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FACTORS AFFECTING FOOD PROVISIONING OF NESTLING BLACK-THROATED BLUE WARBLERS

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ABSTRACT.—Using video cameras at nests, we measured rates, quantities, and types of food delivered by male and female Black-throated Blue Warblers (*Dendroica caerulescens*) to nestlings of different ages and at different times of day and nesting season. Based on 89 1.5–2 h observation periods at 18 nests, all of which contained four young, we found that larval Lepidoptera comprised 60–87% of the estimated prey biomass brought to nestlings and that the female and male parents delivered approximately equal amounts of food over the nesting cycle. Food provisioning rates did not vary with time of day or with parental age, but did increase significantly with age of nestlings and decrease with time of season (early vs mid-summer). The lower rate and quantity of provisioning in mid-summer was reflected in significantly slower growth of nestlings in that part of the season, suggesting constraints on parental food provisioning, perhaps due to lower food availability. *Received 27 Aug. 1995, accepted 2 Feb. 1996.*

Successful production of offspring is an essential component of individual fitness (Stearns 1992), as well as being crucial to the maintenance of population levels for most, if not all, bird species (Nolan 1978, Virolainen 1984, Sherry and Holmes 1992, Holmes, et al. 1992. Robinson et al. 1995). Although predation at the nest is probably the single most important factor affecting breeding success of most passerine birds (Ricklefs 1969, Holmes et al. 1992, Martin 1992a), parental care of nestlings can also be important (Kuitunen and Suhonen 1991). Parental care, which includes nest building, incubation, food provisioning, vigilance, and brooding, is not only energy-demanding but also potentially risky to the survival of the parents and their lifetime reproductive success (Curio 1988). Quantities of food delivered can influence nestling survival as evidenced by brood reduction due to starvation in many passerine birds (Magrath 1990) and in some cases by starvation of whole broods (Rodenhouse and Holmes 1992, Sherry and Holmes 1992). Also, nestlings that are not well fed may beg more, which could result in the attraction of predators, leading to higher nest losses (Skutch 1949, Martin 1992b). The patterns of food delivery to nestlings and the factors that affect them are, therefore, important for understanding population processes. Information about which factors influence food delivery patterns is also useful for designing sampling protocols for future studies of reproductive biology of particular species.

In this study, we examined the rates and quantities of food delivered

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to nestlings by male and female Black-throated Blue Warblers (*Dendroica caerulescens*) breeding in a northern hardwoods forest in north-central New Hampshire. Specifically, we tested whether or not feeding rates and quantities of food delivered by males and females varied with nestling age, time of season, time of day, and/or parental age. We also considered the effect of parental provisioning by measuring the growth rates of young in the nests being videotaped.

STUDY SITE AND METHODS

This study was conducted in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire. This forest consists of northern hardwoods, dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*), with a shrub layer of hobblebush (*Viburnum alnifolium*), saplings of sugar maple and especially beech, and striped maple (*A. pensylvanicum*). The ground stratum consists mostly of herbs, tree seedlings, mosses, and ferns (Bormann and Likens 1979, Holmes 1990).

At Hubbard Brook, Black-throated Blue Warblers nest at an average height of 0.6 m above ground, mostly in hobblebush but also in other shrub-level vegetation (Holmes 1994). We located most nests during the building or incubation stages and then checked them periodically until hatching. Nestlings were weighed with a 10-g Pesola balance on days 2, 4, and 6 (hatching = day 0), the last day they could be handled without causing premature fledging (Holmes et al. 1992). Parents at each nest were color banded, and aged as yearlings (i.e., in their first potential breeding season after hatching) or as older individuals (i.e., in their second or later breeding season), using plumage criteria (U.S. Fish and Wildlife Service 1977, Pyle et al. 1987). Identification of the sexes was unambiguous, due to strong sexual dichromatism in this species.

To record parental feeding rates and foods brought to nests we used two Sony camcorders and one Panasonic S-VHS Recorder (VCR) equipped with 8–10× telephoto lens. Cameras were set on tripods (0.5–1.5 m high) at distances of 3–5 m from the nest, depending on local topography and on density and arrangement of nearby foliage. The video cameras and tripods were covered with black plastic for rain protection and then draped with burlap for camouflage. If necessary, overhanging leaves around the nest were pulled aside and tied so as not to obscure the nest during taping. Any tapes containing evidence that the adults were disturbed were eliminated from the analyses. Taped sequences ranged from 1.5–2 h depending on battery life; data were converted to number of visits, or quantities of food delivered, per hour.

Between 12 June and 17 July 1991, we obtained 89 video samples at nests of 18 Black-throated Blue Warbler pairs. We restricted the nests used for analysis to those containing four young, the mean and modal brood size for Black-throated Blue Warblers at Hubbard Brook (Holmes et al. 1992). Each nest was attended by one male and one female, and none of the males was known to be polygynous (see Holmes et al. 1992, 1996). Visits to nests were video-taped when nestlings were 2, 4, 6, and 8 days of age (hatch = day 0). In this species, nestlings typically fledge late on day 8 or on day 9 (Holmes 1994). Samples were obtained from the same nests on different days, but no nests were sampled more than once per time-of-day/age-of-nestling category. Data from each recording session were categorized according to age of nestlings (see above), time of the season ("early" nests fledged young before 1 July, "late" nests after 1 July, see Holmes et al. 1992 for nesting chronology), the time of day when the nests were videotaped (grouped in three time intervals [EDT]: morning, 06:30–09:45 h, midday, 10:30–13:30, and afternoon, 14:00–17:00), and the age of parents (yearling vs older, see above).

From each taped sample, we recorded the number of visits made by each parent and, where possible, the number, size, and life-form (larval or adult, the latter including Arachnida) delivered to the young. Prey size was determined by comparing the length of prey item (or the prey load when there was more than one item that could not be distinguished) with the 7 mm-long exposed portion of the Black-throated Blue Warbler bill. These data were grouped into four size classes (<7 mm, 7–14 mm, 14–21 mm, >21 mm), regardless of taxa. They were then converted to biomass, based on length-mass regressions for midpoints of each size class. Conversion factors for the four size classes were 1, 2, 8, and 20 mg, respectively, following the rationale and protocol of Omland and Sherry (1994: Table 1). Estimates of food biomass delivered to the nest per hour were then obtained by summing the estimated prey biomass on each trip during the sample period, and expressing these as mg of food delivered $\cdot brood^{-1} \cdot h^{-1}$.

Data for both the number of feeding trips per hour and the food biomass delivered per hour were normalized by square root transformation. The relationships between food provisioning and each variable for both females and males were evaluated by analyses of variance (ANOVA). Differences between the sexes and parental age classes, where appropriate, were examined with *t*-tests. Potential differences in nestling growth in early versus late season nests was assessed by comparing (1) the mean body mass of nestlings on day 6 (mean mass per nestling in nests with 4 young, N = number of nests) and (2) the rate of gain in body mass between day 2 and day 6 (mean mass per nest on day 6 minus that on day 2, N = number of nests).

RESULTS AND DISCUSSION

The number of feeding trips and the biomass of food delivered to broods per hour by adult Black-throated Blue Warblers varied significantly with nestling age (except for feeding trips by females) and with time of season (for both sexes), but not with time of day (Table 1) or with parental age (see below). Two and three-way interactions among these variables were not statistically significant (P values > 0.2). Removal of time of day from the ANOVAS did not alter these results. As mentioned previously, brood size was not a factor in these analyses, because only nests containing four young were considered.

Effects of nestling age.—The most important factor affecting both the number of food delivery trips and amount of food delivered per nestling was nestling age. Both sexes increased their feeding visitation rates from day 2 through day 8 of the nestling phase (Fig. 1A). This trend was not statistically significant for females (Table 1), probably because they were already feeding nestlings relatively frequently on day 2 and did not increase their rate substantially between days 4 and 6. In contrast, males progressively increased their feeding visits as the nestlings became older (Fig. 1A). This difference between the sexes was also evident in comparisons of food visitation rates on particular days: on average, females made significantly more trips to the nest than did males on days 2 and 4 ($t = 4.01$, df = 38, $P = 0.000$, and $t = 3.26$, df = 46, $P = 0.002$,

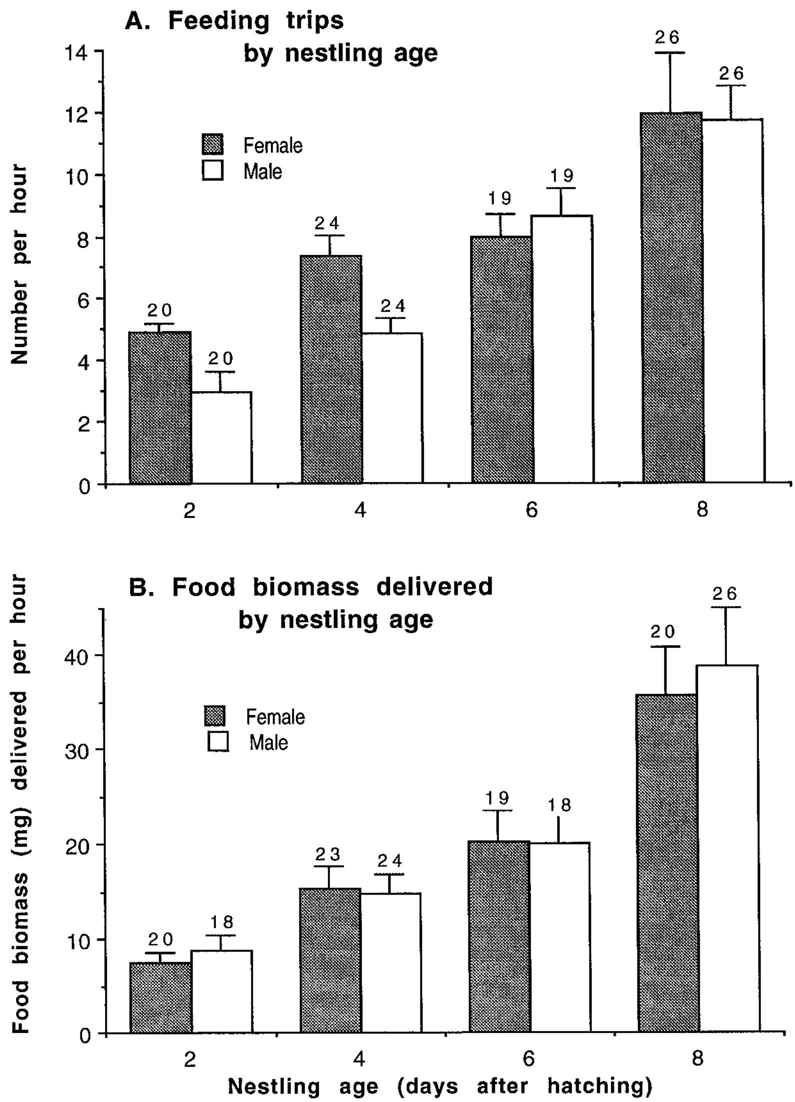

FIG. 1 Feeding rate (A) and estimated food biomass delivered (B) by female and male Black-throated Blue Warblers to broods of four young on days 2, 4, 6, and 8 following hatching (Means ± SE, N = number of 1.5–2 h video-taped samples).

TABLE 1

RESULTS OF ANALYSES OF VARIANCE (ANOVA) TESTS OF FOOD PROVISIONING BY MALE AND FEMALE BLACK-THROATED BLUE WARBLERS AT NESTS WITH FOUR YOUNG[a]

	Females				Males			
	SS[b]	df	*F*	*P*	SS[b]	df	*F*	*P*
Number of food deliveries								
Model[c]	12.50	6	1.74	0.121	41.24	6	15.90	0.000
Age of nestlings	1.25	3	0.35	0.790	38.76	3	29.89	0.000
Time of day	0.95	2	0.40	0.673	0.01	2	0.01	0.988
Time of season	5.18	1	4.34	0.040	2.13	1	4.92	0.029
Residual	110.42	88			76.69	88		
Food biomass delivered								
Model	120.47	6	11.06	0.000	119.47	6	6.93	0.000
Age of nestlings	50.71	3	9.31	0.000	53.15	3	6.16	0.001
Time of day	4.65	2	1.28	0.284	0.69	2	0.12	0.887
Time of season	9.84	1	5.42	0.023	14.24	1	4.95	0.029
Residual	256.62	81			346.52	85		

[a] Analyses were performed separately on the number of food delivery trips·h^{-1} and on the estimated food biomass (mg) delivered·h^{-1}.

[b] Sum of squares.

[c] Explained variance for full models: female number, $r^2 = 0.11$; female biomass, $r^2 = 0.47$, male number, $r^2 = 0.54$; male biomass $r^2 = 0.34$.

respectively), but not on days 6 and 8 ($t = -0.61$, df = 36, $P = 0.546$, and $t = 0.08$, df = 50, $P = 0.938$, respectively).

The quantity of food delivered to the brood increased significantly with nestling age for both sexes (Table 1, Fig. 1B). There were no significant differences between the sexes, however, in the quantity of food delivered per hour at any of the four nestling ages days sampled (*t* tests, *P* values > 0.49). Because males made fewer trips to nests on days 2 and 4 but were contributing about equal biomass (Fig. 1B), they must have been bringing larger and/or more prey per trip (see below).

The positive relationship between nestling age and feeding/food biomass delivery rate was related, as expected, to the increasing energy demands of the young, either for growth or thermoregulation. This same pattern has been reported for most species where it has been studied (e.g., Morehouse and Brewer 1968, Nolan 1978, Johnson and Best 1982, Biermann and Sealy 1982, Bedard and Meunier 1983, Breitwisch et al. 1986, Haggerty 1992). The only apparent exception is the Nashville Warbler (*Vermivora ruficapilla*) in which both males and females were reported to feed nestlings at an essentially constant rate (Knapton 1984). This study, however, examined feeding rates only on days 4 to 8 of the nestling period.

Differences between male and female passerines in the provisioning of their nestlings have been noted frequently, but there appears to be no consistent pattern. In Prairie Warblers (*D. discolor*) and Eastern Phoebes (*Sayornis phoebe*), both sexes fed about equally throughout the nestling period (Nolan 1978 and Conrad and Robertson 1993, respectively). In Yellow Warblers (*D. petechia*), males brought more food to the nest than did females when nestlings were two days old, but by day 8, males and females were delivering food at equal rates (Biermann and Sealy 1982). Female and male Savannah Sparrows (*Passerculus sandwichensis*) made approximately equal number of trips to the nest through the entire nestling period, although this varied some with brood size (Bedard and Meunier 1983). In the latter study, however, when food biomass was considered, males and females brought different quantities of food at different parts of the nestling cycle. Similarly, when food biomass estimates were made for Black-throated Blue Warblers in this study, we found that although the sexes fed at different rates at different parts of the nesting cycle, they delivered approximately equal quantities of food over the nestling period.

Effects of time of season.—Black-throated Blue Warblers made significantly fewer feeding visits and delivered less food biomass per nest per hour in mid-summer (July) than earlier in the season in June (Table 1, Fig. 2). These lowered provisioning rates in the later part of the breeding season were evident for both female and male parents. Furthermore, there were no significant differences between the sexes in their rates of feeding visits or in the quantities of food biomass delivered on any of the four sample days in either the early or the late parts of the season (t tests, P values > 0.13). The lower provisioning at nests in mid summer, therefore, was not due to one sex being a poorer provider at that time.

Other studies have found either no change in food provisioning rates during the course of a breeding season (Johnson and Best 1982), or if changes did occur, they were compensated for by an increase in the quantities of prey brought to the nest (Royama 1966). The fewer trips to the nest/hour and lower food biomass delivered by Black-throated Blue Warblers in this study could be due to several factors. First, nestlings in mid-summer may have lower energy requirements because of lower thermoregulatory costs in the warmer temperatures, although this seems unlikely in these relatively cool northern forests. Second, because the nests in mid-

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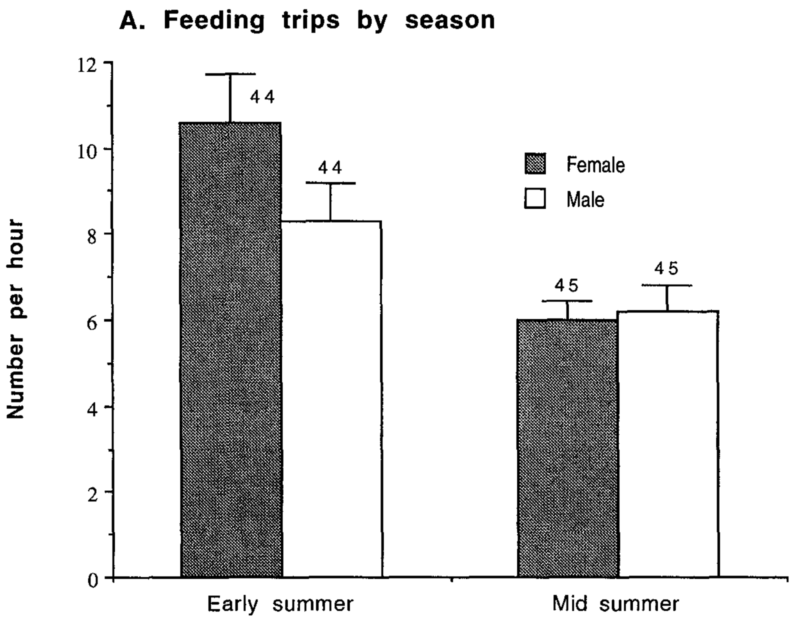
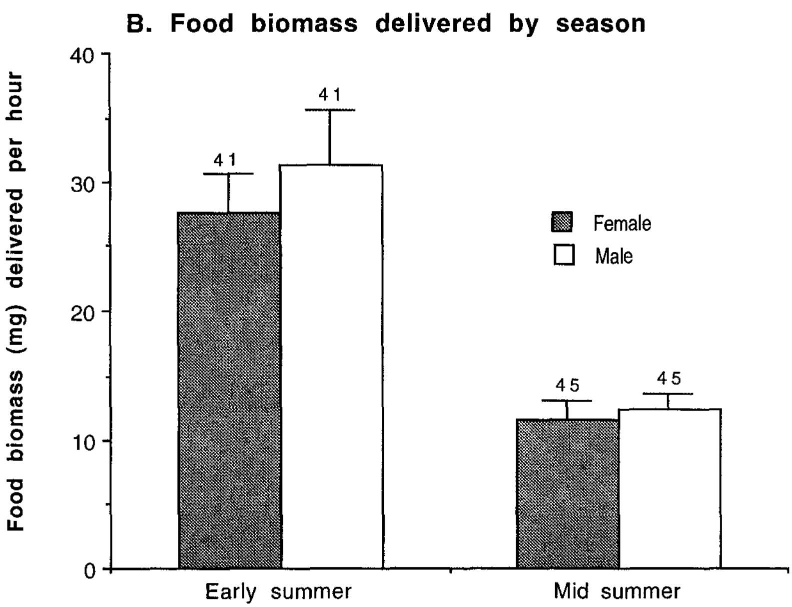
FIG. 2. Feeding rate (A) and estimated food biomass delivered (B) by female and male Black-throated Blue Warblers to broods of four young in June and July (Means ± SE, N = number of 1.5–2 h video-taped samples).


A. Feeding trips by season
Number per hour
12
10
8
6
4
2
0
44
44
45
45
Female
Male
Early summer
Mid summer


B. Food biomass delivered by season
Food biomass (mg) delivered per hour
40
30
20
10
0
41
41
45
45
Female
Male
Early summer
Mid summer

summer were either replacements for ones lost earlier in the season or were second broods (Holmes unpubl. data), perhaps they may be more "expendable" if other energy demands for the parents become more important, e.g., the onset of the annual molt or fat deposition for migration. Molt in this species, however, does not begin until early August and departure on migration doesn't occur until later in the season (Holmes 1994), so this explanation seems unlikely.

A third possible explanation for lower food provisioning of nestlings in mid-summer is that parents had more difficulty in finding food at that time of the season. If so, the reduced level of provisioning should result in slower nestling growth. To test this, we compared growth rates of nestlings in early and late season nests, as indicated by changes in body mass of nestlings between day 2 and day 6 following hatching and body mass on day 6. The mean (±SE) change in body mass of nestlings in early season nests (5.08 ± 0.16 g, N = 8 nests) was significantly higher than that for nestlings in late season nests (4.32 ± 0.21, N = 7; $t = 2.94$, df = 13, $P = 0.012$). Similarly, nestlings on day 6 in the early part of the summer were heavier (7.71 ± 0.02 g, N = 10 nests) than those in mid-summer (7.03 ± 0.30, N = 8), although these differences were only marginally significant ($t = 1.93$, df = 16, $P = 0.07$). Thus, Black-throated Blue Warbler nestlings in late season nests grew more slowly than did their early season counterparts, which could ultimately have a major impact on their post-fledging survival as has been shown by Perrins (1980) for Great Tits (*Parus major*). This finding suggests that food provisioning by Black-throated Blue Warbler parents is not always sufficient to maximize growth of their nestlings and is consistent with the proposition that food is limiting for Black-throated Blue Warblers, at least in some years or seasons (Holmes et al. 1991, Rodenhouse and Holmes 1992).

Effects of time of day.—Food provisioning by Black-throated Blue Warblers did not differ significantly with time of day, either for feeding visitation rate or food biomass delivered (Table 1). Also, there were no significant differences between the sexes in either feeding visits or food delivered at different times of day (t tests, P values > 0.22).

Nolan (1978) found little variation in foraging rate during the day for Prairie Warblers, except for an increase in the morning shortly after dawn (06:00–07:00) and a smaller increase late in the day (19:00–20:00). Similarly, Haggerty found no significant diurnal variation in provisioning rates of Bachman's Sparrow (*Aimophila aestivalis,*). More pronounced diurnal patterns have been reported for other species, e.g., Eastern Kingbirds (*Tyrannus tyrannus,* Morehouse and Brewer 1968) and Nashville Warblers (*Vermivora ruficapilla,* Knapton 1984), in which feeding rates decrease in the middle of the day and increase again later. These are mainly species of more open habitats in which mid-day temperatures may depress insect activity or increase physiological stress on foraging adults. In the present study, Black-throated Blue Warblers nested and foraged largely in the cool, well-shaded understory of a closed-canopy forest, where diurnal variation in summer temperature and insect abundance, especially of Lepidoptera larvae, is not pronounced (R. T. Holmes, unpubl.).

Effects of parental age.—Because of relatively small sample sizes for each parental age class within a sex and the lack of independence arising from multiple samples from individual nests, we were unable to include parental age in the ANOVAs. However, we could test for parental age effects within a restricted part of the nestling period. To do this, we compared the feeding rates of yearling and older parents, both females and males, at nests containing 4 young on day 6 of the nestling period, the time when our sample was largest. The results of one-way ANOVAs indicated no significant difference in feeding visitation rate or food biomass delivered between yearling and older females ($F_{1,17} = 0.06$, $P = 0.81$, and $F_{1,17} = 0.03$, $P = 0.881$, respectively) or between yearling and older males ($F_{1,17} = 0.09$, $P = 0.768$, and $F_{1,16} = 1.51$, $P = 0.237$). Thus, at least on day 6 of the nestling period, there was no effect of age on food provisioning of nestlings for either female or male Black-throated Blue Warblers.

There is little comparative information on food provisioning rates among parental age classes for passerines. Goossen and Sealy (1982) suggested that older Yellow Warblers (*D. petechia*), because of their greater experience, should provide better care for their nestlings than first-time breeding yearlings, but they did not provide supporting data. Studd and Robertson (1989) found no difference in provisioning rate between age classes in Yellow Warblers, nor did Omland and Sherry (1994) for male American Redstarts *Setophaga ruticilla.* Current evidence thus suggests that year-old parents do about as well as older, and presumably more experienced, adults in providing food for their nestlings.

Foods delivered.—For purposes of analysis, food brought to nestlings was divided into two broad categories recognizable in video images, namely larval arthropods (almost entirely lepidopteran caterpillars) and arthropod adults (e.g., crane flies (Tipulidae) and other Diptera, some Hymenoptera and Lepidoptera, and occasional Coleoptera and Arachnida). On a biomass basis, larval insects comprised 60 to 87% of the food brought to nestlings by both females and males (Table 2). Females delivered 43 to 50% of the food biomass to the brood over the course of the nesting cycle. There were no significant differences between the sexes in larval and adult biomass delivered per hour (*t* tests, P values > 0.3),

TABLE 2

ESTIMATES ($\bar{x}$ ± SE) OF FOOD BIOMASS DELIVERED TO BLACK-THROATED BLUE WARBLER NESTLINGS ON DAYS 2, 4, 6, AND 8 FOLLOWING HATCHING

	Food biomass (mg dry weight) delivered·brood^{-1}·h^{-1} for nestling age (in days)			
	2	4	6	8
Food delivered by females				
Larval insect biomass[a]	4.9 ± 0.9	12.2 ± 1.7	14.9 ± 2.4	21.8 ± 3.9
Adult insect biomass[b]	2.5 ± 0.6	3.2 ± 0.8	5.8 ± 1.6	14.0 ± 5.0
% larvae	63%	80%	78%	60%
(N)[c]	(20)	(23)	(19)	(20)
Food delivered by males				
Larval insect biomass[a]	7.7 ± 1.7	12.5 ± 1.9	15.2 ± 2.3	27.4 ± 5.1
Adult insect biomass[b]	1.1 ± 0.5	2.2 ± 0.7	4.9 ± 1.2	11.4 ± 2.5
% larvae	87%	84%	79%	73%
(N)	(18)	(24)	(18)	(26)
% Total food biomass delivered by females	46%	50%	49%	43%

[a] Mostly Lepidoptera larvae.
[b] Flying insects, mostly Diptera, with occasional Hymenoptera and Coleoptera.
[c] Sample sizes represent number of video samples per nestling age class during which prey could be classified.

although variances were high (Table 2). There was a trend for males on day 2 to bring a greater biomass and percentage of larval prey than did females (Table 2), which compensates for their fewer trips at that stage (see below, Fig. 1A). Other studies have noted that male paruline warblers sometimes bring larger prey than do females, especially during the early part of the nestling period (see Nolan 1978, Biermann and Sealy 1982, Omland and Sherry 1994). In the present study, as a result of changing food loads (and partly by changing prey types), male and female Black-throated Blue Warblers contributed about equally in terms of prey biomass delivered to their broods over the course of their nesting cycle.

In conclusion, food provisioning rates of both male and female Black-throated Blue Warblers varied mostly with age of nestlings (especially for males) and with time of season for both parents, with males and females contributing about equally to the provisioning of their offspring. The lower rate of feeding visits and of food biomass delivered in mid-summer was correlated with a decreased rate of nestling growth in those nests compared to earlier in the season. Thus, food availability, at least in some times and places, provides a constraint on nestling growth rates which, in turn, might influence post-fledging survival. Food availability also affects the frequency of double-brooding and, as a consequence, the annual reproductive productivity of this species (Holmes et al. 1992). It is important to acknowledge that these results derive from studies conducted in only one year and one place. Replication in other locations, and especially over more years, will be required to determine the generality of these patterns. Also, because of large variances and intercorrelations between variables, larger sample sizes would be helpful for detecting patterns. Finally, some habitats or even territories within habitats occupied by Black-throated Blue Warblers may be more productive than others, affecting prey availability, and thus influencing food capture and delivery rates of the foraging parents. Thus, food provisioning patterns correlated with measures of food availability in different habitats or on a territory-to-territory basis would help to clarify causes underlying the patterns observed in this study.

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