The interacting effects of food, spring temperature, and global climate cycles on population dynamics of a migratory songbird

ANDREA K. TOWNSEND[1,2,3], EVAN G. COOCH[4], T. SCOTT SILLETT[2], NICHOLAS L. RODENHOUSE[5], RICHARD T. HOLMES[6] and MICHAEL S. WEBSTER[3]

[1]Department of Biology, Hamilton College, Clinton, NY 13323, USA, [2]Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC 20013, USA, [3]Cornell Lab of Ornithology & Department of Neurobiology & Behavior, Cornell University, Ithaca, NY 14853, USA, [4]Department of Natural Resources, Cornell University, Ithaca, NY 14853, USA, [5]Department of Biological Sciences, Wellesley College, Wellesley, MA 12482, USA, [6]Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA

Abstract

Although long-distance migratory songbirds are widely believed to be at risk from warming temperature trends, species capable of attempting more than one brood in a breeding season could benefit from extended breeding seasons in warmer springs. To evaluate local and global factors affecting population dynamics of the black-throated blue warbler (*Setophaga caerulescens*), a double-brooded long-distance migrant, we used Pradel models to analyze 25 years of mark–recapture data collected in New Hampshire, USA. We assessed the effects of spring temperature (local weather) and the El Niño Southern Oscillation index (a global climate cycle), as well as predator abundance, insect biomass, and local conspecific density on population growth in the subsequent year. Local and global climatic conditions affected warbler populations in different ways. We found that warbler population growth was lower following El Niño years (which have been linked to poor survival in the wintering grounds and low fledging weights in the breeding grounds) than La Niña years. At a local scale, populations increased following years with warm springs and abundant late-season food, but were unaffected by spring temperature following years when food was scarce. These results indicate that the warming temperature trends might have a positive effect on recruitment and population growth of black-throated blue warblers if food abundance is sustained in breeding areas. In contrast, potential intensification of future El Niño events could negatively impact vital rates and populations of this species.

Keywords: Black-throated blue warbler, climate change, El Niño Southern Oscillation, mark–recapture, migratory songbird, phenotypic mismatch, population dynamics, Pradel models, recruitment, *Setophaga caerulescens*

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Introduction

Climate change is expected to increase the risk of extinction for many species in the coming century (IPCC, 2014). Long-distance migratory birds are a particular conservation concern (Strode, 2003; Miller-Rushing *et al.*, 2008; Both *et al.*, 2010), because they may be unable to adjust their migration in tempo with the advancement of spring and the consequent earlier peak in food abundance in breeding areas (Both & Visser, 2001; Van Der Jeugd *et al.*, 2009; Saino *et al.*, 2011). Warmer, earlier springs might benefit some migratory species, however. For example, species capable of attempting multiple broods within a single breeding season might produce more offspring when the season is extended (Drever & Clark, 2007; Møller, 2007; Halupka *et al.*, 2008), particularly in populations that

do not experience phenological mismatches with prey (e.g. Halupka *et al.*, 2008; Dunn *et al.*, 2011; Townsend *et al.*, 2013).

Conditions during each stage of the annual cycle (i.e. breeding vs. nonbreeding season) can differentially affect long-distance migrants (Sillett *et al.*, 2000; Sillett & Holmes, 2002). Therefore, a complete understanding of how their populations will respond to climate change requires consideration of weather components across a large geographic scale (Garcia-Perez *et al.*, 2014). Global climate cycles, such as the El Niño Southern Oscillation (ENSO), can be used as an index of integrated weather variables (e.g. sunshine, precipitation, temperature) across the geographic range of Neotropical migrants (Holmgren *et al.*, 2001; Stenseth *et al.*, 2003). El Niño and La Niña events refer to the periodic warm and cold phases, respectively, of the ENSO, and have been shown to alter the survival or productivity of migratory songbirds in different stages of their

Correspondence: Andrea K. Townsend, tel. 315 859 4828, fax 315 859 4807, e-mail: aktownse@hamilton.edu

annual cycles (Sillett *et al.*, 2000; Nott *et al.*, 2002; Wilson *et al.*, 2011; Lamanna *et al.*, 2012; Garcia-Perez *et al.*, 2014). Work by Sillett *et al.* (2000), for example, indicated that annual survival in an overwintering population of black-throated blue warblers (*Setophaga caerulescens*), as well as their recruitment to both the overwintering and breeding grounds, was lower in El Niño years than La Niña years. The effects of global cycles on the populations of migratory songbirds might become increasingly important if elevated greenhouse gas concentrations alter the intensity or frequency of ENSO events (Latif & Keenlyside, 2009; Collins *et al.*, 2010).

The black-throated blue warbler is one long-distance migratory songbird with characteristics that could buffer it from negative impacts of – or even predispose it to benefit from – a warming climate (Townsend *et al.*, 2013), at least in the short term (Rodenhouse *et al.*, 2008). They are insectivores that breed in the forests of eastern North America and overwinter primarily in the Greater Antilles. In contrast with avian systems experiencing phenological mismatches with prey (reviewed in Both, 2010), breeding black-throated blue warblers exploit a prey base that does not exhibit a predictable within-season pulse (Lany *et al.*, in press). They facultatively produce a second clutch after successfully fledging a first (Holmes *et al.*, 1992; Nagy & Holmes, 2005b), initiate breeding earlier in warm springs, and are more likely to attempt second broods (and fledge more young) in years when they begin earlier (Townsend *et al.*, 2013), particularly when food availability is relatively high (Nagy & Holmes, 2005a; Kaiser *et al.*, 2015). Potential increases in annual reproductive output with warming spring temperatures could have positive effects on populations of this migratory bird. Seasonal fecundity in 1 year is correlated with the abundance of new (yearling) breeders recruited in the next breeding season (Sillett *et al.*, 2000), indicating that environmental factors on the breeding ground that influence fecundity are important drivers of their population dynamics (Sillett & Holmes, 2005).

Most previous analyses of the effects of weather and climate trends on migratory songbirds, including studies of black-throated blue warblers, have focused on a single demographic rate, generally survival (Lamanna *et al.*, 2012; Garcia-Perez *et al.*, 2014) or annual fecundity (Visser *et al.*, 1998; Bulluck *et al.*, 2013; Townsend *et al.*, 2013), so that the relative contribution of these vital rates to population change is difficult to assess. Moreover, extrapolating potential population effects from a single demographic rate could be misleading, because fecundity, survival, immigration, and emigration combine to determine population change. Climate-linked changes in one vital rate only would provide a misleading explanation of population dynamics if temperature or other environmental factors have counteracting effects on different demographic rates (Caswell, 1989; Zani, 2008; Pfeifer-Meister *et al.*, 2013), if individuals compensate for changes in one vital rate by adjusting another (Muths *et al.*, 2011), or if population fluctuations are driven primarily by conspecific density or stochastic environmental factors (Reed *et al.*, 2013).

Here, we used a time-symmetric analysis of mark–recapture data (Pradel, 1996; Nichols & Hines, 2002) to simultaneously examine the effects of local weather and global climate cycles on warbler survival, recruitment, and population dynamics. We used 25 years of black-throated blue warbler mark–recapture data from a breeding population in the Hubbard Brook Experimental Forest, New Hampshire, USA (Holmes, 2007, 2011), where warming temperature trends have been both observed (Richardson *et al.*, 2006; Reynolds *et al.*, 2007) and projected (Hayhoe *et al.*, 2007). We evaluate the main and interactive effects of five environmental factors that previous studies indicate are of likely importance to population dynamics in this species: spring temperature (Townsend *et al.*, 2013), global climate cycles (ENSO; Sillett *et al.*, 2000), predator abundance (Nagy & Holmes, 2004), insect biomass (Nagy & Holmes, 2005a), and conspecific density (Rodenhouse *et al.*, 2003; Sillett *et al.*, 2004; Holmes, 2011). The complete set of hypotheses tested for each environmental factor is given in Table 1. We also evaluated population trends over time and used the substantial inter-annual variation in spring temperature recorded between 1985 and 2010 to infer possible population responses of this species to projected future climate change.

Materials and methods

Field data

Black-throated blue warblers breed in mature, northern hardwood forests of eastern North America and winter in the Greater Antilles. We collected data in the 3160-ha Hubbard Brook Experimental Forest (Woodstock, NH, USA), a mature second-growth hardwood forest embedded within the White Mountain National Forest (Holmes, 2007, 2011). Mark–recapture, weather, insect, and predator data were collected from 1986 through 2010 in a 64-ha study plot spanning 450–600 m above sea level. Dominant canopy trees included sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), and red spruce (*Picea rubens*). The patchy understory was composed of hobblebush (*Viburnum alnifolium*) and striped maple (*Acer pensylvanicum*), as well as saplings of canopy species (Holmes, 2011).

Mark–recapture data were recorded annually, resulting in 412 uniquely marked breeders over the 25-year period (1986–2010). Black-throated blue warbler males defend exclusive,

Table 1 Hypotheses for the effects of environmental factors on population growth (λ) tested by our set of approximating models

Parameter	Hypothesis	Citations
Spring temperature	λ Increases with spring temperature in the previous year because of earlier breeding/increased reproductive output	Townsend *et al.* (2013)
Predators	λ Decreases with predator abundance in the previous year because of reduced reproductive success	Nagy & Holmes (2004)
Food	λ Increases with late-season food biomass in previous year because of greater food availability for offspring	Sillett *et al.* (2000), Nagy & Holmes (2005a)
El Niño	λ Lower following El Niño years because of their link to low insect biomass and fledgling weights	Sillett *et al.* (2000)
Temperature*Food	Positive effects of spring temperature on λ greater when late-season food abundance is higher because of increased likelihood of double-brooding	Kaiser *et al.* (2015), Nagy & Holmes (2005a,b)
Density	λ Decreases with conspecific density in the previous year because of reduced reproductive success	Rodenhouse *et al.* (2003)

nonoverlapping territories during the breeding season (Holmes *et al.*, 2005) and adult breeders have strong site fidelity (Cline *et al.*, 2013). Encounter probabilities were therefore very high in this population (>0.8 in all years), resulting in high precision of estimated demographic parameters. We captured and banded adult birds with unique combinations of colored leg bands for individual identification and aged them as yearlings or older breeders based on plumage characters (Holmes *et al.*, 1996). Because our goal was to estimate how environmental factors influence recruitment rate (*per capita* additions of new breeders to the population), only breeders that were first marked as yearlings (new breeding recruits) were included in analyses; older birds immigrating into the study plot were excluded. Inclusion of older age-classes in the analysis would have answered different questions (e.g. the extent to which population density in this plot is buffered by immigration of older birds; the extent to which environmental factors affect absolute abundance). Preliminary analysis revealed no sex-specific differences in survival or recruitment; thus, we pooled data from both sexes for all subsequent analyses to maximize sample size. As pair bonds form at the start of each breeding season, and as most mortality occurs during migration (Holmes *et al.*, 2005), we did not anticipate significant lack of fit of our models to the data by potential nonindependence between members of a breeding pair. This was confirmed by various goodness of fit analyses, as discussed later in this section.

We measured biomass of Lepidopteran larvae by visual surveys at approximately 2-week intervals in each breeding season. On each occasion, 100 understory leaves each of American beech and sugar maple were searched at 10 points separated by 50 m along each of four permanent transects located within the study plot. 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). Biomass was summed for both tree species on each counting occasion, resulting in units of milligram caterpillar biomass per 2000 leaves for each transect on each count date. Food availability was calculated as the sum of the mean caterpillar biomass in two surveys conducted each season between mid-June and mid-July (the time period relevant to birds

attempting double broods), resulting in units of caterpillar biomass per 4000 leaves.

We surveyed eastern chipmunks *Tamias striatus* and eastern red squirrels *Tamiasciurus hudsonicus*, the primary nest predators at Hubbard Brook, with 5 min point counts during the same four biweekly periods used to estimate caterpillar biomass. We conducted four counts during each 2-week period and averaged these to estimate the number of predators detected in each territory per year. Predator surveys were not adjusted for detection probability and thus only indexed predator populations.

Temperature and climate data

We used temperature data from a U.S. Forest Service weather station (490 m above sea level; located <1 km of our study plot), where daily mean temperatures have been recorded since 1956. Following Townsend *et al.* (2013), we defined spring temperature as the annual mean of mean daily temperatures recorded from 15 March through 18 May. Temperature over this interval is relevant to warbler demographic parameters: warblers at Hubbard Brook start breeding earlier when mean temperatures over this interval are higher, and early breeders are more likely to attempt a second brood and have higher fecundity than those starting later in the season (Townsend *et al.*, 2013). Moreover, temperature accumulation after 15 March has been linked to the advancement of spring leaf phenology (Richardson *et al.*, 2006) and development potential of Lepidoptera at Hubbard Brook (Reynolds *et al.*, 2007).

Spring temperatures over this time interval have increased significantly at Hubbard Brook between 1956 and 2010 ($\hat{\beta} = 0.34 \pm 0.11$ °C/10 year; $t = 3.22$; $P = 0.002$), but not over the subset of years for which we have mark–recapture data (1986–2010; $\hat{\beta} = 0.31 \pm 0.37$ °C/10 year; $t = 0.84$; $P = 0.41$). However, the range of temperatures observed in the 25 focal years encompassed nearly the entire range of variation observed in the longer time series, with the exception of two cold springs (1956 and 1967; Fig. S1), facilitating inference about possible responses to continued warming trends (Hayhoe *et al.*, 2007).

We used monthly means of the Southern Oscillation Index scores (www.cpc.ncep.noaa.gov/data/indices/) from January through May of the previous year as an index of annual El Niño Southern Oscillation (ENSO) condition at the start of the breeding season. High, positive values correspond to La Niña conditions and low, negative values correspond to El Niño conditions. El Niño conditions in the previous year have been linked to low Lepidoptera larval biomass mid-June through mid-July and low black-throated blue warbler fledgling weights (Sillett *et al.*, 2000). Preliminary analyses did not reveal any trend in ENSO intensity over the time period of the study (Fig. S1).

Statistical analysis

We used a time-symmetric mark–recapture modeling approach (Pradel, 1996; 'Pradel models' hereafter) in Program MARK v.8.0 (White & Burnham, 1999) to estimate retrospective annual population growth λ_t from our 25 years of mark–recapture data. The Pradel model allows the decomposition of annual estimates of λ_t into two components representing annual apparent survival (φ_t) and annual recruitment (f_t): $\hat{\lambda}_t = \hat{\varphi}_t + \hat{f}_t$. Apparent survival (here, annual survival from May in 1 year to May in the next) reflects overall subtractions from the population, combining both true mortality and permanent emigration. Recruitment refers to the number of new animals in the study area at time $t + 1$ relative to the number of animals present at time t. Recruitment rate reflects the *per capita* additions of new, yearling breeders to the study area, including both those produced within and outside of it. Because natal site fidelity is extremely low in this species (Holmes *et al.*, 2005), here *f* primarily represents recruits produced in other areas, and not *in situ* recruits. Annual fecundity on our site is significantly and positively correlated with the number of yearling recruits in the following spring (Sillett *et al.*, 2000), however, indicating that our study population is representative of *S. caerulescens* population dynamics occurring at a regional scale (see also Jones *et al.*, 2003). The Pradel model accounts for imperfect detection probability (*P*) in the encounter history, reducing potential bias in the estimates of φ, *f*, and λ (Lebreton *et al.*, 1992), and has been applied to demographic analyses of a number of species [e.g. owls (Franklin *et al.*, 2004; Ganey *et al.*, 2014), neotropical parrots (Sandercock & Beissinger, 2002), bears (Boulanger *et al.*, 2002), and migrating songbirds (Schaub *et al.*, 2001)].

Underlying model structure: time-invariant survival and encounter probabilities

Previous analysis indicated little variation in annual adult survival and detection probability of black-throated blue warblers on their breeding grounds (Sillett & Holmes, 2002). We tested the prior assumption of time-invariant survival and detection probability using a Cormack–Jolly–Seber (CJS) modeling approach. As a preliminary step in our analysis, we assessed the identifiability of all parameters using a numerical method based on data cloning (*sensu* Lele *et al.*, 2010; Cooch & White, 2015). Failure to account for nonidentifiable parameters can

yield biased parameter estimates, as extrinsically nonidentifiable parameters can lead to convergence problems during the numerical estimation. It can also lead to errors in model selection based on the AIC$_c$, which is calculated for each model in part as a function of the number of estimable parameters. Previous analysis demonstrated that encounter probabilities were very high in some years (>0.9): in such a case, the true parameter value is sufficiently close to the upper boundary that it may not be properly estimated. Using models with and without time variation in apparent survival and encounter probability, we found that the encounter probability in some years (1987–1988, 1990, 1995–1999, 2001–2002) was 1.0 (i.e. all individuals alive and in the sampling area were encountered during those years). Thus, for all subsequent analyses, we first fixed the encounter probabilities for these years at 1.0.

We next fit a set of five reduced parameter approximating models, nested within a general model that consisted of time-varying survival and time variation in the encounter probability for those years not fixed to 1.0. Goodness of fit of the general model to the data was confirmed using both the median-$\hat{c}$ (White & Burnham, 1999) and Fletcher statistic (Fletcher, 2012). The reduced parameter models constrained either survival or those encounter probabilities for those years not fixed to 1.0, to be either time-invariant or to be constrained as a simple linear trend over time. Over our candidate model set, we found no evidence for time variation in either apparent survival (*sensu* Sillett & Holmes, 2002) or encounter probability for years when $P < 1.0$. The normalized AIC$_c$ weight for the fully time-invariant model (no variation over time in either apparent survival or unconstrained encounter probabilities) was 0.71, while the weight for a model where survival was constrained to change linearly over time was 0.29 (the trend over time in survival was estimated at less than -0.01% per year, which we judge to be biologically insignificant). No other candidate models had any support in the data. Estimated apparent survival from the most parsimonious, fully time-invariant model was $\hat{\varphi} = 0.48$, with a conditional SE = 0.021, while estimated encounter probability for those years where $P < 1$ was $\hat{P} = 0.74$, with a conditional SE = 0.046. Thus, for our subsequent Pradel models, we used a time-invariant parameter structure for both survival and detection probabilities (where some of the encounter probabilities were fixed to 1.0). As $\hat{\lambda}_t = \hat{\varphi}_t + \hat{f}_t$, then in the absence of variation in adult survival (φ), any variation in population growth (λ) would be entirely determined by variation in recruitment (*f*), such that modeling variation in λ or *f* would be equivalent. As variation in population growth is more directly interpretable than variation in *per capita* recruitment, we modeled variation in population growth rate only.

Environmental covariates, recruitment, and populations: main effects

We examined the effects of environmental covariates on population growth, using two distinct but complementary analyses. First, we evaluated a candidate set of 32 fixed-effect approximating models, nested within a general model where growth rate was allowed to vary randomly over time

(hereafter 'main-effects' model set; Table S1). Goodness of fit of the general model to the data was confirmed using both the median-ĉ (White & Burnham, 1999; White, 2002) and Fletcher statistic (Fletcher, 2012). In each model, λ in year t was constrained to be a linear function of one or more environmental covariates: (i) mean temperature in the previous spring (TEMP); (ii) predator abundance in the previous breeding season (PRED); (iii) mid- to late-season caterpillar biomass in the previous breeding season (FOOD); (iv) the Southern Oscillation Index from January through May of the previous year (ENSO); and (v) breeding density in the previous year (DENS). Approximating models were constructed symmetrically over the entire model set such that 16 total models included each covariate. Models were ranked using Akaike's information criterion, corrected for sample size (AIC$_c$; Hurvich & Tsai, 1989; Burnham & Anderson, 2002). We assessed the relative importance of each covariate by summing the normalized AIC$_c$ weights of candidate models containing that covariate. Because our model set was balanced (symmetrical) with respect to all main effects, the predictor variable with the largest cumulative weight was judged to be the most important contributor to annual variation in growth rate λ, whereas the variable with the smallest sum was judged to be the least important (Burnham & Anderson, 2002; Arnold, 2010; Doherty et al., 2012).

Environmental factors, recruitment, and populations: interactive effects

We had strong a priori reasons to expect that interactions of some covariates could significantly influence population growth (Table 1). Specifically, we hypothesized that the effects of warm spring temperatures (and the consequent early breeding; Townsend et al., 2013) could be mediated by food: female black-throated blue warblers at Hubbard Brook are more likely to attempt second broods when late-season food availability is high (Nagy & Holmes, 2005a,b). To evaluate this and other possible interactions among the set of environmental covariates, we also evaluated a different candidate model set, consisting of a general model that included all five main effect covariates (ENSO, FOOD, DENS, TEMP, and PRED), and 10 additional models, where each model contained all five main effect covariates, plus an interaction of two of the five covariates (hereafter 'interaction' model set; Table S2). We considered models with only a single interaction term between pairs of main effects as a compromise between (i) evaluating all possible two-way and higher interactions (which would not only be difficult to interpret biologically, but would result in a candidate model set consisting of ≫30K models; analyzing such a large candidate model set is not only computationally prohibitive, but arguably would represent 'data dredging') and (ii) ignoring possible important interactions among key main effects by restricting the model set to only those models where we had a strong a priori expectation of an interaction based on previous analysis. As the 10 interaction models differed structurally only in the interaction term, we compared normalized AIC$_c$ weights among these candidate models directly.

Estimates of population growth (λ)

To generate robust estimates of annual demographic rates, we used model averaging over both our complete set of fixed effects models (described above; Burnham & Anderson, 2002) and random effects models (Table S1, described above; Burnham & White, 2002) to estimate time-specific (annual) population growth, survival, and recruitment. Model averaging explicitly accounts for model selection uncertainty in inference based on multiple competing models (Burnham & Anderson, 2002) and produces a more stable set of parameter estimates (Doherty et al., 2012). In a separate analysis, we also evaluated a candidate set of random effects models that implicitly accounted for all unstructured time variation in the estimates of λ_t that cannot be modeled with a simple smooth parametric form (e.g. linear trend), yet are potentially important. In such cases, it is realistic to conceptualize the actual unknown λ_t as varying about a conceptual linear structure (i.e. mean or simple trend), with some population variation, σ^2. Such models generally produce less biased estimates of process variance than model averaging alone (Burnham & White, 2002). Consequently, we generated separate estimates of λ_t using both approaches for comparative purposes.

Results

Effects of environmental factors on survival, recruitment, and populations

Annual population growth, which, in the absence of detectable annual variation in survival, was determined by annual recruitment, was strongly affected by global climate cycles (ENSO), local breeding density (DENS), and the interactive effect of spring temperature and late-season food availability (TEMP*FOOD). Cumulative AIC$_c$ weights for ENSO, FOOD, and DENS, calculated over the 32 additive fixed effects models in the 'main-effects' model set (Table S1), were near equal (0.974, 0.856, and 0.974, respectively) and were all much higher than the cumulative weights for PRED (0.310) and TEMP (0.421). Analysis of the 'interaction' model set revealed strong support for an interaction between spring temperature and food; the model including the interaction of spring temperature and food had 3–4 times more support in the data than did the next best interaction model (Table S2).

To provide a robust comparison of the most parsimonious interaction model with our fixed effects models, we reran the fixed effect model set, after including the model with a (TEMP*FOOD) interaction term. This interaction model had a normalized AIC$_c$ weight of 0.894 relative to all other fixed effect models and was almost 25× better supported than the most parsimonious fixed effects model (Table 2).

The model containing the interaction of (TEMP*-FOOD) was estimated on the log scale as (model

Table 2 Model selection results for models with normalized AIC$_c$ weights >0.010 from the analysis of variation in realized growth rates (λ) as a linear function of various environmental and demographic covariates. Apparent survival (φ) and encounter probability were held fixed and are not shown (see explanation in text). K = number of parameters. The likelihood of a model is the AIC$_c$ weight for the model divided by the AIC$_c$ weight of the best model. This value is the strength of evidence of this model relative to other models in the set of models considered

Model	ΔAIC$_c$	AIC$_c$ weight	K	Likelihood
TEMP + FOOD + ENSO + DENS + TEMP*FOOD	0.00	0.894	8	1.000
ENSO + FOOD + DENS	6.46	0.035	6	0.040
TEMP + ENSO + FOOD + DENS	7.05	0.026	7	0.029
PRED + ENSO + FOOD + DENS	7.85	0.018	7	0.018
PRED + TEMP + ENSO + FOOD + DENS	8.72	0.011	8	0.013

presented with parameter estimate in bold font, followed by estimated 95% CI in square brackets):

$$\ln(\lambda) = \mathbf{1.192}\,[0.542 - 1.842]$$
$$-\mathbf{0.145}\,[-0.205, -0.086]\,(ENSO)$$
$$-\mathbf{0.011}\,[-0.018, -0.004]\,(DENS)$$
$$-\mathbf{0.024}\,[-0.041, -0.008]\,(FOOD)$$
$$-\mathbf{0.146}\,[-0.275, -0.016]\,(TEMP)$$
$$+\mathbf{0.005}\,[0.002, 0.008]\,(TEMP*FOOD)$$

As predicted (Table 1), realized growth decreases with increasing Southern Oscillation Index scores (*ENSO*) and local breeding density (*DENS*). Likewise, the interaction term (*TEMP*FOOD*) appears consistent with our predictions. Interpretation of this interaction is shown in Fig. 1, which illustrates the subtle relationships among the four covariates. When food biomass was low (left-most panels, Fig. 1), spring temperature had no measurable effect on population growth in the subsequent year. In marked contrast, population growth rate in the subsequent year increased with spring temperatures when food was abundant (right-most panels, Fig. 1). For either level of food abundance (low, high), growth was always lower following El Niño than La Niña years, and, all other things being equal, population growth to the subsequent year was generally lower when population density was high (indicated by the lower *y*-axis intercepts in high-density years; lower panels).

The coefficients for the main effects of (*FOOD*) and spring temperature (*TEMP*) in our most supported interaction model were both negative, which appears to run counter to our predictions (Table 1). We note, however, that these coefficients are not biologically interpretable given the interaction of the two effects (Gelman & Hill, 2007). In contrast (and in support of our predictions), coefficients for the effect of temperature and food on population growth in the 'main-effects' model set (Table S1) were positive in all models with a temperature or food terms, although the 95% confidence intervals around these estimates included zero, suggesting that neither factor had a significant influence on population growth when considered additively.

Population growth (λ)

We found no evidence that realized annual growth rate changed in a systematic way over the 25 years of the study, although annual growth rate of the warbler population at Hubbard Brook varied markedly across years (Fig. 2). Geometric mean stochastic growth rate was estimated as $\hat{\lambda}_S = 1.03$, with an estimated process variance of $\hat{\sigma}^2 = 0.0526$. The calculated 95% confidence interval for $\hat{\lambda}_S$ [0.928, 1.135] included 1. The estimated slope in the trend model was extremely small ($\hat{\beta} = -0.055$, SE = 0.005). We confirmed the lack of trend in population growth rate by fitting an additional random effects model where random variation in growth was constrained to fall around simple linear trend line (Table 3). A comparison of this model with an intercept-only random effects model showed insufficient evidence to distinguish between the two models. These findings indicate that this warbler population was stable from 1986 to 2010.

Discussion

The mark–recapture modeling approach that we employed allowed us to examine simultaneously multiple factors (i.e. spring temperature, global climate cycles, food availability, predator density, and local conspecific density) that potentially affect survival, recruitment, and population dynamics of a common Neotropical migrant, the black-throated blue warbler. As expected from previous work (Sillett & Holmes, 2002), we found little inter-annual variation in survival probability as measured on the breeding grounds, indicating that changes in population growth were largely mediated by changes in recruitment. Climatic conditions affected recruitment of this migratory songbird on multiple scales. On the global scale, recruitment and population growth were lower following El Niño years
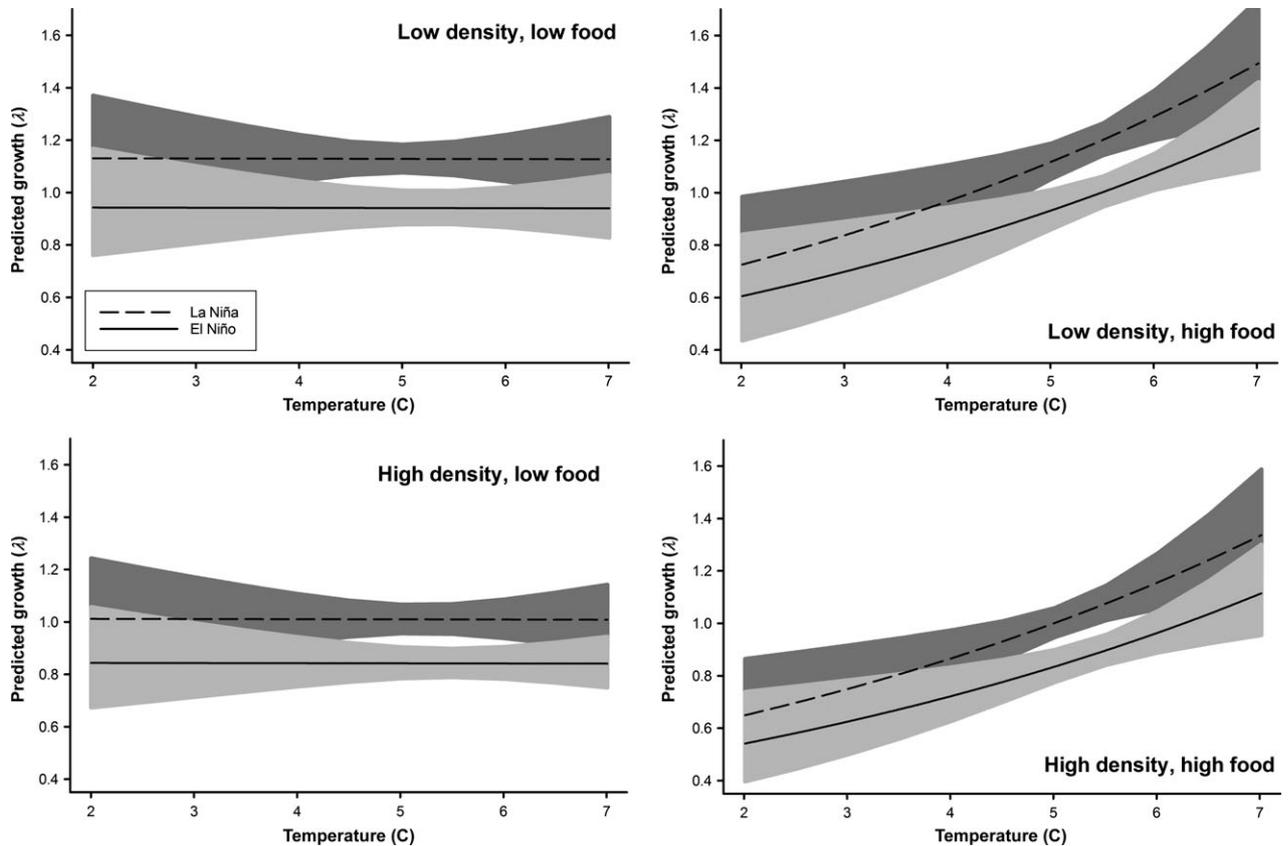
Fig. 1 Plot illustrating interactive effects of local food biomass and spring temperature on annual realized population growth, $\hat{\lambda}$. When late-season food biomass was low (a, b; left-most panels), spring temperature had no detectable effect on population growth. However, when food was abundant (right-most panels), $\hat{\lambda}$ increased markedly with increasing spring temperatures. For either level of food abundance (low, high), $\hat{\lambda}$ was always lower in El Niño years than La Niña years; $\hat{\lambda}$ was generally lower when conspecific population density was high. Food abundance and nesting density discretized as 'low' or 'high', based on 25% and 75% percentiles from overall distribution of both covariates. ENSO discretized as either 'El Niño' or 'La Niña', based on 25% and 75% percentiles from overall distribution of the ENSO index. Plotted lines represent population growth predicted by most parsimonious model (Table 2), as a function of temperature, controlling for discrete levels of breeding density, food abundance, and ENSO index. Shaded areas represent 95% confidence limits to prediction lines.

than La Niña years. On a local scale, spring temperatures on the breeding ground affected population dynamics, but its effect was mediated by late-season food availability. Warm springs were associated with positive population growth in the next year when late-season food biomass was high, but were neutral following years in which food abundance was low. Predator density had no detectable effect on population growth in the next year, whereas the effect of local conspecific density was strong: population density negatively affected recruitment and population growth to the next breeding season.

Local effects: temperature, food, and facultative double-brooding

Warm springs had a positive effect on recruitment and population growth subsequent to years when food abundance was high late in the breeding season. These results are consistent with other studies indicating that the effects of warming spring temperatures on the reproductive season – whether positive, negative, or neutral – depend on within-season food availability (Visser *et al.*, 1998; Møller, 2007; Halupka *et al.*, 2008; Both, 2010; Dunn *et al.*, 2011). Considerable attention has been focused on populations that are experiencing mismatches between timing of egg laying and peak food abundance available for offspring (Visser *et al.*, 1998; Visser & Both, 2005; Both *et al.*, 2006), and some authors suggest that populations with longer 'thermal delays' in migration timing are more likely to experience mismatches and population declines (Saino *et al.*, 2011). However, few studies have explicitly examined mismatches in migratory species (Both, 2010; Knudsen *et al.*, 2011), and such mismatches are likely to be most relevant to species that rely on food abundance for a
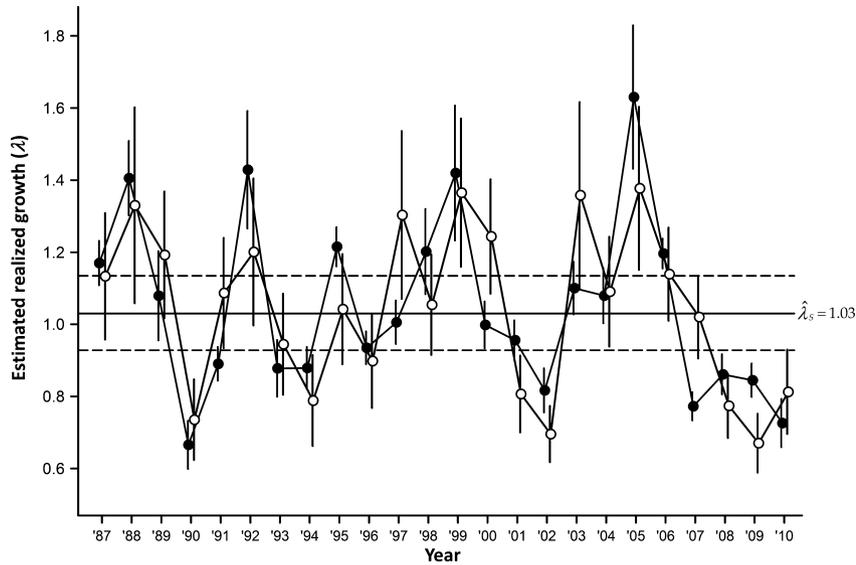
Fig. 2 Annual variation in estimated realized population growth ($\hat{\lambda}$) of black-throated blue warblers at Hubbard Brook (1987–2009). Open circles represent annual shrinkage estimates from the most parsimonious random effects model (intercept-only model; Table 3), whereas solid circles represent annual model-averaged maximum likelihood (ML) estimates from the candidate set of fixed-effect models (Table S1). Shrinkage estimates shown with ±1 *RMSE* (*sensu* Burnham & White, 2002), while model-averaged ML estimates are shown with ±1 SE. The solid horizontal line represents overall mean realized stochastic growth rate ($\hat{\lambda}_S$ = 1.03), with horizontal dashed lines representing 95% confidence limits to the estimated mean. Mean and 95% confidence limits derived from intercept-only random effects model.

Table 3 Model selection results for fixed (FE) and random effects (RE) analysis of trend in realized growth rates (λ) over 25 years of the study. Although temporal variation in apparent survival was not strongly supported in our analyses, we included time variation in survival, φ_t, for some models to account for the possibility that process variation in one parameter was constrained by other model parameters. Detection probability, P, was fixed over time in all models. The likelihood of a model is the AIC$_c$ weight for the model divided by the AIC$_c$ weight of the best model. This value is the strength of evidence of this model relative to other models in the set of models considered

Model	ΔAIC$_c$	AIC$_c$ weight	Likelihood
$\varphi_. \lambda_t$ – RE (trend)	0.000	0.498	1.000
$\varphi_. \lambda_t$ – RE (mean)	0.030	0.492	0.987
$\varphi_. \lambda_t$ – FE	7.88	0.010	0.020
$\varphi_t \lambda_t$ – RE (trend)	30.65	<0.001	<0.001
$\varphi_t \lambda_t$ – RE (mean)	30.81	<0.001	<0.001
$\varphi_t \lambda_t$ – FE	40.85	<0.001	<0.001

relatively short, consistent period within the breeding season (Visser & Both, 2005). The black-throated blue warbler may be buffered from temporal mismatches by its plasticity in the timing of breeding and number of breeding attempts (Townsend *et al.*, 2013), as well as its diverse and seasonally stable prey base (Lany *et al.*, in press).

The mechanism likely linking warm, high-food breeding seasons to higher recruitment and population growth is a higher likelihood of successfully double-brooding (Nagy & Holmes, 2005a,b; Townsend *et al.*, 2013). Only about half of the females in this breeding population, on average, attempt second broods in a given year (Holmes *et al.*, 1992; Nagy & Holmes, 2005b), and this percentage varies dramatically across years (Nagy & Holmes, 2005b). Females are more likely to attempt second broods when they begin breeding earlier (Townsend *et al.*, 2013) and when late-season food abundance is high (Nagy & Holmes, 2005a). Furthermore, longer inter-clutch intervals enabled by extended breeding seasons could contribute to increased fledging success in warm springs (Møller, 2007). Although this idea has received less attention in the literature, it is possible that early springs and extended breeding season could also increase fecundity for single-brooded pairs or populations that facultatively renest after one (or more) nest failures.

For species with relatively little variation in individual clutch size, successful production of a second (or more) broods within a single breeding season can have a profound influence on annual fecundity as well as population growth rates (Nagy & Holmes, 2004, 2005b; Podolsky *et al.*, 2007). Our results are congruent with an increasing number of studies that indicate the importance of double-brooding in predicting

population responses to climate change (Visser *et al.*, 2003; Møller, 2007; Møller *et al.*, 2010; Bulluck *et al.*, 2013; Townsend *et al.*, 2013; Dunn & Møller, 2014). Recent studies indicate that multibrooded species have advanced their lay date more – and have a longer breeding season – than single-brooded species (Dunn & Møller, 2014). Furthermore, the occurrence of multiple brooding has had positive effects on population trends of 71 bird species in France (Jiguet *et al.*, 2007) and 78 species throughout Europe and North America (Dunn & Møller, 2014).

Conspecific density

We found strong evidence of underlying population regulation in the study system: Population density had a negative effect on recruitment and population growth to the next breeding season. This result is consistent with earlier work, as the black-throated blue warblers at Hubbard Brook have become one of the best-documented examples of population regulation in a songbird (Holmes, 2007). Using a shorter term data sets and different analytical methods, previous studies have documented that local population density at Hubbard Brook has a negative impact on fecundity, the likelihood of double-brooding, and the condition of offspring produced (Rodenhouse *et al.*, 2003; Sillett *et al.*, 2004; Sillett & Holmes, 2005). Mechanisms, elucidated through experimental density manipulations, include crowding and occupation of subpar habitat in high-density years (Rodenhouse *et al.*, 2003; Sillett *et al.*, 2004). Operation of these mechanisms is not driven exclusively by offspring produced *in situ*, because natal philopatry is extremely rare in this species; thus, the factors affecting fecundity and recruitment in our study population must also apply to a larger, regional breeding population (Sillett & Holmes, 2002).

Global effects: El Niño Southern Oscillation

Increasing severity of El Niño events could negatively impact warbler populations. Recruitment and population growth were lower following El Niño years (this study), which have been associated with low prey abundance and reduced fledgling mass – but not to adult survival – at Hubbard Brook (Sillett *et al.*, 2000). Annual survival of black-throated blue warblers overwintering in northwestern Jamaica was also lower in El Niño years, associated with reduced rainfall and decreased food availability in Jamaica, than in wetter La Niña years (Sillett *et al.*, 2000). Although some researchers hypothesize that the severity of recent El Niño events is linked to global warming, uncertainty remains as to how much (and in what direction)

increasing greenhouse gas concentrations will affect the ENSO cycle (Fedorov & Philander, 2000; Latif & Keenlyside, 2009; Collins *et al.*, 2010). Warmer temperatures are expected to alter some of the background drivers of ENSO in ways that intensify El Niño events, but will dampen others; depending on the balance of these effects, the end results could be an increase, decrease, or no change in the severity of future El Niño events (Collins *et al.*, 2010).

Population trends

Our population of black-throated blue warblers was stable over the 25-year period of this study ($\hat{\lambda}_S = 1.03$; Fig. 2). This stability is concordant with the results of other studies of this species, using different time series, populations, and analytical techniques (Holmes & Sherry, 2001; Sillett & Holmes, 2005; Sauer *et al.*, 2008). Populations of this warbler have been stable since at least 1969 (Holmes & Sherry, 2001), despite long-term warming temperature trends on breeding grounds (Richardson *et al.*, 2006; Reynolds *et al.*, 2007; Townsend *et al.*, 2013). These results contrast with recent declines reported in many long-distance migratory songbirds across the globe (Robbins *et al.*, 1989; Ballard *et al.*, 2003; Both *et al.*, 2006; Sanderson *et al.*, 2006; Heldbjerg & Fox, 2008; Saino *et al.*, 2011). Some of these declines have been attributed to climate change, at least in part (Sanderson *et al.*, 2006; Lemoine *et al.*, 2007; Van Turnhout *et al.*, 2010). Stability of black-throated blue warbler populations lends support to the idea that double-brooded species might be buffered, to some extent, from warming climate trends (Jiguet *et al.*, 2007; Dunn & Møller, 2014).

Our results emphasize that populations of long-distance, migratory species are affected by a complex interaction between ecological factors, local weather, and global climate cycles. Warming temperature trends appear to have a positive effect on recruitment and population growth of black-throated blue warblers in high-food years, and little effect in low-food years, at least in the short term. This potential benefit is aligned with a small but growing body of evidence that populations of double-brooded species might respond in a more positive way to warming spring temperature trends than do single-brooded species (Jiguet *et al.*, 2007; Townsend *et al.*, 2013; Dunn & Møller, 2014), particularly when they are not constrained by narrow prey peaks (Visser *et al.*, 2003). We note, however, that these potential short-term benefits might be counteracted by climate-driven declines in food and overall habitat quality. High-quality habitat for this species in New England occurs at mid-to-high elevations, where foraging substrate and food biomass is greater (Rodenhouse

et al., 2008). Warming temperatures could cause the extent of this high-food habitat to contract as lower quality habitat expands up the elevational gradient (Rodenhouse *et al.*, 2008). Such a degradation in habitat quality and reduction in food biomass could neutralize benefits of breeding early in warm springs. Furthermore, intensification of El Niño events (if they occur; Collins *et al.*, 2010) could also negatively impact vital rates and populations of this species. Predicting the effects of environmental variation on migratory animals will therefore require analytical approaches that can disentangle the ways that multiple interacting factors shape demographic rates. Pradel's (1996) time symmetrical approach therefore holds great promise in understanding how ongoing climate change determines the dynamics of natural populations.

Acknowledgements

References

Arnold TW (2010) Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management*, **74**, 1175–1178.

Ballard G, Geupel GR, Nur N, Gardali T (2003) Long-term declines and decadal patterns in population trends of songbirds in western North America, 1979–1999. *Condor*, **105**, 737–755.

Both C (2010) Food availability, mistiming, and climatic change. In: *Effects of Climate Change on Birds* (eds Møller AP, Fielder W, Berthold P), pp. 129–148. Oxford University Press, Oxford.

Both C, Visser ME (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, **411**, 296–298.

Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. *Nature*, **441**, 81–83.

Both C, Van Turnhout CM, Bijlsma RG, Siepel H, Van Strien AJ, Foppen RPB (2010) Avian population consequences of climate change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society B*, **277**, 1259–1266.

Boulanger J, White GC, McLellan BN, Woods J, Proctor M, Himmer S (2002) A meta-analysis of grizzly bear DNA mark-recapture projects in British Columbia, Canada: invited paper. *Ursus*, **13**, 137–152.

Bulluck L, Huber S, Viverette C, Blem C (2013) Age-specific responses to spring temperature in a migratory songbird: older females attempt more broods in warmer springs. *Ecology and Evolution*, **3**, 3298–3306.

Burnham KP, Anderson DR (2002) *Model Selection and Inference: A Practical Information Theoretic Approach*. Springer, New York, NY.

Burnham KP, White GC (2002) Evaluation of some random effects methodology applicable to bird ringing data. *Journal of Applied Statistics*, **29**, 245–264.

Caswell H (1989) Analysis of life table response experiments I. Decomposition of effects on population growth rate. *Ecological Modelling*, **46**, 221–237.

Cline MH, Strong AM, Sillett TS, Rodenhouse NL, Holmes RT (2013) Correlates and consequences of breeding dispersal in a migratory songbird. *Auk*, **130**, 742–752.

Collins M, An SI, Cai WJ *et al.* (2010) The impact of global warming on the tropical Pacific ocean and El Niño. *Nature Geoscience*, **3**, 391–397.

Cooch EG, White GC (2015) Appendix F – data cloning. In: *Program MARK – A Gentle Introduction* (14th edn). Available at: http://www.phidot.org/software/mark/docs/book/ (accessed 01 May 2015).

Doherty PF, White GC, Burnham KP (2012) Comparison of model building and selection strategies. *Journal of Ornithology*, **152**, 317–323.

Drever MC, Clark RG (2007) Spring temperature, clutch initiation date and duck nest success: a test of the mismatch hypothesis. *Journal of Animal Ecology*, **76**, 139–148.

Dunn PO, Møller AP (2014) Changes in breeding phenology and population size of birds. *Journal of Animal Ecology*, **83**, 729–739.

Dunn P, Winkler D, Whittingham L, Hannon S, Robertson R (2011) A test of the mismatch hypothesis: how is timing of reproduction related to food abundance in an aerial insectivore? *Ecology*, **42**, 450–461.

Fedorov AV, Philander SG (2000) Is El Niño changing? *Science*, **288**, 1997–2002.

Fletcher D (2012) Estimating overdispersion when fitting a generalized linear model to sparse data. *Biometrika*, **99**, 230–237.

Franklin AB, Gutiérrez RJ, Nichols JD *et al.* (2004) Population dynamics of the California spotted owl (*Strix occidentalis occidentalis*): a meta-analysis. *Ornithological Monographs*, **54**, 1–55.

Ganey JL, White GC, Ward JP, Kyle SC, Apprill DL, Rawlinson TA, Jonnes RS (2014) Demography of Mexican spotted owls in the Sacramento Mountains, New Mexico. *Journal of Wildlife Management*, **78**, 42–49.

Garcia-Perez B, Hobson KA, Albrechts G, Cadman MD, Salvadoris A (2014) Influence of climate on annual survival of Barn Swallows (*Hirundo rustica*) breeding in North America. *Auk*, **131**, 351–362.

Gelman A, Hill J (2007) *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, New York, NY.

Halupka L, Dyrcz A, Borowiec M (2008) Climate change affects breeding of reed warblers *Acrocephalus scirpaceus*. *Journal of Avian Biology*, **39**, 95–100.

Hayhoe K, Wake CP, Huntington TG *et al.* (2007) Past and future changes in climate and hydrological indicators in the US Northeast. *Climate Dynamics*, **28**, 381–407.

Heldbjerg H, Fox T (2008) Long-term population declines in Danish trans-Saharan migrant birds. *Bird Study*, **55**, 267–279.

Holmes RT (2007) Understanding population change in migratory songbirds: long-term and experimental studies of Neotropical migrants in breeding and wintering areas. *Ibis*, **149**, 2–13.

Holmes RT (2011) Avian population and community processes in forest ecosystems: long-term research in the Hubbard Brook Experimental Forest. *Forest Ecology and Management*, **262**, 20–32.

Holmes RT, Sherry TW (2001) Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. *Auk*, **118**, 589–609.

Holmes RT, Sherry TW, Marra PP, Petit KE (1992) Multiple brooding and productivity of a neotropical migrant, the Black-throated Blue Warbler (*Dendroica caerulescens*), in an unfragmented temperate forest. *Auk*, **109**, 321–333.

Holmes RT, Marra PP, Sherry TW (1996) Habitat-specific demography of breeding black-throated blue warblers (*Dendroica caerulescens*): implications for population dynamics. *Journal of Animal Ecology*, **65**, 183–195.

Holmes RT, Rodenhouse NL, Sillett TS (2005) Black-throated Blue Warbler (*Setophaga caerulescens*). In: *The Birds of North America Online* (ed. Poole A). Cornell Lab of Ornithology, Ithaca, NY. Available at: bna.birds.cornell.edu/BNA/account/Black-throated_Blue_Warbler/doi:10.2173/bna.87 (accessed 01 May 2015).

Holmgren M, Scheffer M, Ezcurra E, Gutiérrez JR, Mohren GMJ (2001) El Niño effects on the dynamics of terrestrial ecosystems. *Trends in Ecology & Evolution*, **16**, 89–94.

Hurvich CM, Tsai C-L (1989) Regression and time series model selection in small samples. *Biometrika*, **76**, 297–307.

IPCC (2014) Summary for policymakers. In: *Climate Change 2014: Mitigation of Climate Change. Contribution of Working Group III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Edenhofer O, Pichs-Madruga R, Sokona Y, Farahani E, Kadner S, Seyboth K, Adler A, Baum I, Brunner S, Eickemeier P, Kriemann B, Savolainen J, Schlömer S, von Stechow C, Zwickel T, Minx JC). p. 13. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Jiguet F, Gadot AS, Julliard R, Newson SE, Couvet D (2007) Climate envelope, life history traits and the resilience of birds facing global change. *Global Change Biology*, **13**, 1672–1684.

Jones J, Doran PJ, Holmes RT (2003) Climate and food synchronize regional forest bird abundances. *Ecology*, **84**, 3024–3032.

Kaiser SA, Sillett TS, Risk BB, Webster MS (2015) Experimental food supplementation reveals habitat-dependent male reproductive investment in a migratory bird. *Proceedings of the Royal Society*, **282**, 20142523.

Knudsen E, Linden A, Both C et al. (2011) Challenging claims in the study of migratory birds and climate change. *Biological Reviews*, **86**, 928–946.

Lamanna JA, George TL, Saracco JF, Nott MP, Desante DF (2012) El Niño Southern Oscillation influences annual survival of a migratory songbird at a regional scale. *Auk*, **129**, 734–743.

Lany NK, Ayres MP, Stange EE, Sillett TS, Rodenhouse NL, Holmes RT (in press) Breeding timed to maximize reproductive success in a migratory songbird: the importance of phenological asynchrony. *Oikos*.

Latif M, Keenlyside NS (2009) El Niño/Southern Oscillation response to global warming. *Proceedings of the National Academy of Sciences of the USA*, **106**, 20578–20583.

Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals – a unified approach with case studies. *Ecological Monographs*, **62**, 67–118.

Lele SR, Nadeem K, Schmuland B (2010) Estimability and likelihood inference for generalized linear mixed models using data cloning. *Journal of the American Statistical Association*, **105**, 1617–1625.

Lemoine N, Bauer HG, Peintinger M, Bohning-Gaese K (2007) Effects of climate and land-use change on species abundance in a central European bird community. *Conservation Biology*, **21**, 495–503.

Miller-Rushing AJ, Lloyd-Evans TL, Primack RB, Satzinger P (2008) Bird migration times, climate change, and changing population sizes. *Global Change Biology*, **14**, 1959–1972.

Møller AP (2007) Interval between clutches, fitness, and climate change. *Behavioral Ecology*, **18**, 62–70.

Møller AP, Flensted-Jensen E, Klarborg K, Mardal W, Nielsen JT (2010) Climate change affects the duration of the reproductive season in birds. *Journal of Animal Ecology*, **79**, 777–784.

Muths E, Scherer RD, Pilliod DS (2011) Compensatory effects of recruitment and survival when amphibian populations are perturbed by disease. *Journal of Applied Ecology*, **48**, 873–879.

Nagy LR, Holmes RT (2004) Factors influencing fecundity in migratory songbirds: is nest predation the most important? *Journal of Avian Biology*, **35**, 487–491.

Nagy LR, Holmes RT (2005a) Food limits annual fecundity of a migratory songbird: an experimental study. *Ecology*, **86**, 675–681.

Nagy LR, Holmes RT (2005b) To double-brood or not? Individual variation in the reproductive effort in Black-Throated Blue Warblers (*Dendroica caerulescens*). *Auk*, **122**, 902–914.

Nichols JD, Hines JE (2002) Approaches for the direct estimation of λ, and demographic contributions to λ, using capture-recapture data. *Journal of Applied Statistics*, **29**, 539–568.

Nott MP, Desante DF, Siegel RB, Pyle P (2002) Influences of the El Niño Southern Oscillation and the North Atlantic Oscillation on avian productivity in forests of the Pacific Northwest of North America. *Global Ecology and Biogeography*, **11**, 333–342.

Pfeifer-Meister L, Bridgham SD, Little CJ, Reynolds LL, Goklany ME, Johnson BR (2013) Pushing the limit: experimental evidence of climate effects on plant range distributions. *Ecology*, **94**, 2131–2137.

Podolsky AL, Simons TR, Collazo JA (2007) Modeling population growth of the ovenbird (*Seiurus aurocapilla*) in the southern Appalachians. *Auk*, **124**, 1359–1372.

Pradel R (1996) Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics*, **52**, 703–709.

Reed TE, Jenouvrier S, Visser ME (2013) Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *Journal of Animal Ecology*, **82**, 131–144.

Reynolds LV, Ayres MP, Siccama TG, Holmes RT (2007) Climatic effects on caterpillar fluctuations in northern hardwood forests. *Canadian Journal of Forest Research*, **37**, 481–491.

Richardson AD, Bailey AS, Denny EG, Martin CW, O'Keefe J (2006) Phenology of a northern hardwood forest canopy. *Global Change Biology*, **12**, 1174–1188.

Robbins CS, Sauer JR, Greenberg RS, Droege S (1989) Population declines in North American birds that migrate to the neotropics. *Proceedings of the National Academy of Sciences of the USA*, **86**, 7658–7662.

Rodenhouse NL, Sillett TS, Doran PJ, Holmes RT (2003) Multiple density-dependence mechanisms regulate a migratory bird population during the breeding season. *Proceedings of the Royal Society B*, **270**, 2105–2110.

Rodenhouse NL, Matthews SN, Mcfarland KP et al. (2008) Potential effects of climate change on birds of the Northeast. *Mitigation and Adaptation Strategies for Global Change*, **13**, 517–540.

Rogers LE, Buschbom RL, Watson CR (1977) Length–weight relationships of shrub-steppe invertebrates. *Annals of the Entomological Society of America*, **70**, 51–53.

Saino N, Ambrosini R, Rubolini D et al. (2011) Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society B*, **278**, 835–842.

Sandercock BK, Beissinger SR (2002) Estimating rates of population change for a neotropical parrot with ratio, mark-recapture and matrix methods. *Journal of Applied Statistics*, **29**, 589–607.

Sanderson FJ, Donald PF, Pain DJ, Burfield IJ, Van Bommel FPJ (2006) Long-term population declines in Afro-Palearctic migrant birds. *Biological Conservation*, **131**, 93–105.

Sauer J, Hines J, Fallon J (2008) *The North American Breeding Bird Survey, Results and Analysis 1966–2007*. USGS Patuxent Wildlife Research Center, Laurel, MD.

Schaub M, Pradel R, Jenni L, Lebreton J-D (2001) Migrating birds stop over longer than usually thought: an improved capture-recapture analysis. *Ecology*, **82**, 852–859.

Sillett TS, Holmes RT (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology*, **71**, 296–308.

Sillett TS, Holmes RT (2005) Long-term demographic trends, limiting factors, and the strength of density dependence in a breeding population of a migratory songbird. In: *Birds of Two Worlds: Advances in the Ecology and Evolution of Temperate-Tropical Migration Systems* (eds Greenberg R, Marra PP), pp. 426–436. Johns Hopkins University Press, Baltimore, MD.

Sillett TS, Holmes RT, Sherry TW (2000) Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science*, **288**, 2040–2042.

Sillett TS, Rodenhouse NL, Holmes RT (2004) Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. *Ecology*, **85**, 2467–2477.

Stenseth NC, Ottersen G, Hurrell JW et al. (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society of London B*, **270**, 2087–2096.

Strode PK (2003) Implications of climate change for North American wood warblers (Parulidae). *Global Change Biology*, **9**, 1137–1144.

Townsend AK, Sillett TS, Lany NK, Kaiser SA, Rodenhouse NL, Webster MS, Holmes RT (2013) Warm springs, early lay dates, and double brooding in a North American migratory songbird, the black-throated blue warbler. *PLoS ONE*, **8**, e59467.

Van Der Jeugd HP, Eichhorn G, Litvin KE, Stahl J, Larsson K, Van Der Graaf AJ, Drent RH (2009) Keeping up with early springs: rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply. *Global Change Biology*, **15**, 1057–1071.

Van Turnhout CM, Foppen RPB, Leuven R, Van Strien A, Siepel H (2010) Life-history and ecological correlates of population change in Dutch breeding birds. *Biological Conservation*, **143**, 173–181.

Visser ME, Both C (2005) Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B*, **272**, 2561–2569.

Visser ME, Noordwijk AJV, Tinbergen JM, Lessells CM (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society B*, **265**, 1867–1870.

Visser ME, Adriaensen F, Van Balen JH et al. (2003) Variable responses to large-scale climate change in European *Parus* populations. *Proceedings of the Royal Society B*, **270**, 367–372.

White GC (2002) Discussion comments on: the use of auxiliary variables in capture-recapture modelling. An overview. *Journal of Applied Statistics*, **29**, 103–106.

White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, 120–139.

Wilson S, Ladeau SL, Tottrup AP, Marra PP (2011) Range-wide effects of breeding- and nonbreeding-season climate on the abundance of a Neotropical migrant songbird. *Ecology*, **92**, 1789–1798.

Zani PA (2008) Climate change trade-offs in the side-blotched lizard (*Uta stansburiana*): effects of growing-season length and mild temperatures on winter survival. *Physiological and Biochemical Zoology*, **81**, 797–809.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Mean spring temperatures at the Hubbard Brook Experimental forest (solid circles; daily means from 15 March to 18 May) and ENSO values (open circles; monthly means from January through May) from 1956 to 2010. Shaded area indicates the 25 years of this demographic study (1985–2010). Local temperatures have increased significantly since 1956 but not in the years of the demographic study.

Table S1. Main-effects model set. Candidate set of 33 fixed-effects approximating models: 32 additive fixed effects models nested within a general model that allowed unstructured annual variation, (λ_t). El Niño = *ENSO*; conspecific breeding density = *DENS*, spring temperature = *TEMP*; caterpillar biomass = *FOOD*; AIC$_c$ = Akaike Information Criterion corrected for sample size; K = number of parameters; λ = realized population growth. Model structure for apparent survival (φ) and encounter probability (P) were fixed over all candidate models, and are not shown (see explanation in text).

Table S2. Interaction model set, in which all 10 possible pairwise interactions of the five primary environmental covariates were added to a general (*NULL*) model, which consisted of all five covariates included in the model as additive fixed effects. Models are identified by the interaction term included in the model. Model structure for apparent survival (φ) and encounter probability (P) were fixed over all candidate models and are not shown (see explanation in text). AIC$_c$ = Akaike Information Criterion corrected for sample size. The likelihood of a model is the AIC$_c$ weight for the model divided by the AIC$_c$ weight of the best model. This value is the strength of evidence of this model relative to other models in the set of models considered.

Table S3. Bivariate (Pearson) correlation between environmental covariates. $P \geq 0.15$ (not significant at nominal $\alpha = 0.05$) for all correlations.