and thus survival of overwintering songbirds are likely to be affected by an interaction between population density and habitat availability because: (1) high-quality habitat on winter quarters appears to be limiting (Rappole and McDonald 1994; Sherry and Holmes 1995, 1996; Latta and Baltz 1997; Marra et al. 1998), (2) many species are strongly territorial, and (3) dominant individuals acquire the best territory sites (Marra 2000; Marra and Holmes 2001). Competitor density could also influence physical condition of migrating birds at stopover sites (Moore and Young 1991; Kelly et al. 2002).

Density-independent limiting factors, especially climatic fluctuations, also have important effects on adult and juvenile survival in the nonbreeding season (Baillie and Peach 1992; Sillett et al. 2000) and could overwhelm density-dependent processes. For example, matrix elasticity analyses (Caswell 2001) indicate that population growth rate and equilibrium population size in Black-throated Blue Warblers are most strongly affected by adult survival (Sillett 2000),



which we have shown here to be density-independent. A factor that dramatically limits future adult survival could therefore have a greater influence on warbler population dynamics than density-dependent fecundity. This scenario is likely to have the strongest effect on population size if the rate of winter habitat destruction increases (see Sutherland 1996, 1998).

Because of well-documented population declines, temperate-tropical migratory birds have been the focus of much research on reproductive ecology and habitat selection. Nevertheless, basic demographic information is lacking for most species, data which are needed to parameterize models to assist in species management and conservation (Sherry and Holmes 1995). This study provides evidence that fecundity of at least one species of temperate-tropical migrant is influenced by conspecific density within breeding habitat and that this density dependence can regulate abundance within boundaries observed in the field. Knowledge of density dependence, and of the functional form of density-dependent relationships, is required to make accurate predictions regarding population viability and the response of populations to habitat change (May 1986; Sæther et al. 1998; Runge and Johnson 2002). As a caveat to the above, it is important to note that the relationships between density and demographic rates that we present here come from a source population (Holmes et al. 1996) breeding in fairly uniform, high-quality habitat. The strength of density-dependent processes is unknown for populations breeding in more heterogeneous environments or for sink populations breeding in suboptimal habitat.

## ACKNOWLEDGMENTS

This research was funded by the U.S. National Science Foundation, Sigma Xi, and the Cramer Fund of Dartmouth College. We are grateful to the dozens of people who helped with fieldwork, especially J. Barg, P. Marra, N. Rodenhouse, T. Sherry, and M. Webster. This chapter benefited from the advice and comments of M. Ayres, D. Bolger, B. Dunning, A. Dhondt, P. Doran, G. Hood, P. Marra, M. McPeck, S. Morrison, L. Nagy, N. Rodenhouse, T. Sherry, A. Strong, and S. Zens. We thank the Hubbard Brook Experimental Forest of the U.S. Department of Agriculture Northeastern Research Station for their cooperation.

## LITERATURE CITED

- Anders, A. D., D. C. Dearborn, J. Faaborg, and F. R. Thompson. 1997. Juvenile survival in a population of Neotropical migrant birds. *Conservation Biology* 11:698–707.
- Arcese, P., J. N. M. Smith, W. M. Hochachka, C. M. Rogers, and D. Ludwig. 1992. Stability, regulation, and the determination of abundance in an insular Song Sparrow population. *Ecology* 73:805–822.
- Askins, R. A. 2000. *Restoring North America's Birds: Lessons from Landscape Ecology*. Yale University Press, New Haven.
- Askins, R. A., J. F. Lynch, and R. Greenberg. 1990. Population declines in migratory birds in eastern North America. *Current Ornithology* 7:1–57.
- Baillie, S. R., and W. J. Peach. 1992. Population limitation in Palearctic-African migrant passerines. *Ibis* 134:120–132.
- Begon, M., J. L. Harper, and C. R. Townsend. 1996. *Ecology*. Blackwell Scientific, Boston.
- Bormann, F. H., and G. E. Likens. 1979. *Pattern and Process in a Forested Ecosystem*. Springer-Verlag, New York.
- Both, C. 1998a. Experimental evidence for density dependence of reproduction in Great Tits. *Journal of Animal Ecology* 67:667–674.
- Both, C. 1998b. Density dependence of clutch size: habitat heterogeneity or individual adjustment? *Journal of Animal Ecology* 67:659–666.
- Both, C., M. E. Visser, and N. Verboven. 1999. Density-dependent recruitment rates in Great Tits: the importance of being heavier. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 266:465–469.
- Burnham, K. P., and D. R. Anderson. 1998. *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society Monograph* 5.
- Caswell, H. 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Sunderland, Mass.
- Chamberlain, C. P., J. D. Blum, R. T. Holmes, X. H. Feng, T. W. Sherry, and G. R. Graves. 1997. The use of isotope tracers for identifying populations of migratory birds. *Oecologia* 109:132–141.
- Ekman, J. 1984. Stability and persistence of an age-structured avian population in a seasonal environment. *Journal of Animal Ecology* 53:135–146.
- Ferrer, M., and J. A. Donazar. 1996. Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish Imperial Eagles. *Ecology* 77:69–74.
- Ford, R. G., and J. P. Myers. 1981. An evaluation and comparison of techniques for estimating home range and territory size. *Studies in Avian Biology* 6:461–465.
- Gaston, A. J. 1985. Development of young in the Atlantic Alcidae. Pages 319–354 in *The Atlantic Alcidae* (D. N. Nettleship and T. R. Birkhead, eds.). Academic Press, London.
- Hilborn, R., and M. Mangel. 1997. *The Ecological Detective: Confronting Models with Data*. Princeton University Press, Princeton.
- Hixon, M. A., S. W. Pacala, and S. A. Sandin. 2002. Population regulation: historical context and contemporary challenges of open vs. closed systems. *Ecology* 83:1490–1508.
- Hochachka, W. M., and A. A. Dhondt. 2000. Density-dependent decline of host abundance resulting from a new infectious disease. *Proceedings of the National Academy of Sciences USA* 97:5303–5306.
- Holmes, R. T. 1990. The structure of a temperate deciduous forest bird community: variability in time and space. Pages 121–139 in *Biogeography and Ecology of Forest Bird Communities* (A. Keast, ed.). Academic Publishing, The Hague, The Netherlands.
- Holmes, R. T. 1994. Black-throated Blue Warbler (*Dendroica caerulescens*). Pages 1–24 in *The Birds of North America*,

- no. 87 (A. Poole and F. Gill, eds.). Academy of Natural Sciences, Philadelphia.
- Holmes, R. T., P. P. Marra, and T. W. Sherry. 1996. Habitat-specific demography of breeding Black-throated Blue Warblers (*Dendroica caerulescens*): implications for population dynamics. *Journal of Animal Ecology* 65:183–195.
- Holmes, R. T., and J. C. Schultz. 1988. Food availability for forest birds: effects of prey distribution and abundance on bird foraging. *Canadian Journal of Zoology* 66:720–728.
- Holmes, R. T., and T. W. Sherry. 2001. Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. *Auk* 118:589–610.
- Holmes, R. T., T. W. Sherry, P. P. Marra, and K. E. Petit. 1992. Multiple brooding and productivity of a Neotropical migrant, the Black-throated Blue Warbler (*Dendroica caerulescens*), in an unfragmented temperate forest. *Auk* 109:321–333.
- Holmes, R. T., T. W. Sherry, and L. Reitsma. 1989. Population structure, territoriality and overwinter survival of two migrant warbler species in Jamaica. *Condor* 91:545–561.
- Holmes, R. T., and F. W. Sturges. 1975. Bird community dynamics and energetics in a northern hardwoods ecosystem. *Journal of Animal Ecology* 44:175–200.
- Hood, G. 2000. PopTools, Version 2.06. [www.dwe.csiro.au/vbc/poptools/](http://www.dwe.csiro.au/vbc/poptools/).
- Kelly, J. F., L. S. DeLay, and D. M. Finch. 2002. Density-dependent mass gain by Wilson's Warblers during stopover. *Auk* 119:210–213.
- Kiladis, G. N., and H. F. Diaz. 1989. Global climate anomalies associated with the Southern Oscillation. *Journal of Climate* 2:1069–1090.
- Kimura, M., S. M. Clegg, I. J. Lovette, K. R. Holder, D. J. Girman, B. Mila, P. Wade, and T. B. Smith. 2002. Phylogeographical approaches to assessing demographic connectivity between breeding and overwintering regions in a Nearctic–Neotropical warbler (*Wilsonia pusilla*). *Molecular Ecology* 11:1605–1616.
- Klomp, H. 1980. Fluctuations and stability in Great Tit populations. *Ardea* 68:205–224.
- Kluyver, H. N. 1971. Regulation of numbers in populations of Great Tits (*Parus m. major* L.). Pages 507–524 in *Dynamics of Populations* (P. J. den Boer and G. R. Gradwell, eds.). Center for Agricultural Publishing and Documentation, Wageningen.
- Latta, S. C., and M. E. Baltz. 1997. Population limitation in neotropical migratory birds: comments. *Auk* 114:754–762.
- Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- Lebreton, J.-D., and J. Clobert. 1991. Bird population dynamics, management, and conservation: the role of mathematical modeling. Pages 105–125 in *Bird Population Studies: Relevance to Conservation and Management* (C. M. Perrins, J.-D. Lebreton, and G. J. N. Harens, eds.). Oxford University Press, Oxford.
- Marra, P. P. 2000. The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. *Behavioral Ecology* 11:299–308.
- Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282:1884–1886.
- Marra, P. P., and R. T. Holmes. 2001. Consequences of dominance-mediated habitat segregation in American Redstarts during the nonbreeding season. *Auk* 107:96–106.
- Martin, T. E. 1996. Fitness costs of resource overlap among coexisting bird species. *Nature* 380:338–340.
- May, R. M. 1986. When two and two do not make four: nonlinear phenomena in ecology. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 228:241–266.
- McCallum, H., J. Kikkawa, and C. Catterall. 2000. Density dependence in an island population of silvereyes. *Ecology Letters* 3:95–100.
- Microsoft Corporation. 1999. Excel 2000. Microsoft Corporation, Redmond, Wash.
- Montroy, D. L., M. B. Richman, and P. J. Lamb. 1998. Observed nonlinearities of monthly teleconnections between tropical Pacific sea surface temperature anomalies and central and eastern North American precipitation. *Journal of Climate* 11:1812–1835.
- Moore, F. R., and W. Young. 1991. Evidence of food-based competition among passerine migrants during stopover. *Behavioral Ecology and Sociobiology* 28:85–90.
- Moss, R., I. B. Trenholm, A. Watson, and R. Parr. 1990. Parasitism, predation and survival of hen Red Grouse *Lagopus lagopus scoticus* in spring. *Journal of Animal Ecology* 59:631–642.
- Murdoch, W. W. 1994. Population regulation in theory and practice. *Ecology* 75:271–287.
- Nagy, L. R. 2002. Causes and consequences of individual variation in reproductive output in a forest-dwelling Neotropical migrant songbird. Ph.D. dissertation, Dartmouth College, Hanover, N.H.
- Newton, I. 1998. *Population Limitation in Birds*. Academic Press, London.
- Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory. 2002. Exploring density-dependent relationships in demographic parameters in populations of birds at a large spatial scale. *Oikos* 97:293–307.
- Peach, W. J., S. R. Baillie, and D. E. Balmer. 1998. Long-term changes in the abundance of passerines in Britain and Ireland as measured by constant effort mist-netting. *Bird Study* 45:257–275.
- Pennycuik, L. 1969. A computer model of the Oxford Great Tit population. *Journal of Theoretical Biology* 22:381–400.
- Peterjohn, B. G., J. S. Sauer, and C. S. Robbins. 1995. Population trends from the North American Breeding Bird Survey. Pages 3–39 in *Ecology and Management of Neotropical Migratory Birds: A Synthesis and Review of Critical Issues* (T. E. Martin and D. M. Finch, eds.). Oxford University Press, New York.
- Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture-recapture experiments. *Wildlife Monographs* 107:1–97.
- Pyle, P., S. N. G. Howell, R. P. Yunick, and D. F. DeSante. 1987. *Identification Guide to North American Passerines*. Slate Creek Press, Bolinas, Calif.
- Rappole, J. H., and M. V. McDonald. 1994. Cause and effect in population declines of migratory birds. *Auk* 111:652–660.
- Rawlings, J. O. 1988. *Applied Regression Analysis*. Wadsworth, Pacific Grove, Calif.
- Reitsma, L. 1992. Is nest predation density dependent? A test using artificial nests. *Canadian Journal of Zoology* 70:2498–2500.

- Robbins, C. S., J. R. Sauer, R. S. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the Neotropics. *Proceedings of the National Academy of Sciences USA* 86:7658–7662.
- Robinson, S. K., and R. T. Holmes. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. *Ecology* 63:1918–1931.
- Rodenhouse, N. L. 1986. Food limitation for forest passerines: effects of natural and experimental food reductions. Ph.D. dissertation, Dartmouth College, Hanover, N.H.
- Rodenhouse, N. L. 1992. Potential effects of climatic change on a Neotropical migrant landbird. *Conservation Biology* 6:263–272.
- Rodenhouse, N. L., and R. T. Holmes. 1992. Results of experimental and natural food reductions for breeding Black-throated Blue Warblers. *Ecology* 73:357–372.
- Rodenhouse, N. L., T. W. Sherry, and R. T. Holmes. 1999. Multiple mechanisms of population regulation: contributions of site dependence, crowding, and age structure. Pages 2939–2952 in *Proceedings of the 22nd International Ornithological Congress* (N. J. Adams and R. H. Slotow, eds.).
- Rodenhouse, N. L., T. S. Sillett, P. J. Doran, and R. T. Holmes. In review[AQ2]. Regulation of a migratory bird population by multiple density dependence mechanisms. *Proceedings of the Royal Society of London, Series B, Biological Sciences*.
- Ropelewski, C. F., and M. S. Halpert. 1986. North American precipitation and temperature patterns associated with the El Niño Southern Oscillation (ENSO). *Monthly Weather Review* 114:2352–2362.
- Royama, T. 1977. Population persistence and density dependence. *Ecological Monographs* 47:1–35.
- Rubenstein, D. R., C. P. Chamberlain, R. T. Holmes, M. P. Ayres, J. R. Waldbauer, G. R. Graves, and N. C. Tuross. 2002. Linking breeding and wintering ranges of a migratory songbird using stable isotopes. *Science* 295:1062–1065.
- Runge, M. C., and F. A. Johnson. 2002. The importance of functional form in optimal control solutions of problems in population dynamics. *Ecology* 83:1357–1371.
- Sall, J. P. 1990. Leverage plots for general linear hypotheses. *American Statistician* 44:303–315.
- SAS Institute. 2000. JMP, Version 4. SAS Institute, Cary, N.C.
- Sæther, B.-E., S. Engen, A. Islam, R. McCleery, and C. Perrins. 1998. Environmental stochasticity and extinction risk in a population of a small songbird, the Great Tit. *American Naturalist* 151:441–450.
- Sherry, T. W., and R. T. Holmes. 1995. Summer versus winter limitation of populations: what are the issues and what is the evidence. Pages 85–120 in *Ecology and Management of Neotropical Migratory Birds: A Synthesis and Review of Critical Issues* (T. E. Martin and D. M. Finch, eds.). Oxford University Press, New York.
- Sherry, T. W., and R. T. Holmes. 1996. Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. *Ecology* 77:36–48.
- Sillett, T. S. 2000. Long-term demographic trends, population limitation, and the regulation of abundance in a migratory songbird. Ph.D. dissertation, Dartmouth College, Hanover, N. H.
- Sillett, T. S., and R. T. Holmes. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296–308.
- Sillett, T. S., R. T. Holmes, and T. W. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* 288:2040–2042.
- Sinclair, A. R. E. 1989. Population regulation in animals. Pages 197–241 in *Ecological Concepts: The Contribution of Ecology to an Understanding of the Natural World* (J. Cherrett, ed.). 29th Symposium of the British Ecological Society. Blackwell, Oxford.
- Sokal R. R., and F. J. Rohlf. 1995. *Biometry: The Principles and Practice of Statistics in Biological Research* (third ed.). W. H. Freeman and Co., San Francisco.
- Soler, M., J. J. Soler, J. G. Martinez, T. Perez-Contreras, and A. P. Møller. 1998. Micro-evolutionary change and population dynamics of a brood parasite and its primary host: the intermittent arms race hypothesis. *Oecologia* 117:381–390.
- Sutherland, W. J. 1996. Predicting the consequences of habitat loss for migratory populations. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 263:1325–1327.
- Sutherland, W. J. 1998. The effect of local change in habitat quality on populations of migratory species. *Journal of Applied Ecology* 35:418–421.
- Terborgh, J. 1989. *Where Have All the Birds Gone?* Princeton University Press, Princeton.
- Turchin, P. 1995. Population regulation: old arguments and a new synthesis. Pages 19–40 in *Population Dynamics: New Approaches and Synthesis* (N. Cappuccino and P. W. Price, eds.). Academic Press, San Diego.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–139.