RESEARCH ARTICLE

Variation in nest characteristics and brooding patterns of female Black-throated Blue Warblers is associated with thermal cues

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ABSTRACT

Thermal variation poses a problem for nesting birds and can result in reduced offspring growth rates and survival. To increase the thermal stability of the nest, females can adjust nest characteristics and nest attendance in response to changes in environmental conditions. However, it is unclear how and to what extent females modify parental behaviors during various stages of offspring development. We tested the hypothesis that females adjust nest characteristics and brooding patterns in response to thermal variation during the nest-building and nestling stages, respectively. We examined elevational variation in nest location, nest construction, and brooding patterns in the migratory Black-throated Blue Warbler (*Setophaga caerulescens*) across a 2°C gradient at the Hubbard Brook Experimental Forest, New Hampshire, USA. Density of woody stems at nest sites and nest wall thickness increased from low to high elevation, corresponding to decreasing temperatures, but we found no relationship between weather during nest building and nest characteristics. However, weather during the nestling stage was associated with female brooding patterns: at lower temperatures and with higher rainfall, females spent more time off the nest, which was associated with lower nestling mass near fledging. These results suggest that thermal cues during nest building may be unreliable as predictors of future conditions for developing nestlings and also that females might favor their own self-maintenance and compromise nestling growth under adverse thermal conditions.

Keywords: behavioral plasticity, brooding, environmental cues, nest construction, nest microclimate, nestling condition

La variación en las características del nido y en los patrones de crianza de las hembras de *Setophaga caerulescens* está asociada con señales térmicas

RESUMEN

La variación térmica representa un problema para las aves que anidan y puede resultar en una reducción en las tasas de crecimiento y en la supervivencia de las crías. Para aumentar la estabilidad térmica del nido, las hembras pueden ajustar las características del nido y la presencia en el nido en respuesta a los cambios en las condiciones ambientales. Sin embargo, está poco claro cómo y en qué medida las hembras modifican los comportamientos de los progenitores durante varios estadios del desarrollo de las crías. Evaluamos la hipótesis que las hembras ajustan las características del nido y los patrones de crianza en respuesta a la variación térmica durante las etapas de construcción del nido y de polluelos, respectivamente. Examinamos la variación altitudinal en la localización del nido, la construcción del nido y los patrones de crianza en la especie migratoria *Setophaga caerulescens* a través de un gradiente de 2°C en el Bosque Experimental Hubbard Brook, NH, EEUU. La densidad de tallos leñosos en los sitios de anidación y el espesor de la pared de los nidos aumentó desde la elevación baja hacia la alta, correspondiendo a una disminución de la temperatura, pero no encontramos una relación entre el clima durante la construcción del nido y las características del nido. Sin embargo, el clima durante la etapa de polluelo estuvo asociado con los patrones de crianza de la hembra: a bajas temperaturas y con mayor precipitación, las hembras pasaron más tiempo afuera del nido, lo que estuvo asociado con una menor masa de los polluelos cerca del emplumamiento. Estos resultados sugieren que las señales térmicas durante la construcción del nido pueden ser poco confiables como predictores de las futuras condiciones para desarrollar volantones y también que las hembras podrían favorecer su propio auto mantenimiento y comprometer el crecimiento de los volantones bajo condiciones térmicas adversas.

Palabras clave: condición del volantón, construcción del nido, crianza, microclima del nido, plasticidad comportamental, señales ambientales

INTRODUCTION

Temperature fluctuations pose a challenge for nesting birds (DuRant et al. 2013). Offspring developing under extreme or highly variable temperatures can suffer reduced growth rates (Olson et al. 2006), leading to lower survival (Ardia 2013). Such temperature conditions might be particularly problematic for altricial species because their young are incapable of thermoregulating during early development (Whittow and Tazawa 1991, Dawson et al. 2005). Altricial species should therefore use environmental cues to modify their parental behaviors to maintain thermal stability for their developing offspring and to maximize offspring survival and their own fitness (Britt and Deeming 2011, Deeming et al. 2012). However, there is still uncertainty regarding how and to what extent females respond adaptively to environmental cues by adjusting their parental behaviors during different stages of offspring development.

Females can increase thermal stability at their nests by adjusting nest location and construction (Walsberg 1985, Windsor et al. 2013). For example, selection of nest sites in densely vegetated or sheltered areas can influence nest microclimate by decreasing cooling from wind and radiative heat loss (Walsberg 1985, D'Alba et al. 2009). Constructing nests in patches of dense, woody vegetation may minimize cooling of nest contents and shield nest contents from precipitation (Walsberg 1985). Microclimate can, in turn, influence nest construction and insulation properties. More protected nest sites may require less investment by females during nest building to insulate the nest and less effort during incubation and brooding to maintain thermal stability. Building more insulated nests in cooler areas has been shown to mitigate the effects of lower ambient temperatures. For instance, birds at high elevations and latitudes, where breeding conditions are cooler and more variable, may construct nests with denser or thicker walls than birds at low elevations (Kern and van Riper 1984) and latitudes (Rohwer and Law 2010, Crossman et al. 2011, Mainwaring et al. 2014). However, nest wall thickness generates a trade-off, in that thicker nests lose heat less rapidly (Whittow and Berger 1977) but absorb more water and dry more slowly, increasing evaporative cooling (Rohwer and Law 2010). Females may adjust nest characteristics differently across populations, given the relative importance of cooling and water absorption (Botero-Delgadillo et al. 2017). Moreover, few studies have been designed to test for a direct link between functional differences in nest characteristics and temperature and rainfall during nest building (Suárez et al. 2005, Deeming et al. 2012, Mainwaring et al. 2014).

Nest temperature also can be mediated through changes in female attentiveness at the nest (Sanz and Tinbergen 1999, DuRant et al. 2013). For example, adjustments in incubation patterns in response to changes in environmental conditions, such as temperature and rainfall, are well documented (Haftorn 1978, 1988, Morton and Pereyra 1985, Joyce et al. 2001, Kovařík et al. 2009). Generally, females take shorter incubation off-bouts under cooler and wetter conditions to maintain a relatively constant nest temperature (DuRant et al. 2013). However, other adverse conditions for the nest may include times when females experience increased energetic demands, potentially creating conflicts over self-maintenance and incubating or brooding (Morton and Pereyra 1985, MacDonald et al. 2013). Overall, female adjustments in brooding patterns in response to environmental variation and how these patterns are influenced by the nest microclimate and nest construction are not well understood.

We tested the hypothesis that females adjust nest characteristics and brooding patterns in response to thermal variation during different nest stages. We examined nest-building and brooding behaviors in a population of migratory Black-throated Blue Warblers (*Setophaga caerulescens*) breeding on 3 study plots at different elevations that spanned a 2°C gradient (Rodenhouse et al. 2003). We first assessed plot-level variation in nest location, nest construction, and brooding patterns. Next, we investigated whether nest characteristics were associated with temperature and rainfall experienced during nest building. We then examined whether nest characteristics and/or variation in temperature and rainfall during the nestling stage were correlated with female brooding patterns. Lastly, we determined whether brooding patterns were associated with the mass of nestlings near fledging, which can be a determinant of fledgling survival (Monrós et al. 2002, Greño et al. 2008).

METHODS

Study Population

We studied a breeding population of the migratory Black-throated Blue Warbler at the Hubbard Brook Experimental Forest (HBEF), Woodstock, New Hampshire, USA (43.93°N, 71.75°W). The study area is a northern hardwood forest dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*), with red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), and white birch (*B. papyrifera*) increasing in abundance on the ridges (Schwarz et al. 2003). Basic breeding biology for our study population is detailed in Holmes et al. (2017). In brief, females choose nest sites in the understory, primarily in dense hobblebush (*Viburnum lantanoides*), and build nests over 3–5 days. At the HBEF, nests are constructed with strips of bark from yellow or white birch and formed

by spider webs. Nests are lined with rootlets, pine needles, moss, and mammal hair. Females lay 1 egg day^{-1} (mean clutch size = 3.6, range: 2–5 eggs) and incubate without assistance from males for ~12 days. Both sexes feed nestlings (mostly lepidopteran larvae) for ~9 days until fledging. Females brood nestlings frequently, particularly early in the nestling stage.

Field Methods

We collected data on 3 study plots classified as low-elevation (250–350 m; 85 ha), mid-elevation (450–600 m; 65 ha), and high-elevation (750–850 m; 35 ha) during May–August, 2010–2013. All plots were on south-facing slopes. We marked adults, mapped male territories, and monitored all nesting attempts. Adults were captured in mist nets and marked with a unique combination of 3 colored leg bands and a federal leg band. Nests were found through intensive searching and were monitored every other day throughout all nest stages, with daily checks near building completion, clutch initiation and completion, and anticipated hatch and fledge dates. We weighed and placed a federal band on young on day 6 (hatching = day 0) of the nestling stage. Because brood size can affect the thermal environment of the nest (Chaplin et al. 2002), we accounted for cases of brood reduction by calculating the average brood size over nestling days 3–5.

We measured the density of woody stems at the nest site and nest wall thickness after each nest became inactive. Stem density was measured as the number of stems per square meter within a 1 m radius of the nest. Mean nest height was 53.2 cm (range: 11–700 cm). A horizontal plane was created on the ground by placing the end of a pole 1 m in length underneath the nest and rotating the pole in a circle around the nest. We counted all bases of woody stems >0.1 m in height that emerged from the ground within the plane. Nest wall thickness was measured as the difference in the diameter of the outer nest cup and inner nest cup (both measured to the nearest 0.1 cm). We measured stem density at all nest sites (*n* = 490) and nest wall thickness of intact nests that were not deformed by weather or nest depredation (*n* = 388).

Temperatures inside the nest cup and from the ambient microclimate of each nest site were measured with iButton thermochrons (DS1921G-F5; Embedded Data Systems, Lawrenceburg, Kentucky, USA). Similar thermochron models have been shown to be accurate within ±0.5°C of reference temperatures when tested in cold and warm conditions and are highly consistent (Davidson et al. 2003, Hubbart et al. 2005, Smith et al. 2010). The afternoon before data recording, we placed one thermochron in the nest cup to collect "nest temperature." We affixed a second thermochron to a small piece of cardboard 5 m from the nest, and tied to vegetation of a similar type and height as the vegetation supporting the nest, to collect mean maximum daily ambient "microclimate temperature" at the nest site. Thermochrons were automated to begin recording near dawn (0400 hours) on nestling day 3 and recorded temperature to the nearest 0.5°C at 4 min intervals until they were retrieved after the nest fledged or failed.

For each nest, we calculated weather conditions during nest building (5 days prior to clutch initiation) and the early nestling stage (nestling days 3–5) when brooding is most likely to occur. When nests were found after laying, the date of clutch initiation was estimated to within 1 day by back-dating 1 egg day^{-1} from the date of the first egg of known lay date and/or the hatch date. We assumed a 12-day incubation period (Holmes et al. 2017). Plot-level daily ambient temperature (°C) and rainfall (millimeters) were measured at 3 permanent U.S. Forest Service weather stations adjacent to each study plot. On average, birds nesting at high elevations experienced cooler (2°C) and wetter (30 mm more rainfall) conditions over the course of the study than birds nesting at low elevations. We measured total daily rainfall accumulated at weather stations during both the nest-building and nestling stages. "Nest-building temperature" is the mean maximum daily temperature measured at weather stations. For "nestling-stage temperature," we used microclimate temperature collected by thermochrons (defined above), which better represents the temperature experienced by females nesting in the understory than temperature measured at weather stations.

We estimated female brooding patterns using data recorded by thermochrons. We paired and aligned temperature data from nest and ambient thermochrons at a nest site by time of day and calculated the difference between nest and ambient temperatures for each 4 min interval. We defined female off-bouts as intervals with a monotonic decrease in the difference between nest and ambient temperatures of ≥0.5°C, indicating that the nest was cooling in relation to the ambient temperature. We identified off-bouts by visualizing output files produced by Rhythm (Cooper and Mills 2005) in Raven Pro 1.4 (Bioacoustics Research Program 2011). We provide a validation of thermochrons for detecting female off-bouts (Appendix). We excluded data collected after sunset (i.e. between 2030 and 0500 hours) because the difference between nest and ambient temperature showed a continuous decrease during this time, making off-bout assignment difficult without a validation method (e.g., video recording of nests at night). From these data, we calculated 3 measures of brooding patterns: mean off-bout duration, mean off-bout frequency, and total proportion of time off the nest over the early nestling stage (i.e. nestling days 3–5). We also calculated these brooding measures during 2 hr time windows to analyze fine-scale patterns because averaging over several days could potentially obscure

short-term effects of temperature on brooding. We excluded from analyses thermochron data collected after day 5, when nestlings began to generate more heat, which reduced the accuracy of off-bout detection by thermochrons (for details, see Appendix).

Using thermochron data, we identified a total of 25,801 daytime off-bouts over nestling days 3–5 from 193 nests. In models of brooding patterns, we included only nests with complete temperature data from 0500–2030 hours on nestling days 3–5 ($n = 146$). Nests with incomplete temperature data resulted from late deployment of thermochrons due to logistical difficulties or failure to find the nest prior to nestling day 3 ($n = 27$), nest failures prior to nestling day 5 ($n = 19$), and thermochron malfunctioning ($n = 1$).

Statistical Analyses

We used a 2-stage process to investigate how nest characteristics and brooding patterns varied with (1) study plot and (2) nest-stage-specific temperature and rainfall. We first used analysis of variance (ANOVA) and Tukey's test with $\alpha = 0.05$ to test for significant differences in nest location, nest construction, and brooding patterns among study plots at low-, mid-, and high-elevation zones. We calculated η^2 (Lakens 2013) and the estimated change in mean values between elevations (β) with associated 95% confidence intervals (CI) as measures of effect size for ANOVAs and Tukey's tests, respectively, using the R package "lsr" (Navarro 2015). We then built linear mixed models (LMMs) and used an information-theoretic approach to identify which weather and nest-site predictor(s) best explained differences in nest characteristics, female brooding behavior, and nestling mass. We constructed LMMs using "lme4" (Bates et al. 2015) and fitted models with maximum likelihood (ML) to account for different fixed-effects model structures (Zuur et al. 2009). Study plot and elevation were not included in LMMs because elevation was correlated with temperature (linear model; $P < 0.001$, adjusted $R^2 = 0.04$). We conducted all analyses in R 3.2.4 (R Core Team 2016).

For LMMs, we used our knowledge of the study system to select 2–4 predictor variables per model to test a priori hypotheses that nest microclimate was correlated with nest characteristics, brooding behavior, and nestling mass. Models testing for associations between microclimate and brooding and between microclimate and nestling mass also included nest-site variables (e.g., nest wall thickness) as predictors. Each candidate model set (range: 3–17 models) included a global model with all fixed effects, an additive model with each combination of fixed effects, and a model with the intercept only. We examined models for homogeneity of variance by plotting model residuals against fitted values (Pinheiro and Bates 2000) and for normality of model residuals by visually inspecting

quantile-quantile plots (Crawley 2013). We conducted a square-root transformation of stem density and a natural-log transformation of mean bihourly off-bout duration to satisfy model assumptions (McDonald 2014).

We examined associations of (1) temperature and rainfall during nest building with square-root-transformed stem density at the nest site ($n = 297$ nests); (2) temperature and rainfall during nest building and stem density with nest wall thickness ($n = 297$ nests); and (3) microclimate temperature and rainfall during the nestling stage, stem density, and nest wall thickness with off-bout duration, off-bout frequency, and proportion of time off the nest ($n = 144$ nests). To examine potential short-term adjustments in brooding patterns, we built 3 LMMs ($n = 104$ nests) for which the response variables were log-transformed bihourly off-bout duration, off-bout frequency, and proportion of time off the nest during 2 hr periods. We divided daylight (0500–2030 hours) into eight 2 hr periods (1.5 hr for the last period, 1900–2030 hours), for a total of twenty-four 2 hr periods over the 3 days, and included mean microclimate temperature over each 2 hr period ("bihourly microclimate temperature") as a fixed effect. In summary, average brooding patterns were examined both over the early nestling stage and bihourly; rainfall and nest characteristics were included as fixed effects only in models for brooding patterns over the early nestling stage. Brood size has been found to be associated with variation in brooding: females spend less time brooding larger broods because they retain heat better than smaller broods during periods of parental inattention (Clark 1985, Sanz and Tinbergen 1999, Chastel and Kersten 2002, Archard et al. 2006). Therefore, in all 6 model sets for brooding patterns, we included mean brood size as a predictor in each model to account for known variation. We included year and female identity (or, for bihourly models, nest identity nested within female identity) as random effects in each model. We did not include year as a random effect in the final models for mean off-bout duration (nestling stage), proportion of time off the nest (nestling stage), and mean off-bout duration (bihourly) because its estimated variance was equal to zero (Zuur et al. 2009).

The final LMMs examined the factors influencing mean nestling mass near fledging, which has been correlated with survival probability in birds (Monrós et al. 2002, Greño et al. 2008). Each analysis used a subset of nests that had the same set of measurements without missing data. The 2 candidate model sets were (1) weather and brooding ($n = 149$ nests), which included microclimate temperature, rainfall during the nestling stage, and proportion of time off the nest (nestling stage) as fixed effects; and (2) nest location and construction ($n = 169$ nests), which included stem density and nest wall thickness as fixed effects. In all models for mean nestling mass, we included (1) mean

brood size to account for known variation and (2) hatch date to account for unmeasured conditions (e.g., food resources) that vary over the breeding season (Holmes et al. 1986) and could influence nestling mass. To further examine potential fitness consequences on nest success, we constructed 2 generalized linear mixed models with fledge (1) or fail (0) as a response variable with a binomial error distribution with a logit link function. We included the same fixed effects as for the nestling mass models but removed hatch date and mean brood size to facilitate model convergence. Model-selection and model-averaging results were qualitatively and quantitatively similar to the nestling mass results, except that proportion of time off the nest was not associated with fledging probability (Supplemental Material Tables S3 and S4).

Model selection for all LMM candidate model sets was based on second-order Akaike's Information Criterion adjusted for small sample sizes (AIC$_c$; Burnham and Anderson 2002) using "MuMIn" (Barton 2014). We report maximized log likelihood (logL) and number of estimated parameters (K) for each model. We ranked models within a candidate set by the difference in AIC$_c$ between each model and the best model (Δ_i). We averaged all models in each candidate model set to obtain coefficient estimates for each fixed effect. We summed Akaike weights (w_i) across all models containing a given fixed effect to evaluate the importance of each model parameter. If a parameter had a summed $w_i \geq 0.75$ and a confidence interval that did not include zero, we considered it important in explaining a given response variable. If a parameter had a 95% CI containing zero, we concluded that the parameter and response variable were not associated. The full list of models included in each candidate model set is given in Supplemental Material Table S1. We detected no multi-collinearity among variables included as fixed effects in the global model for each candidate model set; all variance inflation factors were <1.5 (Supplemental Material Table S2), well below the threshold of 10 suggested by Hair et al. (2010). Results are reported as means ± SE.

RESULTS

Nest characteristics and brooding patterns differed among study plots (Figure 1). Mean stem density and nest wall thickness increased with plot elevation (ANOVA; stem density: $F = 5.5$, df = 2 and 487, $P = 0.004$, $\eta^2 = 0.02$; nest wall thickness: $F = 5.3$, df = 2 and 385, $P = 0.005$, $\eta^2 = 0.03$). Mean stem density at nest sites was significantly higher at high-elevation sites than at low-elevation sites (Tukey's test; $P = 0.01$, $\beta = 0.49$ stems m^{-2}, 95% CI: 0.09–0.90) and mid-elevation sites ($P = 0.005$, $\beta = 0.48$ stems m^{-2}, 95% CI: 0.12–0.85), but we detected no statistical difference in stem density between high- and mid-elevation sites ($P = 0.99$, $\beta = 0.01$ stems m^{-2}, 95% CI:

−0.31 to 0.33). Mean nest wall thickness was significantly greater at high-elevation sites than at low-elevation sites ($P = 0.004$, $\beta = 0.46$ cm, 95% CI: 0.13–0.79), but we detected no statistical difference between mid- and low-elevation sites ($P = 0.06$, $\beta = 0.30$ cm, 95% CI: −0.01 to 0.60) or between high- and mid-elevation sites ($P = 0.32$, $\beta = 0.17$ cm, 95% CI: −0.10 to 0.43). Variation in mean off-bout duration and proportion of time off the nest differed significantly among plots (ANOVA; off-bout duration: $F = 5.5$, df = 2 and 190, $P = 0.005$, $\eta^2 = 0.05$; proportion of time off nest: $F = 3.6$, df = 2 and 190, $P = 0.03$, $\eta^2 = 0.04$). Females had longer off-bouts and spent more time off their nests at high-elevation sites than at mid-elevation sites (Tukey's test; off-bout duration: $P = 0.003$, $\beta = 23.50$ s, 95% CI: 6.59–40.41; proportion of time off nest: $P = 0.03$, $\beta = 0.02$, 95% CI: 0.002–0.04). However, we detected no statistical difference in brooding patterns between mid- and low-elevation sites (off-bout duration: $P = 0.31$, $\beta = -12.21$ s, 95% CI: −32.00 to 7.59; proportion of time off nest: $P = 0.32$, $\beta = -0.01$, 95% CI: −0.04 to 0.01) or between high- and low-elevation sites (off-bout duration: $P = 0.43$, $\beta = 11.29$ s, 95% CI: −10.19 to 32.77; proportion of time off nest: $P = 0.76$, $\beta = 0.01$, 95% CI: −0.02 to 0.03). We detected no statistical difference in mean off-bout frequency among plot elevations (ANOVA; $F = 0.1$, df = 2 and 190, $P = 0.90$, $\eta^2 = 0.001$).

Daily brooding patterns varied over the early nestling stage (Figure 2). Mean off-bout duration and proportion of time off the nest decreased from dawn to dusk and from nestling day 3 to day 5. Mean off-bout frequency remained relatively constant on day 3 and peaked between 0900 and 1100 hours on days 4 and 5. Ambient temperature at nest sites reached a maximum at midday (1300–1500 hours).

Variation in stem density and nest wall thickness was not associated with temperature or rainfall during nest building (Tables 1 and 2). The top-ranked model for stem density included the intercept only (Table 1). Confidence intervals for nest-building temperature and rainfall in models for both stem density and nest wall thickness encompassed zero (Table 2). Although weather did not explain variation in nest construction, stem density was associated with nest wall thickness; nest walls were thicker at nest sites with higher stem density.

Variation in some female brooding patterns was associated with weather, but none was influenced by nest characteristics (Tables 1 and 2). Mean off-bout duration and proportion of time off the nest, measured over the nestling stage or at bihourly intervals, increased with decreasing microclimate temperatures. Mean off-bout duration and proportion of time off the nest increased with increasing rainfall during the nestling stage and with decreasing brood size (Table 2). Mean off-bout duration and proportion of time off the nest were not associated with stem density or nest wall thickness; confidence
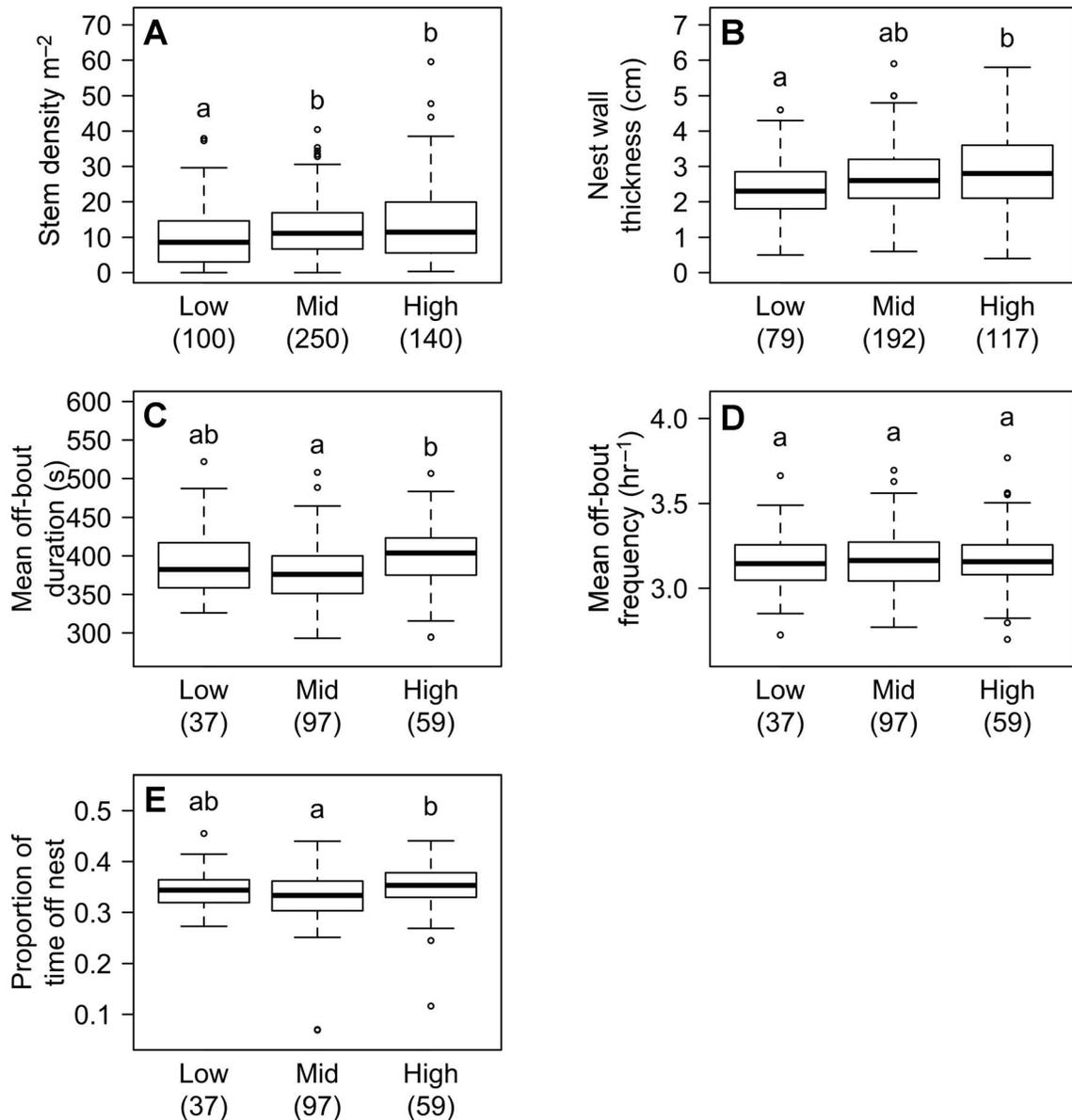
FIGURE 1. Median values, quartiles, and range in parameters across low-elevation, mid-elevation, and high-elevation study plots at Hubbard Brook Experimental Forest, New Hampshire, USA, May–August, 2010–2013. Parameters include (**A**) stem density at the nest site, (**B**) nest wall thickness, (**C**) mean off-bout duration, (**D**) mean off-bout frequency, and (**E**) proportion of time off the nest for female Black-throated Blue Warblers. Letters denote statistically significant differences ($P < 0.05$). Sample sizes are given along the x-axes.

intervals encompassed zero. Mean off-bout frequency over the nestling stage, which showed little variation across plot elevations (Figure 1), was not associated with any of the measured environmental factors; the top-ranked model included the intercept only (Table 1). Mean bihourly off-bout frequency increased with decreasing microclimate temperature (Table 2).

Mean nestling mass near fledging was associated with the proportion of time females were off nests and with mean brood size (Tables 1 and 2). Females that spent more time off nests fledged offspring with lower mass. By contrast, nest microclimate temperature, rainfall, stem density, nest wall thickness, and hatch date (Table 2) were not correlated with nestling mass.

DISCUSSION

Maintaining a stable thermal environment is necessary for the development of altricial young, yet the extent to which females respond behaviorally to changes in nest microcli-
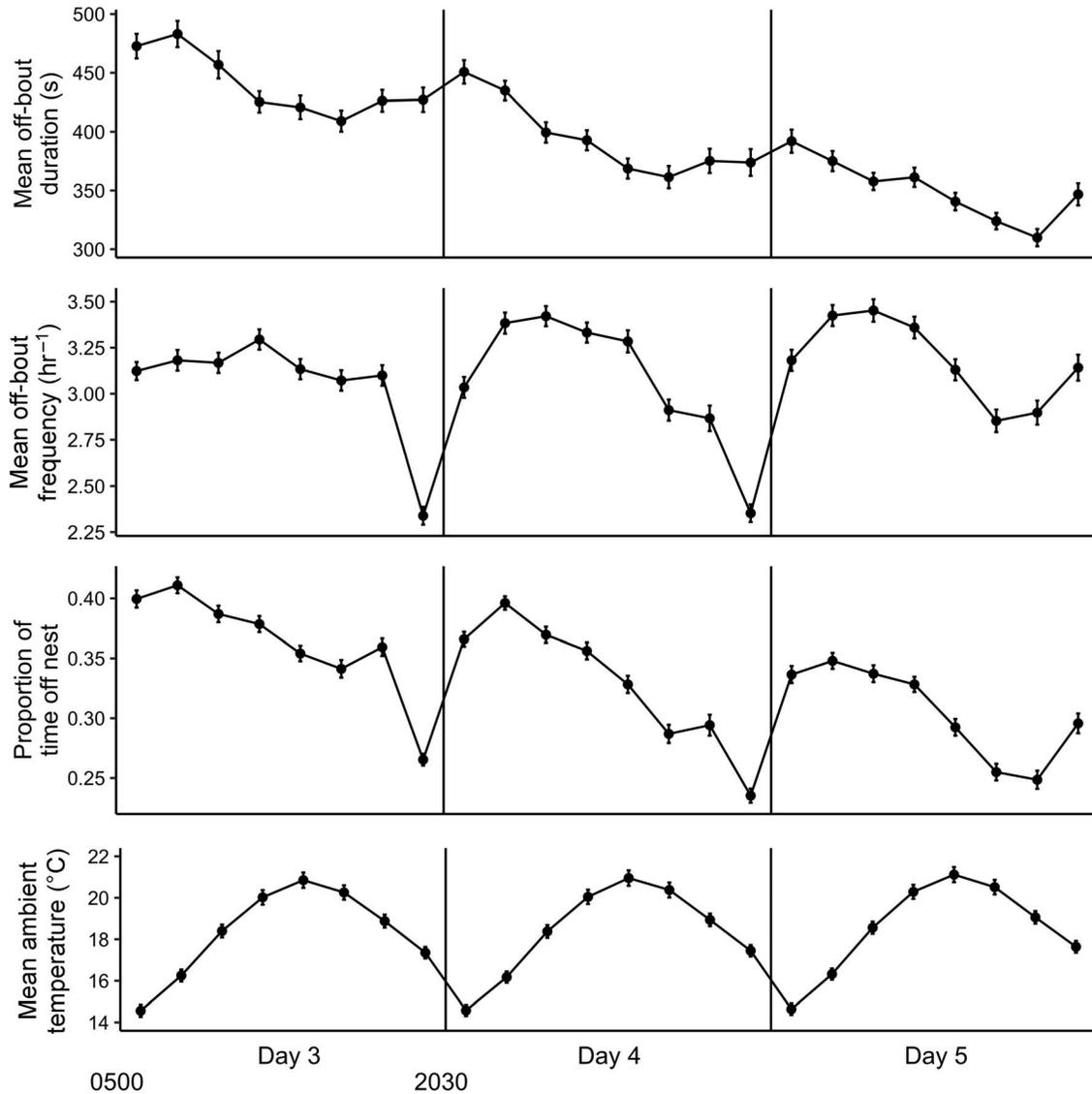
FIGURE 2. Mean (± SE) brooding patterns of female Black-throated Blue Warblers, measured every 2 hr during the daytime (0500–2030 hours) over nestling days 3–5 ($n = 146$ nests), at Hubbard Brook Experimental Forest, New Hampshire, USA, May–August, 2010–2013. Vertical black lines separate days.

mate is not well understood. At the scale of our 3 study plots, stem density at nest sites and nest wall thickness increased from low to high elevation, corresponding to a broad pattern of decreasing temperatures (Rodenhouse et al. 2003). However, we found no direct link between temperature and rainfall during nest building and either stem density at nest sites or nest wall thickness. Adjustments in brooding patterns, by contrast, were associated with weather. Moreover, females that brooded less under cooler and wetter conditions produced nestlings with lower mass near fledging. This indicates that females might favor their own self-maintenance and compromise nestling growth under adverse thermal conditions.

Stem density at nest sites and nest wall thickness were generally greater at higher elevations, although the proportion of the variance in these factors explained by study plot was low. Breeding conditions are cooler and wetter and understory vegetation is more dense at high elevations (Rodenhouse et al. 2003, 2008). The finding that stem density at nest sites increased with elevation could reflect the overall pattern of higher stem density at higher elevations. However, previous work at the HBEF has shown that female Black-throated Blue Warblers select nest sites with denser vegetation than at random points, which may be due, in part, to microclimate benefits (Holway 1991). Moreover, females constructed nests with thicker walls at higher elevation, which suggests a mechanism to insulate

TABLE 1. Model-selection results examining the effects of microclimate temperature, rainfall, stem density, nest wall thickness, and mean brood size on nest location, nest construction, brooding patterns (nestling stage and bihourly), and nestling mass near fledging in Black-throated Blue Warblers at Hubbard Brook Experimental Forest, New Hampshire, USA, May–August, 2010–2013.

Model type	Response variable	Model	logL	K	Δ_i	w_i
Nest characteristics	Stem density	Intercept only	−486.74	4	0.00	0.52
		Nest-building temperature	−486.61	5	1.81	0.21
		Nest-building rainfall	−486.69	5	1.96	0.20
	Nest wall thickness	Nest-building temperature + stem density	−390.63	6	0.00	0.34
		Nest-building rainfall + stem density	−390.94	6	0.63	0.25
		Stem density	−392.09	5	0.85	0.22
		Nest-building temperature + nest-building rainfall + stem density	−390.19	7	1.22	0.19
Brooding patterns	Mean off-bout duration (nestling stage)	Microclimate temperature + nestling-stage rainfall + brood size	−730.79	6	0.00	0.32
		Nestling-stage rainfall + brood size	−732.83	5	1.89	0.12
		Microclimate temperature + nestling-stage rainfall + nest wall thickness + brood size	−730.65	7	1.92	0.12
		Microclimate temperature + nestling-stage rainfall + stem density + brood size	−730.66	7	1.93	0.12
	Mean off-bout frequency (nestling stage)	Intercept only	35.15	4	0.00	0.34
	Proportion of time off nest (nestling stage)	Microclimate temperature (nestling stage) + nestling-stage rainfall + stem density + brood size	243.52	7	0.00	0.27
		Microclimate temperature (nestling stage) + nestling-stage rainfall + brood size	242.04	6	0.74	0.19
		Microclimate temperature (nestling stage) + nestling-stage rainfall + stem density + nest wall thickness + brood size	243.69	8	1.89	0.11
	Mean off-bout duration (bihourly)	Microclimate temperature (bihourly) + brood size	−253.62	6	0.00	1.00
	Mean off-bout frequency (bihourly)	Microclimate temperature (bihourly) + brood size	−244.90	7	0.00	0.57
		Intercept only	−247.56	5	1.31	0.30
	Proportion of time off nest (bihourly)	Microclimate temperature (bihourly) + brood size	−591.14	7	0.00	1.00
Nestling mass	Mean nestling mass (weather and brooding)	Nestling-stage rainfall + proportion of time off nest (nestling stage) + brood size + hatch date	−144.74	8	0.00	0.46
		Proportion of time off nest (nestling stage) + brood size + hatch date	−146.38	7	1.04	0.28
	Mean nestling mass (nest location and construction)	Brood size + hatch date	−174.15	6	0.00	0.30
		Intercept only	−176.33	4	0.08	0.28
		Stem density + brood size + hatch date	−173.41	7	0.69	0.21
		Nest wall thickness + brood size + hatch date	−174.01	7	1.90	0.11

Notes: Maximized log likelihood (logL), number of estimated parameters (K), difference in AIC$_c$ between current and best model (Δ_i), and Akaike weight (w_i) are reported for each candidate model set. Models with ΔAIC$_c$ <2 are shown. Additive effects are indicated by a plus sign. The lowest values of AIC$_c$ for each model set are as follows: stem density, 981.62; nest wall thickness, 793.54; mean off-bout duration (nestling stage), 1,474.20; mean off-bout frequency (nestling stage), −62.02; proportion of time off nest (nestling stage), −472.21; mean off-bout duration (bihourly), 519.27; mean off-bout frequency (bihourly), 503.84; proportion of time off nest (bihourly), 1,196.32; mean nestling mass (weather and brooding), 306.50; mean nestling mass (nest location and construction), 360.82.

their developing offspring from cooler temperatures. These results are also consistent with other studies that have found that nest wall thickness and/or stem density was greater at higher elevations or latitudes (Kern and van Riper 1984, Rohwer and Law 2010, Crossman et al. 2011).

Differences in nest characteristics were, however, not associated with thermal cues or rainfall during nest building. Nest wall thickness increases with decreasing temperatures during nest building in some open-cup-nesting species (e.g., Eurasian Skylark [*Alauda arvensis*]

and Greater Short-toed Lark [*Calandrella brachydactyla*]; Herranz et al. 2004) but not in others (e.g., Tawny Pipit [*Anthus campestris*]; Suárez et al. 2005). Some species may show less plasticity, or high within-individual repeatability, in nest construction behavior (Schleicher et al. 1996, Møller 2006, Walsh et al. 2010) or may modify nest characteristics other than nest wall thickness to increase nest insulation. For instance, in some cavity-nesting species, such as Blue Tits (*Cyanistes caeruleus*) and Great Tits (*Parus major*), females increased nest insulation properties or nest mass in response to lower temperatures during nest building (Britt and Deeming 2011, Deeming et al. 2012). Rainfall during nest building has not been associated with nest characteristics (Mainwaring et al. 2014). Our results suggest that thermal cues during nest building may not be reliable indicators of nestling developmental conditions in the open-cup-nesting Black-throated Blue Warbler. Alternatively, females might adjust characteristics other than those we measured. Further work should evaluate whether nest characteristics are associated with unmeasured environmental variation and/or with individual variation in nest building that may be correlated with elevation (i.e. differences in habitat quality and associated individual settlement patterns).

Mean off-bout duration and proportion of time off the nest decreased as nestlings aged and with larger brood sizes, but off-bout frequency varied little over the nestling stage. Increased nest attendance over the early nestling stage is likely unrelated to thermoregulation, given that older nestlings should require less warming by the female (Archard et al. 2006). As nestlings grow, they can consume larger prey items or larger amounts of food (Haggerty 1992, Goodbred and Holmes 1996). Females may therefore be able to increase nest attentiveness, and decrease their time spent provisioning, if they or their social mates bring larger prey loads during each visit to the nest (Stodola et al. 2010). Because higher nest temperature is associated with greater nestling mass and greater nestling survival (Dawson et al. 2005), females should devote as much time to brooding early in the nestling stage as energetic constraints allow, in order to maximize their reproductive success. We included mean brood size in each model of brooding behavior to account for the known relationship between brooding patterns and brood size. Females spent less time attending nests with smaller broods, contrary to results of previous studies (Sanz and Tinbergen 1999, Chastel and Kersten 2002, Archard et al. 2006). This result may reflect differential investment by females in small vs. large broods. For instance, although a small brood may be less insulated and therefore may require more brooding (Clark 1985, Chastel and Kersten 2002), females may spend more time brooding larger broods because they are more valuable and are worth the additional parental investment (Coleman and Gross 1991, Hanssen et al.

2003). Alternatively, nests may sufficiently insulate a small brood such that heat loss does not pose a large problem. In this case, warming a small brood may simply require less brooding time than warming a large brood.

Both mean off-bout duration and proportion of time off the nest increased with decreasing temperatures and with increasing rainfall, although effect sizes were relatively small. Female adjustments in brooding in response to weather conditions, though slight, were opposite to patterns reported in other studies (Beintema and Visser 1989, Rosa and Murphy 1994, Sanz and Tinbergen 1999, Archard et al. 2006; but see Poiani 1993). For example, female Eastern Kingbirds (*Tyrannus tyrannus*) spent more time brooding at lower temperatures (Rosa and Murphy 1994), whereas female Black-throated Blue Warblers spent less time brooding at lower temperatures. Several possibilities could explain the brooding patterns we observed. First, females might increase off-bout duration at low temperatures and during heavy rainfall to shift the allocation of limited time to self-maintenance activities, such as foraging. Such a pattern has been documented in some incubating songbirds (Haftorn 1978, 1988, Morton and Pereyra 1985, MacDonald et al. 2013). Second, females may require more time off the nest to forage to provision their offspring, given that decreased prey activity at low temperatures effectively reduces food availability (Bryant 1975, Davies 1977, Jones 1987). Lastly, the off-bout pattern we observed could be due to increased nest attentiveness at higher temperatures to shade nestlings (Murphy 1985, Archard et al. 2006). For example, in 2010, a record-breaking hot and dry year in the Northeast (Blunden et al. 2011), females on video recordings were observed shading nestlings more than in other years (e.g., panting and holding their wings outstretched over nestlings; S.A. Kaiser personal observation). The effect of shading on nest temperature is poorly understood, and further validation of thermochrons under such conditions would be necessary to determine how to identify shading events using nest temperature data.

Females that brooded less had nestlings with lower mass near fledging. The effect size was considerable, given that a decrease in 0.4 g with a 10% increase in the female's time off the nest is likely meaningful for a nestling with a mass of 6–9 g. However, fledging probability was not correlated with proportion of time off the nest (Supplemental Material Tables S3 and S4). Offspring that are left exposed for longer periods, especially at low temperatures, may need to reallocate energy from growth to thermoregulation (Dawson et al. 2005). Experimental reductions of nest temperature have not been conducted during the brooding stage. However, nestling Tree Swallows (*Tachycineta bicolor*) in experimentally heated nest boxes had higher mass and survival to fledging (Dawson et al. 2005), which suggests that higher nest temperatures increase nestling

TABLE 2. Full model-averaged parameter estimates ($\pm$ unconditional SE), unconditional 95% confidence intervals (CI), and summed Akaike weights (w_i) for each parameter included in linear mixed models examining the effects of microclimate temperature, rainfall, stem density, nest wall thickness, and mean brood size on nest location, nest construction, brooding patterns, and nestling mass near fledging in Black-throated Blue Warblers at Hubbard Brook Experimental Forest, New Hampshire, USA, May–August, 2010–2013. Summed w_i values are not provided for brood size or hatch date because these factors were included in each model in a given candidate model set to account for known variation. Parameters in bold have confidence intervals that do not include zero.

Model type	Response variable	Parameter	Estimate	CI	w_i	Effect [a]
Nest characteristics	Stem density (square-root transformed)	Nest-building temperature	−0.003 ± 0.011	−0.045, 0.027	0.29	+9 × 10^6 stems/1 m²/1°C
		Nest-building rainfall	0.0002 ± 0.002	−0.005, 0.007	0.27	+4 × 10^8 stems/1 m²/1 mm rain
	Nest wall thickness	Nest-building temperature	0.011 ± 0.014	−0.006, 0.048	0.53	+0.011 cm nest wall/1°C
		Nest-building rainfall	−0.001 ± 0.002	−0.008, 0.002	0.43	−0.001 cm nest wall/1 mm rain
		Stem density	0.023 ± 0.006	0.012, 0.035	1.00	+0.023 cm nest wall/stem/1 m²
Brooding patterns	Mean off-bout duration (nestling stage)	**Microclimate temperature (nestling stage)**	−1.388 ± 1.105	−3.588, −0.103	0.75	−1.388 s duration off/1°C
		Nestling-stage rainfall	0.514 ± 0.319	0.104, 1.108	0.85	+0.514 s duration off/1 mm rain
		Nest wall thickness	−0.692 ± 2.389	−10.267, 5.438	0.29	−0.692 s duration off/1 cm nest wall
		Stem density	0.064 ± 0.264	−0.680, 1.146	0.27	0.064 s duration off/stem/1 m²
		Brood size	−20.576 ± 4.345	−29.166, −11.986	–	−20.576 s duration/nestling
	Mean off-bout frequency (nestling stage)	Microclimate temperature (nestling stage)	−0.001 ± 0.002	−0.011, 0.005	0.21	−0.001 off-bouts/1 hr/1°C
		Nestling-stage rainfall	0.0003 ± 0.001	−0.001, 0.003	0.23	+0.0003 off-bouts/1 hr/1 mm rain
		Nest wall thickness	0.006 ± 0.014	−0.014, 0.061	0.27	+0.006 off-bouts/1 hr/1 cm nest wall
		Stem density	0.0002 ± 0.001	−0.003, 0.006	0.18	+0.0002 off-bouts/1 hr/stem/1 m²
		Brood size	−0.002 ± 0.017	−0.045, 0.038	–	−0.002 off-bouts/1 hr/nestling
	Proportion of time off nest (nestling stage)	**Microclimate temperature (nestling stage)**	−0.002 ± 0.001	−0.004, −0.0002	0.79	−0.2% change in time off/1°C
		Nestling-stage rainfall	0.001 ± 0.0003	0.0001, 0.001	0.87	+0.1% change in time off/1 mm rain
		Nest wall thickness	0.001 ± 0.003	−0.006, 0.013	0.31	+0.1% change in time off/1 cm nest wall
		Stem density	0.0005 ± 0.001	−0.0002, 0.002	0.55	+0.05% change in time off/stem/1 m²
		Brood size	−0.018 ± 0.005	−0.028, −0.008	–	−1.8% change in time off/nestling

TABLE 2. Continued.

Model type	Response variable	Parameter	Estimate	CI	w_i	Effect [a]
	Mean off-bout duration (bihourly; natural-log transformed)	**Microclimate temperature (bihourly)**	−0.020 ± 0.002	−0.022, −0.017	1.00	−1.98% change in duration off (s)/1°C
		Brood size	−0.056 ± 0.012	−0.080, −0.032	–	−5.44% change in duration off (s)/nestling
	Mean off-bout frequency (bihourly)	**Microclimate temperature (bihourly)**	−0.002 ± 0.002	−0.006, −0.0004	0.57	−0.002 off-bouts/1 hr/1°C
		Brood size	0.003 ± 0.008	−0.013, 0.021	–	+0.003 off-bouts/1 hr/nestling
	Proportion of time off nest (bihourly)	**Microclimate temperature (bihourly)**	−0.023 ± 0.002	−0.026, −0.019	1.00	−2.3% change in time off/1°C
		Brood size	−0.051 ± 0.014	−0.079, −0.023	–	−5.1% change in time off/nestling
Nestling mass	Mean nestling mass (weather and brooding)	Microclimate temperature (nestling stage)	0.0004 ± 0.008	−0.030, 0.033	0.25	+0.0004 g/1°C
		Nestling-stage rainfall	−0.004 ± 0.004	−0.014, 0.001	0.62	−0.004 g/1 mm rain
		Proportion of time off nest (nestling stage)	−4.234 ± 1.189	−6.533, −1.980	0.99	−4.234 g/100% change in time off
		Brood size	−0.207 ± 0.078	−0.360, −0.054	–	−0.207 g/nestling
		Hatch date	−0.003 ± 0.004	−0.010, 0.004	–	−0.003 g/day
	Mean nestling mass (nest location and construction)	Stem density	0.003 ± 0.006	−0.004, 0.022	0.31	+0.003 g/stem/1 m²
		Nest wall thickness	−0.008 ± 0.030	−0.149, 0.075	0.21	−0.008 g/1 cm nest wall
		Brood size	−0.102 ± 0.088	−0.282, −0.001	–	−0.102 g/nestling
		Hatch date	0.001 ± 0.003	−0.005, 0.008	–	+0.001 g/day

[a] Effect of 1-unit increase in parameter in terms of response variable.

growth rate. When nests were cooled experimentally during incubation, females spent less time incubating, resulting in lower nestling mass and immunity (Ardia et al. 2010). Our results suggest that females may modify their parental investment during cooler and wetter periods, but possibly at a cost to their offspring's growth and survival.

The ability of females to adjust nest characteristics may be an important determinant of reproductive success. We found no association between either stem density around nests or nest wall thickness and (1) nestling mass, an index of reproductive success (Monrós et al. 2002, Greño et al. 2008); or (2) nesting success (Supplemental Material Tables S3 and S4). We know of no similar studies of open-cup-nesting passerines. Studies of cavity-nesting species have found a positive relationship between fledging success and nest mass (Britt and Deeming 2011), nest size (Álvarez and Barba 2008, 2011), and nest insulation (Lombardo et al. 1995), but other studies have not found these relationships (Alabrudzińska et al. 2003, Tomás et al. 2006). Black-throated Blue Warbler nests in areas of higher stem density and with thicker nest walls were typically at higher elevations at the HBEF. Thus, cooler ambient temperatures experienced by young in those nests could have counteracted any effects of nest characteristics on nestling mass. Alternatively, brooding may be more effective than nest structure at buffering nestlings from thermal fluctuations in this and similar species.

In conclusion, our findings demonstrate that nest characteristics and brooding behavior of female Black-throated Blue Warblers may be related to nest-site temperatures and rainfall. At higher elevations, where conditions are cooler, females construct nests in areas of higher stem density and with thicker nest walls. However, females do not adjust nest characteristics in response to weather conditions experienced during nest building. Females do, however, modify brooding patterns in response to nest-stage-specific thermal variation in ways that could influence fledgling survival. During cooler and wetter periods, brooding females spent more time off the nest, which suggests that they may have been investing in self-maintenance activities at the expense of offspring growth and development. Plasticity in brooding behavior provides a mechanism by which open-cup-nesting song-birds can cope with thermal stress, but this might be constrained by female energetic thresholds. Further studies designed to quantify the effects of local temperature on parental investment and offspring growth and development will be useful for understanding how wild bird populations will respond to environmental change (Du-Rant et al. 2013). Longitudinal studies examining within-individual plasticity in female response to various weather conditions, including extreme weather events, across years and locations would help in predicting the effects of rapid environmental change on reproductive success.

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APPENDIX

Validation of Thermochrons for Detecting Female Off-Bouts

We verified the accuracy of off-bout identification using thermochron data by comparing off-bouts detected using thermochrons to off-bouts documented in 2 hr video recordings of nestling provisioning on nestling days 3 and 7 from a complementary study conducted during 2010–2012 (Kaiser et al. 2014). We randomly selected 10 video recordings across all plots and years taken at different times during the breeding season for each nestling age to compare with thermochron data. In 2013, we collected 5 video recordings on nestling day 5 to test the accuracy of the thermochrons midway through the nestling stage. We recorded start and end times of all off-bouts, defined here as any time the female was not sitting inside the nest cup to brood. We included time spent perched on the nest rim as an off-bout. When analyzing thermochron data, we defined female off-bouts as intervals with a monotonic decrease in the difference between nest and ambient temperatures of $\geq 0.5°C$, indicating that the nest was cooling in relation to the ambient temperature.

For days 3, 5, and 7 of the nestling stage, we calculated the percentage of off-bouts that were detected by thermochrons and whose durations as recorded by thermochrons were within 4 min of the actual durations recorded by video. When videos showed 2 off-bouts separated by an on-bout of <2 min, we counted this as a single off-bout because thermochron resolution was not fine enough to record 2 off-bouts in these situations. Thermochrons accurately detected 74.24% ($n = 66$ off-bouts from 10 nests), 70.37% ($n = 27$ off-bouts from 5 nests), and 30.61% ($n = 49$ off-bouts from 10 nests) of off-bouts on days 3, 5, and 7, respectively. Of all off-bouts recorded by thermochrons, the percentages that did not correspond to actual off-bouts (false positives) were 7.55% ($n = 53$ off-bouts recorded by thermochrons), 20.83% ($n = 24$ off-bouts recorded by thermochrons), and 55.88% ($n = 34$ off-bouts recorded by thermochrons) on days 3, 5, and 7, respectively. When a thermochron recorded an actual off-bout as multiple off-bouts, we evaluated whether the first off-bout recorded was within 4 min of the actual duration and did not count subsequent off-bouts as false positives because they occurred during a known off-bout. We examined whether ambient temperature during off-bouts was associated with whether thermochrons detected actual off-bouts, missed off-bouts, or recorded false positives but found no differences (ANOVA; $F = 0.2$, df $= 2$ and 167, $P = 0.80$).

On the basis of these results, we excluded thermochron data after day 5 from all analyses. Although thermochron accuracy was poorer for day 5 than for day 3, accuracy was substantially lower on day 7 of the nestling stage than on day 3 or 5. Nestling homeothermy begins on day 5 or 6 in the Field Sparrow (*Spizella pusilla*) and Chipping Sparrow (*S. passerina*), which develop over 8–10 days (Dawson and Evans 1957). The Black-throated Blue Warbler has a similar nestling development period (Holmes et al. 1992), so this seems to be an appropriate cut-off to avoid the effects of heat produced by thermoregulating nestlings. Given the fairly high accuracy of thermochrons prior to nestling day 5, we retained our initial off-bout criterion of any monotonic decrease in the difference between nest and ambient temperatures. We imposed no minimum duration or rate of cooling when determining off-bouts. Although off-bout data from thermochrons were not completely accurate, using thermochrons in place of video recording allowed us to have a much larger sample size.

We excluded nocturnal data from all analyses because we often observed a decrease in the difference between nest and ambient temperatures throughout the night, likely due to consistent cooling of the nest contents as ambient temperature decreased. We could not verify female activity after sundown, so we could not identify female off-bouts during 2030–0500 hours with any certainty.