

Breeding timed to maximize reproductive success for a migratory songbird: the importance of phenological asynchrony

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Phenological advances and trophic mismatches are frequently reported ecological consequences of climate warming. Trophic mismatches occur when phenological responses to environmental conditions differ among trophic levels such that the timing of resource demand by consumers becomes decoupled from supply. We used 25 years of demographic measurements of a migratory songbird (the black-throated blue warbler *Setophaga caerulescens*) to compare its breeding phenology to the phenology of both its caterpillar prey and the foliage on which caterpillars feed. Caterpillar biomass in this forest did not show a predictable seasonal pulse. Nest initiation by warblers in this northern hardwood forest was therefore not timed to coincide with a peak in food availability for nestlings. Nonetheless, timing of first clutches was strongly associated with spring leaf expansion (slope \pm SE = 0.56 ± 0.08 days per day of change in leaf phenology, $R^2 = 0.66$). Warblers adjusted the timing of breeding to early springs mainly by shortening the interval between arrival and clutch initiation, but this likely has limits because recent early springs are approaching the relatively inflexible dates when birds arrive on the breeding grounds. Although the timing of first nests did not match 1:1 with leaf-out phenology, the adjustments in breeding time maximized mean annual reproductive success. Nest predation had the greatest effect on annual reproductive success, but the ability of nesting warblers to appropriately track leaf phenology accounted for effects on annual reproductive success comparable to the influence of variation in caterpillar abundance and conspecific density. Nesting phenology in black-throated blue warblers was generally well matched to the timing of leaf-out, even though the match was not 1:1. Without measurements of reproductive success, these unequal phenological shifts might otherwise have been interpreted as having negative ecological consequences.

Changes in phenology are among the most widely reported consequences of climate warming (Parmesan and Yohe 2003). The ecological effects of these changes have often been investigated by using the phenological shift of an organisms' food supply as a measure of the amount that an optimizing organism would shift the timing of life cycle events such as reproduction (Cushing 1990, Visser and Both 2005). For example, a temporal decoupling of an organism's breeding season from the peak availability of food resources for its young (i.e. a trophic mismatch) can have negative consequences for reproductive success (Visser et al. 2006, Post and Forchhammer 2008), and has been linked to population declines in some species (Both et al. 2006, Plard et al. 2014). Such mismatches are not accompanied by decreasing trends in population size across all species, implying that other ecological or life history factors may influence abundances more than breeding phenology (Dunn and Møller 2014). For example, breeding phenology may not affect demography for populations in environments with relatively constant

food availability (Dunn et al. 2011) or that experience strong density-dependent regulation (Reed et al. 2013).

Organisms can potentially respond to environmental variation, including climate change, via phenotypic plasticity: the ability of a single genotype to express a different phenotype in response to different environmental conditions (Gienapp et al. 2008). When the phenological response to environmental variation is presented as the relationship between the phenology of interacting species – for example days of change in the timing of breeding by birds versus days of change in the timing of a food peak – a slope of one indicates equal plasticity across trophic levels and thus synchronous phenological shifts. However, such phenological synchrony may not be an appropriate baseline assumption (Johansson et al. 2015) if life-history tradeoffs favor unequal plasticity across trophic levels (an apparent mismatch as described in Singer and Parmesan 2010, Lof et al. 2012).

In some avian systems, breeding is timed such that the peak food demand of nestlings coincides with a peak in food

availability (Lack 1954, Perrins 1970, Visser et al. 2006, Gaston et al. 2009, Regular et al. 2014), and long-term demographic studies of birds have revealed varying degrees of phenotypic plasticity in the timing of egg-laying (Dunn and Winkler 2010). Much of this research has been done with cavity-nesting songbirds, especially tits (Paridae) and flycatchers (Muscicapidae) that breed in nest boxes in European oak woodlands, for which rates of nest predation are relatively low (Perrins 1965). In these systems, the matching of breeding time with a predictable peak of caterpillar availability is among the important determinants of reproductive success (reviewed by Both 2010), although density dependent regulation can buffer against negative effects of lower reproductive success on demographic rates (Reed et al. 2013). However, avian breeding is not always timed to match peak food availability for young (Wesolowski and Rowinski 2014), and the availability of food for nesting birds does not always exhibit a strong seasonal peak, e.g. the insect prey of tree swallows *Tachycineta bicolor* (Dunn et al. 2011) and of reed warblers *Acerocephalus scirpaceus* (Halupka et al. 2008). In addition, seasonal patterns of food availability can differ among habitats used by a single species. For example, pied flycatchers *Ficedula hypoleuca* in oak forests experience a narrow peak in caterpillar availability, while those in mixed deciduous and coniferous forests experience a gradual increase over the breeding season (Burger et al. 2012). Taken together, these findings suggest that the importance of phenotypic plasticity in breeding time may depend on whether or not food supplies exhibit a predictable seasonal peak, and on the importance of food limitation versus other demographic drivers such as predation and density dependent regulation.

The window of potential breeding times in birds is generally controlled by photoperiod (Dawson 2008). Plasticity within that window can be influenced by temperature (Schaper et al. 2012), spring budburst phenology (Bourgault et al. 2010), and food availability (Perrins 1970, Dawson 2008, Dunn et al. 2011). Predator activity (Hušek et al. 2012), as well as intrinsic factors such as breeder age (Nussey et al. 2005) and conspecific density (Votier et al. 2009), may also affect avian nesting phenology. Constraints on plasticity can arise due to body condition (e.g. when only high-quality individuals can advance lay date in an early spring; Verhulst and Nilsson 2008). A relatively fixed timing of departure from winter quarters and subsequent arrival on breeding grounds for migratory birds can also limit adjustment of breeding dates (Both et al. 2005).

We studied the reproductive phenology of individually-marked black-throated blue warblers *Setophaga caerulescens*, in an unfragmented North American temperate hardwood forest over a 25-year period. Our goal was to assess how population-level plasticity in the timing of breeding relative to spring leaf-out and food availability affected mean annual reproductive success in this Nearctic – Neotropical migratory passerine. We exploited the naturally high inter-annual variation in the phenology of spring leaf expansion and bird breeding to: 1) characterize the population-level plasticity of breeding time and the factors that influence it, 2) evaluate the timing of breeding relative to seasonal patterns of caterpillar abundance, 3) test whether the population-level plasticity in breeding time has maximized mean annual reproductive

success, and 4) compare the effects on annual reproductive success of breeding phenology relative to those of nest survival, food abundance, and conspecific density.

Methods

Study system

Black-throated blue warblers were studied between 1986 and 2010 in the Hubbard Brook Experimental Forest in north-central New Hampshire, USA (43°56', 71°45'). This 3160-ha forest is part of the much larger White Mountain National Forest and consists of uneven-aged, mature, unmanaged second-growth northern hardwoods. The canopy trees consist primarily of American beech *Fagus grandifolia* sugar maple *Acer saccharum* and yellow birch *Betula alleghaniensis*, with scattered red spruce *Picea rubens* and eastern hemlock *Tsuga canadensis*. Hobblebush *Viburnum lantanoides* and striped maple *Acer pensylvanicum* are the most common woody understory plants.

The black-throated blue warbler breeds in relatively undisturbed deciduous and mixed deciduous forests in the eastern and northeastern United States and Canada and winters mostly in the Greater Antilles (Holmes et al. 2005). Males defend exclusive territories and females build open-cup nests in low, dense shrubs in the forest understory. Clutch size is usually four but ranges from three to five eggs in first broods and from two to four in second broods (Holmes et al. 2005). The warblers typically renest following nest failure and often attempt a second brood after successfully fledging a first (i.e. double-brood) if sufficient food is available (Holmes et al. 1992, Rodenhouse and Holmes 1992).

Lepidoptera larvae (caterpillars) are an important food source for black-throated blue warbler adults and young (Robinson and Holmes 1982, Holmes et al. 2005). Caterpillars comprise approximately 60–90% of prey biomass provisioned to young (Goodbred and Holmes 1996), with the remainder of prey consisting of a wide variety of adult insects and other arthropods. Caterpillars comprise proportionally fewer of the food items provisioned to nestlings in years of low caterpillar abundance and on plots with experimentally reduced caterpillar abundance (Rodenhouse and Holmes 1992). Food availability, nest survival, and conspecific density limit and regulate this population (Sillert and Holmes 2005), and data on caterpillar abundance, in particular, are essential for understanding inter-annual variation in reproductive output (Nagy and Holmes 2004).

Data

Black-throated blue warblers were studied between 1986 and 2010 ($n = 25$ years) on the 64-ha plot (450–600 m a.s.l.) described by Sillert and Holmes (2005). Each year, fieldwork began in early May and continued until all nesting ceased, typically in early August. The 64-ha study plot was marked with a 25×25 -m grid by using flagging tape, which allowed us to map warbler arrival patterns and determine the density of breeding pairs ($n = 25$ years, Sillert and Holmes 2005). Adult birds were captured, individually marked with a unique combination of colored leg bands, and aged

as yearlings (SY) or older adults (ASY) by plumage characteristics (Pyle 1997). We attempted to locate and determine the fate of all nesting attempts made by females on the 64-ha plot. Adults were monitored after a nest fledged or failed to ensure that renesting and double-brooding attempts were discovered. Young were weighed, measured, and banded 2–3 days prior to fledging.

To document arrival of warblers on the study plot each spring, we mapped the occurrence of males on the study area each day from their first arrival in early May through early June when territory establishment was completed (1989–2010). Because only about half of the males each season were returnees from the previous year and thus already color-banded, we could not unambiguously determine the date of first arrival for all individuals. We used the median arrival date of males for comparison to arrival phenology across years ($n = 22$ years). We focused on arrival dates of males because male arrival is relatively easy to document in black-throated blue warblers and provides a robust index of annual arrival dynamics. We did not use data on female arrival because females arriving in spring were difficult to detect and often were unbanded. Females have a lower survival rate (Sillert and Holmes 2002) and lower site fidelity (Cline et al. 2013), resulting in the arrival of few color-banded females each spring. Females, which do not sing, were typically detected through cues from male behaviors. The first females always arrive within one week of the first males (Lany et al. unpubl.).

Nests, which were usually discovered during the building phase, were monitored every two days until fledging or failure. Clutch initiation was defined as the first day on which an egg was laid in a nest. When nests were found during incubation or nestling periods, clutch initiation dates were back-dated from hatching or fledging dates (Holmes et al. 1992). We excluded from analysis pairs ($n = 29$) for which the first recorded clutch initiation was more than the length of one nesting cycle (24 days) after the tenth percentile of first clutch initiation for that year. This was done because these pairs probably represented cases in which we missed the initial nesting attempt of the season. This resulted in a final sample size for our study of 463 dates for first clutch initiation (median = 15 nests per year; range = 9–37 nests per year). Annual estimates of daily survival probability of nests were calculated via logistic regression and maximum likelihood using the ‘nest survival’ model in program MARK (Shaffer 2004). We calculated one constant daily nest survival probability for each year of study using an intercept-only model fit with a sine link function. We calculated mean annual reproductive success for warblers on the study area as the average of the total number of young fledged per pair per year (excluding the young fledged from the second mate of the few bigamous males that had two mates simultaneously).

We measured directly the abundance and biomass of the two main types of prey used by the warblers – Lepidoptera larvae and adult flying insects (Rodenhous and Holmes 1992, Goodbred and Holmes 1996, Holmes et al. 2005). Caterpillars were visually surveyed from 1986–2010 at approximately two-week intervals beginning when leaves in the understory reached full expansion (about 1 June). In each interval, 2000 leaves on each of four permanent transects within the study plot were searched (100 understory

leaves each of American beech and sugar maple at 10 points separated by 50 m along each transect). Sampling during each two-week interval typically occurred over one to four days (not necessarily consecutive), and the date of sampling was considered to be the middle of these days. Seasonal caterpillar abundance varied synchronously among years on the four dominant woody understory species in this forest – American beech, sugar maple, striped maple and hobblebush (Lany et al. unpubl.). Therefore, our measure of caterpillar abundance on American beech and sugar maple saplings provided reliable index food availability to black-throated blue warblers. The length of each individual caterpillar was recorded and converted to dry biomass using the equation $0.004 \times \text{length (mm)}^{2.64}$ (Rogers et al. 1977), resulting in units of dry caterpillar biomass per 2000 leaves. Total food availability over the entire season was calculated for each transect as the sum of the mean caterpillar biomass on each of the four counting occasions, resulting in units of dry caterpillar biomass per 8000 leaves. Adult flying insects (mainly Diptera) were sampled with two 2-m tall Malaise traps that were placed at ground level in the same location each year and operated from mid May through early August (1996–2010). Two 24-h samples were collected each week from these traps, dried, and then weighed to obtain dry biomass of flying insects per trap per 24 h.

We used thermal sums instead of calendar day in analyses of seasonal patterns of insect prey availability to standardize across warm and cool seasons. We calculated the thermal sum (growing degree days accrued above a 4°C base) for each caterpillar count and Malaise trap collection date from daily maximum and minimum temperatures, and used quantile regression to test for directional trends and unequal variance in biomass across the breeding season. We also tested for correlations between thermal sums and both caterpillar biomass (mg/2000 leaves, transformed as $\ln(x + 1)$) and the average length of individual caterpillars (mm, transformed as $\ln(x)$) with an ANOVA model that included year, sampling occasion within year, and their interaction. We defined the day of maximum caterpillar abundance for each year as the date of the count with the highest mean caterpillar biomass, and we used the mean caterpillar biomass of the first count (~29 May to 5 June) as a measure of food availability during egg laying in the first clutches of the season. Unless indicated otherwise, all statistics were performed in R ver. 3.0.2 (< www.r-project.org >).

We used the timing of sugar maple leaf expansion as a metric of spring temperatures and tree phenology. Of the three co-dominant canopy species (sugar maple, American beech and yellow birch), we chose sugar maple phenology as our baseline because this species is the first to leaf-out (budburst) in spring but also completes canopy expansion at about the same time as the other two species. Sugar maple phenology in the Hubbard Brook forest is well described with a simple thermal time model (Richardson et al. 2006). Our approach is therefore conceptually congruent with studies that use mean temperature or thermal sums accrued over a fixed interval of calendar days as the baseline metric against which breeding plasticity is calculated (McCleery and Perrins 1998, Visser et al. 2006).

Sugar maple spring phenology was modeled based on a 'thermal time' approach following Richardson et al. 2006 (detailed methods in Supplementary material Appendix 1 Fig. A1) using 22 years (1989–2010) of leaf phenology observations and daily maximum/minimum temperatures (data available at < www.hubbardbrook.org >). To confirm that these observations of the forest canopy taken across the experimental forest matched the understory leaf phenology on our study plot, we used four years of temperature and leaf expansion data gathered between 0.5 and 3 m above ground level directly on the bird study plot (2005–2007, 2010); both methods arrived at similar thermal thresholds for each stage of leaf expansion (Supplementary material Appendix 1 Fig. A2). We calculated the day of budburst and full canopy expansion (the day leaves reached 90% of final length) for sugar maples on our 64-ha study plot for all years of bird study (1986–2010) using daily maximum/minimum temperatures recorded at the Hubbard Brook weather station adjacent to the study plot, and used this measure in subsequent analyses. We tested for time trends in budburst phenology using the nonparametric Mann–Kendall test with Sen slope estimate.

Analyses

We quantified the factors that predict warbler breeding time using multiple linear regression and an information-theoretic approach (Burnham and Anderson 2002). We identified the best predictive model for median clutch initiation date for the bird population (1986–2010; $n = 25$ years); candidate predictors included 1) the date of maximum caterpillar biomass, 2) the date of full canopy expansion, 3) caterpillar abundance (ln mg/2000 leaves) on the first sampling date of the season (approximately when leaves complete spring expansion), 4) the proportion of older than second year (ASY) females in the population, 5) conspecific density (breeding black-throated blue warblers per 64 ha), and 6) the daily nest survival probability. The residuals were not serially autocorrelated (Durbin–Watson test, $D = 1.47$, $n = 25$, $p = 0.08$), and years were treated as independent. Regression diagnostics did not detect multicollinearity (max VIF = 2.95), and the day of maximum caterpillar biomass was negatively correlated with caterpillar biomass on the first sampling date of the season ($R^2 = 0.50$). We quantified the relationship between median arrival dates of male warblers and sugar maple budburst ($n = 22$ years) as the slope of the linear regression between the two variables.

We evaluated whether the population-level plasticity in the timing of breeding – defined as the slope of the median clutch initiation date versus date of full spring tree canopy development regression – maximized reproductive success. To do so, we identified the best model (based on Akaike information criteria) predicting mean annual reproductive success (young fledged per pair per year) from candidate models that included the previously known predictors of black-throated blue warbler reproductive success at Hubbard Brook (Nagy and Holmes 2004, Sillett and Holmes 2005): daily survival probability of nests, conspecific density (birds/64 ha), food availability over the entire breeding season (mg caterpillar biomass/8000 leaves) and all possible interactions. We also considered as an additional predictor the residuals (X) from

the regression of clutch initiation date versus the date of full canopy development both as a linear and quadratic term ($Y = \beta_0 + \beta_1 X$ versus $Y = \beta_0 + \beta_1 X + \beta_2 X^2$). Support for the quadratic term, but not the linear term would indicate that the observed plasticity maximized reproductive output, on average, for the population. Because the residuals were not serially autocorrelated (Durbin–Watson test, $D = 2.6$, $n = 25$, $p = 0.12$), years were treated as independent. Regression diagnostics did not detect multicollinearity (max VIF = 1.59 with interaction products excluded), although caterpillar abundance was positively associated with the population-level phenotypic plasticity residuals ($R^2 = 0.24$) and the daily nest survival probability was positively associated with the squared population-level phenotypic plasticity residuals ($R^2 = 0.24$). The best model also allowed us to compare the responsiveness of mean annual reproductive success to the range of empirical variation in each predictor (by substituting values for the 10th and 90th percentiles of the predictor of interest, while holding the other predictors at their mean value). We used annual reproductive success as our measure of reproductive success because natal dispersal is high in this species (Holmes et al. 2005). Annual reproductive success is strongly correlated with recruitment in the following year (Sillett et al. 2000), indicating that the number of young fledged in a breeding season is a good measure of the number of young recruited the following year.

Data deposition

Data available from the Dryad Digital Repository: < <http://dx.doi.org/10.5061/dryad.g1m27> > (Lany et al. 2015).

Results

Seasonal patterns of food availability

Average caterpillar biomass per 2000 leaves varied dramatically at Hubbard Brook among years (range = 40-fold, main effect of year: $F_{24,50} = 5.2$, $p < 0.001$), but showed no predictable seasonal peak. Depending on the year, caterpillar abundance decreased, increased, or remained stable over the course of the warblers' breeding season (Fig. 1). Caterpillar biomass was most variable among years in the early part of the season: the 90th quantile regression slope was -2.37 ($-3.18, -0.753$) mg caterpillar/2000 leaves per 100 growing degree-days. However, the slope of the 50th percentile regression was not significantly different from zero (Fig. 2A), indicating that caterpillar biomass, on average, neither increased nor decreased over the breeding season. Furthermore, the average size of individual caterpillars available in the forest as potential food for birds was surprisingly stable over the summer (back-transformed mean length = 9.5 mm), and seasonal patterns that did occur varied among years (year \times thermal sum interaction: $F_{24,2995} = 6.3$, $p < 0.001$, Supplementary material Appendix 1 Fig. A4). Caterpillar biomass was proportional to abundance ($n = 25$ years, $r = 0.93$), indicating that a period of higher caterpillar biomass was the result of more, not bigger, larvae in the forest. Caterpillar biomass in the early season was not associated with spring

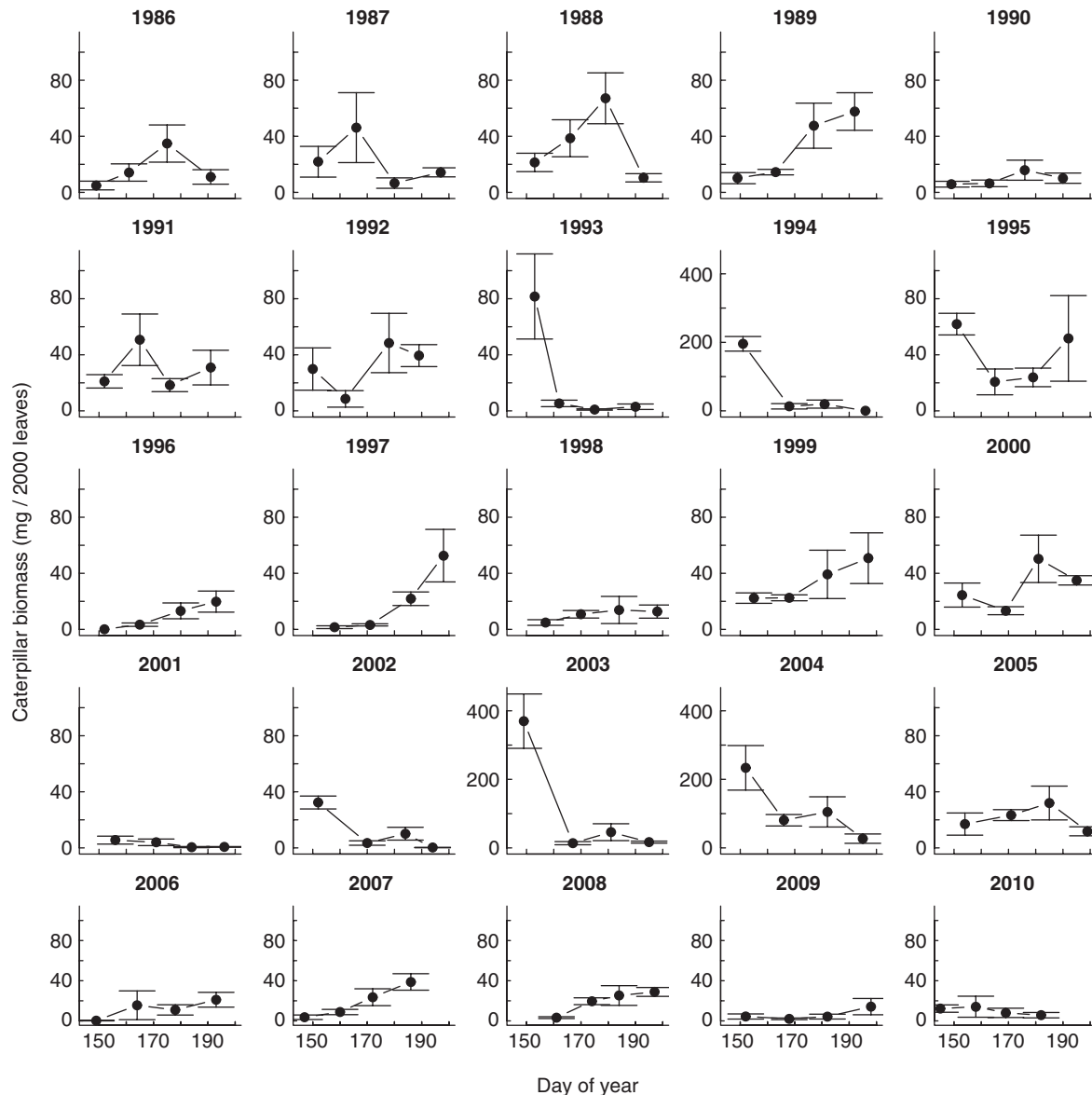


Figure 1. Seasonal patterns of caterpillar biomass for 25 years (1986–2010) at the Hubbard Brook Experimental Forest. Points represent mean caterpillar dry biomass (mg/2000 leaves) of four transects observed four times each season at approximately two-week intervals, from about late May through late July. Bars represent the standard errors ($n = 4$ transects). The y-axes are scaled differently for 1994, 2003 and 2004. Conspicuous peaks of caterpillar biomass were evident in some years but not in others; no consistently-timed biomass peak was observed across years. Day 150 = 30 May.

leaf-out date (linear regression, $n = 25$ years, $p = 0.90$), indicating that early springs did not consistently have higher (or lower) than average caterpillar abundance.

The biomass of the other main prey for the warblers – flying insects as measured in Malaise traps – also lacked a predictable seasonal peak (Fig. 2B), and instead tended to increase steadily (by about 60% from early to late summer; $F_{1,250} = 21.8$, $p < 0.001$). For flying insects, unlike caterpillars, we found no tendency for higher inter-annual variation early in the breeding season (the 50th percentile regression slope was indistinguishable from the 90th percentile regression slope). Inter-annual variation in the biomass of flying insects was small compared to variation in caterpillar biomass (less than three-fold for flying insects versus 40-fold

for caterpillars). Taken together, seasonal patterns of both flying insect and caterpillar abundance indicated that peak food availability could occur at any time during the breeding season and was independent of leaf-out date.

Spring tree phenology

The timing of sugar maple budburst on the study plot during this study was highly variable among years (range = 26 April – 26 May, Fig. 3). We found no significant trend in budburst dates over the 25 years of this study (1986–2010, $p = 0.62$), and budburst trended earlier at a rate of 1.25 days per decade (95% confidence interval = -2.70 , 0 days per decade) over the entire period that temperature has been

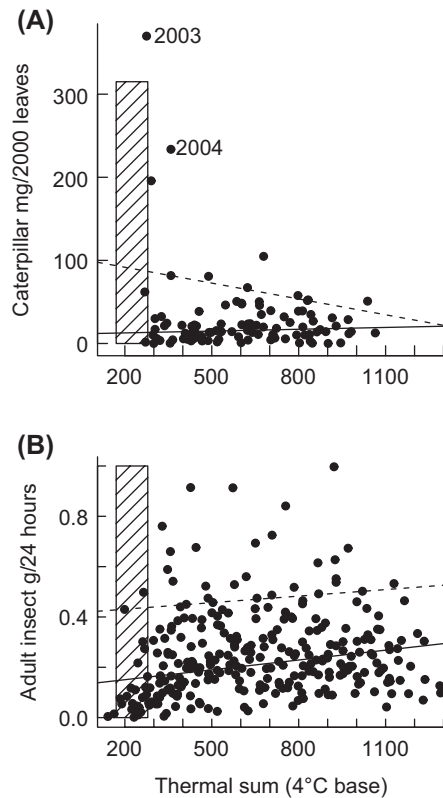


Figure 2. Seasonal patterns in biomass of caterpillars and adult flying insects at Hubbard Brook Experimental Forest. Neither caterpillar dry biomass (mg/2000 leaves, (A)) nor adult insect dry biomass (g/24 h, (B)) showed a predictable peak during the breeding season of migratory birds. The x-axis is scaled as thermal time (degree days) instead of calendar day to standardize comparisons across warmer and cooler years. Each point represents one sampling occasion in one year ($n = 100$ caterpillar sampling occasions (A) and 279 adult insect sampling occasions (B)); solid lines represent the 50th percentile regression and dashed lines represent the 90th percentile regression; shaded boxes represent the period from budburst to full canopy expansion for sugar maples on the study plot.

recorded at the Hubbard Brook Experimental Forest (1957–2010, $p = 0.04$).

Factors that influence variation in arrival and breeding time

Arrival dates of male black-throated blue warblers for each year (mean \pm SD = 12 May \pm 2.9 days) were much less variable than budburst dates (mean \pm SD = 11 May \pm 7.1 days) and were weakly associated with budburst phenology (slope = 0.16 ± 0.08 days per day of change in budburst phenology, $p = 0.06$, $R^2 = 0.17$, Fig. 4A). The annual median date of clutch initiation (31 May \pm 4.3 days) more closely matched spring phenology and changed by 0.56 ± 0.08 days per day of change in the date of full canopy expansion (the population-level plasticity of breeding time; $p < 0.01$, $R^2 = 0.66$, Table 1, Fig. 4B). Warblers adjusted the timing of first clutch initiation to early springs mainly by shortening the length of the period between arrival and clutch initiation date (0.38 ± 0.10 days for each day advance in full canopy

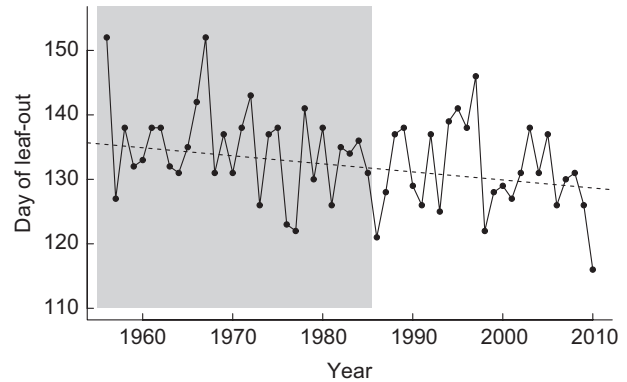


Figure 3. Modeled spring leaf phenology of sugar maples at the Hubbard Brook Experimental Forest, 1956–2010. Spring leaf phenology showed high inter-annual variation and advanced by 1.25 days per decade (dashed line, Sen slope estimate from Mann-Kendall trend test). While budburst did not trend earlier during the 25-year period of the bird study (unshaded region, 1986–2010), these years captured the full range of environmental variability since the beginning of the instrument record at Hubbard Brook, with both one of the warmest (2010) and one of the coldest (1997) seasons on record. Day 135 = 15 May.

expansion, $p < 0.01$, $R^2 = 0.43$, Fig. 4C). The smallest interval observed between median arrival of males and median clutch initiation for the warbler population was 12 days.

We found strong evidence that median clutch initiation dates were also influenced by caterpillar biomass during the first survey period of the season, which coincides with when warblers initiate their first clutches of the season ($\Delta AIC_c = 7.55$ for a model that does not include early season caterpillar biomass, Table 1). Variation in early-season caterpillar biomass explained 11% of the variation in annual mean clutch initiation dates (Table 1). The age structure of the population was also a predictor of annual mean clutch initiation dates in the lowest AIC_c model ($\Delta AIC_c = 2.17$ for a model that does not include the proportion of ASY females) such that on average, birds bred earlier in years with a greater proportion of older females in the population (Table 1). Models that additionally included the daily survival rate of nests, conspecific density, or the timing of maximum caterpillar biomass were not strongly supported ($\Delta AIC_c > 2.95$ for each, Table 1, comparisons of all candidate models in the Supplementary material Appendix 1 Table A1).

Effects of breeding time plasticity on seasonal reproductive output

Success of the first nesting attempt represents only part of annual reproductive success for the multi-brooded black-throated blue warbler (mean \pm SD of fledglings per first attempt versus fledglings per season per pair = 1.95 ± 0.63 versus 3.42 ± 0.96 ; $Y = 1.86 + 0.80 X$, $n = 25$, $R^2 = 0.27$). An average of 46% of warbler first clutches failed during the 25 years of our study, with 71% of those failures attributable to predation events and the remainder to abandonment (14%), extreme weather events (4%), or unidentified causes (14%).

Average annual reproductive success of the warblers over the 25-year study period (mean \pm SE = 3.42 ± 0.19

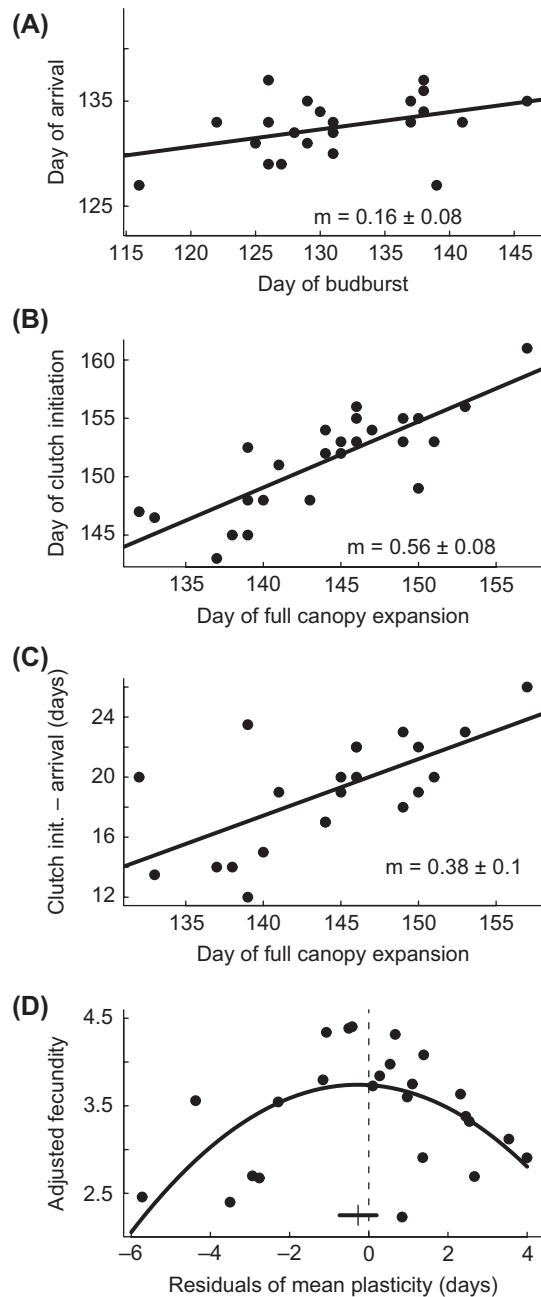


Figure 4. (A) Median arrival dates ($n = 22$ years) of male black-throated blue warblers relative to spring budburst ($m = \text{slope} \pm \text{SE}$, day 130 = 10 May). (B) Median clutch initiation dates ($n = 25$ years) of black-throated blue warblers relative to day of full canopy expansion. (C) Interval between median arrival and clutch initiation dates ($n = 22$ years) relative to the day of full canopy expansion. (D) Average number of fledglings per warbler pair per year relative to residuals from (B); the vertex of the function $\pm \text{SE}$ (-0.27 ± 0.47 days) is indicated with a cross on the x-axis and the vertical, dashed line identifies the line $x = 0$.

fledglings pair⁻¹ year⁻¹) was affected by nest survival ($R^2 = 0.36$), caterpillar abundance ($R^2 = 0.07$), the interaction of nest survival and caterpillar abundance ($R^2 = 0.08$), conspecific density ($R^2 = 0.11$), and deviation from the population-level plasticity of breeding time ($R^2 = 0.05$; Table 2; comparisons of all candidate models in Supplemen-

tary material Appendix 1 Table A2). After accounting for predators, food and density, we found a negative quadratic relationship between the population-level phenotypic plasticity residuals (from Fig. 4B) and average annual reproductive success (Fig. 4D, Table 2). The vertex of this quadratic function was approximately zero (vertex $\pm \text{SE} = -0.27 \pm 0.47$ days), indicating that the observed adjustments among years in breeding time were, on average, that which maximized mean annual reproductive success. Additionally supporting this result, the residuals of the plasticity regression as a linear predictor were not included in the lowest AIC_c model (Table 2). Thus, average annual reproductive success did not tend to be higher or lower when spring phenology was early or late (linear regression of adjusted annual reproductive success versus timing of budburst, $n = 25$ years, $p = 0.82$).

Effects on annual reproductive success of breeding phenology relative to other environmental factors

Although birds adjusted their breeding time in accordance with the timing of canopy leaf expansion (Fig. 4B), which benefited their annual reproductive success (Fig. 4D, Table 2), these adjustments were apparently imperfect. Deviations from the population-level plasticity shown in Fig. 4B corresponded to swings in annual reproductive success of about 22%, which was comparable to demographic effects from inter-annual variation in warbler nesting density (22%) and caterpillar biomass (17%) (Table 3). Fluctuations in annual nest survival accounted for the largest portion (39%) of variation in annual reproductive success (Table 3).

Discussion

Our analyses for black-throated blue warblers showed that plasticity in the timing of breeding was an important determinant of mean annual reproductive success despite the absence of a seasonal caterpillar biomass peak at Hubbard Brook. The absence of a predictable seasonal caterpillar pulse is likely related to Lepidoptera diversity. Several hundred species of Lepidoptera with variable life histories and a wide array of larval feeding times contribute to caterpillar abundance in the temperate mixed hardwood forest at Hubbard Brook (Stange et al. 2011). Thus, the pool of caterpillars available to breeding black-throated blue warblers consists of a shifting array of species – with earlier-feeding species lost from the biomass pool to predation and pupation while neonates of later species hatch and join the pool at variable times during the season.

Deciduous tree species differ in the caterpillar species that feed on them (Summerville et al. 2003), and forest types can vary in the species richness of numerically important caterpillars (Murakami et al. 2007). The Lepidoptera fauna of oak woodlands in the Netherlands and England for example, where phenological mismatches between birds and their prey have been most often documented (Both 2010), are dominated by relatively few common species such as winter moth *Operophtera brumata* and oak leaf roller *Tortrix viridana* (Betts 1955, Visser et al. 2006). Oak forests in general might be prone to early season peaks in caterpillar abundance (Murakami et al. 2005, Forkner et al. 2008) because oaks typically display a strong decline in foliage quality after leaf

Table 1. Environmental factors associated with the timing of first clutch initiation of black-throated blue warblers at Hubbard Brook. Annual mean clutch initiation dates ($n = 25$ years) were predicted by spring phenology (the day of full canopy expansion), caterpillar abundance (ln mg/2000 leaves) as measured in spring as egg laying began, and the population age structure. Clutch initiation dates were not related to the daily survival rate of nests, conspecific density, or timing of maximum caterpillar biomass.

	Estimate \pm SE	Partial R^2	Estimate \pm SE	Estimate \pm SE	Estimate \pm SE	Estimate \pm SE
Intercept	78.2 \pm 10.0		103.3 \pm 38.9	76.4 \pm 11.0	78.7 \pm 12.6	75.5 \pm 12.1
Spring tree phenology	0.54 \pm 0.07	0.63	0.54 \pm 0.07	0.55 \pm 0.07	0.54 \pm 0.07	0.55 \pm 0.08
Caterpillar biomass, early season	-0.70 \pm 0.21	0.11	-0.69 \pm 0.21	-0.69 \pm 0.22	-0.72 \pm 0.33	
Population age structure (proportion ASY females)	-5.42 \pm -2.4	0.07	-4.9 \pm 2.6	-5.3 \pm 2.5	-5.6 \pm 2.9	-5.4 \pm 2.9
Nest survival (daily probability)			-25.6 \pm 38.3			
Density (breeding birds/64 ha)				0.02 \pm 0.05		
Day of maximum caterpillar biomass					-0.003 \pm 0.04	
R^2		0.81	0.81	0.81	0.81	0.70
ΔAIC_C		0	2.95	3.27	3.50	7.55

Table 2. Determinants of mean annual reproductive success (young fledged per pair per year) of black-throated blue warblers at Hubbard Brook. The model with the most support (in bold) includes the residual of the median clutch initiation date versus date of spring leaf maturation regression as a quadratic term, indicating that annual reproductive success was lower in years when breeding was either early or late compared to the average match between spring leaf phenology and breeding ($n = 25$ years).

Variable	Estimate \pm SE	Estimate \pm SE	Estimate \pm SE
Intercept	129.4 \pm 81.5	84.2 \pm 88.5	141.1 \pm 85.4
Nest survival (daily probability)	-129.2 \pm 84.0	-82.8 \pm 91.0	-141.5 \pm 88.1
Density (breeding birds/64 ha)	-0.031 \pm 0.016	-0.033 \pm 0.018	-0.032 \pm 0.016
Caterpillar biomass (ln mg/8000 leaves)	-39.5 \pm 17.9	-26.6 \pm 19.0	-42.2 \pm 18.7
Nest survival \times caterpillars	41.0 \pm 18.4	27.6 \pm 19.5	43.7 \pm 19.3
Residual of plasticity			0.039 \pm 0.067
Residual of plasticity, squared	-0.047 \pm 0.020		-0.044 \pm 0.021
R^2	0.67	0.57	0.68
ΔAIC_C	0	2.71	3.95

expansion is complete (Forkner et al. 2004). Thus, low Lepidoptera diversity, coupled with feeding constraints for caterpillars imposed by plant chemistry, may account for the sharp peak in food abundance for birds in oak-dominated habitats. Forests with many caterpillar species of variable feeding phenologies are less likely to have predictable seasonal pulses in food for insectivorous birds. For example, pied flycatchers in oak forests, but not in mixed hardwood/deciduous forest types, fed proportionally fewer caterpillars to nestlings as summer progressed (Burger et al. 2012). Even though the diverse oak–lime–hornbeam forest of the Białowieża National Park, Poland, typically displayed an early season peak in caterpillar abundance, blue tits *Cyanistes caeruleus* provisioned an increasing proportion of caterpillars to their young as the season progressed (Wesołowski and Rowinski 2014). We expect that birds in habitats with a diverse Lepidoptera fauna, e.g. those in the White Mountains of New Hampshire

where our study was conducted, will be less susceptible to trophic mismatches from climatic variation.

The timing of warbler first clutches was strongly associated with timing of spring leaf expansion, but the timing of clutch initiation was not isometric (1:1) with that of the foliage that supports the caterpillar food base (Fig. 4B). Phenological shifts across trophic levels were unequal. Nevertheless, the population-level plasticity in breeding time maximized mean annual reproductive output (Fig. 4D). We interpret this pattern as an example of adaptive asynchrony or adaptive mismatch (as described by Singer and Parmesan 2010, Lof et al. 2012) that is the result of a life history tradeoff for the warblers between the benefits of a longer season versus the costs of being too early.

The capacity to initiate breeding earlier in warm springs is an advantage to black-throated blue warblers because it extends the length of the breeding season and thereby increases

Table 3. Responsiveness of mean annual reproductive success (young fledged per pair per year) to inter-annual variation in four variables that influence reproduction of black-throated blue warblers at Hubbard Brook Experimental Forest ($n = 25$ years).

Variable	Mean of variable	Range in variable ^a	Range of expected reproductive success ^b	Range	% change ^c
Nest survival (daily probability)	0.971	0.957–0.983	2.92–4.25	1.33	39
Density (breeding birds/64 ha)	44.8	34.0–58.2	3.97–3.21	0.76	22
Caterpillar biomass (ln mg/8000 leaves)	4.42	3.44–5.70	3.39–3.96	0.57	17
Residual of plasticity (days ²)	5.98	0.2–15.9	3.62–2.88	0.74	22

^a10th – 90th percentiles shown.

^bcalculated as mean fledglings \cdot pair⁻¹ year⁻¹ from reproductive success model (Table 2) by using values for 10th and 90th percentiles of the variable of interest and mean values for all other parameters.

^crelative to mean of 3.42 young fledged per territory per year.

the time for re-nesting after nest failure and for attempting a second brood after successfully fledging a first (Townsend et al. 2013). The number of nesting attempts is particularly important to annual reproductive success for bird species, such as the black-throated blue warbler, that have relatively small clutch sizes and high rates of nest predation (Holmes et al. 1992, Martin 1995, Sillett and Holmes 2005). The naturally high rates of predation on black-throated blue warbler nests contrasts with the relatively low nest predation in the cavity nesting birds that have been the focus of breeding phenology studies in European forests (Perrins 1965). The difference in nest predation rates between open cup nesters and cavity nesters might be of general importance in the ecology of avian breeding phenology (Martin and Li 1992), although nest mortality can also be high for cavity nesting species when they are using tree holes (Wesolowski and Tomialojć 2005).

Our analyses also revealed that breeding too early imposes reproductive costs on black-throated blue warblers (left side of Fig. 4D), although the explanation for this pattern is less clear than for the costs of breeding too late. Nest survival probability may be lower early in the season if nests are easier to detect by predators when the leaves are not fully expanded, or if weather-related nest failures are more likely. An alternative or complementary explanation is that females which attempt to breed too early – before sufficient food is available to sustain that effort – pay a cost in body maintenance and capacity for subsequent nesting attempts (Nilsson 1994, Perrins 1970). Female black-throated blue warblers that started breeding early lost more mass between the incubation and nestling periods than females that started to nest later (Nagy et al. 2007), indicating that early breeding was energetically costly. Black-throated blue warblers, like tree swallows (Dunn et al. 2011), initiated their first clutches earlier in years with greater food availability (Rodenhouse and Holmes 1992; this study). Improved understanding of the costs of early breeding would help to evaluate the effects of climatic change on bird populations.

A population-level phenotypic response such as we have documented here is the result of individual-level plasticity, and individuals within a population do not necessarily have identical reaction norms (Nussey et al. 2007). We were unable to test for genetic variation in the warbler breeding-time reaction norm (as in Nussey et al. 2005), because natal dispersal of the warblers is high and yearlings rarely return to their natal site (Holmes et al. 2005). However, analyzing individual- versus population-level responses to the environment for these warblers revealed congruent results. Individual-level analysis of this same population has shown that although individuals that breed earlier than others in a given year have the highest reproductive output (there was selection for early breeding in 18 of the 25 years of this study), selection for early breeding did not intensify in warm years, implying that warblers are able to appropriately adjust the timing of breeding to spring conditions (Townsend et al. 2013).

The observed phenotypic plasticity in the timing of clutch initiation by black-throated blue warblers implies that this migratory species uses proximate cues to predict the suitability of their breeding environment (Levins 1963, Lof et al. 2012). Most of the inter-annual plasticity comes

from varying the time lag from arrival on breeding grounds until the first nest is initiated. Therefore, the most important cues must come during this period, the most likely of which are: direct perception of temperatures (Schaper et al. 2012), visual cues from developing leaves (Bourgault et al. 2010), and increasing food abundance (Dunn et al. 2011). Because these three factors are highly correlated and causally linked, disentangling them would require experimental manipulations. We also show that low food abundance in the early season is associated with later clutch initiation dates, on average, indicating that both cues and constraints determine the timing of breeding for these warblers.

We did not find evidence that first clutch initiation dates were constrained by the timing of arrival in black-throated blue warblers, although the interval between male arrival and breeding was short (minimum of 12 days) in early springs. The mechanisms underlying the correlation between budburst and arrival phenology of migratory passerines are poorly known. Conditions on the wintering grounds, such as insect availability or temperature, can modify northward departure dates (Studds and Marra 2011), but for this mechanism to affect nesting phenology would require a climatic correlation between tropical and temperate sites separated by thousands of kilometers. Conditions en route (fewer stops and faster refueling) are more likely to influence arrival dates (Knudsen et al. 2011). Either way, relatively invariant migration times for the warblers could prevent earlier egg laying in future climates.

Conclusions

Our study suggests that black-throated blue warblers have been resilient to the challenges of early springs by virtue of flexibility in their breeding time. This could be due, in part, to the high historical climatic variation in the start of the plant-growing season at this temperate site. Climate warming at Hubbard Brook has been modest relative to the range of conditions the population has experienced (Fig. 3). The warblers' flexibility in breeding time, however, likely has limits because recent early springs are approaching the relatively inflexible date when birds arrive on the breeding grounds. An additional factor that eases the challenges of climate change for black-throated blue warblers is that their habitat does not experience the distinct seasonal pulse of food availability that constrains the reproduction of some bird populations (Visser et al. 2006). Nevertheless, the capacity for black-throated blue warblers to adjust their breeding times relative to the start of the plant growing season was still a strong determinant of number of offspring fledged per pair per season, a key determinant of population dynamics in this species (Sillett et al. 2000). An important result was that nesting phenology in black-throated blue warblers was generally well matched to the timing of leaf-out, even though the match was not 1:1 and the timing of nest initiation varied less than the timing of leaf-out. Without the measurements of reproductive success, these unequal phenological shifts might otherwise have been interpreted as having negative ecological consequences.

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Supplementary material (available online as Appendix oik-02412 at <www.oikosjournal.org/appendix/oik-02412>). Appendix 1.