

EXPERIMENTALLY REDUCING NEIGHBOR DENSITY AFFECTS REPRODUCTION AND BEHAVIOR OF A MIGRATORY SONGBIRD

T. SCOTT SILLETT,^{1,3} NICHOLAS L. RODENHOUSE,² AND RICHARD T. HOLMES¹

¹Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755 USA

²Department of Biological Sciences, Wellesley College, Wellesley, Massachusetts 02181 USA

Abstract. Because populations of territorial birds are relatively stable compared to those of other animal taxa, they are often considered to be tightly regulated. However, the mechanisms that produce density-dependent feedbacks on demographic rates and thus regulate these populations are poorly understood, particularly for migratory species. We conducted a three-year density-reduction experiment to investigate the behavioral mechanisms that regulate the abundance of a Nearctic–Neotropical migrant passerine, the Black-throated Blue Warbler (*Dendroica caerulescens*), during the breeding season. We found that the number of young fledged per territory, territory size, and the proportion of time males spent foraging were significantly greater on territories around which neighbor density was experimentally reduced compared to control territories. Territory quality, proportion of nests depredated per territory, and male countersinging rates were not statistically different between treatments. These results indicate that individuals with more neighbors (i.e., in neighborhoods with greater conspecific density) have reduced breeding productivity. The results also suggest that a crowding mechanism that mediates interactions among territory-holders could generate the density dependence needed to regulate local abundance, at least in areas of homogeneous, high-quality habitat. The effect of the neighbor-density reduction on warbler fecundity and behavior varied with annual fluctuations in weather and food availability, and was strongest in 1997, an El Niño year, when conditions for breeding were least favorable. This variation in our experimental results among years implies that density dependence due to crowding may have its strongest impact on local abundance when environmental conditions are relatively poor.

Key words: Black-throated Blue Warbler; *Dendroica caerulescens*; density dependence; Hubbard Brook Experimental Forest; Nearctic–Neotropical migratory birds; neighbor density; population regulation; territorial behavior.

INTRODUCTION

The identification of regulatory mechanisms and the strength of density dependence is critical to understanding and managing natural populations (Murdoch 1994, Hixon et al. 2002, Runge and Johnson 2002). However, research on population regulation has focused primarily on measuring density dependence, whereas the proximate mechanisms by which density can affect demographic rates are less well understood (Sinclair 1989, Krebs 1991, Mylius and Diekmann 1995, Ferrer and Donazar 1996, Rodenhouse et al. 1997, May 1999, Turchin 1999, Hixon et al. 2002). Indeed, direct evidence of regulation and of the action of regulatory mechanisms remains elusive, despite several decades of research. This is due, in part, to the scarcity of long-term data (Sinclair 1989, Newton 1998) and to the rarity of experimental perturbations of density (Murdoch 1994, Harrison and Cappuccino

1995, Krebs 2002). Experimental manipulations are often necessary to disentangle the interactions of multiple limiting and regulatory processes on population size (Turchin 1995, den Boer and Reddingius 1996, Moss et al. 1996, Rodenhouse et al. 1999). For example, the intensity of intraspecific competition may be density dependent, but its effect on population size may be weak and overwhelmed by a stronger density-independent process, such as climate variation.

Populations of territorial birds appear to be tightly regulated because they are relatively stable compared to those of other animal taxa (Hanski and Tiainen 1989, Murdoch 1994). Many studies of density dependence in territorial birds assume that a crowding mechanism regulates abundance (Dhondt et al. 1992, Rodenhouse et al. 1997, 1999, Bonsall et al. 1998). Resource competition associated with crowding is the basis of density-dependent regulation as described by Lack (1954, 1966) and Fretwell and Lucas (1970). Under a crowding mechanism, regulation could be accomplished through density-dependent interactions between crowded individuals and their natural enemies, such as predators (e.g., Martin 1996) or disease organisms (e.g., Hochachka and Dhondt 2000), or through a density-dependent increase in agonistic interactions among

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³ Present address: Smithsonian Migratory Bird Center, National Zoological Park, Washington, D.C. 20008 USA. E-mail: silletts@si.edu

crowded conspecifics; both processes can decrease demographic rates. The ultimate causes of agonistic interactions include competition for limited resources such as food (Newton 1998), territory space (McCleery and Perrins 1985, Stamps 1990, Mougeot et al. 2003), nest sites (Brawn and Balda 1988), and mating opportunities (Chuang-Dobbs et al. 2001). Crowding probably has the strongest regulatory effect where species exist at high densities in relatively homogenous habitat.

Crowding during the breeding season could amplify resource limitation for adult birds and their young by reducing territory size, by increasing time spent in agonistic interactions and thus reducing time spent foraging or provisioning young, or by a combination of these factors. The best evidence in passerines for density-dependent feedbacks caused by crowding during the breeding period comes from species using nest boxes (Alatalo and Lundberg 1984, Stenning et al. 1988, Torok and Toth 1988, Perrins 1990, Both 1998a) or from those confined to islands (e.g., Arcese et al. 1992, McCallum et al. 2000). Although these studies indicate that density-dependent feedbacks can occur, they do not identify the mechanisms by which crowding reduces fecundity. Furthermore, the presence of density-dependent negative feedbacks generated by crowding during the breeding season has not been determined or experimentally tested in open-cup-nesting passerines.

In this paper, we examine the effect of neighbor density on the demography and behavior of a Nearctic–Neotropical migrant songbird, the Black-throated Blue Warbler (*Dendroica caerulescens*), and discuss its role in population regulation. This research was motivated by several lines of evidence that indicated that our study population in New Hampshire, USA was regulated and that a key mechanism involved was crowding-induced resource competition during the breeding season. First, Black-throated Blue Warbler abundance has been relatively stable and has not shown any directional trend at our study site since 1969, a period of more than 30 years (Holmes and Sherry 2001). Second, population growth rate and multiple measures of annual warbler fecundity (mean number of young fledged per territory, mean fledgling mass, and proportion of territories with females attempting second broods, but not mean clutch sizes of first- or second-brood nests) were strongly and negatively correlated with local population density (Rodenhouse et al. 2003, Sillett and Holmes, *in press*). Third, density-dependent fledging success, as illustrated by simulation models parameterized with field data, is sufficient to constrain abundance within the range observed on the study area (Sillett and Holmes, *in press*). Fourth, Black-throated Blue Warblers are highly territorial during the breeding season (Holmes 1994), and forage almost exclusively on their territories. Fifth, annual fecundity is limited, in part, by food availability (Rodenhouse and Holmes 1992, Sillett et al. 2000, Nagy 2002). Sixth, predation on Black-throated Blue Warbler nests, although an im-

portant factor limiting annual fecundity, does not appear to be density dependent at Hubbard Brook (Reitsma 1992, Sillett and Holmes, *in press*). Finally, variance in warbler fledging success does not increase with population density on our 150-ha study area (Sillett and Holmes, *in press*), suggesting that all individuals breeding here are affected equally by density-dependent processes (see Ferrer and Donazar 1996, Both 1998a).

We present the results of a three-year density-reduction experiment designed to test if crowding is an important mechanism regulating Black-throated Blue Warbler abundance. At the start of our experiment, we hypothesized that the number of neighbors (i.e., local neighbor density) would affect reproductive output and breeding behavior of Black-throated Blue Warblers. We predicted that: (1) territories with a reduced number of neighbors would fledge more young than control territories; (2) territories would be larger in the reduced-density treatment; (3) nest predation rates would not differ between treatments; (4) levels of male–male interactions would be lower at reduced density, enabling these males to spend more time foraging; and (5) parental feeding rates of nestlings would be higher in the reduced-density treatment. As a corollary of prediction 5, we predicted that fledgling mass would be greater in the reduced-density treatment. We analyze and discuss differences in warbler fecundity, behavior, and territory quality between control territories and territories around which the density of neighboring conspecifics was experimentally reduced. We consider these results in relation to annual variation in weather and food availability during the three years of our study.

METHODS

Study site and species

Field research was conducted from May to August 1997–1999 in the 3160-ha Hubbard Brook Experimental Forest in Woodstock, New Hampshire, USA. The forest was extensively logged in the early 1900s. Our gridded, 150-ha study site extended from 520 to 610 m above sea level on one south-facing hillside. This site represented high-quality, high-density breeding habitat for Black-throated Blue Warblers (Holmes et al. 1996), with each warbler pair having 4–6 neighboring conspecific pairs. The relatively homogeneous vegetation on the study site consisted of a 20–25 m tall canopy of American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*), and a thick understory dominated by hobblebush (*Viburnum alnifolium*), striped maple (*A. pensylvanicum*), and beech saplings. Further details on characteristics of the study site can be found in Holmes et al. (1996) and Holmes and Sherry (2001).

The Black-throated Blue Warbler is a common breeder in hardwood forests of northern New England

TABLE 1. Interannual variation in climate, clutch completion dates, and food abundance for Black-throated Blue Warblers at Hubbard Brook Experimental Forest, New Hampshire, USA, 1997–1999. Except where noted, values are given as means \pm 1 SE.

Year	Mean daily temperature, May ($^{\circ}$ C) [†]	Total rainfall, June (mm) [†]	Mean clutch completion date [‡]	Mean caterpillar biomass (mg) [§]
1997	6.5 \pm 1.6	79.5	170.4 \pm 3.7	8.4 \pm 2.0
1998	13.3 \pm 2.2	325.0	154.1 \pm 3.2	6.0 \pm 1.1
1999	12.8 \pm 2.5	78.6	154.3 \pm 1.8	13.5 \pm 2.5
Long-term mean	11.5 \pm 0.5	89.7 \pm 6.4	158.3 \pm 1.7 [¶]	11.5 \pm 1.4 [¶]

[†] Climate data obtained by scientists of the Hubbard Brook Ecosystem Study [Online, URL: (<http://www.hubbardbrook.org>)]. The Hubbard Brook Experimental Forest is operated and maintained by the Northeastern Research Station, U.S. Dept. of Agriculture, Newtown Square, Pennsylvania, USA.

[‡] Julian date for first clutches, where day 1 = 1 January.

[§] Mean dry biomass of caterpillars/200 American beech and sugar maple leaves recorded at 40 points; biomass data were collected during four biweekly surveys (once every two weeks) from late May to late July (see Rodenhouse et al. 1992, Jones et al. 2003) and were summed for each point.

^{||} 50-year mean.

[¶] Mean for 1986–1999.

(Holmes 1994). This sexually dichromatic species is insectivorous and males defend exclusive, non-overlapping territories during the breeding season. At Hubbard Brook, Black-throated Blue Warblers are multiple-brooded and socially monogamous, although 5–10% of males are bigamous in an average year (Holmes et al. 1992; T. S. Sillett, N. L. Rodenhouse, and R. T. Holmes, *unpublished data*). Females build nests in understory shrubs and incubate eggs; mean and modal clutch size is 4 (Holmes 1994). Both parents feed nestlings and fledglings. Adults have strong fidelity to breeding territories between years (Holmes 1994), but natal dispersal is high, judging from the low return rate of fledglings banded on the study plot (T. S. Sillett, N. L. Rodenhouse, and R. T. Holmes, *unpublished data*). Nevertheless, reproductive success of warblers breeding on our site each year is significantly and positively correlated with the number of yearling recruits in the following spring (Sillett et al. 2000), indicating that our study population is representative of warbler population dynamics occurring at a larger, regional scale (see also Jones et al. 2003).

Weather and warbler food availability on our study site differed dramatically between the 1997 through 1999 breeding seasons (Table 1), and this natural environmental variation formed an important backdrop for our research. In 1997, an El Niño year, conditions for Black-throated Blue Warblers were least favorable (Sillett et al. 2000, Sillett and Holmes, *in press*). Mean daily temperature in May was lower in 1997 than in either 1998 or 1999, or in any year since 1986, and this resulted in a later mean date of first clutch completion (Table 1). Mean food availability in 1997 was also lower than average. In June 1998, record-high rainfall was recorded in many parts of New Hampshire (Bell et al. 1999). At Hubbard Brook, approximately four times as much rain fell in June 1998, the height of the Black-throated Blue Warbler breeding season,

compared to either 1997, 1999, or the 50-year mean (Table 1). Mean food availability in 1998 was the lowest of the three years. In 1999, La Niña conditions predominated, food was most abundant, and the weather was most benign (Table 1).

Experimental design and field methods

Our experimental design built upon prior research at Hubbard Brook, which demonstrated that the territory space occupied by a Black-throated Blue Warbler pair remained empty for an entire breeding season if both the female and male were permanently removed after the end of spring migration (Marra and Holmes 1997). Thus, by removing already settled pairs of warblers in late May and early June, we were able to create two neighbor-density treatments: a reduced-density treatment in which we removed all conspecifics whose territories abutted those of focal pairs, and a control consisting of focal territories with a normal, high density of neighbors. Control ($n = 9$ in 1997; $n = 12$ in 1998; $n = 11$ in 1999) and reduced-density territories ($n = 4$ /yr) were randomly selected from those present on the 150-ha study plot. Warbler density was not manipulated within a 64-ha section of the plot to avoid compromising an ongoing, long-term population study (see Holmes et al. 1992, 1996, Holmes and Sherry 2001, Sillett and Holmes 2002, *in press*). Control territories were separated from areas where density was reduced by at least one and usually several intervening, occupied territories. Focal territories for the reduced-density treatment were chosen after a preliminary 3–5 day survey to map locations of all countersinging males. In this treatment, conspecific pairs on territories adjoining those of focal pairs were permanently removed by shotgun under approval from the Institutional Animal Care and Use Committee, Dartmouth College (protocol number 96-09-07) and from appropriate federal and state agencies. Removals were conducted during nest-

building and laying, with a few pairs being removed during early incubation, and were completed by early June. After removals were completed, adults were captured in mist nets, individually marked with a unique combination of one numbered aluminum leg band and two colored plastic leg bands, and aged as either second-year (SY) or after second-year (ASY) using plumage characters. However, we did not consider female age in our analyses because some could not be aged with certainty. Both male age classes were present in each treatment each year (for 1997 control, 5 ASY, 4 SY; for 1997 reduced density, 1 ASY, 3 SY; for 1998 control, 8 ASY, 4 SY; for 1998 reduced density, 3 ASY, 1 SY; for 1999 control, 7 ASY, 4 SY; for 1999 reduced density, 3 ASY, 1 SY). All males in the reduced-density treatment, and all but one (in 1999) of the control males, were mated. No unmated females were detected in the study area.

To test our general hypothesis, that local neighbor density would affect warbler reproductive output and breeding behavior, and specifically, predictions 1–3, we intensively monitored focal territories, found and documented fates of nests, and measured territory sizes. Nests were usually found during nest-building and were checked every two days until fledging or failure. Cause of failure (e.g., predator, abandoned by female) was determined from the condition of failed nests (see Holmes et al. 1992, 1996). Parental identity was verified by observing leg band combinations when birds visited nests, and nest success was confirmed by noting parents feeding fledglings. Adults were monitored after a nest fledged or failed to ensure that further re-nesting and double-brooding attempts were discovered. Movements of male warblers were mapped every 2–3 days from mid-May through late June each year. Males were followed closely without disturbing them for 15–20 min periods, and their positions were recorded on graph paper based on their movements within the 25-m plot grid. These field maps were transferred to weekly summary maps that were used to construct a final territory map for each male in each breeding season. Territories were delineated with the minimum convex polygon method (Ford and Myers 1981). Three-factor, fixed-effect ANOVAs were used to test if the number of young fledged per territory, territory size, and the proportion of nests depredated per territory differed between the two treatments. Independent variables were year, male age, neighbor-density treatment, and all interaction terms.

Predictions 4 and 5 were tested by quantifying and analyzing singing and foraging behavior of monogamous males between early June and early July, 1997 and 1999. No observations were made on males in the reduced-density treatment until at least two days after removals were completed. Behavioral data were analyzed with split-plot, univariate repeated-measures ANOVAs (Milliken and Johnson 1992). Fixed effects were year, nest stage, male age class, neighbor-density

treatment, and all two- and three-factor interactions between these variables. Individual male nested within year, male age class, and treatment (i.e., male[year, male age, treatment]) was included in models as a random effect. Dependent variables will be described. Models were fit using the Restricted Maximum Likelihood (REML) method (SAS Institute 1996).

Male song rate.—Male countersinging rate was used to measure male–male interactions because fighting and chasing were rarely observed after establishment of territory boundaries in mid-May, before we started removals. A countersong was defined as a song from a focal male that was followed immediately by a song of one or more neighboring males; at least two sets of songs had to be exchanged between males before the behavior was recorded as countersinging. Song data were collected while mapping the territorial movement of a subset of males. Countersinging rates were measured during the nest-building–egg-laying, incubation, and nestling stages of first broods. Song data were not collected for males after first broods fledged. For analysis, data for each male were summarized by calculating the number of countersongs per minute per stage.

Male foraging time.—Time budgets were quantified for males encountered opportunistically during the nest-building–egg-laying, incubation, nestling, and fledgling stages of first broods. Females were too cryptic to observe regularly. Once a male was located and identified, he was observed for 30 seconds before his behaviors were dictated onto microcassette. This delay minimized biasing estimated time budgets toward conspicuous activities (e.g., acrobatic foraging maneuvers). Behavioral data were recorded continuously until an individual was either lost from sight, observed for 10 consecutive minutes, or perched for five consecutive minutes. Behavior categories noted were: foraging, perching, patrolling (moving without foraging), preening, and mate guarding. The latter two behaviors were rarely observed, and we were principally interested in the time that males spent foraging. Black-throated Blue Warblers are active foragers that move quickly and capture prey by gleaning, hovering, and snatching them from foliage and twigs (Robinson and Holmes 1982, Holmes 1994), making the classification of a behavioral sequence as “foraging” unambiguous. A maximum of 20 minutes of data were collected per male per day. Microcassette tapes were transcribed, and the duration of each observation bout and the time each male foraged per bout were recorded. After discarding observation bouts <2 minutes long, we summed foraging time and total observation time per male per nest stage and then calculated the proportion of time each male spent foraging per stage. Only summed observation periods ≥ 5 minutes per male per nest stage were included in data analyses.

Nestling provisioning rate and fledgling mass.—Parental feeding rates and fledgling mass were quantified for first brooding nests each year. Nests were video-

taped for continuous 2.5-h periods during the morning on day 7 of the nestling period. Previous research indicated that the nestling provisioning rate of Black-throated Blue Warblers increased daily until fledging, but did not vary significantly with time of day or with parental age (Goodbred and Holmes 1996). Cameras were placed 10–15 m from nests and concealed in vegetation. Nestlings were counted immediately prior to filming. Nests were not filmed in rain or when vegetation was dripping wet. When transcribing video tapes, we discarded the first 15 minutes of data to ensure that parents were acclimated to the camera's presence. The number of food deliveries per nestling per hour was analyzed separately by sex because male and female provisioning rates were not significantly correlated ($r = 0.25$, $P = 0.29$). Food biomass delivered per adult visit could not be reliably determined from video tapes. Nestling mass on day 6 of the eight-day nestling period, the last day to safely handle young without causing premature fledging, was used as an estimate of fledgling mass. Mean deliveries per nestling per hour and mean fledgling mass were analyzed with two-factor, fixed-effect ANOVAs with year, neighbor-density treatment, and year \times treatment as independent variables. Data from territories with bigamous males (control, $n = 1$ in 1997; reduced-density, $n = 3$ in 1998) were excluded from statistical analyses because these males typically provision nestlings less than do monogamous males (T. S. Sillett, N. L. Rodenhouse, and R. T. Holmes, unpublished data).

To verify that any differences found between treatments were not due to differences in territory quality, i.e., a site-dependent mechanism (Rodenhouse et al. 1997), we measured and compared the quality of all focal territories in both treatments. Previous research indicated that high-quality territories for Black-throated Blue Warblers at Hubbard Brook would have a high density of hobblebush and other vegetation in the shrub layer, ample arthropod prey, and low predator abundance (Rodenhouse and Holmes 1992, Steele 1993, Holmes et al. 1996). Territory quality data were analyzed with a two-factor, fixed-effect MANOVA with year, neighbor-density treatment, and year \times treatment as independent variables. Dependent variables for the territory model will be described. Model sphericity (i.e., the assumption of an equal covariance structure between responses for all possible pairs of response variables) was assessed with the Mauchly criterion and, when necessary, the Geisser-Greenhouse (hereafter G-G) correction was used to estimate degrees of freedom for F tests (Muller and Barton 1989).

Vegetation.—Understory leaf density was measured at five randomly selected, 394-m² circular plots per territory; plots were ≥ 50 m apart. In each plot, 11.2-m transects were delineated in the understory in cardinal directions. At the distal end of each transect, all leaves of hobblebush and those of the two other dominant understory species, American beech and striped

maple, that intersected a ground-level, 9-m² plane (demarcated by two 3-m vertical poles set 3 m apart) were counted. Leaf density data were summed for each territory site.

Prey abundance.—Availability of the warbler's primary prey in summer, lepidopteran larvae and spiders, was quantified per territory on four biweekly surveys beginning in late May each year. Black-throated Blue Warblers typically forage for arthropods in the understory (Robinson and Holmes 1982), and prey biomass is not strongly stratified by height on our study plot (Holmes and Schultz 1988). A survey entailed non-destructive, visual inspections of 16 50-leaf samples from hobblebush, American beech, and striped maple in the forest understory. Surveys were conducted in 25 m radius circles centered at nests. Note that these surveys only indexed the actual arthropod populations because we did not adjust for detection probability. Lengths of all caterpillars and spiders detected were recorded; lengths were converted to biomass using length-mass regressions (Rodenhouse 1986). The biweekly biomass data were summed for each territory to produce annual estimates of food availability (see Rodenhouse et al. 2003).

Predator abundance.—Abundances of eastern chipmunks *Tamias striatus*, eastern red squirrels *Tamiasciurus hudsonicus*, and Blue Jays *Cyanocitta cristata*, the warblers' principal nest predators at Hubbard Brook (Holmes 1994), were surveyed with 5-min point counts conducted during the same four biweekly periods used to estimate food biomass. Like the prey abundance surveys previously described, predator surveys were not adjusted for detection probability and thus only indexed predator populations. Four counts were performed in each period and were then averaged to estimate the number of predators counted per survey per territory per year.

All statistics were calculated with the JMP computer program (SAS Institute 2003). Model residuals were examined to verify that model assumptions were met, and only the male countersong data had to be transformed (square-root). Results are presented as untransformed, least-squares means ± 1 SE from the relevant model effect tests.

RESULTS

The neighbor-density manipulation clearly influenced Black-throated Blue Warbler reproductive success and behavior. However, some effects varied among the three years of the experiment and were counter to our predictions. We first present results of the density-reduction experiment on warbler reproductive success and territory size, and then the differences in warbler behavior and territory quality between control and reduced-density territories.

Fledging success.—As predicted, birds on reduced-density territories fledged significantly more young per year than did those on control territories (treatment $F_{1,32}$

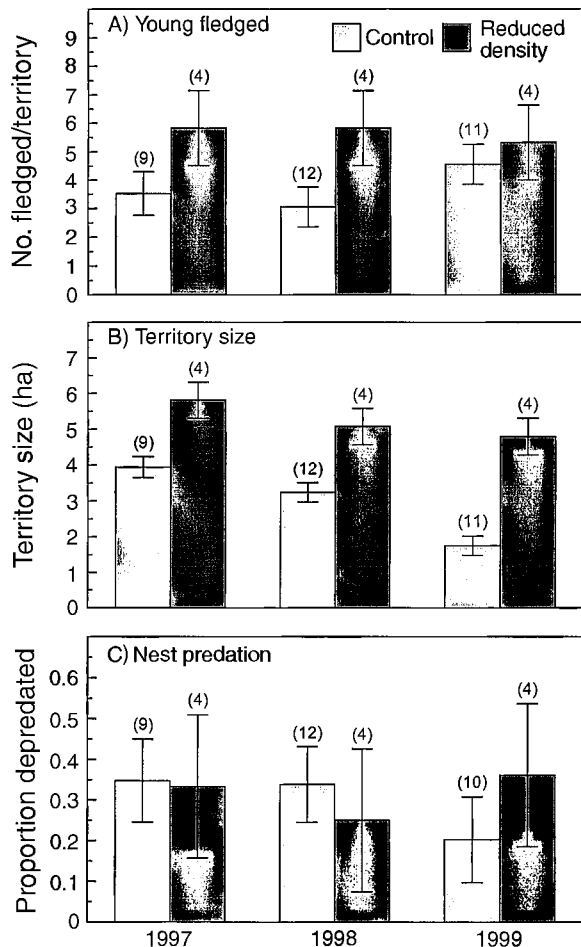


FIG. 1. Annual variation (1997–1999) in the effects of the density-reduction experiment on Black-throated Blue Warbler (A) fledging success, (B) territory size, and (C) nest predation rates. Bars show least-squares means (± 1 SE) from treatment \times year effect tests (see *Methods*). Numbers of territories per treatment \times year combination are given in parentheses.

= 4.78, $P = 0.04$; Fig. 1A). This treatment effect did not vary with male age (treatment \times age $F_{1,32} = 0.24$, $P = 0.63$), with year (treatment \times year $F_{2,32} = 0.61$, $P = 0.55$), or with the three-way interaction among independent variables (treatment \times age \times year $F_{2,32} = 0.11$, $P = 0.90$). Birds in the reduced-density treatment therefore fledged more young than did control birds, regardless of male age or year, although the treatment effect was largest in 1997 and smallest in 1999 (Fig. 1A). In both treatments, ASY males fledged, on average, more young per year than did SY males (age $F_{1,32} = 5.30$, $P = 0.03$). Relative to controls, a greater proportion of reduced-density territories fledged multiple broods due to double brooding and bigamy, with the largest differences in 1997 and 1998 (reduced density, three of four territories each year; control in 1997, two of nine territories, in 1998, six of 12 territories, in 1999, eight of 11 territories). Mean clutch sizes for

both first and second brood nests per territory did not differ between neighbor-density treatments in any year (T. S. Sillett, N. L. Rodenhouse, and R. T. Holmes, unpublished data).

Territory size.—Reduced-density territories were significantly larger than control territories (treatment $F_{1,32} = 42.40$, $P < 0.0001$; Fig. 1B). This relationship did not vary by male age, by year, or by any interactions of independent variables ($F < 1.28$, $P > 0.29$). Mean territory size was smaller in each successive year of the experiment (year $F_{1,32} = 7.06$, $P = 0.003$), probably because the number of warblers breeding on our study area increased from 1997 to 1999 (see Holmes and Sherry 2001).

Nest predation.—As predicted, the proportion of nests depredated did not significantly differ between reduced density and control territories (treatment $F_{1,31} = 0.03$, $P = 0.87$; Fig. 1C). Nest predation also did not significantly differ by year ($F_{2,31} = 0.09$, $P = 0.91$), by male age ($F_{1,31} = 2.03$, $P = 0.16$), or by any combinations of model effects (interaction F tests < 0.80 , $P > 0.43$). Variation in the proportion of nests depredated among territories, particularly in the reduced-density treatment, was high (Fig. 1C).

Male countersong rate.—Contrary to our prediction, the neighbor-density manipulation did not have a significant effect on countersinging rates (treatment $F_{1,20} = 1.30$, $P = 0.27$), although reduced-density males tended to countersing less than control males when females were building nests and laying eggs (Fig. 2A). Countersinging behavior did differ between ASY and SY males (age $F_{1,20} = 7.29$, $P = 0.01$), with older birds countersinging at a higher mean rate (0.57 ± 0.08 songs/min) than yearlings (0.28 ± 0.07 songs/min), regardless of nest stage, year, or neighbor-density treatment (interaction F tests < 2.23 , $P > 0.13$). Countersinging rate was also significantly different among stages of the nesting cycle (stage $F_{2,31} = 4.63$, $P = 0.02$), being highest when females were incubating (Fig. 2A). Mean countersinging rates were lower in 1999 (0.21 ± 0.07 songs/min) than in 1997 (0.65 ± 0.06 songs/min; year $F_{1,20} = 16.30$, $P = 0.0006$), irrespective of treatment or nest stage (interaction F tests < 1.17 , $P > 0.31$). Countersinging behavior did not vary significantly among individual males ($F_{20,31} = 0.19$, $P > 0.99$).

Male foraging behavior.—The proportion of time that males foraged varied with neighbor-density treatment, year, and nest stage. Consistent with our prediction, males in the reduced-density treatment spent a significantly greater proportion of their time foraging than did control males (treatment $F_{1,16} = 7.50$, $P = 0.01$), and this difference tended to be greatest when females were building nests, laying eggs, and incubating (Fig. 2B; treatment \times stage $F_{3,18} = 2.06$, $P = 0.14$). Foraging time was most similar between treatments when males were feeding nestlings and dependent fledglings (Fig. 2B). The effect of the neighbor-

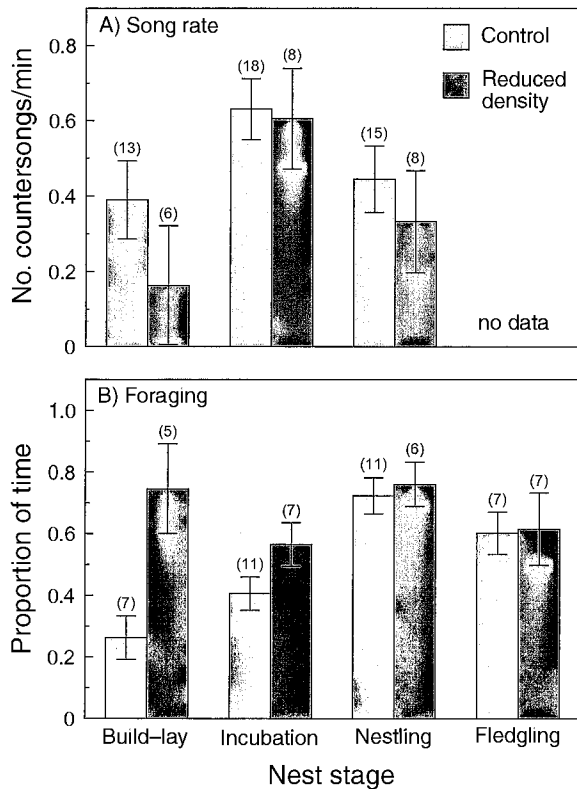


FIG. 2. (A) Countersinging rates and (B) proportion of time spent foraging for male Black-throated Blue Warblers in the two neighbor-density treatments (control and reduced density). Least-squares means (± 1 SE) from treatment \times nest-stage effect tests (see *Methods*) are given for the nest-building and egg-laying, incubation, nestling-feeding, and fledgling-feeding stages in the warbler reproductive cycle. Numbers of males per treatment \times nest stage combination are given in parentheses.

density manipulation on foraging behavior did not differ significantly with year (treatment \times year $F_{1,16} = 0.37$, $P = 0.55$) or with age class, although the divergence in the mean proportion of time that individuals foraged tended to be greater between ASY males (reduced density, 0.75 ± 0.09 ; control, 0.49 ± 0.05) than between SY males (reduced density, 0.60 ± 0.05 ; control, 0.51 ± 0.05 ; treatment \times age $F_{1,16} = 2.23$, $P = 0.15$). On average, all males foraged proportionally more in 1997 (0.70 ± 0.05) than in 1999 (0.47 ± 0.05 ; year $F_{1,16} = 11.41$, $P = 0.004$), regardless of their age class (year \times age $F_{1,16} = 0.0005$, $P = 0.98$) or nesting stage (year \times stage $F_{3,18} = 1.15$, $P = 0.35$). Foraging time differed strongly among stages of the nesting cycle (stage $F_{3,18} = 6.32$, $P = 0.004$), independent of male age (stage \times age $F_{3,18} = 1.03$, $P = 0.40$). Males foraged least when females were building and laying, and most when they were feeding nestlings and dependent fledglings (Fig. 2B). No three-way interactions among model effects were significant (interaction F tests < 1.05 , $P > 0.32$), and foraging behavior did not vary signif-

icantly among individual males ($F_{16,18} = 0.36$, $P = 0.98$).

Nestling provisioning rates and fledgling mass.—Parental provisioning rates and mean fledgling mass were not conclusively different between neighbor-density treatments in every year. Female food deliveries per nestling per hour differed by neighbor-density treatment and by year (treatment \times year $F_{2,21} = 9.63$, $P = 0.02$; Fig. 3A). Reduced-density females fed nestlings at a higher rate than did control females in 1997 (orthogonal contrast, $t_{21} = 3.36$, $P = 0.003$), but not in 1998 ($t_{21} = -0.99$, $P = 0.33$) or 1999 ($t_{21} = 0.04$, $P = 0.97$). Male provisioning rates tended to be greater in the reduced-density treatment (treatment $F_{1,21} = 2.71$, $P = 0.11$; Fig. 3B), but did not differ significantly between years (year $F_{2,21} = 0.03$, $P = 0.97$). Our data also did not reveal any significant annual differences

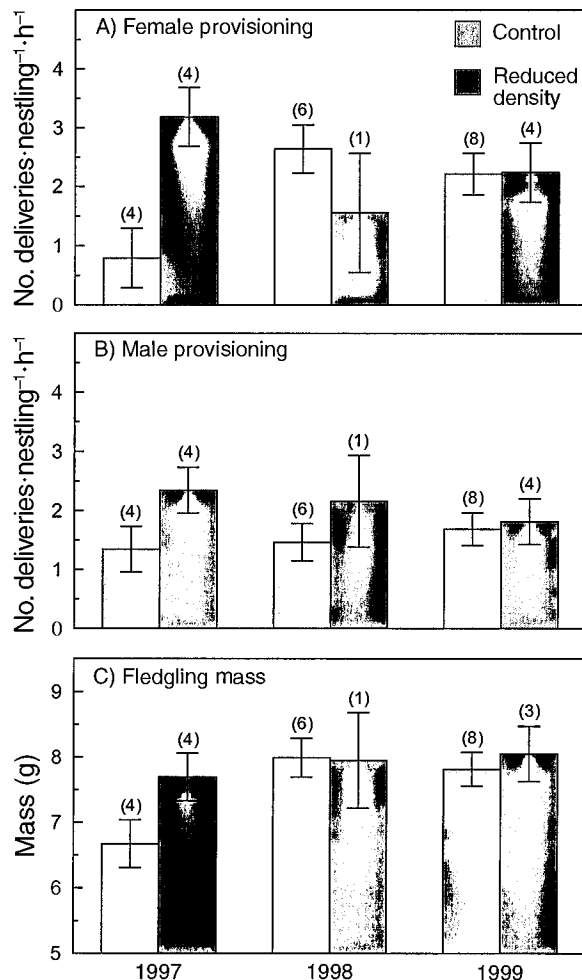


FIG. 3. Annual variation (1997–1999) in nestling provisioning rates by (A) females and (B) males, and (C) annual variation in fledgling mass for first-brood nests in the two neighbor-density treatments. Bars indicate least-squares means (± 1 SE) from treatment \times year-effect tests (see *Methods*). Numbers of territories per treatment \times year combination are given in parentheses.

in the treatment effect for males (treatment \times year $F_{2,21} = 0.74$, $P = 0.49$). However, like the females, male deliveries per nestling per hour were most dissimilar between neighbor-density treatments in 1997 (Fig. 3B). The treatment effect on fledgling mass was marginally significant in the direction predicted (treatment $F_{1,20} = 2.63$, $P = 0.10$; Fig. 3C). Fledgling mass did not differ significantly by year ($F_{2,20} = 1.31$, $P = 0.27$). Although annual differences among control and reduced-density territories were not statistically significant (treatment \times year $F_{2,20} = 0.89$, $P = 0.43$), fledgling mass appeared to be most divergent between treatments in 1997 (Fig. 3C).

Territory quality.—Based on MANOVA, nest predator abundance (control vs. reduced density, 1.03 ± 0.10 vs. 0.98 ± 0.17 predators/5-min survey; mean \pm), mean food biomass (104.31 ± 14.03 vs. 102.97 ± 23.27 mg dry biomass of caterpillars and spiders/2400 leaves), and number of deciduous leaves in the shrub layer (564.83 ± 18.67 vs. 592.29 ± 30.26 leaves/180 m² sample), respectively, did not differ significantly between control and reduced-density territories (G-G $F_{1,13,43,10} = 0.39$, $P = 0.56$). Territory quality differed among years (G-G $F_{2,27,43,10} = 20.39$, $P < 0.0001$) due to annual variation in food and predator abundance. However, no statistically significant treatment \times year interaction was detected (G-G $F_{2,27,43,10} = 0.83$, $P = 0.45$), indicating that territory quality among control and reduced-density territories was similar within seasons.

DISCUSSION

Our experiment demonstrated that local neighbor density affects Black-throated Blue Warbler reproductive output. To our knowledge, only six other published studies of passerines have experimentally manipulated intraspecific density to investigate density-dependent fecundity: Tompa (1967), Alatalo and Lundberg (1984), Torok and Toth (1988), Dhondt et al. (1992), Both (1998B), and Both and Visser (2000). All six were conducted on European cavity-nesting species that bred in nest boxes, and with the exception of Tompa (1967), all found a negative effect of density on some variable related to reproductive success, such as clutch size, fledgling survival, or territory size. However, only two of these studies identified the mechanisms responsible for density dependence. Dhondt et al. (1992) concluded that site preemption coupled with heterogeneity in territory quality (i.e., a site-dependent mechanism; Rodenhouse et al. 1997) regulated their study population. In contrast, Both and Visser (2000) concluded that crowding and resource competition reduced mean territory size, which was, in turn, positively related to fledgling success and adult fitness. As we will discuss, our results are generally consistent with a crowding regulatory mechanism based on intraspecific resource competition.

Density-dependent fecundity is predicted to be a key outcome if bird territories become compressed at high densities and conspecifics compete primarily for food, rather than for nest sites (e.g., tree cavities or nest boxes) during the breeding season (Both and Visser 2003). Territories in the reduced-density treatment, on average, were 70% larger than control territories. Density of conspecific competitors has been shown to influence territory size in several bird species (reviewed by Newton 1998). Furthermore, in studies in which food levels and territory sizes were quantified in each year, a negative correlation was found between conspecific density and territory size, irrespective of whether food availability was relatively high or low per unit area (Krebs 1971, Klomp 1980, Smith et al. 1980, McCleery and Perrins 1985, Arvidsson and Klaesson 1986, Arcese and Smith 1988, Stamps 1990; T. S. Sillett, N. L. Rodenhouse, and R. T. Holmes, *unpublished data*). In other words, an increase in conspecific density can reduce the size of territories, even when food is scarce. Because territory size can be decreased by supplementing food after territory establishment (Boutin 1990, Newton 1998), it seems that individuals typically defend only the area necessary to meet their food requirements. Therefore, a reduction in territory size as a result of crowding could yield territories that are food limited.

The differences between neighbor-density treatments in male foraging behavior, in adult provisioning rates of nestlings, and in fledgling mass suggest that food limitation was greater for control birds, at least in some years of our study. Compared to males in the reduced-density treatment, control males spent less time foraging in both 1997 and 1999, and thus devoted more time to other activities like territory defense and mate guarding. Although we did not quantify prey-capture rates of foraging males, this result suggests that crowding at high densities may further reduce food availability by limiting the time that males spend foraging. A density-dependent increase in adult interactions and a concomitant increase in food limitation could also be regulatory if they reduce parental care of young. Our results supported this possibility in 1997, when adults in the reduced-density treatment tended to provision nestlings at a higher rate (Fig. 3A, B) and fledge heavier young (Fig. 3C) relative to controls. However, results from 1998 were inconclusive due to small sample sizes, and provisioning rates and fledgling mass did not differ between treatments in 1999. We are unaware of any other published experimental studies that measure whether parental care or foraging behavior varies with population density. Additional research is therefore needed to understand how crowding-induced competition for limited food acts to regulate populations of territorial passerines during the breeding season.

Our experiment indicated that the proportion of nests depredated per territory was not influenced by the number of conspecific neighbors, although variance among

territories was high, especially in the reduced-density treatment (see *Results*). Nevertheless, these results, along with those from an artificial nest experiment conducted in the shrub layer at Hubbard Brook (Reitsma 1992), and from our long-term demographic research (Sillett and Holmes, *in press*), indicate that predation on Black-throated Blue Warbler nests is independent of conspecific density and thus does not exert a strong regulatory influence on this species in areas of high-quality, homogeneous habitat. However, other studies have demonstrated density-dependent rates of nest predation (Martin 1996, Newton 1998), and nest predators do appear to play a role in the site-dependent regulation of warbler abundance at the broader spatial scale of the entire Hubbard Brook valley (Rodenhouse et al. 2003).

The neighbor-density manipulation did not reveal density-dependent variation in countersinging rates, our best index of direct agonistic behavior. This is probably due to the fact that aggression between males peaks during territory establishment in mid-to-late May, before we initiated removals. Despite this, the differences between density treatments in annual fecundity, in territory size, and in adult foraging and nestling provisioning behavior argue that either the real or perceived presence of neighbors did have a regulatory effect on our study population. Density-dependent aggression has been documented in many bird species, and can affect fecundity (Watson 1970, Williams et al. 1994) and regulate population size (Moss et al. 1994, Mougeot et al. 2003). Intraspecific interactions were not quantified in any of the six experimental manipulations of breeding passerine density previously cited. Thus, further experimental work is needed to determine how aggression generated by crowding might regulate passerine populations.

A regulatory process such as crowding should have the strongest effect on abundance in years when weather and resource levels are most limiting, and the weakest effect when weather is benign and resources are abundant (Newton 1998). Much of the annual variation in our experimental results probably can be attributed to the striking annual variation in weather and food availability during this study. The neighbor-density manipulation had the largest impact on warbler reproductive success and behavior in 1997, when environmental conditions for Black-throated Blue Warblers were poorest (Table 1). The late start to breeding in 1997, coupled with lower than average food availability, probably amplified crowding effects. Indeed, parental provisioning rates and fledgling mass from first-brood nests were lower on control territories than on territories in the reduced-density treatment in 1997. Three of four females in our reduced-density treatment double-brooded in this year, compared to only one of nine control females. The extreme amount of rain in June 1998 caused many Black-throated Blue Warbler nests to fail throughout the Hubbard Brook valley, and some individuals abandoned their breeding territories

(T. S. Sillett, N. L. Rodenhouse, and R. T. Holmes, *unpublished data*). Several birds, especially unmated yearling males, appeared during June 1998 in areas where warbler pairs previously had been removed (those that established territories adjacent to experimental pairs were immediately removed). One apparent consequence of this late influx of new birds was that three of the four experimental males became bigamous in June 1998, and one had three females nesting on his territory. Thus, the high reproductive success on reduced-density territories in 1998 was due to bigamy, not to double-brooding. Female Black-throated Blue Warblers paired to bigamous males usually do not double-brood (T. S. Sillett, N. L. Rodenhouse, and R. T. Holmes, *unpublished data*). Environmental conditions were most favorable in the 1999 breeding season (Table 1). Males in both neighbor-density treatments spent less time foraging in 1999 than in 1997. Furthermore, number of young fledged per territory, nestling provisioning rates, and fledgling mass differed least between density treatments in 1999. Thus, the variation in our experimental results among the three years suggests that: (1) the regulatory potential of a crowding mechanism can be affected by annual variation in weather and food abundance, and (2) crowding may have its strongest effect on local warbler abundance in years when environmental conditions are relatively poor.

In conclusion, results presented in this paper, in combination with our other recent work (Rodenhouse et al. 2003, Sillett and Holmes, *in press*), indicate that the Black-throated Blue Warbler population at Hubbard Brook is regulated, in part, by breeding season events. In high-quality, relatively homogeneous habitat, a negative feedback on fecundity generated by crowding-induced resource competition appears to be an important regulatory mechanism. The strength of this behaviorally mediated density dependence seems to be sufficient to maintain abundance within the levels observed locally for at least the last three decades (Sillett and Holmes, *in press*). At a landscape scale, a site-dependent mechanism also appears to regulate abundance via territory-level differences in food availability, vegetation density, and nest predation (Rodenhouse et al. 2003). Therefore, multiple regulatory mechanisms are likely to operate on the Black-throated Blue Warbler population sampled at Hubbard Brook, but at different spatial scales. This finding emphasizes the importance of studying populations in a representative range of habitats and environmental conditions in order to understand the processes involved in regulation.

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