BIOTIC AND ABIOTIC FACTORS GOVERNING NESTLING-PERIOD LENGTH IN THE OVENBIRD (*SEIURUS AUROCAPILLA*)

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ABSTRACT.—In many songbirds, the nesting period for a breeding attempt is extremely short, often lasting only a few weeks. Breeding adults can shorten this period by decreasing the number of eggs laid or reducing the length of the nestling period. Nestling-period length has received little attention in the literature but could have profound effects on annual fecundity, because each day represents a risk of nest depredation. Consequently, we were interested in assessing the biotic and abiotic factors that govern the nestling period in the Ovenbird (*Seiurus aurocapilla*). We provide evidence that food availability, more than predation pressure and climatic factors, influences nestling-period length, with increases in food availability decreasing the nestling period. We suggest that the nestling period is dictated by physiological constraints, which may be influenced by food availability and, thus, the ability to provision young. However, the greatest variation in nestling period was individual variation among breeding pairs. Thus, we believe that large-scale variation in ecological and environmental factors may determine the physiological constraints of the nestling period but parental behavior and quality within this framework dictate the actual length of the nestling period. *Received 6 November 2008, accepted 18 June 2009.*

Key words: fecundity, fledging period, nest success, nestling period, Ovenbird, parental behavior, *Seiurus aurocapilla*.

Factores Bióticos y Abióticos que Determinan la Duración del Periodo de Pichón en *Seiurus aurocapilla*

RESUMEN.—En muchas aves canoras, el periodo de pichón de un intento reproductivo es extremadamente corto, durando frecuentemente sólo unas pocas semanas. Los adultos reproductivos pueden acortar este periodo disminuyendo el número de huevos que ponen o reduciendo la duración del periodo de pichón. La duración del periodo de pichón ha sido poco tratada en la literatura, pero podría tener efectos profundos en la fecundidad anual debido a que cada día representa un riesgo de depredación del nido. En consecuencia, estábamos interesados en evaluar los factores bióticos y abióticos que determinan el periodo de pichón en *Seiurus aurocapilla*. Brindamos evidencia de que la disponibilidad de alimentos, más que la presión de depredación y los factores climáticos, influencian la duración del periodo de pichón. Los incrementos en la disponibilidad de alimento acortaron el periodo de pichón. Sugerimos que el periodo de pichón está determinado por restricciones fisiológicas, que podrían estar influenciadas por la disponibilidad de alimento y, por lo tanto, determinar la habilidad de alimentar a los pichones. Sin embargo, la mayor variación en el periodo de pichón fue la variación individual existente entre las parejas que se encontraban criando. Por ende, creemos que la variación a gran escala de factores ecológicos y ambientales puede determinar las limitaciones fisiológicas del periodo de pichón, pero el comportamiento y la calidad parental dentro de este marco determinan la duración real del periodo de pichón.

ELUCIDATING THE PROCESSES that influence fecundity is vital to our knowledge of the basic ecology and conservation of birds and is central to our understanding of population dynamics. Most studies of avian demography have focused on nest survival, which is a dominant factor influencing annual fecundity in numerous insectivorous songbird species (Underwood and Roth 2002, Nagy and Holmes 2005b, Mattsson and Cooper 2007). In many of these species, the nesting period for a single breeding attempt is extremely short, often lasting only a few weeks. Breeding adults can modify the length of this period by adjusting the number of eggs

or changing the time from hatching to fledging. Nestling-period length has received little attention in the literature but could have profound effects on nest survival and reproductive success because the nestling period can be the period of greatest mortality during a songbird's life (Ricklefs 1969a).

To maximize annual fecundity, single-brooded species need to balance the costs associated with fledging young early with the risks of total nest loss due to predation, because both of these factors can strongly influence annual productivity (Mattsson and Cooper 2007). Fledgling survival, which can be a fraction of adult survival (Berkeley et al. 2007, Rush and Stutchbury 2008), may be influenced by the condition of young near the end of the nestling period (Blancher and Robertson 1987, Krementz et al. 1989, Monros et al. 2002), and prolonged parental care should presumably help increase nestling quality. However, a protracted nestling period may have disadvantages if it increases the probability of total nest loss. Consider 2 nests, each with a probability of daily survival of 0.95, where the first nest fledges in 8 days and the second in 10 days. The probability of surviving to fledging is 10% greater for the first nest than for the second (0.66 vs. 0.60). Thus, all else being equal, reducing the length of the nestling period should increase nest survival. Furthermore, after leaving the nest, fledglings face chance events such as predation singly, rather than as a group, which reduces the probability that a single event will eliminate all young. Consequently, from an inclusive fitness standpoint, it may be advantageous for breeding adults to expedite fledging, so long as fledgling survival is not negatively affected.

Understanding the factors that govern time spent in the nest can increase understanding of songbird demography. Biotic and abiotic factors such as nest predation, food availability, and ambient temperatures may play a role in determining fledging times. Martin (1995) showed that differences in nest predation rates explained most interspecific differences in nestling period length, whereas food availability is the major determinant of nestling growth and development (Naef-Daenzer and Keller 1999), and nestling size can determine differences in intraspecific fledging time (Johnson et al. 2004). Abiotic factors could also directly or indirectly influence the length of the nestling period. Temperature and precipitation should directly affect the costs associated with thermoregulatory ability in newly fledged young while indirectly affecting the length of the nestling period through effects on food abundance and search time.

Little empirical research has been conducted on intraspecific differences in nestling-period length. The limited research that has been done has generally focused on a single factor and not on the relative importance of multiple biotic and abiotic factors. In addition, most studies investigating fledging times have dealt with species that use cavities and readily take to nest boxes, but life-history strategies often differ between open-cup and hole-nesting species (Martin 1992b). Consequently, our objective was to provide one of the first evaluations of the relative influence of abiotic and biotic factors on the length of the nestling period in an open-cup-nesting species.

METHODS

Study area.—We conducted the study at the Coweeta Hydrologic Laboratory (hereafter "Coweeta") within the Nantahala National Forest in the southern Appalachian Mountains, Macon County, North Carolina (35.1°N, 83.4°W), between April and July, 2002–2004. We established three study plots (>10 ha each) at approximate elevations of 900 m, 1,050 m, and 1,200 m, all within 15 km of one another. The vegetative composition of the forest is dominated by cove and northern hardwood forest vegetation (Day et al. 1988), with an understory dominated by Great Laurel (*Rhododendron maximum*) and Mountain Laurel (*Kalmia latifolia*) (Day and Monk 1974).

Study species.—We focused our study on the Ovenbird (*Seiurus aurocapilla*), a small insectivorous Neotropical migrant songbird that breeds throughout the eastern United States (Van Horn and Donovan 1994). Ovenbirds are typically single brooded and lay a clutch of 2–6 eggs; clutches of 4 or 5 eggs were the most common during the present study. Young reportedly leave the nest 7–10 days after hatching (Van Horn and Donovan 1994). When foraging, Ovenbirds spend >80% of the time on the ground, gleaning prey from the leaf litter and nearby foliage (Holmes and Robinson 1988). Coleopterons, dipterans, and lepidopteran larvae constituted the majority of prey items for adults in a study in New Hampshire (Holmes and Robinson 1988), and lepidopteran larvae are a major component of items brought to nestlings (Van Horn and Donovan 1994).

Nest finding and monitoring.—We systematically searched all study plots for Ovenbird nests and searched surrounding areas to increase sample sizes. We were present on each plot at least every other day. To facilitate nest searching, we created territory maps of all individuals on the study plots by following individual singing males and marking locations on grid paper that corresponded to each plot. Over the 3 years of the study, we located 107 Ovenbird nests, of which 60 successfully fledged young. We monitored nests every 2–4 days to note the dates of clutch completion and hatching and at least every day near the end of the nestling period to note success or failure of nests.

Fledging date.—Nestlings typically leave the nest in the morning on fledging day, and all nestlings leave within several hours of one another (Van Horn and Donovan 1994, K. W. Stodola pers. obs.). To determine the day of fledging, we visited all active nests in the morning of all days after day 6 of the nesting cycle and again later in the day, weather and time permitting. Nest monitoring was performed with binoculars at a distance (often >3 m) to minimize our influence. If we did not observe parental activity at the nest, we approached until we could observe nest contents without disturbing the nestlings if they were still in the nest. When nestlings fledged between nest checks on successive days, we scored fledging day as the midpoint between those 2 days. If a nest was not checked on successive days, it was removed from the analysis because we could not accurately determine the day of fledging within a 1-day time frame. This procedure eliminated 3, 5, and 1 nests from analyses in 2002, 2003, and 2004, respectively, resulting in a total sample size of 51 successfully fledged nests. Although disturbance at the nest may influence the day of fledging, we checked all nests on day 6 of the nestling stage, so nest disturbance was constant across study plots and years.

Statistical inferences.—We evaluated fledging times using a general linear mixed model incorporating plot-level and nest-level variables that we thought might affect the nestling period. We created a two-level hierarchical model in which predation pressure, food, and average temperature during May and June were plot-level effects because they were all specific to a plot for each year. Nest-level effects were all specific to a particular nest and included litter depth, vegetative cover, minimum temperature on day of fledging, and average precipitation during the nestling stage.

Finally, we incorporated brood size in all models because this has been shown to be an important determinant of nestling-period length in other songbird species (Zach and Mayoh 1982, Husby and Slagsvold 1992, Michaud and Leonard 2000). A description of the variables of interest and how they were measured follows.

PLOT-LEVEL PREDICTORS

Nest depredation.—We calculated daily nest mortality rate for each plot and year using the logistic exposure method (Shaffer 2004) and used this measure as an index of predation pressure. We used an information-theoretic approach to obtain unbiased estimates of daily nest mortality rates. More specifically, we calculated Akaike's information criterion (Akaike 1973) adjusted for small sample size (AIC_c; Burnham and Anderson 2002) for 5 models relating the probability of nest mortality to plots and years, along with their combination and interaction, and a model with constant probability of survival. We then used model averaging (Burnham and Anderson 2002) to incorporate the weight of evidence that the probability of nest mortality differed between sites and years. Of the 47 failed nests that we followed during the study, 45 were missing all or some of their eggs, which indicated that they were depredated rather than abandoned. We therefore believe that this is a good measure of the predation pressure experienced by a nesting pair.

Temperature.—We used average temperature during May and June as an indicator of climatic conditions on a plot, because this represented the time when most young fledged from nests. Average temperature measurements were obtained at Coweeta at 3 elevations: 865 m, 1,001 m, and 1,347 m. Although these elevations are not the same as those of our study plots and the difference is slightly larger, we believe that the relative temperature differential between each location should indicate the temperature differential encountered by Ovenbirds on the plots.

Food abundance.—We used lepidopteran larvae as our measure of food abundance because they are included in ~90% of all feeding trips to the nest (K. W. Stodola unpubl. data). Lepidopteran abundance and growth are associated with temperature (Simonet et al. 1981, Levesque et al. 2002), and our measurements of lepidopteran abundance were moderately correlated with temperature ($r = 0.47$, $n = 8$, $P = 0.23$). However, we were interested in specific effects of each and modeled each seperately. Lepidopteran abundance was sampled at the end of May and in the middle of June in all 3 years. Although this method did not evaluate food abundance during laying and early incubation, it provided a measure of food abundance during the nestling and fledging periods, which were of primary concern. Ovenbirds fledged 82%, 88%, and 92% of all broods within 3 days of the lepidopteran sampling periods in 2002, 2003, and 2004, respectively. Average fledging day from the 60 nests analyzed was 5 June (± 1.4 SE), irrespective of year and site.

To estimate lepidopteran abundance, we counted all lepidopteran larvae on the undersides of shrub- and ground-level leaves of American Chestnut (*Castanea dentata*) and Red Maple (*Acer rubrum*) following the methods of Holmes et al. (1986). Lepidopteran surveys were conducted along 4 parallel 500-m transects separated by ≥50 m. When possible, two 50-leaf samples of each tree species were obtained every 50 m. For each sample, we counted ~3,500 leaves of each tree species on each study plot. The length of each lepidopteran larva was measured to the nearest millimeter, and dry-weight biomass was calculated following

the length–mass regression equations from Rodenhouse (1986). We then summed the average biomass found on 50-leaf samples from each tree species for each sample on each plot (e.g., average biomass of larvae on 50 American Chestnut leaves between the 2 sampling periods plus average biomass of larvae on 50 Red Maple leaves between the 2 sampling periods).

NEST-LEVEL PREDICTORS

Litter depth.—Litter depth is an important habitat characteristic for Ovenbirds that may be tied to food availability (Burke and Nol 1998). To estimate litter depth in and around the nest we took five measurements, one centered on the nest and the other four 5 m from the nest in the four cardinal directions. We gathered this measurement at the end of the breeding season (July) and used the average of these measurements when predicting nestling-period length.

Vegetative coverage.—Vegetative coverage around a nest may affect the ability of predators to find a nest (e.g., Martin 1992a). We determined vegetative cover by placing a 0.2 × 2 m cover board vertically on the ground at the nest and then visually estimating the percent that was covered from a distance of 5 m in the four cardinal directions. We took this measurement at the end of the breeding season (July).

Minimum temperature.—We used the minimum temperature on the day of fledging as a possible explanatory variable influencing nestling-period length. We thought that the thermoregulatory benefits of remaining in the nest on cold days would outweigh the benefits of fledging early and, thus, would influence nestling-period length. We attained minimum temperature measurements at Coweeta from the same sites as our May–June temperatures.

Precipitation.—Precipitation can also influence the ability of adults to adequately provision young (Johnson and Best 1982, Rosa and Murphy 1994), which could influence nestling-period length. Consequently, we used average precipitation during the week before fledging as a predictor variable. This period represented the entire posthatching time for most nests.

Model specifics.—We first calculated the amount of variation in the length of the nestling period by fitting an unconditional hierarchical model that grouped nests by plot–year combinations. We used the covariance estimate from this model to estimate the percent of variation that was explainable by differences in the plot–year groups. This estimate was also used as a baseline for evaluating the explanatory strength of the plot-level predictors: predation pressure, food, and temperature. We then fit linear models relating these predictors to days spent in the nest. We allowed the intercept to vary randomly to evaluate the effects of predation pressure, food, and temperature on variation in nestling-period length among plot–year groups. Finally, we used the covariance estimate of this model to evaluate how much variation in fledging times was attributable to these predictor variables and used the slopes from these models to indicate the effect these variables have on the length of the nestling period.

To assess the importance of the nest-level predictors, litter depth, shrub coverage, minimum temperature, and precipitation, we fit linear models relating these variables to nestling-period length. When evaluating nest-level predictors, we allowed these predictors to vary randomly because we believed that their effect on the nestling period might differ among plot–year groups. We then used the residual variance for these models to assess the amount of variation in

nestling-period length among plot–year groups that was explained by the nest-level predictors. In addition, we used the slopes of these predictors to estimate their effects on nestling-period length.

Statistical analyses.—We assessed the relative fit of the different models at each iterative step using an information-theoretic approach (Burnham and Anderson 2002). Model fit was calculated using AIC_c. The relative fit of each model was determined using AIC_c weights, where the best-fitting model corresponds to the highest weight (Burnham and Anderson 2002). All models were fit using maximum-likelihood specification using PROC MIXED in SAS, version 9.1.3 (SAS Institute, Cary, North Carolina). A Shapiro-Wilk's test of normality on nestling-period length indicated that the data were not normally distributed. Standard transformations failed to remedy the problem because of the lack of time resolution (i.e., 0.5-day increments). However, modeling the length of the nestling period using linear regression in PROC MIXED provided a better fit than a multinomial random-effects model in PROC NL-MIXED ($AIC_c = 131.8$ and 192.1, model fit using the normal distribution with random intercept and multinomial distribution with random intercept). Therefore, for ease of interpretation, we used the random-effects linear regression model in PROC MIXED, but caution the reader that our results may be subject to problems associated with non-normality of data and linear regression. Unless otherwise noted, we present all data as averages ($\pm$ SE).

RESULTS

Average nestling-period length was 7.6 ± 0.12 days. Ovenbirds fledged young in 8.0 ± 0.26 days in 2002 ($n = 14$); in 7.8 ± 0.16 days in 2003 ($n = 20$), and 7.0 ± 0.17 days in 2003 ($n = 17$) irrespective of plot; and in 7.5 ± 1.00 days at the 900-m plot ($n = 2$), 7.4 ± 0.15 days at the 1,050-m plot ($n = 28$), and 7.9 ± 0.19 days at the 1,200-m plot ($n = 21$) irrespective of year. Larger broods fledged sooner than smaller broods (Fig. 1). We estimated predation pressure to be greatest at the 900-m site (24 nests), whereas the 1,050-m
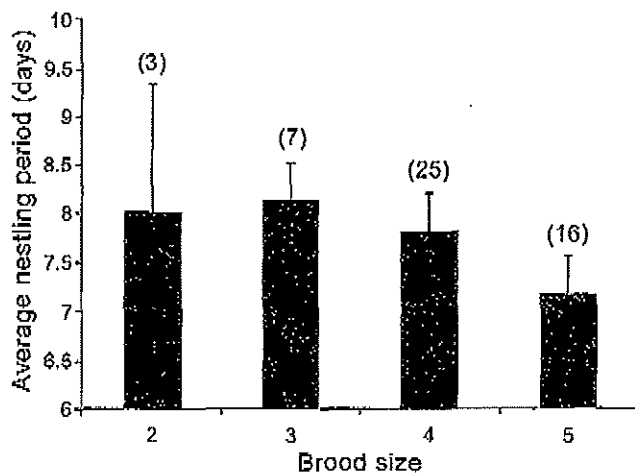

FIG. 1. Average nestling period (2002–2004) of Ovenbirds at Coweeta Hydrologic Laboratory, Nantahala National Forest, North Carolina, for different brood sizes, with 95% confidence intervals. Sample sizes are given in parentheses.
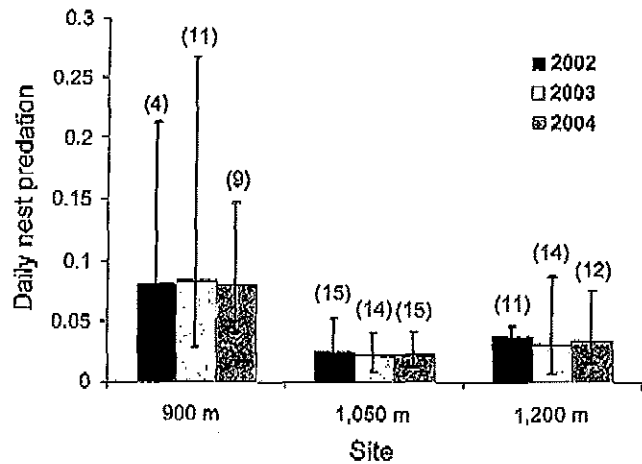

FIG. 2. Model-averaged probability of daily nest predation (DNP) of Ovenbirds at Coweeta Hydrologic Laboratory, Nantahala National Forest, North Carolina. We calculated 95% confidence intervals by predicting DNP for each site and year from 5 models (see text) and then used derived estimates and standard errors from the logistic exposure model in 100,000 Monte Carlo simulations, assuming a normal distribution, to attain confidence intervals and incorporate model selection uncertainty. Sample sizes are given in parentheses.

(44 nests) and 1,200-m sites (37 nests) experienced similar predation pressure (Fig. 2). Average temperatures decreased with elevation and were highest in 2004 and lowest in 2003 (Table 1). Estimated food biomass was greatest in 2004 on all study plots, but there was no consistent difference between study plots (Fig. 3).

Plot–year predictors.—Most of the variation in the length of the nestling period was within plot–year groups, although 18% of the variation could be explained by differences among these groups. Differences in food availability explained 84% of the variation among plot–year groups, whereas temperature differences among plot–year groups explained 56% of the variation. However, predation pressure explained only 1% of the variation in the nestling period among plot–year groups. Food availability was the only model that received substantial support in comparison to the null model (Table 2). We found strong support that increased high food availability was associated with a shorter average nestling period (Table 3 and Fig. 4). Increased May–June temperature also corresponded to a decrease in the nestling period, although the evidence was weak (Table 3). Finally, there was no evidence that predation pressure had any directional effect on average nestling period (Table 3).

TABLE 1. Average May–June temperature (°C) at Coweeta Hydrologic Laboratory, Nantahala National Forest, North Carolina.

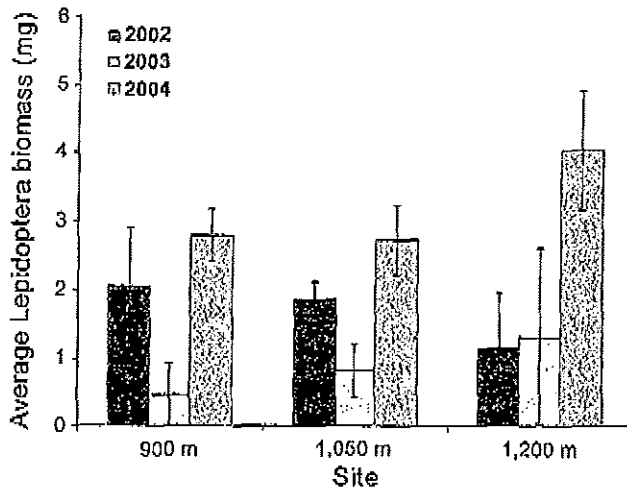| Year	Elevation		
	865 m	1,001 m	1,347 m
2002	17.80	16.87	14.62
2003	15.54	14.36	14.24
2004	18.89	17.24	15.56

FIG. 3. Estimated biomass of lepidopteran larvae, among plots and years, at Coweeta Hydrologic Laboratory, Nantahala National Forest, North Carolina. 95% confidence intervals were derived from 10,000 Monte Carlo simulations.

Nest-level predictors.—None of the nest-level predictors adequately explained nestling-period length within a plot–year group (Table 2) and, consequently, none of the variables explained any of the variation within a plot–year group (<1%). All predictor variables had estimated effects on nestling-period length with 95% confidence intervals that included zero, which indicated little discernible effect (Table 3).

DISCUSSION

Nest depredation was the primary cause of reproductive failure in our study population, with 45 of the 47 nest losses directly attributable to depredation, which is the norm in many systems (Ricklefs 1969a, Martin 1995). In addition, daily nest depredation rates more than doubled, from 0.03 during the incubation stage to 0.07 during the nestling stage (K. W. Stodola unpubl. data), which suggests that predation events exert strong selective pressure for nestling Ovenbirds to leave the nest as soon as possible. An earlier

TABLE 2. Comparison of candidate models for factors predicted to affect nestling-period length in Ovenbirds at Coweeta Hydrologic Laboratory, Nantahala National Forest, North Carolina, 2002–2004. Number of nestlings was included in all models as a grouping variable. Log likelihood (Log L), AIC_c values, AIC_c differences (Δ_i), and AIC weights (w_i) are given.

	Log L	AIC_c	Δ_i	w_i
Food	112.2	128.8	0	0.55
Temperature	115.1	131.7	2.9	0.13
Null	117.9	131.8	3.0	0.12
Minimum temperature	116.8	133.4	4.6	0.05
Precipitation	117.3	133.9	5.1	0.04
Cover	117.3	133.9	5.1	0.04
Predation	117.9	134.5	5.7	0.03
Litter	117.2	134.7	5.9	0.03

TABLE 3. Model-averaged coefficients and 95% confidence intervals for variables predicted to affect nestling-period length in Ovenbirds at Coweeta Hydrologic Laboratory, Nantahala National Forest, North Carolina, 2002–2004.

Variable	Coefficient ± SE	95% confidence interval
Food	−0.32 ± 0.16	−0.55 to −0.09
Temperature	−0.18 ± 0.10	−0.38 to 0.02
Predation	0.01 ± 0.11	−0.20 to 0.22
Litter	0.04 ± 0.05	−0.06 to 0.15
Precipitation	0.01 ± 0.01	−0.01 to 0.02
Minimum temperature	−0.04 ± 0.04	−0.13 to 0.05
Cover	−0.00 ± 0.01	−0.02 to 0.01

departure from the nest should reduce the likelihood of complete nest loss, because fledglings are often separated and fed individually upon nest departure (Van Horn and Donovan 1994, K. W. Stodola pers. obs.). Abundant food during the nestling stage and at the time of fledging may help facilitate a shorter nestling period, which our data suggest.

The nestling period of Ovenbirds in our study was directly related to food: shorter nestling periods were associated with greater food abundance. Food abundance has long been known to influence songbird reproductive success (Lack 1954, 1966; Martin 1987). Although the effect of food abundance is probably most important in determining the total number of offspring, whether through increased clutch sizes, number of young fledged, or number of nesting attempts (Hussell and Quinney 1987, Martin 1987, Arcese and Smith 1988, Nagy and Holmes 2005a), our results show that it may also reduce predation risk by allowing breeding adults to fledge young sooner. In support of this, offspring growth in songbirds is affected by abundant food resources and delivery rates to young (Naef-Daenzer and Keller 1999), which suggests that nestling-period length can be influenced by food abundance.
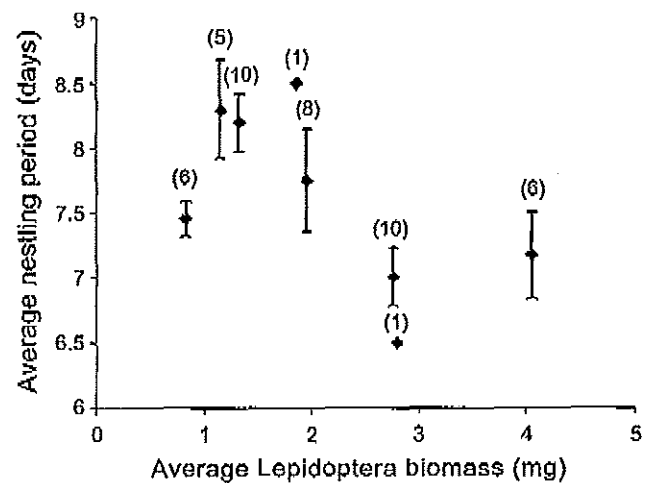

FIG. 4. Average nestling-period length (2002–2004) of a plot–year group in relation to estimated biomass (mg) of lepidopteran larvae, in Ovenbirds at Coweeta Hydrologic Laboratory, Nantahala National Forest, North Carolina. Sample sizes are given in parentheses.

Ovenbirds did not alter the length of the nestling period in response to predation pressure. However, we may not have had the ability to detect such a response because of low sample sizes and lack of variation between years. Breeding adults of other species display the ability to assess predation risk and adjust behavior. Fontaine and Martin (2006) showed that breeding adults adjusted their parental activity in response to predation risks. In addition, comparative studies have indicated that differences in the length of the nestling period among species correspond to daily nest depredation rates (Martin and Li 1992, Bosque and Bosque 1995, Martin 1995, Yanes and Suarez 1995). Unfortunately, the magnitude of predation at our 900-m plot resulted in few successful nests. Thus, although the 900-m plot experienced the greatest predation pressure, the low number of successful nests precludes detection of an influence of nest predation on nestling period, given that the 1,050-m and 1,200-m sites varied little in predation pressure. Therefore, we stress that our results do not imply that predation risk is not influential in determining nestling period; rather, we were unable to detect an influence.

Although we do not know whether breeding Ovenbirds in our study were influenced by predation pressure at the ecological scale, the selective pressure of predation over evolutionary time may favor accelerated nestling growth and decreased nestling periods. As our data suggest, predation risk is extremely high during the nestling period, and decreasing the length of time that nestlings spend in the nest may increase reproductive output by increasing nest survival. However, nestling growth and development may be limited by physiological constraints (Ricklefs 1969b, 1979; Ricklefs et al. 1998) that preclude young from fledging sooner even if adults perceive high predation risk. More than half the nests (9 of 17) in 2004 fledged 6 days after hatching, which is earlier than the reported 7–10 days for this species (Van Horn and Donovan 1994) and extremely fast for any altricial songbird species (based on a review of The Birds of North America Online). Because nestlings that spend less time in the nest have higher daily energy requirements (Weathers 1992, 1996) and provisioning of young is energetically costly (Vander Haegen and DeGraaf 2002), only factors that affect the energetics of development (i.e., food resources or temperature) can help offspring reach maximum growth rate. Thus, although predation pressure acting over evolutionary time may have selected for accelerated nestling growth and decreased nestling periods, this may be accomplished only by overcoming ecological constraints, which is suggested by our finding that food availability influenced nestling-period length.

Abundant food resources may also help offset the potential cost of lower survival in light-weight young that may arise when young fledge too soon. Fledgling mortality in Ovenbirds (King et al. 2006), as in other species (Berekely et al. 2007, Rush and Stutchbury 2008), is greatest during the first few days after fledging. A reduced nestling period could potentially increase this risk if it resulted in fledglings of lower quality. However, food availability can influence nestling quality (Naef-Daenzer and Keller 1999, Granbom and Smith 2006), and nestlings of higher quality may have greater postfledging survival (Krementz et al. 1989, Naef-Daenzer et al. 2001, Monros et al. 2002). Thus, abundant food may not only allow for accelerated fledging but also decrease the associated risks by helping to increase nestling or fledgling quality and survival.

Most of the variation in nestling-period length occurred within plot–year groups, yet none of the nest-level variables performed well in predicting the length of the nestling period. We believe that these results highlight the importance of individual variation in behavior and quality among breeding adults. There is strong empirical support for individual variation in parental quality and care in birds, which is often associated with parental age (Ross 1980, Hegyi et al. 2006). Generally, older individuals produce more young of higher quality (Perrins and Moss 1974, Nol and Smith 1987). Unfortunately, we did not know the age of the breeding pairs that we followed over the course of the study, and this may have contributed to the majority of the variation in nestling-period length.

Food availability was the only variable that was able to predict the length of the nestling period of Ovenbirds at our study area. In all years, nest predation was greatest during the nestling period and fledgling Ovenbirds left the nest extremely early for an altricial songbird. Therefore, developmental rates of Ovenbirds in our study area may be limited by physiological processes, which are determined by ecological (food) and environmental (temperature) factors. Finally, we found that most of the variation in the length of the nestling period occurred within a plot–year group and none of our predictor variables at this scale performed well in explaining this length. We suggest that this highlights the importance of individual variation in breeding adults. Consequently, we believe that the physiological constraints of the nestling period may be affected by large-scale variation in ecological and environmental factors but that parental behavior and quality, acting within this framework, dictate actual fledging time.

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