

# MULTIPLE BROODING AND PRODUCTIVITY OF A NEOTROPICAL MIGRANT, THE BLACK-THROATED BLUE WARBLER (*DENDROICA CAERULESCENS*), IN AN UNFRAGMENTED TEMPERATE FOREST

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**ABSTRACT.**—We studied a population of Black-throated Blue Warblers (*Dendroica caerulescens*) in the White Mountains of central New Hampshire to determine the reproductive performance of this Neotropical migrant species in an unfragmented north-temperate forest. Over a four-year period (1986–1989), female Black-throated Blue Warblers laid an average of 6.6 eggs per season of which 5.2 hatched and 4.3 fledged. This high annual production of young was due to a combination of overall high nesting success (63%), low nest depredation rates (22%), no brood parasitism, and, most importantly, frequent multiple brooding (48%). Over the four years, 35% (range = 14–50%) of the individually-marked females in this population successfully fledged two or more broods; one female fledged three successive broods in one season. Multiple brooding accounted for most of the annual variation in numbers of young fledged per female, and its frequency was related to annual differences in food abundance and, potentially, to time constraints imposed by the intensity and timing of nest depredation. Multiple brooding was significantly and positively related to age of the male parent, and possibly the female parent. Older males were also more likely to be polygynous, although such matings were infrequent (4–16% of mated males each year). Higher reproductive output by older individuals implies that demographic structure of Neotropical migrant populations may have important consequences for maintenance of population size. Recruitment of yearling male Black-throated Blue Warblers into the population was positively related to the number of young fledged per female in the preceeding summer. Although not statistically significant, this finding in combination with the above results and other published information suggests that reproductive success and the factors affecting it may be particularly important in influencing the abundance and population dynamics of this Neotropical migrant passerine, and may override the impact of events occurring in winter or on migration. Received 6 May 1991, accepted 2 December 1991.

RECENT evidence suggests that many North American bird populations are declining, especially those that breed in temperate forests and winter in the Neotropics (Robbins et al. 1989, Askins et al. 1990). These declines may be caused by: (1) factors affecting reproductive success and adult mortality while these species are in their temperate breeding areas (Whitcomb et al. 1981, Lynch and Whigham 1984, Probst 1986, Sherry and Holmes 1992); (2) mortality during winter (Robbins et al. 1989, Holmes et al. 1989) or on migration (Moore and Yong 1991); or (3) some combination of these factors (Cox 1985).

At present, there is little consensus concerning which ecological processes are most important in limiting populations of Neotropical migrant birds or where such limitation might take place (Keast and Morton 1980, Hagan and Johnston 1991). Data on these questions are critical before effective measures can be implemented to halt the current decline of Neotropical migrants.

Several lines of evidence suggest that events in the breeding areas may be particularly important in population regulation. First, fragmentation of breeding habitat results not only in loss of suitable breeding areas of Neotropical migrants, but also in disproportionately fewer species and lower population levels of migrants within the remaining habitat patches (Whitcomb et al. 1981, Lynch and Whigham 1984). This may be due in part to lowered reproductive output caused by increased nest depredation and nest parasitism in fragmented habitats

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(Wilcove 1985, Robinson 1992). Second, population trends in north temperate breeding bird populations often are correlated with local changes in food abundance (e.g. defoliator irruptions), successional changes in habitat structure, and other events in the breeding areas, suggesting that breeding habitat and conditions are important to maintenance of population size (Holmes et al. 1986, 1991, Holmes and Sherry 1988). As an example, in a study on replicated plots in New Hampshire, Holmes et al. (1991) found that bird population trends and reproductive performance of intensively studied species were significantly correlated with caterpillar abundances in the preceding summers, corroborating an effect of food supply on reproductive success and subsequent recruitment of new individuals into the populations. Demographic data for two migratory species of paruline warblers also support this relationship between nesting success and subsequent recruitment of yearlings at the population level (e.g. for Prairie Warblers, *Dendroica discolor*, Nolan 1978; for American Redstarts, *Setophaga ruticilla*, Sherry and Holmes 1992).

To evaluate further the importance of breeding events to population dynamics of migratory birds, studies are needed of productivity and related demographic parameters of species over a diverse range of habitats, including those that are intact and relatively undisturbed and those that are fragmented to varying degrees. Despite the seeming plethora of studies on the life histories and breeding biologies of North American passerine birds (e.g. Bent 1953, Morse 1989), few studies have been sufficiently detailed and have involved sufficiently large numbers of individually-marked birds over a series of years to provide reliable information on the diverse components of reproductive performance and productivity (Martin 1991). For paruline warblers, such data are available only (and even then in varying degrees of detail) for the Kirtland's Warbler (*D. kirtlandii*) in Michigan (Mayfield 1960, Walkinshaw 1983, Probst 1986), Prairie Warbler in Indiana (Nolan 1978), Yellow-breasted Chat (*Icteria virens*) in Indiana (Thompson and Nolan 1973), Yellow Warbler (*D. petechia*) in Manitoba (Goossen and Sealy 1982), and Prothonotary Warbler (*Protonotaria citrea*) in Tennessee (Petit 1989). All of these species live in riparian, scrub or open-pine habitats. Little detailed information exists on the reproductive productivity of paruline warblers or

other Neotropical migrant species breeding in north-temperate forests.

In this study, we investigated the reproductive performance and nesting effort of a Neotropical migrant species, the Black-throated Blue Warbler (*D. caerulescens*), in an unfragmented temperate deciduous forest in New Hampshire. When comparable information becomes available for other species, these baseline data from a species breeding in an undisturbed habitat will help in evaluation of the impact of habitat disturbance or fragmentation on reproductive performance of Neotropical migrant species. Specifically, we determined: (1) the reproductive output; (2) the factors influencing reproductive success; and (3) the relationship, if any, between reproductive success and population size. With reference to objective (3), we hypothesized that, if reproductive success were important in affecting subsequent populations, there should be a positive correlation between reproductive success and recruitment of yearlings into the population in the next season.

#### STUDY AREA AND METHODS

The study was conducted from 1986 to 1989 on a gridded 70-ha study plot in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire, which encompassed the 10-ha census plot used by Holmes and colleagues since 1969 (Holmes and Sturges 1975, Sherry and Holmes 1985, Holmes et al. 1986, Holmes 1990). The forest at Hubbard Brook consists of unfragmented northern hardwoods, contiguous with large expanses of similar forests in the surrounding White Mountain National Forest, and is dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*), with occasional white ash (*Fraxinus americana*), red spruce (*Picea rubens*), eastern hemlock (*Tsuga canadensis*), and balsam fir (*Abies balsamea*). The shrub layer is composed primarily of hobblebush (*Viburnum alnifolium*) and saplings of beech and sugar maple. The vegetation of the 70-ha plot was similar to that described for the census area (see references just cited), but was more heterogeneous, especially with respect to shrub density and the presence of more coniferous vegetation.

In each year, we caught and color marked about 90–95% of all Black-throated Blue Warblers inhabiting the 70-ha study area. Most males were caught using the playback method described by Holmes et al. (1989) for luring birds into a net. Other males, as well as most females, were caught in mist nets placed at regular intervals through parts of the study area and near nests. All birds were fitted with a U.S. Fish and Wildlife Service band and two distinctive color bands.

Males were aged, when in hand, by subtle plumage characteristics as being either second year (SY, i.e. yearlings hatched the previous breeding season), or after second year (ASY, i.e. older birds hatched at least two seasons previously) in accordance with procedures described in the North American Bird Banding Manual (U.S. Fish and Wildlife Service 1977). Beginning in 1988, captured females were aged as SY or ASY by plumage characteristics described by Pyle et al. (1987) and verified by us through recaptures of birds of known ages (R. T. Holmes, unpubl. data).

Each year, territories of Black-throated Blue Warblers occupying the 70-ha study area were determined by mapping movements and nesting locations of color-marked birds. From their arrival in early to mid-May until the time they began to wander in mid-July to mid-August, we recorded locations of singing males, foraging sites, territorial disputes and active nests.

Nests were found by intensive searching, usually by following nest building or incubating females. When clutch initiation dates were known, nests were checked every second or third day. Nests found with completed clutches (or with nestlings) were visited daily until hatching (or fledging), and then dates of clutch initiation (or hatching) were determined by back-dating. Nestlings were weighed and measured, usually on days 2, 4 and 6 (hatching = day 0) using procedures of Rodenhouse (1986). After nestlings were banded on day 6, nests were checked daily to determine the time of fledging (usually day 8 or 9; see Results). We continued to observe pairs after they successfully fledged a brood to see if additional nests were attempted. Although we visited nests frequently and handled young for weighing, measuring and banding, in only four cases was there any evidence of reduced success due to our disturbance; these cases were excluded from the analyses. Although losses to predation could have increased because of our activity near nests, we have no evidence of this. Moreover, the relatively low predation rates recorded during this study (see Results) argue against this possibility.

## RESULTS

*Population structure.*—From 1986–1989, the number of male Black-throated Blue Warblers defending territories on the 70-ha study area ranged from 18 to 32 (Table 1) and averaged 22.5, or 3.2/10 ha. During the same four summers, male Black-throated Blue Warblers occurred at densities averaging 5.8/10 ha on the 10-ha, long-term census plot, which was located within the 70-ha study area (R. T. Holmes, unpubl. data), indicating that some sections of the 70-ha plot were less suitable than the census plot.

Most mated males (84–96%) were monoga-

mous and maintained a pairbond with a single female throughout a season. Each year, however, one to three males (4–16%,  $\bar{x} \pm SD = 10.8 \pm 5.1\%$ ) were mated simultaneously to two females (Table 1; see Petit et al. 1988). In three of the four years, unmated males (as evidenced by the lack of any female seen within their territories and by the more persistent singing of these males compared to mated males during the same periods) varied from 0–21.9% ( $\bar{x} = 10.9 \pm 10.1\%$ ) of all males (Table 1). The maximum number of unmated males (7) occurred in 1989, the year of highest Black-throated Blue Warbler density (Table 1).

Numbers of older (ASY) males remained relatively stable (10–13) over the four-year period, whereas the abundance of yearling (SY) males fluctuated widely (5–14, or 31–56% of all males; Table 1). As a consequence, the ratio of SY/ASY males varied among years, with the highest percentage of SYs occurring in years of highest Black-throated Blue Warbler densities (1987 and especially 1989; Table 1). Thus, density changes appear to reflect different recruitment levels of yearling males.

Seventeen to 26 female Black-throated Blue Warblers occurred on the 70-ha plot each year (Table 1). Most females were mated monogamously, but a few were involved in bigamous associations. No unmated females were detected in any year. In the two years in which we were able to age females, yearlings (SY) comprised about one-half (46–61%) of the females present (Table 1).

*Arrival, pair formation, and nest-site selection.*—Black-throated Blue Warblers began arriving at Hubbard Brook between 5–10 May each year. Males always appeared first, with a few females appearing one to three days thereafter. Most females arrived about a week later (10–15 May). Aggressive interactions were observed frequently between males, between females, and between males and females. Most interactions involved aerial chases, but physical combat took place early in the season, especially between neighboring males and in several instances between two females. Males often chased females through the understory and occasionally into the canopy. Once a female seemed to be established, the male stayed close to her, often singing softly overhead as she investigated possible nest sites and constructed the nest.

Females began building nests within a week after arrival. The majority of first nests were

TABLE 1. Numbers, mating patterns, and age structure of Black-throated Blue Warblers on 70-ha study area at Hubbard Brook, 1986–1989.

|                                  | 1986      | 1987      | 1988      | 1989       |
|----------------------------------|-----------|-----------|-----------|------------|
| <b>Numbers/70 ha</b>             |           |           |           |            |
| <b>Males</b>                     |           |           |           |            |
| Monogamous                       | 13        | 16        | 18        | 24         |
| Bigamous                         | 2         | 3         | 2         | 1          |
| Unmated                          | 3         | 1         | 0         | 7          |
| Total males                      | 18        | 20        | 20        | 32         |
| Total females                    | 17        | 22        | 22        | 26         |
| Males + females                  | 35        | 42        | 42        | 58         |
| <b>Age ratio SY: ASY* (% SY)</b> |           |           |           |            |
| Males                            | 5:11 (31) | 9:10 (47) | 7:13 (35) | 14:11 (56) |
| Females                          | —         | —         | 11:7 (61) | 11:13 (46) |

\* Ratio of number of second-year (SY) and after-second-year (ASY) birds caught and aged on study area (see text).

completed between 21 May and 10 June (Fig. 1). Nests were usually situated within 1 m of the ground ( $\bar{x} = 0.43 \pm 0.20$  m,  $n = 148$ ), mostly in hobblebush, but also low in saplings of sugar

maple, beech, red spruce, and occasionally in dense clumps of fern.

*Nest initiation and clutch sizes.*—First eggs were laid on 19, 20, 24, and 28 May in 1986–1989, respectively. The late clutch initiation date in 1989 reflected cool, wet weather in mid-May of that year. One egg was laid per day, usually in the early morning, and incubation regularly started with the laying of the penultimate egg (R. T. Holmes, unpubl. data). The mean incubation period was  $13.0 \pm 0.5$  days ( $n = 42$ ), and the mean nestling period was  $8.6 \pm 0.6$  days ( $n = 77$ ). There were no statistically significant year-to-year differences in either incubation or nestling period length (R. T. Holmes, unpubl. data).

Clutch size for all nests reaching the incubation stage averaged  $3.8 \pm 0.4$  eggs ( $n = 131$ ), with a range of 2 to 5, and both a median and a mode of 4 (Table 2). Clutch size did not differ significantly between years, but in some cases there were small but significant declines in clutch sizes within a season (Table 2). These were most notable in 1986 and 1987 between first and second clutches laid by individually-marked females and between clutches grouped by laying date (those initiated before or after 15 June), but also for early versus late clutches in 1989 and for all four years combined (Table 2).

*Nesting attempts and multiple brooding.*—In a previous study of Black-throated Blue Warblers at Hubbard Brook, Rodenhouse (1986) recorded a bimodal peak in nest initiations and documented double brooding as the underlying cause, although females were not banded. During our study, the bimodal pattern of clutch

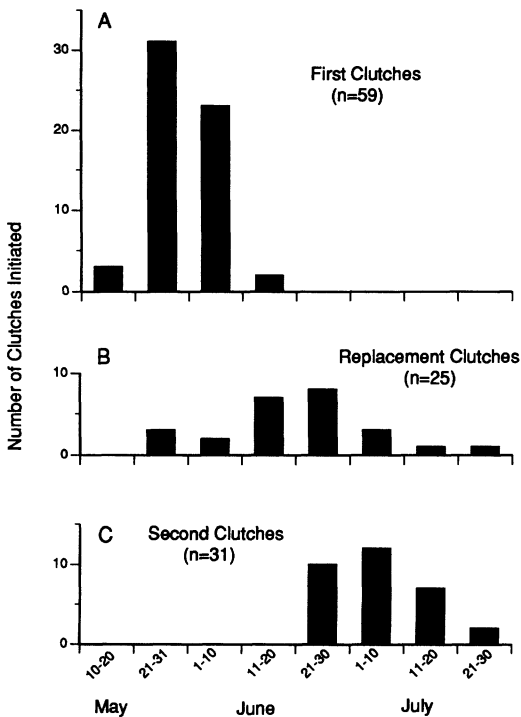


Fig. 1. Clutch initiation by individually-marked female Black-throated Blue Warblers at Hubbard Brook (data combined from four summers, 1986–1989). Replacement clutches are those initiated after failure of a previous attempt; second clutches are those following successful fledging of an earlier brood.

TABLE 2. Mean clutch sizes of Black-throated Blue Warblers within and between years at Hubbard Brook, 1986–1989. First, second, and third clutches represent those known to be laid by individually-marked females, including their renests following nest loss, and second or third clutches following successful fledging (see text and Table 3). Early clutches are those with egg laying initiated before 15 June and late clutches on or after 15 June. Asterisks placed between values indicate statistically significant differences (*t*-test; \*,  $P \leq 0.05$ ; \*\*,  $P \leq 0.01$ ; \*\*\*,  $P \leq 0.005$ ).

|                         | 1986                | 1987                | 1988           | 1989                 | 1986–1989             |
|-------------------------|---------------------|---------------------|----------------|----------------------|-----------------------|
| First clutches          | 4.0 ± 0.4 (15)<br>* | 4.0 ± 0 (19)<br>*** | 3.9 ± 0.4 (14) | 3.9 ± 0.7 (20)       | 3.9 ± 0.4 (68)<br>*   |
| Second clutches         | 3.7 ± 0.2 (9)       | 3.6 ± 0.5 (16)      | 4.0 ± 0.3 (12) | 3.6 ± 0.5 (8)        | 3.7 ± 0.5 (45)<br>*   |
| Third clutches          | —                   | 3.6 ± 0.9 (4)       | 3.5 ± 0.6 (4)  | 3.5 ± 0.6 (4)        | 3.6 ± 0.7 (10)        |
| Early clutches          | 4.0 ± 0.4 (16)<br>* | 4.0 ± 0 (17)<br>**  | 3.9 ± 0.1 (16) | 4.0 ± 0.4 (17)<br>** | 4.0 ± 0.3 (66)<br>*** |
| Late clutches           | 3.7 ± 0.5 (9)       | 3.7 ± 0.6 (23)      | 4.0 ± 0 (17)   | 3.6 ± 0.6 (16)       | 3.7 ± 0.6 (65)        |
| All clutches            | 3.9 ± 0.4 (25)      | 3.8 ± 0.5 (40)      | 3.9 ± 0.2 (33) | 3.8 ± 0.5 (33)       | 3.8 ± 0.4 (131)       |
| Median and mode (range) | 4 (3–5)             | 4 (2–4)             | 4 (3–4)        | 4 (2–5)              | 4 (2–5)               |

initiation also was evident, with the first peak of nesting occurring between 21–31 May and the second from 21–30 June (Fig. 1). For these analyses, a nesting attempt was defined as having occurred if a female completed a nest and initiated egg laying. Not counted as nesting attempts were nests that were built but abandoned before egg laying, as happened frequently most years, especially early in the season. We define multiple brooding as the initiation of egg laying in a second or subsequent nest after having successfully fledged young from a previous nesting attempt that season.

Records from individually-marked females show that they made 1 to 4 nesting attempts per season, with an average of 1.7 and a median and a mode of 2 (Table 3). Such nesting attempts

reflect: (1) loss of an earlier clutch to predation or other factors (see below); and (2) multiple brooding. In our study population, the proportion of females initiating second clutches after having successfully fledged a first brood ranged from 29% to 64% over four years, for an average of 48% over all four years (Table 3).

In the first three years of this study, 40 to 50% of the females successfully fledged two broods per season and, in 1987, one female fledged three successive broods (Table 3). In 1989, most females (71%) fledged one brood, and only 14% fledged two. In each season, some females (7–14%) failed in their nesting attempts and fledged no young (Table 3).

*Nesting success.*—To estimate annual nesting success, we used the Mayfield (1961, 1975)

TABLE 3. Nesting attempts by female Black-throated Blue Warblers at Hubbard Brook, 1986–1989 ( $n$  = number of females).

|   | 1986<br>( $n = 15$ ) | 1987<br>( $n = 21$ ) | 1988<br>( $n = 14$ ) | 1989<br>( $n = 21$ ) | 1986–1989<br>( $n = 71$ ) |
|---|----------------------|----------------------|----------------------|----------------------|---------------------------|
| <b>All nesting attempts</b>                   |                      |                      |                      |                      |                           |
| Mean ± SD                                     | 1.7 ± 0.6            | 1.9 ± 0.7            | 2.0 ± 0.8            | 1.4 ± 0.6            | 1.7 ± 0.7                 |
| Median and mode (range)                       | 2 (1–3)              | 2 (1–3)              | 2 (1–4)              | 1 (1–3)              | 2 (1–4)                   |
| <b>Second-clutch attempts (%)<sup>a</sup></b> |                      |                      |                      |                      |                           |
|   | 47                   | 57                   | 64                   | 29                   | 48                        |
| <b>Broods successfully fledged (%)</b>        |                      |                      |                      |                      |                           |
| 0   | 6.7                  | 9.5                  | 7.1                  | 14.3                 | 9.9                       |
| 1   | 53.3                 | 42.9                 | 42.9                 | 71.4                 | 53.5                      |
| 2   | 40.0                 | 42.9                 | 50.0                 | 14.3                 | 35.2                      |
| 3   | 0.0                  | 4.7                  | 0.0                  | 0.0                  | 1.4                       |

<sup>a</sup> Percent of females initiating egg laying after successfully fledging a first brood.

TABLE 4. Nesting success of Black-throated Blue Warblers at Hubbard Brook, 1986–1989.

|           | Mean nest survival rates |                          |                                |                         |             |                   |
|-----------|--------------------------|--------------------------|--------------------------------|-------------------------|-------------|-------------------|
|           | Early nests <sup>a</sup> |                          |                                | Late nests <sup>a</sup> |             |                   |
|           | Daily <sup>b</sup>       | Nest period <sup>c</sup> | Exposure days <sup>d</sup> (n) | Daily                   | Nest period | Exposure days (n) |
| 1986      | 0.981 (0.008)            | 0.66                     | 320 (40)                       | 0.986 (0.010)           | 0.74        | 143 (21)          |
| 1987      | 0.976 (0.009)            | 0.59                     | 287 (35)                       | 0.981 (0.008)           | 0.66        | 316 (42)          |
| 1988      | 0.979 (0.008)            | 0.63                     | 284 (32)                       | 0.986 (0.006)           | 0.74        | 421 (39)          |
| 1989      | 0.953 (0.017)            | 0.35                     | 149 (31)                       | 0.974 (0.012)           | 0.57        | 191 (35)          |
| All years | 0.975 (0.005)            | 0.58                     | 1,040 (138)                    | 0.982 (0.004)           | 0.68        | 1,071 (137)       |

<sup>a</sup> Early nests with clutches initiated prior to 15 June, and late nests with clutches initiated on or after 15 June.

<sup>b</sup> Mean daily nest survival rate ( $\pm 1$  SE) based on Mayfield (1961, 1975) technique (see also Hensler and Nichols 1981).

<sup>c</sup> Nest survival probability for combined incubation (13 days) and nestling periods (8.6 days).

<sup>d</sup> Exposure days are the pooled incubation and nestling periods (21.6 days).

method, which takes into account the fact that nests were found (and lost) at different stages during the nesting cycle. During the four years of study, annual estimates of nest success from the start of incubation through fledging ranged from 46% (1989) to 69% (1986), for an overall average of 63% (Table 4). Nesting success did not differ significantly between years ( $X^2 = 2.97$ ,  $df = 3$ ,  $P > 0.39$ ), nor between the incubation and nestling stages within years ( $X^2$ ,  $df = 1$ ,  $P > 0.19$ ). Nests initiated early in the season (before 15 June) had lower survivorship than nests completed after 15 June (Table 4), but the differences were not statistically significant, either within years ( $X^2$ ,  $df = 1$ ,  $P > 0.30$ ) or for all years combined ( $X^2 = 1.20$ ,  $df = 1$ ,  $P = 0.27$ ).

For an analysis of the causes of nest failure, we catalogued the fate of each nest that was lost during either incubation or nestling periods. Annual nest loss ranged from 20 to 33%, for an average of 27.2% over the four years (Table 5). The major cause of nest failure was predation, which accounted for 21.6% of all clutches laid (Table 5). Significantly more nests were lost to predation during incubation than in the nestling period ( $X^2 = 28.1$ ,  $df = 6$ ,  $P < 0.001$ ). Of the 34 clutches lost to some mortality factor over the four-year study, 27 (79.4%) were taken by predators, the remaining losses being attributable to severe weather or abandonment (Table 5). Brown-headed Cowbird (*Molothrus ater*) parasitism was not recorded during this study period, nor has it been documented within this study area at Hubbard Brook since our research began in 1969 (Sherry and Holmes 1992).

*Effects of age on multiple brooding and polygyny.*—Multiple brooding by Black-throated Blue Warblers was significantly related to age of the

male parent: proportionately more ASY males (61.6%,  $n = 34$ ) were paired with females that multiple brooded than were yearling (SY) males (23.1%,  $n = 26$ ;  $G = 9.252$ ,  $df = 1$ ,  $P < 0.01$ ). A similar relationship appears to hold for females: in 1988, seven of the nine females producing second clutches after fledging their first were ASYs. Further testing of this relationship was not possible, however, because females were not aged in the first two years of the study and few females double brooded in 1989 (see Table 3). In this context, note that the one female that laid and fledged three successive clutches in 1987 had been banded as an adult in 1982; thus, she was at least seven years of age in 1987.

Seven of the eight bigamous males recorded during this study (Table 1) were ASYs. Assuming that males associating with two females and observed feeding at their nests were actually the parents of the young in those nests, bigamy should result in more young produced per male per season. Based on the six bigamous males for which we had complete nesting information (including the one SY male, see below), the number of young fledged per bigamous male per season averaged  $7.2 \pm 3.1$  (range = 3–12). This is significantly higher than the average of  $4.4 \pm 2.2$  (range = 0–8,  $n = 59$ ) young fledged per monogamous male per season ( $t$ -test,  $P < 0.01$ ).

The experience or other advantages of age, however, are not prerequisite to successful production of young. One of the two females (age unknown) associated with the single bigamous SY male in our sample (Table 1) made three nesting attempts, successfully fledging two broods; the other female (age unknown) laid and successfully fledged two clutches. Assum-

TABLE 4. Extended.

| Mean nest survival rates |             |                   |
|--------------------------|-------------|-------------------|
| Combined                 |             |                   |
| Daily                    | Nest period | Exposure days (n) |
| 0.983 (0.006)            | 0.69        | 463 (61)          |
| 0.978 (0.006)            | 0.62        | 603 (77)          |
| 0.983 (0.005)            | 0.69        | 705 (71)          |
| 0.965 (0.010)            | 0.46        | 340 (66)          |
| 0.979 (0.003)            | 0.63        | 2,011 (275)       |

ing this yearling male was responsible for fertilizing all eggs in both clutches, he and his mates fledged 12 young that season (1987).

*Reproductive effort in terms of seasonal productivity.*—To determine seasonal productivity, we examined the number of eggs laid and their fate for the population of individually marked females. Of the 470 eggs laid by such females during the four-year period, 369 (78.5%) hatched and 304 (64.6%) young fledged (Table 6). Thirty (6.4%) eggs failed to hatch and were probably infertile or suffered embryo death, 57 (12.1%) were lost to depredation, and 11 (2.3%) were abandoned during the incubation period. Losses during the nestling stage were due to predation (7.9% of eggs laid), starvation (3.6%), and other factors such as abandonment (4.3%).

On a per-capita basis, female Black-throated Blue Warblers laid an average of 6.6 eggs each season, of which 5.2 hatched and 4.3 fledged

(Table 6). The only significant differences among these values involved comparisons with 1989, a year in which females laid fewer eggs compared to 1987 and 1988 ( $t$ -tests,  $P < 0.025$  and  $P < 0.01$ , respectively), hatched fewer young compared to 1987 ( $P < 0.05$ ), and fledged fewer young compared to both 1987 and 1988 ( $P < 0.05$ ; Table 6). As a consequence, the lowest per-capita production of young per season was in 1989, when most females fledged only one brood (Table 3) and an average of 3.5 young (Table 6). These lower values in 1989 apparently were due to fewer nesting attempts in that season (Table 3) and not to differences in clutch sizes (Table 2).

*Reproductive effort and recruitment.*—We predicted that, if reproductive success were important in affecting subsequent population levels, there should be a positive correlation between reproductive performance and the recruitment of yearlings into the population the next season. Following Sherry and Holmes (1991), we calculated recruitment as the number of yearling males entering the population on the study area each spring, expressed as a percentage of the number of adult males present in the preceding year (from Table 1 and R. T. Holmes, unpubl. data). Yearling recruitment, so defined, was positively correlated (Fig. 2) with the mean number of young fledged per female in the preceding season (from Table 6 and Rodenhouse 1986), although not significantly so ( $r = 0.808$ ,  $R^2 = 0.653$ ,  $P = 0.098$ ). Considering the few years for which we have data, however, the trend is highly suggestive.

TABLE 5. Causes of nest failure in Black-throated Blue Warblers at Hubbard Brook, 1986–1989 ( $n$  = number of nests).

|                  | Number (% in parentheses) |                      |                      |                      |                            |
|------------------|---------------------------|----------------------|----------------------|----------------------|----------------------------|
|                  | 1986<br>( $n = 25$ )      | 1987<br>( $n = 40$ ) | 1988<br>( $n = 30$ ) | 1989<br>( $n = 30$ ) | 1986–1989<br>( $n = 125$ ) |
| Clutches lost to |                           |                      |                      |                      |                            |
| Depredation      | 1 (4.0)                   | 5 (12.5)             | 5 (16.7)             | 5 (16.7)             | 16 (12.8)                  |
| Abandonment      | 1 (4.0)                   | 1 (2.5)              | 1 (3.3)              | 0 (0.0)              | 3 (2.4)                    |
| Subtotal         | 2 (8.0)                   | 6 (15.0)             | 6 (20.0)             | 5 (16.7)             | 19 (15.2)                  |
| Broods lost to   |                           |                      |                      |                      |                            |
| Depredation      | 3 (12.0)                  | 3 (7.5)              | 3 (10.0)             | 2 (6.7)              | 11 (8.8)                   |
| Weather          | 0 (0.0)                   | 1 (2.5)              | 0 (0.0)              | 1 (3.3)              | 2 (1.6)                    |
| Abandonment      | 0 (0.0)                   | 0 (0.0)              | 0 (0.0)              | 2 (6.7)              | 2 (1.6)                    |
| Subtotal         | 3 (12.0)                  | 4 (10.0)             | 3 (10.0)             | 5 (16.7)             | 15 (12.0)                  |
| Total            | 5 (20.0)                  | 10 (25.0)            | 9 (30.0)             | 10 (33.3)            | 34 (27.2)                  |

TABLE 6. Total reproductive effort of female Black-throated Blue Warblers on 70-ha study area at Hubbard Brook, 1986–1989 ( $n$  = number of individually marked females).

|  | 1986<br>( $n = 15$ ) | 1987<br>( $n = 21$ ) | 1988<br>( $n = 14$ ) | 1989<br>( $n = 21$ ) | 1986–1989<br>( $n = 71$ ) |
|--|----------------------|----------------------|----------------------|----------------------|---------------------------|
| <b>No. eggs</b>                            |                      |                      |                      |                      |                           |
| Laid                                       | 95                   | 152                  | 110                  | 113                  | 470                       |
| Unhatched                                  | 7                    | 12                   | 6                    | 5                    | 30                        |
| Depredated                                 | 3                    | 20                   | 18                   | 16                   | 57                        |
| Abandoned                                  | 2                    | 4                    | 5                    | 0                    | 11                        |
| <b>No. young</b>                           |                      |                      |                      |                      |                           |
| Hatched                                    | 83                   | 116                  | 78                   | 92                   | 369                       |
| Starved                                    | 1                    | 8                    | 4                    | 4                    | 17                        |
| Depredated                                 | 13                   | 12                   | 5                    | 7                    | 37                        |
| Lost to other factors <sup>a</sup>         | 1                    | 4                    | 4                    | 11                   | 20                        |
| Fledged                                    | 69                   | 92                   | 69                   | 74                   | 304                       |
| <b>Mean <math>\pm</math> SD per female</b> |                      |                      |                      |                      |                           |
| No. eggs laid                              | 6.3 $\pm$ 1.9        | 7.2 $\pm$ 2.7        | 7.9 $\pm$ 3.1        | 5.4 $\pm$ 2.4        | 6.6 $\pm$ 2.7             |
| No. young hatched                          | 5.5 $\pm$ 2.0        | 5.5 $\pm$ 2.3        | 5.6 $\pm$ 2.4        | 4.4 $\pm$ 2.1        | 5.2 $\pm$ 2.2             |
| No. young fledged                          | 4.6 $\pm$ 2.2        | 4.4 $\pm$ 2.3        | 4.9 $\pm$ 2.9        | 3.5 $\pm$ 1.8        | 4.3 $\pm$ 2.3             |

<sup>a</sup> Including weather and abandonment (see Table 5).

## DISCUSSION

With an average of 4.3 young fledged per female per year, Black-throated Blue Warblers during our study were producing more young than needed for replacement. This high annual production was due most directly to high nesting success (63%), low nest predation rates (22%), a lack of brood parasitism, and relatively frequent (48%) multiple brooding. Also, during this same period, nesting success was positively correlated with available food resources (Holmes

et al., 1991; see below). This set of factors may be typical of those affecting annual production of Neotropical migrant species inhabiting unfragmented temperate forests in contrast to disturbed or fragmented habitats, where nest predation and parasitism rates are high, and nesting success is low (Askins et al. 1990; see below). Data in support of these commonly assumed differences between large forest tracts and fragmented ones are surprisingly scarce and sketchy. In this discussion, we consider the factors that influence the annual reproductive output of Black-throated Blue Warblers during our study, make comparisons with other species and across habitats, and evaluate the hypothesis that breeding productivity is a major factor influencing population size and dynamics in this Neotropical migrant species.

*Nesting success and predation.*—The nesting success of Black-throated Blue Warblers at Hubbard Brook (63% by Mayfield method, Table 4; 72.8% as fraction of nests fledging young, Table 5) was considerably higher than the overall average rate of 42% ( $n = 17$  studies using Mayfield method) and 44% ( $n = 32$  studies using fraction of nests fledging young) reported by Martin (1992). Because Martin's data came from a review of studies of Neotropical migrants breeding in a variety of habitats, they probably include species in both unfragmented and fragmented habitats. Recent evidence indicates that nest success in small forest fragments (Rob-

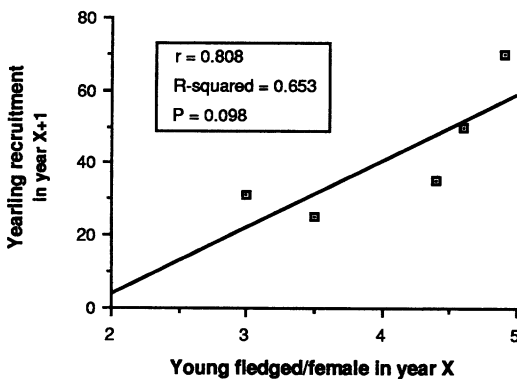


Fig. 2. Relationship between annual breeding productivity of Black-throated Blue Warblers at Hubbard Brook in one year (year  $x$ , 1985–1988) and recruitment of yearling (SY) males into the population in subsequent seasons (year  $x + 1$ , 1986–1990). See text for discussion.



inson 1992) and along edges of larger forest tracts (Temple and Cary 1988) is often less than 20%. This is due primarily to high nest depredation rates, which increase with forest fragmentation (Wilcove 1985, Small and Hunter 1988) and also to cowbird parasitism, which increases in habitats close to agricultural areas, including many forest fragments (Brittingham and Temple 1983, Temple and Cary 1988).

In his review, Martin (1992) reported that predation accounted for the loss of 42.8% (range = 11–67%) of active nests initiated by Neotropical migrants, whereas cowbird parasitism caused an average loss of 9% (range = 0–65%). In the present study, only 22% of the clutches initiated by Black-throated Blue Warblers were lost to predation (Table 5), but of those that did fail, predation was the main cause of mortality (79%,  $n = 34$ , see Table 5) and, as indicated, cowbird parasitism did not occur. At Hubbard Brook, experimental studies using artificial nests indicate that predation events in these undisturbed forests are very patchy and, thus, variable in both space and time (Reitsma et al. 1990, Sloan 1991; Reitsma, unpubl. data). This variability in predation pressure, coupled with a relatively sparse but locally diverse predator community, may lead to the low nest predation rates recorded in our study. Based on observations and photographs taken at artificial nests, seven species of mammal and one bird species have been recorded depredating nests at Hubbard Brook (Reitsma et al. 1990; L. R. Reitsma, T. W. Sherry, and R. T. Holmes, unpubl. data), the most important being red squirrels (*Tamiasciurus hudsonicus*), Blue Jays (*Cyanocitta cristata*), and eastern chipmunks (*Tamias striatus*).

The high nesting success rates of Black-throated Blue Warblers at Hubbard Brook, thus, can be accounted for by the low nest depredation rates and the absence of cowbird parasitism in the undisturbed, unfragmented forest where this study was conducted.

*Multiple brooding and reproductive output.*—In contrast to temperate-zone resident species, Neotropical migrant passerines often are characterized as birds that usually produce no more than one successful brood per season (Wiens 1989, Morse 1989). It is evident from our study that Black-throated Blue Warblers regularly produce two broods, or even occasionally three per season (Table 3; see also Rodenhouse and Holmes 1992). Furthermore, since nesting success did not vary significantly among years in

this study, the differences in annual productivity (numbers of young produced per female per season) by female Black-throated Blue Warblers were strongly influenced by the frequency of multiple brooding.

How common is double or multiple brooding among Neotropical migrant birds? For paruline warblers, there are a few reports indicating that double brooding does occur, and its frequency and extent rarely have been documented. Nolan (1978:430) found that 35% of the female Prairie Warblers that fledged young before mid-July ( $n = 51$ ) attempted second broods, and double brooding occurred in 10 of the 11 years of his study. Petit (1989) reported that 77% of 66 female Prothonotary Warblers fledging a first brood laid a second clutch, 55% of which successfully fledged second broods. In Maine, 65% of 20 female Blackpoll Warblers (*D. striata*) laid second clutches (Eliason 1986). Based on male singing activity and the occurrence of nests late in the breeding season, other species at Hubbard Brook (e.g. Black-throated Green Warblers [*D. virens*], Red-eyed Vireos [*Vireo olivaceus*], and Scarlet Tanagers [*Piranga olivacea*]) may also produce multiple broods, at least in years when food is plentiful (R. T. Holmes and T. W. Sherry, unpubl. data). In Ontario, Keast (1990) reported double brooding in about one-third of the bird species in a deciduous forest-edge community, but most of the forest-dwelling migratory species were reported as single brooded. As more studies of migrant birds measure the reproductive histories of marked individuals, double brooding may be shown to be more common than previously thought. Whether or not it occurs more frequently in bird populations inhabiting large tracts of undisturbed habitats, or at lower latitudes where frost-free seasons are longer, remains to be determined. This gap in our knowledge underscores the paucity of quantitative information on the basic breeding biology of Neotropical migrant species (Martin 1992).

Some Neotropical migrant species do not double brood, or at least do so infrequently. We have not observed double brooding in a 10-year study of color-marked American Redstarts at Hubbard Brook, although redstarts regularly replace nests following early nest failure (T. W. Sherry and R. T. Holmes, unpubl. data). Goossen and Sealy (1982) stated that Yellow Warblers in Manitoba "rarely attempted" second broods, and Walkinshaw (1983) reported only

11 cases of double brooding in Kirtland's Warbler out of an unstated but apparently large number examined.

*Factors affecting multiple brooding.*—Because multiple brooding appears to be a process that significantly influences the annual reproductive output of Black-throated Blue Warblers, it is important to understand the factors that determine its frequency. We are aware of at least two such factors: (1) time constraints during the temperate summer season; and/or (2) food abundance.

Given the climatic constraints on length of favorable season, a major factor influencing the frequency of multiple brooding appears to be the fate of early-season nests, and, thus, whether there is sufficient time available to build new nests and lay additional clutches after completing earlier ones. Nolan (1978) found that Prairie Warbler females that successfully fledged a brood early in the season were more likely to produce a second clutch. The same held for Black-throated Blue Warblers in our study. Relatively wet weather in late May and June 1989 delayed the onset of laying and/or led to early-season nest failures. These conditions, coupled with relatively high depredation rates early in the 1989 season (Table 5; R. T. Holmes, unpubl. data), probably account for the fact that only 35% of females initiated second clutches that season and only 10% fledged second broods (Table 3).

Another factor influencing nesting success and annual production of young is food available to breeding birds at particular times of the breeding season. Although actual starvation of young was infrequent in this study (Table 6, but see Rodenhouse and Holmes 1992), the mean number of young fledged per nesting attempt by female Black-throated Blue Warblers on our study area during the same time period (1986–1990) was positively and significantly correlated with mean caterpillar abundance (both numbers and biomass) present each season (Holmes et al., 1991). Further, in an earlier study (1981–1985), using natural and experimentally-produced variations in caterpillar abundance, Rodenhouse and Holmes (1992) found that the annual reproductive output of Black-throated Blue Warblers at Hubbard Brook was positively and significantly related to caterpillar biomass, more young fledging in seasons when more caterpillars were available. This effect was due largely to a greater frequency of double brood-

ing in years with higher food abundance in midsummer, just as we have found in more recent years. Thus, food supply apparently influences the number of young fledged, primarily by influencing double brooding, and probably post-fledging survival, both of which potentially influence population dynamics of this species.

The impact of these two processes affecting multiple brooding may differ among habitats. The time-constraint effect may be more critical in disturbed or fragmented habitats, where predation and/or parasitism rates are high (see references above). In such situations, birds re-nest frequently and may lack the time needed to fledge more than one brood per season, further lowering their nesting productivity. In contrast, variations in food abundance may occur in both fragmented and unfragmented habitats, but would be the major factor affecting multiple brooding in intact, undisturbed habitats. Further studies of the reproductive ecology and breeding effort of Neotropical migrants in relation to food abundance and predation are needed to test these predictions.

*Effects of age and pairing success on reproductive output.*—Our results indicate that two-year or older male Black-throated Blue Warblers were more likely to mate polygynously and to be mated to females that double brooded. The available evidence also suggests that older females were also more productive (see Results). Such concentration of reproductive success in relatively few individuals may be a demographic characteristic of populations in undisturbed habitats, and may contribute towards their high production of young. If the birds occupying woodlots, fragmented forests, and other modified habitats are mostly yearlings (S. K. Robinson, pers. comm.) and, if site tenacity to these areas is low (see Robinson 1992), the absence of older, more experienced individuals may contribute to the relatively low productivity in such habitats. Thus, changes in the demographic structure of these populations as a result of habitat modification may have important consequences for reproductive output and population dynamics, particularly the maintenance of population size.

During our study, most male Black-throated Blue Warblers were successfully paired to one or, in a few cases, two females. Also, most adult Black-throated Blue Warblers fledged at least one brood each season, indicating full involve-

ment of all or most individuals in nesting efforts. This may not be the case in highly modified or fragmented forests, as evidenced by the finding that a high proportion of male Ovenbirds (*Seiurus aurocapillus*) in forest fragments were unpaired (Gibbs and Faaborg 1990). Such biases in sex ratio could seriously jeopardize reproductive success in these species (Sherry and Holmes 1991).

*Effects of productivity on recruitment and abundance.*—Does the reproductive success of Neotropical migrants breeding in temperate forests influence subsequent population size or composition? Studies of bird and caterpillar abundances on four replicate plots over five seasons in New Hampshire have shown that bird abundances were significantly correlated with caterpillar biomass in the previous summers (Holmes et al. 1991). In our study, the number of yearlings present each year was positively correlated with the mean number of young fledged per female in the previous season (Fig. 2). Similar and statistically significant correlations between yearling recruitment and reproductive success have been found for two other Neotropical migrant warblers (Prairie Warbler, Nolan 1978; American Redstart, Sherry and Holmes 1992) that have been studied over periods of up to a decade. Furthermore, in redstarts, reproductive success clearly predicts yearling recruitment, suggesting that reproductive success may drive population changes in this species (Sherry and Holmes 1991).

None of the more than 300 nestling Black-throated Blue Warblers banded on the Hubbard Brook study area has been resighted in subsequent years (R. T. Holmes and T. W. Sherry, unpubl. data). Thus, the yearling Black-throated Blue Warblers recruited to the Hubbard Brook study area each year were not the individuals fledged on that area. Returns of birds to natal areas usually are very low (Nolan 1978, Stewart et al. 1978, Carey and Nolan 1979, Eliason 1986; see Greenwood and Harvey 1982), and often are difficult to detect if study areas are small. If returning yearlings of migrant species, such as the Black-throated Blue Warbler, typically disperse widely in their breeding areas, then local areas with high reproductive success in one year will likely influence the population levels in surrounding areas in the next season (i.e. these represent "source" populations; Pulliam 1988). Thus, the high reproductive output per capita of Black-throated Blue Warblers (Table 6) and

their increasing densities on the Hubbard Brook study area between 1986 and 1989 (Table 1) are probably causally related.

Our results suggest that factors determining breeding success and annual productivity of Black-throated Blue Warblers have important subsequent effects on local population size. Similar findings have been reported for several other migrant species (Nolan 1978, Virolainen 1984, Sherry and Holmes 1992). Because these effects occur in spite of mortality during the post-fledging period, on migration, and on the winter grounds, breeding productivity appears to be particularly critical in maintaining the viability of at least some long-distance migrant species. Similarly, poor reproductive success in other migrant bird populations, particularly those in fragmented or otherwise degraded habitats, may be a primary cause of their population declines, and may be related to increasing nest depredation or parasitism rates (see Askins et al. 1990, Robinson 1992, Sherry and Holmes 1992). These findings, taken together, suggest that declining reproductive success due to human modifications of temperate landscapes may be a crucial factor in the decline of Neotropical migratory birds (Sherry and Holmes 1991).

Baseline reproductive and related demographic data on more Neotropical migrant species in diverse habitats, both fragmented and unfragmented, are needed to test the validity and generality of the findings reported here. The challenges ahead include identifying the important factors limiting or regulating these long-distance migratory bird populations, whether these operate more importantly in the summer, in winter, or on migration, and how the impact of these factors varies with density, habitat, land-use patterns, climate change, and other environmental parameters.

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