

EFFECTS OF INSECTICIDE-INDUCED REDUCTION IN LEPIDOPTERAN LARVAE ON REPRODUCTIVE SUCCESS OF HOODED WARBLERS

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ABSTRACT.—We examined the effects of an insecticide-induced reduction of lepidopteran larvae due to spraying of *Bacillus thuringiensis* to eradicate gypsy moths (*Lymantria dispar*) on the reproduction of Hooded Warblers (*Wilsonia citrina*). Treatment plots had two applications of *Bacillus* in 1994. No *Bacillus* application occurred in 1995. Reductions in lepidopteran larvae were demonstrated by pheromone traps and arthropod samples from oak (*Quercus* spp.) foliage. We analyzed the following reproductive parameters: nesting success, number of eggs, number of fledglings, egg mass, mass of nestlings at day 5, growth rates, feeding rates, and prey items brought to nestlings. Of these reproductive parameters, three showed both statistical and biological differences. Nesting success was higher in the control than in the treatment zone in 1995, but not in 1994. Nestling masses at day 5 increased over the duration of the breeding season in the treatment zone but not in the control zone. Differences in feeding rates between treatment and control zones occurred only for small clutches. Overall, the reduction of lepidopteran larvae due to *Bacillus* application appeared to have only minimal effects on reproduction in Hooded Warblers. Received 9 September 1996, accepted 8 April 1997.

THE EFFECTS OF CHANGES IN FOOD AVAILABILITY on breeding forest birds are unclear. The contention that food is superabundant during the breeding season (e.g. Morse 1978, Rabenold 1978, Rosenberg et al. 1982) has been contradicted by claims that food can be limited during the breeding season (Martin 1987, Boutin 1990). Most studies that used food supplementation showed increases in at least one reproductive parameter, such as number of young produced, nestling mass, feeding rates, or annual productivity (see Martin 1987, Simons and Martin 1990, Lozano and Lemon 1995). Few studies, however, have examined the ecology of food limitation.

Questions of food limitation often are addressed by the use of pesticides that reduce food availability (Doane and Schaefer 1971, DeWeese et al. 1979, DeReede 1982, Hunter and Witham 1985, Cooper et al. 1990, Shearer 1990, Rodenhouse and Holmes 1992, Sample et al. 1993, Fair et al. 1995). Three of these studies (DeReede 1982, Shearer 1990, Rodenhouse and Holmes 1992) investigated reproductive parameters, and only Rodenhouse and Holmes

(1992) addressed the ecology of food limitation. Rodenhouse and Holmes (1992) found that clutch size, hatching success, number of young fledged, growth rates, and nestling masses of Black-throated Blue Warblers (*Dendroica caerulescens*) did not differ between control areas and areas where lepidopterans were reduced. During one year of their study, however, lower percentages of lepidopteran larvae were fed to nestlings in the lepidopteran-reduced areas.

We attempted to replicate the study of Rodenhouse and Holmes (1992). The application of *Bacillus thuringiensis* (var. *kurstaki*; hereafter "Bacillus") in an attempt to eradicate an infestation of gypsy moths (*Lymantria dispar*) in the Arkansas Ozarks created a reduction in the number of lepidopteran larvae. We examined the effects of this reduction in food on the reproductive parameters of an insectivorous Neotropical migrant, the Hooded Warbler (*Wilsonia citrina*). We chose Hooded Warblers as a study species because they were abundant on the study plots, they fed extensively on lepidopteran larvae (Evans Ogden and Stutchbury 1994, M. Revels pers. comm.), and their nests were easily monitored. We tested the hypothesis that the reduction of lepidopteran larvae would have no effect on the Hooded Warbler

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nesting success, clutch size, egg mass, number of fledglings, nestling mass, and growth rates. We also hypothesized that feeding rates would be lower and prey types would be different in areas of pesticide application, with fewer lepidopteran larvae being consumed in the treated areas.

STUDY AREA AND METHODS

Study area.—We conducted this study from 1 May to 31 July 1994 and 1 May to 30 July 1995 in the Ozark Mountains, northwestern Arkansas. Four study plots were selected on the basis of presence or absence of gypsy moths, presence of suitable habitat for Hooded Warblers (i.e. dense understory), and requirements for arthropod sampling of Lih et al. (1995). Study plots were visually similar, but due to the heterogeneous nature of the vegetation, we did not sample the vegetation. Control plots and one treatment plot had small clearcuts created within the last five years. All plots were high-graded for timber at the turn of the century (Smith and Petit 1988) and currently range between 82 to 87% oak/hickory and mixed hardwood forest (Limp et al. 1996) at elevations from 548 to 701 m. No noticeable defoliation due to gypsy moths occurred on any of the plots in either year.

Reduction and sampling of lepidopteran larvae.—Two treatment plots of 80 and 15 ha were located in Carroll and Newton counties (ca. 36°6'N, 93°21'W) within the areas sprayed with *Bacillus* (see below). Treatment plots were separated by approximately 6 km. Control plots of 25 and 42 ha were located in Newton County (ca. 35°53'N, 93°28'W) about 25 km south of the treatment plots and were separated by approximately 4 km. The treatment plots and the control plots collectively were referred to as the treatment zone and the control zone, respectively.

Abundance of lepidopteran larvae was reduced following application of *Bacillus*, a bacterial pesticide used to control lepidopteran larvae, particularly the gypsy moth. Two applications (19.2 to 14.4 billion international units/ha) of *Bacillus* were applied to a 10,150-ha spray block between 1 and 12 May 1994 using fixed-wing aircraft and helicopters during fair weather. Spray dates were based on emergence of second-instar larvae. The spray block was selected based on the presence of gypsy moths in pheromone traps in 1993 (Arkansas State Plant Board unpubl. data). The treatment plots did not receive *Bacillus* application in 1995, and the control plots did not receive *Bacillus* application in either year. Treatment plots were considered separate replicates because *Bacillus* was applied on different series of days by different aircraft.

Success of the *Bacillus* application to eradicate gypsy moths, which were not common on the spray

block, was evaluated through pheromone trapping and foliage sampling of lepidopteran larvae. In the summer of 1994, only 21 of 287 males in 12,725 traps were captured within the area sprayed earlier in 1994 (Blackburn 1994). In the summer of 1995, 11 male gypsy moths were captured in approximately 5,000 pheromone traps within the area sprayed in 1994 and an adjacent area sprayed in 1995 (Blackburn 1995) that was not included in this study, leading the Arkansas State Plant Board to tentatively declare that the gypsy moth had been eradicated from Arkansas (Blackburn 1995). No gypsy moths were captured on control plots in either 1994 (Blackburn 1994) or 1995 (Blackburn 1995).

Lepidopteran larvae (as well as other arthropods) were sampled weekly between late April and June. One (in 1994) or two (in 1995) additional foliage collections were made in July. Samples were based on foliage clipping of selected oak (*Quercus* spp.) trees (see Stephen et al. 1990). Specimens were held for identification in 70% ethyl alcohol, and all lepidopteran larvae were counted. Lepidopteran larvae per kg dry mass of foliage decreased 84.7% between 1 and 17 May 1994 in the treatment zone, compared with a 22.2% increase in the control zone over the same period (Lih et al. 1995). In 1995, abundance of lepidopteran larvae per kg dry mass of foliage was 80.2% lower in the treatment plots on 1 May 1995 compared with 1 May 1994. In contrast, the abundance of larval lepidopterans declined by only 10.1% in the control zone during the same dates (Lih et al. unpubl. data).

Study organism.—Hooded Warblers arrive in Arkansas in late March and early April and begin laying eggs from 5 to 21 May (James and Neal 1986, M. Revels pers. comm.). Breeding habitat varies from moist valleys to dry deciduous forest, with preference for areas with shrub understory due to tree fall gaps or selective logging (James and Neal 1986, Evans Ogden and Stutchbury 1994). Open-cup nests range from 0.3 to 1.4 m above the ground (Evans Ogden and Stutchbury 1994). Typical clutch size is three to four eggs, which the female incubates for 12 days (Bent 1953, Evans Ogden and Stutchbury 1994). The young are altricial and leave the nest eight to nine days after hatching; both adults feed the nestlings and fledglings. Double clutching is common (Evans Ogden and Stutchbury 1994). Major food items in the diets of the Hooded Warbler are caterpillars, locusts, moths, grasshoppers, beetles, flies, and spiders (Bent 1953, Evans Ogden and Stutchbury 1994). Fall migration begins in September, and there are no Arkansas records after mid-October (James and Neal 1986).

Nest monitoring.—Nest searches began on 5 May in 1994 and on 1 May in 1995. Nesting areas were defined by behavioral cues of adults such as singing, call notes, and adults carrying food or nesting material. Nests were located by systematically search-

ing vegetation and/or flushing the female from the nest. Eggs of Brown-headed Cowbirds (*Molothrus ater*) were removed to reduce confounding factors in the analyses.

Nests were monitored every one to three days after discovery. Data collected included clutch size, average egg mass (for nests located after 19 June in 1994 and after 20 May in 1995), number of eggs hatched, and number of nests destroyed by predators. Nests were considered successful if at least one young fledged; nesting success was calculated using the Mayfield method (Mayfield 1961, 1975). Egg mass refers to the average mass per egg per nest.

Nestling mass and growth rates.—Nestlings were uniquely marked on the tarsus on day 0 (i.e. at hatching) and were weighed (± 0.25 g) at days 1, 3, and 5. If nestling age and hatching date were unknown, they were estimated by nestling mass. To prevent premature fledging, we handled nestlings after day 5 only when nestlings had fledged on their own. Although nestlings were weighed individually, data were analyzed as the mean nestling mass per nest to maintain statistical independence. Owing to travel time between plots and because some nests hatched simultaneously, masses were recorded between 0618 and 1815 CST in 1994 and between 1000 and 1200 in 1995. Masses were adjusted to 1200 under the assumption of linear growth throughout the day (Rodenhouse 1986, Smith et al. 1995). Mean mass per bird per nest on day 5 was used as an indicator of fledging mass. Growth rate was defined as the difference between first and last mean mass per nestling per nest divided by the number of days between measurements.

Feeding rates and prey items—Data recorded included number of feeding events and prey type. Feeding rates were defined as number of times adult Hooded Warblers brought prey items to their nestlings per hour. Observations were recorded with a 20 \times spotting scope or video camera (Panasonic WV-3240 12X or Sharp Slimcam VL-L 64 U 12X) for a two-hour period when nestlings were between two and five days old. Nests were observed a maximum of two times. Nest watches started between 0610 and 1135. Time of day was not included in the analysis because other studies have shown that it does not affect feeding rates or prey types fed to nestlings (Pinkowski 1978, Biermann and Sealy 1982, Bennun 1994). Prey items were identified as lepidopteran, non-lepidopteran, or unknown.

Statistical analyses.—Differences in nesting success between treatment and control zones were evaluated following Hensler and Nichols (1981). We used Fisher's exact test to compare the distribution of the number of eggs or fledglings between treatment and control zones (depredated nests excluded for analysis of fledglings). Years were analyzed separately in all three analyses.

Average egg mass, day-5 nestling mass, growth

rates, and feeding rates were analyzed using a split split-plot ANOVA where the whole-plot factor was zone and the split-plot factor was year. Appropriate biological factors, including clutch size, nestling age, and hatching date (and associated interactions) were included in preliminary models at the split split-plot level. Only final models are described here.

Biological factors included in the ANOVA for egg mass included clutch size, the interaction between clutch size and zone, and the interaction between clutch size and year. The three-way interaction between zone, clutch size, and year was not included due to limited sample size. The day-5 nestling mass ANOVA included hatching date as a covariate at the split split-plot level. Hatching date was a numerical value from 1 to 365. This model also included the interaction of hatching date with zone. Biological factors added to the growth-rate model ANOVA included hatching date as a covariate and the interaction of hatching date and year.

Because the variable feeding rate potentially had two feeding-observation periods per nest, it required an additional split at the nest level. The biological factor added to feeding-rate analysis was clutch size, which was arbitrarily pooled into "small" (one or two nestlings) and "large" (three or four nestlings) values. To accommodate data from nests that were observed at two different time periods, nestling age ("young" = 2 to 3 days; "old" = 4 to 5 days) was included as an additional split in the model. Because there were at most two observation periods per nest, the potential correlation between feeding rates from the same nest would not affect the *F*-test for nestling age. Least significant differences among interaction means involving factors at different design levels were calculated following Cochran and Cox (1957).

To analyze prey type, two sets of proportions of lepidopteran larvae were calculated, one using only identified items and the other including unknown items in the total. Proportions were averaged in nests with multiple observations. Both sets of data were subjected to a split-plot ANOVA where the whole-plot factor was zone and the split-plot factor was clutch size. Years were analyzed separately. Because individual feeding trips were not assumed to be independent, the analysis was not based on the binomial distribution. Unless specified otherwise, analyses were carried out using SAS (SAS Institute Inc. 1990). Results were considered significant if $P < 0.05$.

RESULTS

Nesting success and number of eggs and fledglings.—We located 31 and 40 active nests in 1994 and 1995, respectively. The treatment zone contained 19 nests in 1994 and 25 nests in 1995. Because adults were not uniquely

TABLE 1. Nesting success of Hooded Warblers during 1994 and 1995 in the Arkansas Ozarks. Nesting success and daily survival rates based on Mayfield (1961, 1975).

Variable	Treatment ^a	Control
No. of nests located	44	27
No. of successful nests	22	17
No. of depredated nests	16	7
Nesting success (overall)	0.39	0.53
Daily survival rate (incubation) ^b	0.488	0.729
Daily survival rate (nestling period) ^c	0.728	0.812
No. of exposure days	444	319

^a Treatment zone received two applications of *Bacillus thuringiensis* in 1994 and none in 1995. Control zone was never sprayed.

^b Based on 12-day incubation period.

^c Based on 8-day nestling period.

marked, we were unable to determine if nests were first or second nesting attempts. Nesting success was not statistically different in the treatment and control zones in 1994 (0.50 vs. 0.41, respectively; $Z = 0.40$, $P = 0.68$), but was higher in the control zone than in the treatment zone in 1995 (0.71 vs. 0.30; $Z = 2.15$, $P = 0.03$). Most nesting failures resulted from predation (Table 1).

Plots within the treatment and control zones did not differ in the number of eggs or fledglings (Fisher's exact tests, $P_s > 0.40$), so plots were combined. There were no significant differences in the distribution of number of eggs or number of fledglings between treatment and control zones in 1994 (eggs, $P = 0.83$, $n = 30$; fledglings, $P = 0.99$, $n = 21$) or 1995 (eggs, $P = 0.12$, $n = 40$; fledglings, $P = 0.08$, $n = 19$). The average egg mass was higher in the control zone ($1.80 \pm \text{SE of } 0.04 \text{ g}$) than in the treatment zone ($1.68 \pm 0.03 \text{ g}$; $F = 46.30$, $df = 1$ and 26 , $P = 0.02$).

Nestling mass and growth rates.—Based on day-5 nestling mass, a significant interaction existed between hatching date and zone ($F = 7.59$, $df = 1$ and 24 , $P = 0.01$; Table 2). At nests in the treatment zone, the slope between hatching date and day-5 mass was 0.03 g/day ($P = 0.02$), representing a net gain of 1.80 g in day-5 mass over the 60-day breeding season (Fig. 1). In contrast, the slope for nests in the control zone was not significantly different from zero (Fig. 1).

In the analysis of growth rate, the hatching date \times year interaction was significant ($F = 5.63$, $df = 1$ and 28 , $P = 0.02$). When slopes of

TABLE 2. Split split-plot ANOVA comparing mass at day 5 of Hooded Warbler nestlings during 1994 and 1995 in the Arkansas Ozarks.

Source	Mean square	F	P	df
Zone ^a	2.86	19.66	0.05	1, 2
Year	0.12	0.70	0.49	1, 2
Year \times zone	0.03	0.16	0.72	1, 2
Hatching date	0.42	1.09	0.31	1, 24
Hatching date \times zone	2.91	7.59	0.01	1, 24

^a Treatment (sprayed with *Bacillus thuringiensis* in 1994) vs. control (no spray).

hatching day by year were examined, the 1994 slope was -0.005 ($P = 0.02$), representing a net decrease of 0.28 g over the 60-day breeding season. Conversely, the slope based on control nests was not significantly different from zero ($P = 0.45$), suggesting no change in growth rate over the breeding season.

Feeding rates and prey types.—We recorded 657 feeding trips during 63 two-hour observation periods at 37 nests over both years. The interaction among zone, clutch size, and nestling age was significant ($F = 6.35$, $df = 1$ and 18 , $P = 0.02$; Table 3). When clutch size and nestling age were held constant, there was no difference in feeding rates between treatment and control zones in nests containing large clutches. Feeding rates for nests containing small clutches with young nestlings were higher in the control (LSD = 1.98 , $P \leq 0.05$) than in the treatment zone, whereas the opposite occurred for nests containing small clutches with old nestlings (LSD = 1.41 , $P \leq 0.05$; Fig. 2). However, mean values for nests with small clutches and young nestlings in the control zone were based on only two observations, one had a value of 6.94 feeding trips per nestling per hour, which was 28% higher than the next highest value. When this nest was removed from the analysis, the small clutches with young nestlings were no longer statistically different between treatment and control zones. Thus, these results should be treated with caution.

The proportion of lepidopteran larvae delivered to nestlings was not significantly affected by zone, clutch size, or their interaction regardless of whether unknown prey items were included in the analyses. These results were consistent for 1994, when all prey items were known (control = 0.50 ± 0.14 ; spray = 0.54 ± 0.10) or when unknown prey items were in-

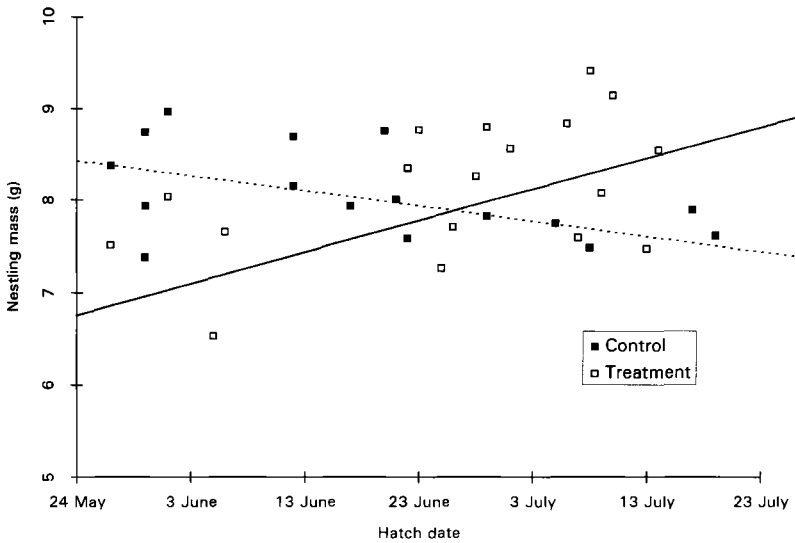


FIG. 1. Mass at day 5 of Hooded Warbler nestlings during 1994 and 1995 in the Arkansas Ozarks. Treatment zone received two applications of *Bacillus thuringiensis* in 1994 and none in 1995. Lines represent change in mass over the duration of the breeding season. Asterisk indicates significant trend ($P < 0.05$).

cluded (control = 0.23 ± 0.08 ; spray = 0.29 ± 0.07), and in 1995, when all prey items were known (control = 0.71 ± 0.08 ; treatment = 0.73 ± 0.08) or when unknown prey items were included (control = 0.43 ± 0.06 ; spray = 0.37 ± 0.09).

DISCUSSION

An 85% reduction in the number of lepidopteran larvae early in 1994 and the subsequent

reduction early in 1995 (Lih et al. 1995) affected few aspects of the reproductive biology of the Hooded Warbler. Our hypothesis of no differences in nesting success between treatment and control zones was supported in 1994 and refuted in 1995 when nesting success was higher in the control zone. Despite these contradicting results, we believe that nesting success was not affected by food limitation in either year. Under conditions of food limitation, either partial or complete brood starvation would be expected

TABLE 3. Split split-plot ANOVA comparing nestling feeding rates (no. of trips per nestling per hour) of Hooded Warblers during 1994 and 1995 in the Arkansas Ozarks.

Source	Mean square	F	P	df
Zone ^a	2.17	2.22	0.27	1, 2
Year	0.68	0.58	0.53	1, 2
Year × zone	0.46	0.39	0.60	1, 2
Clutch size	7.53	7.36	0.01	1, 26
Zone × clutch size	1.11	1.09	0.31	1, 26
Clutch size × year	0.16	0.16	0.69	1, 26
Zone × clutch size × year	3.08	3.01	0.09	1, 26
Age group	0.42	0.42	0.53	1, 18
Age group × clutch size	3.92	3.89	0.06	1, 18
Age group × zone	4.21	4.18	0.06	1, 18
Age group × year	2.97	2.95	0.10	1, 18
Age group × zone × year	0.02	0.02	0.90	1, 18
Age group × zone × clutch size	6.40	6.35	0.02	1, 18
Age group × year × clutch size	0.45	0.45	0.51	1, 18

^a Treatment (sprayed with *Bacillus thuringiensis* in 1994) vs. control (no spray).

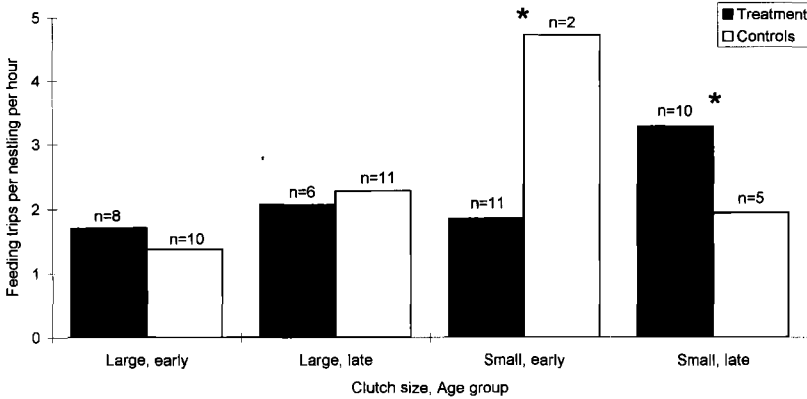


FIG. 2. Mean nestling feeding rates (no. of trips per nestling per hour) of Hooded Warblers during 1994 and 1995 in the Arkansas Ozarks. Treatment zone received two applications of *Bacillus thuringiensis* in 1994 and none in 1995. Asterisks indicate significant difference ($P < 0.05$) between treatment and control zones within a clutch-size (large vs. small)/age-group (early vs. late) combination.

(e.g. Holmes et al. 1991). However, predation was the main cause of nest failure in our study (Table 1). We observed no partial brood starvation, and in only one nest did all of the chicks die (after a severe storm). Thus, differences between nesting success in the treatment and control zones were due to differences in rates of predation. Also, nesting success in the treatment zone was comparable to the 37.5% success rate in the Ozark National Forest (Li 1994), suggesting not that nesting success in the treatment zone was low, but rather that nesting success in the control zone was unusually high.

Although the number of eggs per nest did not differ between control and treatment zones, mean egg mass was significantly higher in the control zone (1.79 vs. 1.68 g). These findings are consistent with other studies (Murphy 1983, 1986; Perrins and McCleery 1994) that found either a reduction in egg mass under conditions of food limitation or an increase in egg mass during food supplementation. However, we recorded egg masses for entire clutches to the nearest 0.25 g, whereas the difference in mean values between the zones was only 0.11 g. Therefore, we suggest that the difference in egg masses between treatment and control zones is not biologically meaningful.

The model of day-5 nesting mass revealed a significant interaction between hatching date and zone (Fig. 1). Day-5 masses in the treatment zone were lowest at hatching dates nearest to the dates of *Bacillus* application (i.e. the period of maximum reduction of lepidopteran

larvae). This reduced nestling mass early in the season suggests that the quantity of available lepidopteran larvae influenced nestling quality. In contrast, when lepidopteran larvae were at natural levels in the controls, nestlings maintained the same mean mass throughout the season. Thus, because nestling mass has been shown to represent the likelihood of survival (see Magrath 1991: table 5), survivorship may be reduced in individuals hatched closest to the date of *Bacillus* application.

Growth rates showed statistical significance without apparent biological significance. Thus, we assumed that there was no difference in growth rates of nestlings in treatment or control zones, as has been found in other experimental studies (Rodenhouse and Holmes 1992, DeReede 1982; but see Bancroft 1984). The observed differences in day-5 nestling mass between treatment and control zones suggested that there was some difference in parental care, potentially through feeding rates or prey type. However, differences in feeding rates between treatment and controls were found only for small clutches. The direction of the differences was dependent on nestling age, with feeding rates being higher in the controls when nestlings were two to three days old and higher in the treatments when nestlings were four to five days old. There was no difference between the treatment and control zones in the proportion of lepidopteran larvae delivered to nestlings, regardless of whether unknown prey items were included. These results are inconsistent

with other *Bacillus* studies that have shown lower proportions of lepidopteran larvae delivered to nestlings in treated areas (Gaddis and Cockran 1986, Gaddis 1987, Rodenhouse and Holmes 1992). However, in a study examining the effects of the pesticide Dimilin on bird diets, species responded differently to arthropod reductions (Sample et al. 1993). We hypothesize that adult Hooded Warblers either reduced their overall biomass intake (Sample et al. 1993) or expanded their foraging range to compensate for a reduction in the number of lepidopteran larvae available (Cooper et al. 1990).

In summary, the application of *Bacillus* had little influence on the reproductive parameters we measured, but the reduction in numbers of lepidopteran larvae appeared to have a negative influence on nestling masses early in the season and to alter feeding rates in small clutches. We offer two non-mutually exclusive explanations to account for the minimal influence of reduced lepidopteran larvae on the reproductive ecology of Hooded Warblers. First, long-distance insectivorous migrants should encounter years of food scarcity during the breeding season due to annual fluctuations in arthropod abundance (Holmes 1988, Holmes et al. 1991). In eastern deciduous forests, years of low arthropod abundance appear to be more common (Holmes 1988) than years of high abundance (e.g. Williams et al. 1993). Therefore, migratory birds in these forests should be adapted to breed during periods of relatively low food abundance because they do not appear to seek out areas of high caterpillar abundance from year to year (as do birds in eastern coniferous forests; Kendeigh 1947). Although application of *Bacillus* reduced the number of lepidopteran larvae in the treatment zone (Lih et al. 1995), the relative abundance of prey may not have been affected enough to influence breeding.

Second, there may be a critical threshold of prey abundance below which breeding of Hooded Warblers would be affected, as suggested by Rodenhouse and Holmes (1992). At times (i.e. during severe drought), the level of arthropod abundance may decline to a point where breeding is greatly affected or prohibited (see Smith 1982). Although *Bacillus* reduced the number of lepidopteran larvae in the treatment zone, the amount of available prey still may have exceeded the threshold neces-

sary for successful breeding by Hooded Warblers.

The majority of studies examining the influence of food on breeding birds use food supplementation to test effects of food abundance (Martin 1987). Determination of the effects of food limitation often is based on the assumption that the effects will be in the opposite direction of those resulting from food supplementation. However, the hypothesis of a critical food threshold (Rodenhouse and Holmes 1992) suggests that this assumption is not valid, because a reduction in food may not reduce reproductive success unless the food reduction falls below some critical level. Thus, future research must examine questions of food limitation in terms of reduction studies, and efforts should include estimates of territory size, prey biomass, and annual productivity.

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