

Distribution-wide effects of climate on population densities of a declining migratory landbird

ANGELA D. ANDERS and ERIC POST

Department of Biology, Program in Ecology, 208 Mueller Laboratory, The Pennsylvania State University, University Park, PA 16802, USA

Summary

1. Increases in global temperatures have created concern about effects of climatic variability on populations, and climate has been shown to affect population dynamics in an increasing number of species. Testing for effects of climate on population densities across a species' distribution allows for elucidation of effects of climate that would not be apparent at smaller spatial scales.

2. Using autoregressive population models, we tested for effects of the North Atlantic Oscillation (NAO) and the El Niño Southern Oscillation (ENSO) on annual population densities of a North American migratory landbird, the yellow-billed cuckoo *Coccyzus americanus*, across the species' breeding distribution over a 37-year period (1966–2002).

3. Our results indicate that both the NAO and ENSO have affected population densities of *C. americanus* across much of the species' breeding range, with the strongest effects of climate in regions in which these climate systems have the strongest effects on local temperatures. Analyses also indicate that the strength of the effect of local temperatures on *C. americanus* populations was predictive of long-term population decline, with populations that were more negatively affected by warm temperatures experiencing steeper declines.

4. Results of this study highlight the importance of distribution-wide analyses of climatic effects and demonstrate that increases in global temperatures have the potential to lead to additional population declines.

Key-words: climate change, El Niño Southern Oscillation, migratory landbird, North Atlantic Oscillation, yellow-billed cuckoo

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Introduction

Global temperatures have increased by approximately 0.6 °C over the 21st century and are predicted to increase by an additional 2–6 °C over the next century (Houghton *et al.* 2001). Such rapid changes in global climate have spurred research on the effects of climatic variability on the phenology and population dynamics of many species of plants and animals (Walther *et al.* 2002; Root *et al.* 2003). Studies of several species of landbirds have shown effects of variation in large-scale climate and local temperatures on migration and breeding phenology (Dunn & Winkler 1999; Forchhammer, Post & Stenseth 2002; Visser *et al.* 2003; Wilson & Arcese 2003; Both *et al.* 2004) and on population

productivity and adult survival (Saether *et al.* 2000; Sillett, Holmes & Sherry 2000; Nott *et al.* 2002). However, these climatic effects have translated to changes in population densities in only a few studies (Forchhammer, Post & Stenseth 1998; Saether *et al.* 2000; Jonzen *et al.* 2002). This is perhaps not surprising, as spatial variation in biotic and abiotic factors makes it likely that ecological effects of climate are spatially heterogeneous, and most field studies are necessarily conducted at small geographical scales. Consequently, studies are needed that test for effects of climate on population densities across species' distributions.

Among North American landbirds, more than 30% of migratory species have declined significantly over the past 37 years (Robbins *et al.* 1989; Askins, Lynch & Greenberg 1990; Sauer, Hines & Fallon 2003). With species declining to this extent, research on the factors that limit populations is imperative in focusing our conservation efforts. To date, most of the research on

Correspondence: Angela D. Anders, Department of Biology, 208 Mueller Laboratory, The Pennsylvania State University, University Park, PA 16802, USA. E-mail: ada128@psu.edu

factors that limit migratory birds in North America has focused on endogenous factors, including nest predation, brood parasitism and density-dependent habitat limitation (Robinson *et al.* 1995; Sherry & Holmes 1996; Porneluzi & Faaborg 1999), and these endogenous factors are now known to be important in limiting migratory populations. In contrast, there is no evidence for an effect of climate on annual population densities in these species, despite several studies that have found climatic effects on phenology, productivity and survival. Thus, the extent to which changes in climate may lead to population declines in North American landbirds has remained unclear.

Here, we quantify the relationships between large-scale climate, local temperatures and population dynamics of a North American migratory landbird, the yellow-billed cuckoo *Coccyzus americanus*, throughout its breeding distribution. Using survey data from throughout the USA and Canada over the past 37 years (Sauer *et al.* 2003), we examine the influence of annual variation in large-scale climate and local temperatures on annual *C. americanus* population densities. Much of the annual variation in temperatures across North America is attributable to two large-scale climate systems, the North Atlantic Oscillation (NAO) and the El Niño Southern Oscillation (ENSO) (Hurrell 1995; Trenberth & Caron 2000); in addition, recent evidence indicates that the NAO may be an important vehicle through which anthropogenic causes of climatic warming are manifest (Visbeck *et al.* 2001). Here, we document geographical variation in the strength of the NAO and ENSO on interannual fluctuations in population densities. We furthermore document that the strength of the effects of these climate systems on regional population dynamics is strongly correlated with the strength of the effects of these systems on local temperatures. Finally, we show that the strength of the effect of local temperatures on annual population densities is correlated with the magnitude of population decline: the more strongly any particular population has been affected by local temperatures, the more precipitous has been that population's decline over the past 37 years.

Materials and methods

SURVEY DATA

Coccyzus americanus is a Neotropical migratory landbird, breeding in the USA and Canada from May through September, and wintering from Venezuela through central Argentina from October through April (Hughes 1999). Among the 137 species of long-distance migratory birds that breed in North America, *C. americanus* ranks 14th in its rate of population decline. Although declines are most severe for this species in the western USA, it ranks 11th of 88 species in its rate of decline in the eastern USA (Sauer *et al.* 2003). As indices of annual *C. americanus* densities, we

used data from the US Geological Survey's Breeding Bird Survey (BBS) from 1966 through 2002, using data from 41 physiographic regions incorporating 43 US states and three Canadian provinces (<ftp://ftpext.usgs.gov/pub/er/md/laurel/BBS/DataFiles>). Each physiographic region was defined as a population, and annual population densities were calculated as mean number of *C. americanus* detected per survey route within a region within a year. Western cuckoo populations were excluded from analyses, as we analysed only regions in which more than 20 cuckoos were observed in total between 1966 and 2002.

CLIMATE AND LOCAL TEMPERATURE DATA

The winter NAO index (mean of monthly NAO index values from December through March; www.cgd.ucar.edu/~jhurrell/nao.stat.winter.html#winter) was used to represent annual NAO conditions from 1966 through 2002, and the mean of monthly values of the Southern Oscillation Index (SOI) from May through April was used to represent annual ENSO conditions (www.cpc.ncep.noaa.gov/data/indices). Local temperature data were obtained from the US National Climatic Data Center (NCDC; www.ncdc.noaa.gov/oa/climate/onlineprod/drought/ftppage.html) from NCDC divisions that overlapped the BBS physiographic regions used to define *C. americanus* populations. Mean monthly temperatures for all NCDC divisions within a BBS region were calculated, and we used mean of December through March temperatures within each year in our analyses, as both the NAO and ENSO show the strongest effects on temperatures in North America during these months (Hurrell 1995; Trenberth & Caron 2000).

POPULATION MODELS

To quantify the influences of the NAO, ENSO and local temperatures on changes in annual *C. americanus* population densities, we incorporated the climate indices and local temperatures into models of cuckoo population dynamics. We hypothesized that climate and local temperatures would have 1-year lagged effects on annual population densities on the breeding grounds by influencing cuckoo productivity in the previous year (separate analyses indicate unlagged effects of ENSO on *C. americanus* population densities, suggesting effects on survival on the wintering grounds independent of effects on cuckoo productivity; A.D. Anders unpublished data). We used density-dependent autoregressive population models, which allow for examination of the strength of previous population densities and other factors, such as climate or temperature, on annual population densities (Royama 1992). The general form of the model was:

$$X_t = a_0 + a_1(X_{t-1}) + a_2(X_{t-2}) + a_3(X_{t-3}) + b_1(Y_t - 1) + \epsilon_t \quad \text{eqn 1}$$

where X_t are log of population density, a_0 is the intrinsic rate of increase, a_i are estimates of the strength of statistical density dependence, b_1 quantifies the influence of climate or local temperature on population density, Y_{t-1} is the NAO index, SOI, or mean local temperature in year $t-1$, and ε_t represents the effects of other perturbations. Year was included as a covariate for all populations displaying a significant temporal trend (Post & Stenseth 1999). First-, second- and third-order models were tested to determine which best predicted log annual population density for each population. We then included in the best-fit model terms for climate or local temperature to determine whether inclusion of these parameters improved model fit. Parameter coefficients were estimated using ARIMA in SPSS (SPSS Inc., Chicago, IL), and model fit was examined using Akaike's Information Criterion (Burnham & Anderson 1998).

We next investigated whether spatial variation in the influences of the NAO and ENSO on population dynamics reflected variation in the response of local temperatures to these climate systems. We first conducted correlation analyses of the NAO index and local temperatures across the 37-year period for each of the 41 physiographic regions. Then, to test whether the strength of the NAO's effect on annual population density is predicted by the strength of the connection between the NAO and local temperatures, we conducted a correlation analysis of the Pearson's r for each region and the NAO coefficient from the cuckoo population model for each region. We then conducted these same analyses for ENSO.

Finally, we quantified the relationship between the influence of local temperature on annual cuckoo population densities and the magnitude of long-term population change. We calculated magnitude of population change as the slope of the regression of mean population density over time, scaled by population density at the midpoint of the survey period, for each population, using only those populations that exhibited a linear trend over the period 1966–2002 ($N = 31$ populations). We then conducted a linear regression analysis of the local temperature coefficients from each population model and the slopes of the regression of population density over time for each region.

POTENTIAL MECHANISMS OF CLIMATIC EFFECTS

Although extreme climatic events may directly affect landbird population dynamics by increasing mortality, limiting effects of climate are more likely mediated through effects on food availability (Silllett *et al.* 2000; Jones, Doran & Holmes 2003). Food availability has been shown to impact landbird productivity (Arcese & Smith 1988; Rodenhouse & Holmes 1992; Marshall *et al.* 2002), and both the NAO and ENSO have been shown to affect North American landbird productivity through effects on lepidopteran larvae (Silllett *et al.*

2000; Nott *et al.* 2002), the primary food resource for landbirds during the breeding season. We had thus hypothesized that the NAO and ENSO would have 1-year lagged effects on annual *C. americanus* densities by affecting productivity, through effects on lepidopteran larvae abundance, the previous breeding season (Post 2004).

To determine whether climate may potentially affect cuckoo dynamics by affecting food availability, in 2003 and 2004 we collected field data on lepidopteran larvae abundance and cuckoo productivity in the Ridge and Valley region of Pennsylvania. Using two 150-ha sites, we located and monitored cuckoo territories throughout the breeding season to quantify the number of nesting attempts by each pair. Lepidopteran larvae were surveyed along randomly located fixed transects within each cuckoo territory ($N = 18$ territories) during a 2–4-day period in mid- and late June. We counted the number of caterpillars per 1000 understory leaves and measured the length of each caterpillar to the nearest millimetre (caterpillars were not removed from the vegetation). In 2003, we surveyed a single $50 \text{ m} \times 1 \text{ m} \times 1 \text{ m}$ transect per territory, and in 2004 we surveyed four $12.5 \text{ m} \times 1 \text{ m} \times 1 \text{ m}$ transects per territory.

Results

Results of population models indicated that 31 *C. americanus* populations showed first-order density dependence, eight populations showed second-order density dependence, and two showed third-order density dependence. The lagged NAO climate parameter entered the best-fit population model for eight cuckoo populations, all in the southern and eastern USA (Fig. 1). The model coefficient quantifying the lagged effect of the NAO was positive for five of these populations and negative for three populations. The lagged ENSO parameter entered the best-fit model for five additional cuckoo populations, all in the north-central USA (Fig. 1); the model coefficient quantifying the lagged effect of ENSO was negative for all five populations.

In examining the relationship between large-scale climate, local temperatures, and population dynamics for each of the 41 *C. americanus* populations, model coefficients quantifying the lagged influences of the NAO and ENSO on annual population densities were positively related to the correlations between the NAO index and local temperatures ($r = 0.309$, $P = 0.026$; Fig. 2a) and SOI and local temperatures ($r = 0.498$, $P = 0.001$; Fig. 2b). Hence, the more strongly these large-scale climate systems affected local temperatures, the greater was their influence on *C. americanus* population dynamics. Because only positive correlations existed between the NAO index and local temperatures in all regions studied (Fig. 2a), we repeated our analysis using only those regions in which the population model NAO coefficients were positive ($N = 17$ populations). Results of this analysis also showed a significant positive



Fig. 1. Physiographic regions in which the NAO and ENSO entered the best-fit population model for *Coccyzus americanus* populations from 1966 to 2002. Black outline delineates the 41 physiographic regions analysed in this study. Dark grey indicates regions in which lagged NAO occurred in the best-fit population model; light grey indicates regions in which lagged ENSO occurred in the best-fit model (background map of BBS physiographic regions from Sauer *et al.* (2003)).

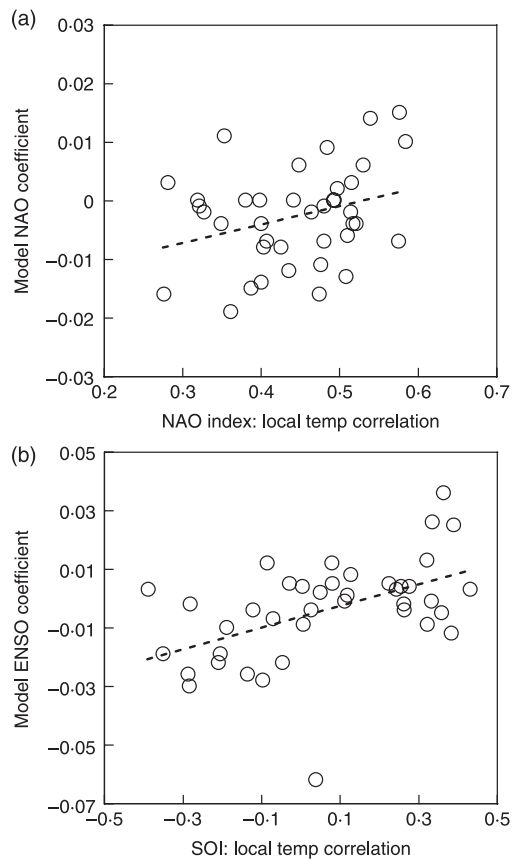


Fig. 2. Relationships between the lagged influences of the NAO and ENSO on *C. americanus* population dynamics and the strength of the correlations between these climate systems and local temperatures. (a) NAO parameter coefficient from each cuckoo population model vs. strength of the Pearson's correlation between the NAO Index and local temperature within that physiographic region. (b) ENSO parameter coefficient from each population model vs. strength of the Pearson's correlation between the Southern Oscillation Index (SOI) and local temperature within the physiographic region.

correlation between the model NAO coefficients and the Pearson's r 's from the NAO index and local temperature correlations ($r = 0.426$, $P = 0.044$).

Inclusion of local temperature in each population model indicated a lagged negative influence of temperature on 30 *C. americanus* populations: between 1966 and 2002, these populations experienced declines following warmer temperatures during the preceding breeding season. Linear regression analysis revealed a positive relationship between the magnitude of the influence of local temperatures on annual population densities and the magnitude of long-term population change ($t = 4.668$, $P < 0.0001$, $R^2 = 0.429$; Fig. 3). Hence, the more strongly local temperatures influenced a population's dynamics, the more precipitously that population declined.

In examining the potential of food availability as a mechanism by which climate affects annual population densities, we found that cuckoos attempted to nest on only a subset of occupied territories in 2003 and 2004, and lepidopteran larvae abundance was higher on those territories on which cuckoos nested than on occupied territories on which cuckoos did not nest (repeated measures ANOVA: $F_{1,14} = 5.28$, $P = 0.037$), with no effect of year ($F_{1,14} = 2.52$, $P = 0.135$) and no interaction between year and nesting status ($F_{1,14} = 0.47$, $P = 0.505$). Restricting the analysis to the lepidopteran survey conducted in mid-June, when cuckoos typically initiate nesting, territories on which cuckoos subsequently nested had higher lepidopteran larvae abundance (23.1 ± 6.8 SE caterpillars/1000 leaves vs. 7.0 ± 2.3 ; t -test: $t_{16} = 2.81$, $P = 0.013$) and more lepidopteran larval biomass, as indexed by summing the lengths of caterpillars per 1000 leaves (41.2 ± 13.8 mm of caterpillar/1000 leaves vs. 11.9 ± 4.5 ; $t_{16} = 2.56$, $P = 0.021$) than those territories without nests.

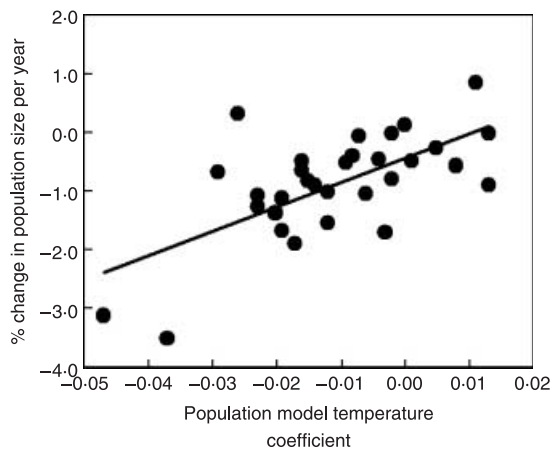


Fig. 3. Magnitude of change in *C. americanus* population density over time vs. magnitude of the lagged influence of local temperature on cuckoo population dynamics within a physiographic region.

Discussion

This study documents the spatially heterogeneous effects of large-scale climate on population densities of a North American migratory landbird across the species' breeding distribution. Our results indicate that two climate systems, the NAO and ENSO, have affected annual population densities of *C. americanus* over the past 37 years, and that the strength of the effect of climate on populations is correlated with the strength of the relationship between large-scale climate and local temperatures. In addition, the magnitude of the effect of local temperature on cuckoo populations is predictive of population decline: the more strongly and negatively any particular cuckoo population was affected by local temperatures on its breeding grounds, the more precipitous has been that population's decline over the past 37 years.

Geographic variation in the effects of the NAO and ENSO on cuckoo populations points to the importance of studying climatic effects at the scale of the species' distribution. Recent large-scale studies of the breeding phenology of European landbirds, including great tits *Parus major*, blue tits *P. caeruleus*, collared flycatchers *Ficedula albicollis*, and pied flycatchers *F. hypoleuca*, have shown geographical variation in effects of climate: in those areas of Europe that have experienced warming trends over the past one to two decades, landbird populations have displayed shifts in their breeding phenologies (Visser *et al.* 2003; Both *et al.* 2004). For the *Ficedula* species, there is a strong positive correlation between the extent of change in local temperatures and the extent of advancement of egg-laying date (Both *et al.* 2004). Field studies of North American landbirds, including black-throated blue warblers *Dendroica caerulescens* and song sparrows *Melospiza melodia*, have documented effects of

climate on productivity and adult survival at the scale of the study population (Sillett *et al.* 2000; Wilson & Arcese 2003), but those studies showed no subsequent effect on annual population densities, primarily because of recruitment of juveniles from other areas into the study populations (Sillett *et al.* 2000; Wilson & Arcese 2003). Because such field studies were necessarily conducted at relatively small geographical scales, it is possible that climatic effects on productivity or survival in these species may cause important but undetected changes in population densities at larger, regional scales.

Studies of the mechanisms by which large-scale climate could affect landbird populations have shown that the NAO and ENSO influence the abundance of lepidopteran larvae, the primary food resource for landbirds during breeding (Sillett *et al.* 2000; Nott *et al.* 2002). Research on *D. caerulescens* has shown an effect of ENSO on lepidopteran larvae abundance, and an effect of lepidopteran availability on warbler productivity (Sillett *et al.* 2000). Our field work with *C. americanus* indicates that only a subset of cuckoos attempted to breed in 2003 and 2004, and those territories on which cuckoos nested had more than three times the number and biomass of lepidopteran larvae than the occupied territories on which cuckoos did not attempt to nest. These results suggest that food availability may limit *C. americanus* productivity, as has been seen in other landbird species (Arcese & Smith 1988; Rodenhouse & Holmes 1992; Marshall *et al.* 2002).

Results of our analyses indicate that cuckoo population densities declined following warm years. There is evidence to indicate that outbreaking species of lepidopterans are more abundant in cold years: Myers (1998) found in a meta-analysis of 26 outbreaking lepidopteran species that outbreaks were more likely in cold years, and Williams & Liebhold (1995) and Miller, Mo & Wallner (1989) found higher abundances of gypsy moth *Lymantria dispar* L. larvae following cooler winter and spring temperatures. *Coccyzus americanus* is known to take advantage of outbreaking species such as gypsy moths, and warmer temperatures may act to decrease the availability of these food resources. However, it is also possible that warm winter temperatures lead to earlier spring peaks in the abundance of nonoutbreaking lepidopteran species, such that *C. americanus*, a relatively late-arriving species on the breeding grounds, misses this peak in food abundance. This type of climate-induced trophic mismatch has been seen in nonmigratory *P. major* (Visser *et al.* 1998; Stevenson & Bryant 2000) and may be even more likely in migratory species that are unable to time their spring migration in response to food availability on the breeding grounds (Both & Visser 2001).

In conclusion, we found lagged effects of two large-scale climate systems, the NAO and ENSO, on annual *C. americanus* population densities. Geographic variation in the strength of these climate systems on cuckoo

populations was underlain by geographical variation in the effects of the NAO and ENSO on local temperatures. We also found that the strength of the effect of local temperatures on populations was predictive of long-term population decline, with those populations that are more negatively affected by warm temperatures experiencing steeper declines over the past 37 years. Field data showing that cuckoo productivity is limited by lepidopteran larvae abundance point to the possibility that climate may affect *C. americanus* population densities by affecting food availability; however, data are needed to test our hypothesized mechanisms by which warm temperatures may decrease food availability. Overall, the results of this study indicate that, although endogenous factors such as nest predation, brood parasitism and habitat availability limit populations of migratory birds, exogenous factors such as large-scale climate and local temperatures also affect changes in the population densities of these species and do so in a spatially heterogeneous manner. An understanding of the limiting effects of climate on additional species, and knowledge of the mechanisms by which climate has such effects, is critical in an environment of increasing climate change.

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References

- Arcese, P. & Smith, J.N.M. (1988) Effects of population density and supplemental food on reproduction in Song Sparrows. *Journal of Animal Ecology*, **57**, 119–136.
- Askins, R.A., Lynch, J.F. & Greenberg, R. (1990) Population declines in migratory birds in eastern North America. *Current Ornithology*, **7**, 1–57.
- Both, C. & Visser, M.E. (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, **411**, 296–298.
- Both, C., Artemyev, A.V., Blaauw, B., Cowie, R.J., Dekhuijzen, A.J. *et al.* (2004) Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proceedings of the Royal Society of London Series B*, **271**, 1657–1662.
- Burnham, K.P. & Anderson, D.R. (1998) *Model Selection: a Practical Information-Theoretic Approach*. Springer-Verlag, New York.
- Dunn, P.O. & Winkler, D.W. (1999) Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society of London B*, **266**, 2487–2490.
- Forchhammer, M.C., Post, E. & Stenseth, N.C. (1998) Breeding phenology and climate. *Nature*, **391**, 29–30.
- Forchhammer, M.C., Post, E. & Stenseth, N.C. (2002) North Atlantic Oscillation timing of long- and short-distance migration. *Journal of Animal Ecology*, **71**, 1002–1014.
- Houghton, J.T., Ding, Y., Griggs, D.J., Noguera, M., van der Linden, P.J. & Xiaosu, D., eds. (2001) *Climate Change 2001: the Scientific Basis*. Cambridge University Press, Cambridge.
- Hughes, J.M. (1999) Yellow-billed cuckoo (*Coccyzus americanus*). *The Birds of North America*, no. 418 (eds A. Poole & F. Gill). The Birds of North America, Inc., Philadelphia.
- Hurrell, J.W. (1995) Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science*, **269**, 676–679.
- Jones, J., Doran, P.J. & Holmes, R.T. (2003) Climate and food synchronize regional forest bird abundances. *Ecology*, **84**, 3024–3032.
- Jonzen, N., Hedenstrom, A., Hjort, C., Lindstrom, A., Lundberg, P. & Andersson, A. (2002) Climate patterns and the stochastic dynamics of migratory birds. *Oikos*, **97**, 329–336.
- Marshall, M.R., Cooper, R.J., DeCecco, J.A., Strazanac, J. & Butler, L. (2002) Effects of experimentally reduced prey abundance on the breeding ecology of the red-eyed vireo. *Ecological Applications*, **12**, 261–280.
- Miller, D.R., Mo, T.K. & Wallner, W.E. (1989) Influence of climate on gypsy moth defoliation in southern New England. *Environmental Entomology*, **18**, 646–650.
- Myers, J.H. (1998) Synchrony in outbreaks of forest Lepidoptera: a possible example of the Moran effect. *Ecology*, **79**, 1111–1117.
- Nott, M.P., Desante, D.F., Siegel, R.B. & 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 Ecological and Biogeography*, **11**, 333–342.
- Porneluzi, P.A. & Faaborg, J. (1999) Season-long fecundity, survival, and viability of ovenbirds in fragmented and unfragmented landscapes. *Conservation Biology*, **13**, 1151–1161.
- Post, E. (2004) Time lags in terrestrial and marine environments. *Marine Ecosystems and Climate Variation* (ed. N.C. Stenseth, *et al.*), pp. 165–167. Oxford University Press, Oxford.
- Post, E. & Stenseth, N.C. (1999) Climatic variability, plant phenology, and northern ungulates. *Ecology*, **80**, 1322–1339.
- Robbins, C.S., Sauer, J.R., Greenberg, R.S. & Droege, S. (1989) Population declines in North American birds that migrate to the neotropics. *Proceedings of the National Academy of Science USA*, **86**, 7658–7662.
- Robinson, S.K., Thompson, F.R., III, Donovan, T.M., Whitehead, D.R. & Faaborg, J. (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science*, **267**, 1987–1990.
- Rodenhouse, N.L. & Holmes, R.T. (1992) Effects of experimental and natural food reductions for breeding Black-throated Blue Warblers. *Ecology*, **73**, 357–372.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.
- Royama, T. (1992) *Analytical Population Dynamics*. Chapman & Hall, London.
- Saether, B.E., Tufto, J., Engen, S., Jerstad, K., Rostad, O.W. & Skatun, J.E. (2000) Population dynamical consequences of climate change for a small temperate songbird. *Science*, **287**, 854–856.
- Sauer, J.R., Hines, J.E. & Fallon, J. (2003) *The North American Breeding Bird Survey, Results and Analysis 1966–2002*, Version 2003.1. USGS Patuxent Wildlife Research Center Laurel, Maryland.
- Sherry, T.W. & Holmes, R.T. (1996) Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. *Ecology*, **77**, 36–48.
- Sillett, T.S., Holmes, R.T. & Sherry, T.W. (2000) Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science*, **288**, 2040–2042.
- Stevenson, I.R. & Bryant, D.M. (2000) Climate change and constraints on breeding. *Nature*, **406**, 366–367.
- Trenberth, K.E. & Caron, J.M. (2000) The Southern Oscillation revisited: sea level pressures, surface temperatures, and precipitation. *Journal of Climate*, **13**, 4358–4365.

- Visbeck, M.H., Hurrell, J.W., Polvani, L. & Cullen, H.M. (2001) The North Atlantic Oscillation: past, present, and future. *Proceedings of the National Academy of Science USA*, **98**, 12876–12877.
- Visser, M.E., van Noordwijk, A.J., Tinbergen, J.M. & Lessells, C.M. (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London B*, **265**, 1867–1870.
- Visser, M.E., Adriaensen, F., van Balen, J.H., Blondel, J., Dhondt, A.A., van Dongen, S., du Feu, C., Ivankina, E.V., Kerimov, A.B., de Laet, J., Matthysen, E., McCleery, R., Orell, M. & Thomson, D.L. (2003) Variable responses to large-scale climate change in European *Parus* populations. *Proceedings of the Royal Society of London B*, **270**, 367–372.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.
- Williams, D.W. & Liebhold, A.M. (1995) Influence of weather on the synchrony of gypsy moth (Lepidoptera: Lymantriidae) outbreaks in New England. *Environmental Entomology*, **24**, 987–995.
- Wilson, S. & Arcese, P. (2003) El Niño drives timing of breeding but not population growth in the song sparrow (*Melospiza melodia*). *Proceedings of the National Academy of Science USA*, **100**, 11139–11142.

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