

In press for the journal Mitigation and Adaptation Strategies for Global Change, as part of the special issue entitled:
“Northeast United States Climate Impact Assessment”

guest edited by:

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July 2007

POTENTIAL EFFECTS OF CLIMATE CHANGE ON BIRDS OF THE NORTHEAST

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Abstract. We used three approaches to assess potential effects of climate change on birds of the Northeast. First, we created distribution and abundance models for common bird species using climate, elevation, and tree species variables and modeled how bird distributions might change as habitats shift. Second, we assessed potential effects on high-elevation birds, especially Bicknell's Thrush (*Catharus bicknelli*), that may be particularly vulnerable to climate change, by using statistical associations between climate, spruce-fir forest vegetation and bird survey data. Last, we complemented these projections with an assessment of how habitat quality of a migratory songbird, the Black-throated Blue Warbler (*Dendroica caerulescens*) might be affected by climate change. Large changes in bird communities of the Northeast are likely to result from climate change, and these changes will be most dramatic under a scenario of continued high emissions. Indeed, high-elevation bird species may currently be at the threshold of critical change with as little as 1 °C warming reducing suitable habitat by more than half. Species at mid elevations are likely to experience declines in habitat quality that could affect demography. Although not all species will be affected adversely, some of the Northeast's iconic species, such as Common Loon and Black-capped Chickadee, and some of its most abundant species, including several neotropical migrants, are projected to decline significantly in abundance under all climate change scenarios. No clear mitigation strategies are apparent, as shifts in species' abundances and ranges will occur across all habitat types and for species with widely differing ecologies.

Key words: Bicknell's Thrush, *Catharus bicknelli*, bird species modeling, climate change, Black-throated Blue Warbler, *Dendroica caerulescens*, habitat, high elevation, Northeast, northern hardwoods, spruce-fir, Random Forests

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1. Introduction

Climate exerts both direct and indirect effects on bird populations. Direct effects, such as late spring storms, may kill migrating birds (e.g., Zumeta and Holmes 1978). Indirect effects are mediated by one or more other species. For example, Both et al. (2006) found that Great Tit (*Parus major*) populations collapsed where climate warming disrupted the synchrony between breeding pairs and the caterpillars they feed their nestlings. Climate change will therefore affect bird species in myriad ways, as it always has in the past. So what is new about anthropogenic climate change in the 21st century such that it may have unprecedented effects on bird populations?

Ongoing and projected climate change in the Northeast differs from that experienced by bird species in recent evolutionary history in a number of critical ways: the magnitude of change is expected to be larger, the rate of change will be more rapid and directional (warmer and wetter), and the variability of weather is expected to increase, increasing the likelihood of extreme events (Hayhoe et al. 2007). Change will also occur in all seasons, and the phenology of weather events will shift. Bird populations will experience these long-term changes in climate via shorter-term changes in the weather because relatively few species have generation times lasting for more than a few years. However, even short-term weather conditions—a few good days or bad months—can have significant and lasting effects on abundance and population processes (Saether et al. 2004).

Past studies and reviews of the observed and potential effects of climate change on birds in North America have highlighted: the relationships between bird distributions and climate (Root 1988); the effects of changes in precipitation on breeding productivity (Rodenhouse 1992); phenological changes in the timing of migration and arrival (Bradley et al. 1999) and the onset of breeding (Brown et al. 1999); the relationship of global climate patterns to food supplies, breeding productivity and survival of migratory birds (Sillett et al. 2000); the potential effects of climate change on bird species distributions as habitats shift northward and upward in elevation (Matthews et al. 2004); and the extent to which high-elevation habitat and its associated avifauna may be lost due to climate warming (Lambert and McFarland 2004).

Here, we combine multiple approaches to provide a new assessment of the potential effects of climate change on the distribution and demography of birds of the Northeast. First, we integrate the modeling of bioclimatic envelopes for common bird species with that of tree species (Iverson et al., this issue), extending the work of Matthews et al. (2004). Second, we use the bird survey data of Lambert et al. (2005) and current climate projections in a geographic information system (GIS) model to assess how climate might alter the distribution of high-elevation bird species. Last, because both of these approaches are based on projected shifts in available habitat, we ground these discussions with an assessment of how habitat quality, and hence, the reproduction and survival of one common, well studied bird species, the Black-throated Blue Warbler (*Dendroica caerulescens*), might also be affected by climate change.

2. Potential habitat changes for 150 common bird species

Our goal was to project the potential future distribution and abundance of 150 bird species that are common in the eastern United States, based on their present patterns of distribution and abundance. The large sample of species allows generalizations regarding species using different habitat types (e.g., wetland, forest, shrubland, grassland) or having different migratory habits (e.g., neotropical migrant, temperate migrant, resident).

2.1. Methods

Bird distribution and abundance data were derived from the North American Breeding Bird Survey (BBS) (Sauer et al. 2001). O'Connor et al. (1996) extracted a set of 1223 BBS routes that were representative of the coterminous United States and that had frequent and high quality surveys over the period 1981-1990. Incidence data, or the proportion of routes with the species present, are typically correlated with abundance (Hanski 1992) and were available for each route and species. O'Connor et al. (1996) compiled these data to the 640-hexagonal grid of White et al. (1992). For the present analysis, we selected hexagons east of the 100th meridian to match the environmental and tree species predictors available (Iverson et al., this issue), although many of the bird species included have ranges that extend beyond this western boundary. In order to match the spatial resolution of the predictor variables (20 x 20 km), the 640 km² hexagonal grid of the bird data was adjusted by area-weighted resampling to 20 x 20 km. Statistical models were generated for each bird species using Random Forests, an advanced data mining tool that uses bootstrap sampling and a random set of predictors, averaged over a thousand regression trees, to produce a robust prediction that does not overfit the data (Breiman 2001; Prasad et al. 2006).

Bioclimatic models for each of 150 bird species common somewhere within the eastern United States were generated, with a total of 99 predictor variables related to climate, elevation, and abundance for 88 tree species (Matthews et al. 2004). Tree species compositions have shifted individually in the past and in all likelihood will continue to do so, resulting in unique combinations of species in the future (Jacobson et al. 1987; Webb 1992). When we use individual tree species as potential predictors, it allows us to build more robust models for contemporary bird distributions as compared to using aggregated forest types that will likely disassociate with a changing climate. However, it is also important to emphasize that tree range and abundance will likely change slowly, as trees usually live a long time; therefore, we cannot paint an accurate picture of the timing and rate of changes for trees or birds. The predictive bioclimatic models of current incidence for each species were then projected onto the climate change scenarios used by Hayhoe et al. (2007) for the climate variables, and onto shifts in tree species abundance (Iverson et al., this issue) for changes in bird habitats. We report model results for the most extreme (Hadley A1fi), least extreme (PCM B1), and average high and low emissions across HadleyCM3, GFDL, and PCM scenarios (GCM3-A1fi and B1). Because bioclimatic models such as the ones used in this study rely on the present associations between birds and vegetation, we assume that these relationships will remain constant through time. As such, changes in bird species requirements through adaptation, interspecific interaction among bird species, and lag times between climate and vegetation change cannot be accommodated in the models. However, this modeling approach provides the best estimates currently available for understanding how a large segment of the avifauna may shift in range and abundance as climate changes.

The bird species models were generated from 7 climate variables, 4 elevation variables, and 88 tree species distributions. The five variables contributing most to each of the 150 bird species models included 64 of these variables. All climate variables and elevation variables were represented along with 53 tree species. Across all species, the mean model $r^2 = 0.65$ (s. dev. = 0.17) with a range of 0.20 to 0.91. In order to capture the maximum variation within a bird's distribution, we built each of the 150 bird models using the entire area of the eastern United States. For the results reported here, we extracted the information for the Northeast from the broader modeling efforts. This approach also allowed us to include species that do not currently occur within, or that are only marginally abundant within the Northeast and might expand into the region.

2.2. Results

Projected change in suitable habitat under the four climate change scenarios indicates the potential for relatively large changes in the bird community throughout the Northeast. Any location can simultaneously gain and lose bird species. Areas where habitat may be suitable for the largest increases in bird richness include Maine and New Hampshire, while large losses of species richness may occur in the southern portion of the Northeast (most notably Pennsylvania and western New York) (Figure 1). Furthermore, changes in the incidence of bird species differ greatly among species, highlighting the potential changes in the abundance of birds throughout the region (Figure 2). More species are projected to change at least 25% (increase or decrease) in incidence than in the extent of the species' range within the Northeast (Table 1). Therefore, species that are projected to decrease, such as Wood Thrush (*Hylocichla mustelina*) and Baltimore Oriole (*Icterus galbula*) may occupy much of the same area, but at lower densities. Less change in range than in incidence was expected because most bird species can tolerate a relatively wide range in climate, elevation, and vegetation composition. However, the range of habitat characteristics that support the highest density of individuals can be quite narrow.

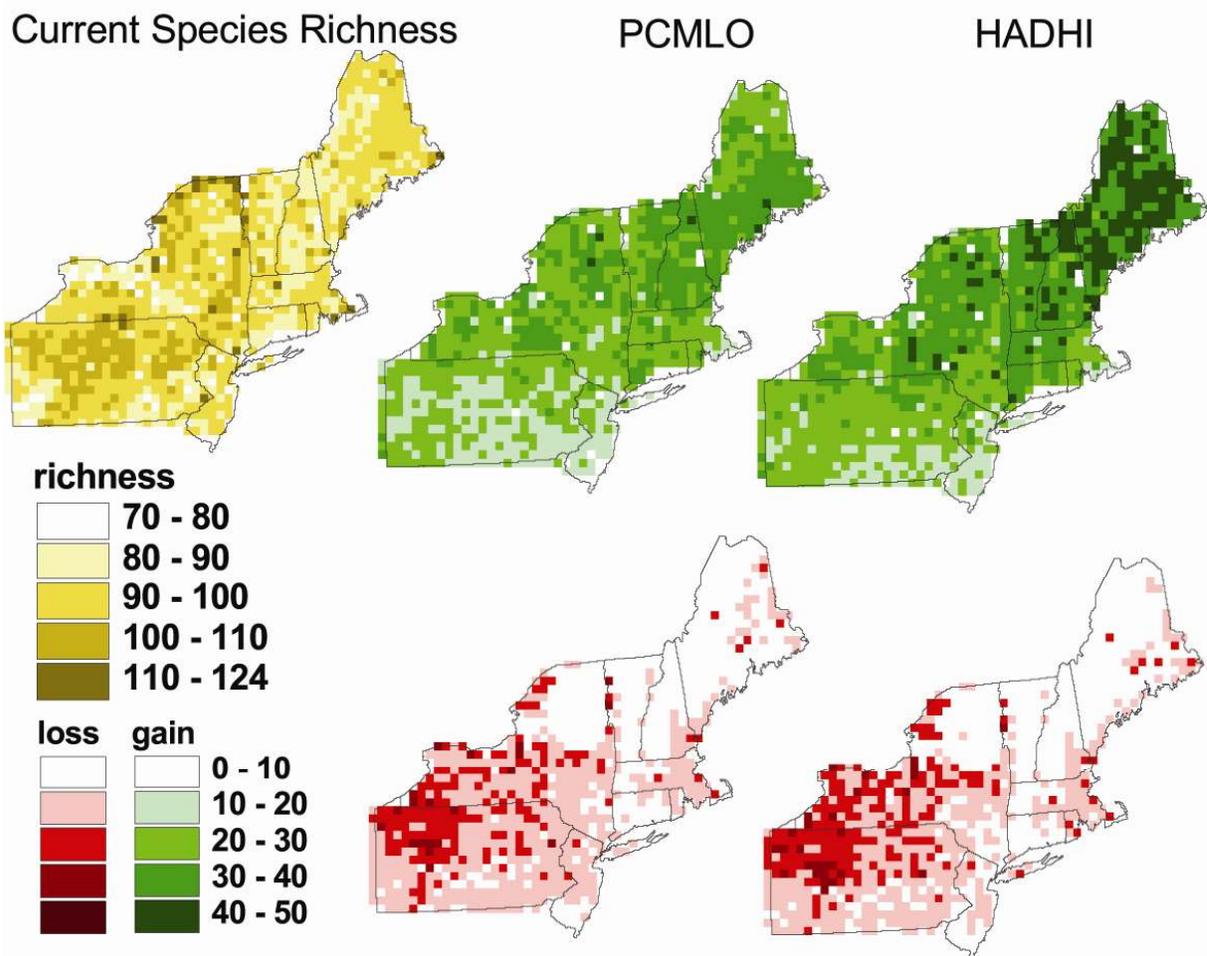


Figure 1. Projected gains and losses of bird species richness across the northeastern US under the Hadley Center Coupled Model hi emissions scenario (HADHI) and the Parallel Climate Model low emissions scenario (PCMLO) (see text for details) relative to current species richness.

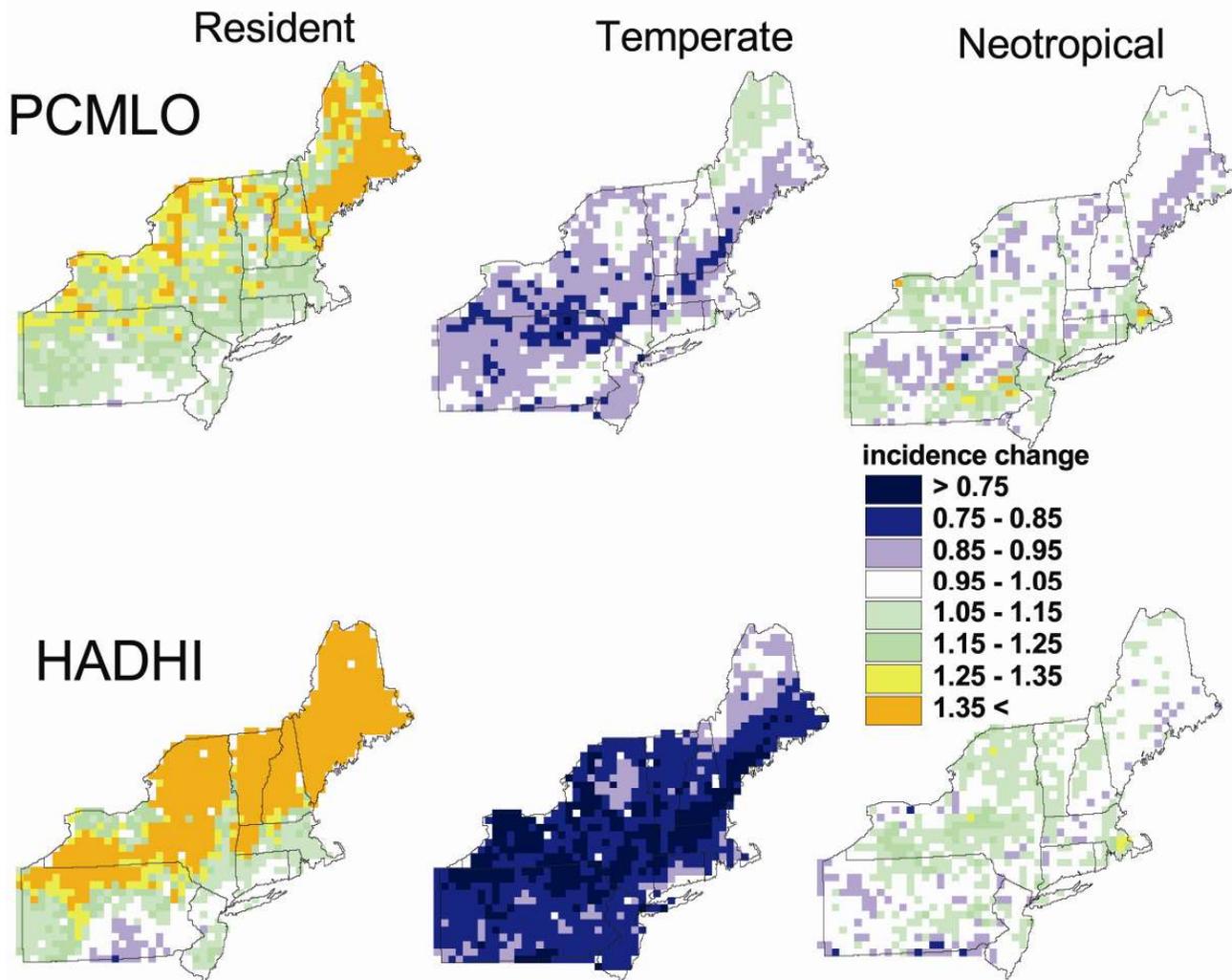


Figure 2. Projected change in total incidence for neotropical migrants, temperate migrants, and residents under climate change scenarios for the northeastern US under the Hadley Center Coupled Model hi emissions scenario (HADHI) and the Parallel Climate Model low emissions scenario (PCMLO). A change in incidence is defined as the ratio of the summed incidence under a specific climate change scenario to the summed incidence under current conditions per 20 km grid cell.

Projected changes are consistent across the four climate change scenarios, with largest changes projected under the Hadley A1fi and smallest changes projected under the PCM B1 scenario (see Appendix 1 for species-specific results). These results are consistent with the anticipated response of birds to climate change, i.e., that more change would be associated with more severe environmental perturbations. The association between the projected change in incidence and range is high for each scenario (Spearman rank correlation coefficient greater than $r_s = 0.75$ for all combinations).

Table 1. Number of species projected to change in incidence or range as a result of shifting habitat in the Northeast US under four climate change scenarios. Species were counted as declining or increasing only when the projected change exceeded 25% of current incidence or range.

	<i>Incidence</i>			<i>Range</i>		
	Declining	Stable	Increasing	Declining	Stable	Increasing
HAD-hi [†]	60	22	68	33	60	57
GCM3-hi	56	27	67	32	62	56
GCM3-lo	42	49	59	19	79	52
PCM-lo	38	64	48	15	94	41

[†] Full descriptions of the climate simulation models (HAD, GCM, PCM) and emissions scenarios, high (hi) or low (lo) can be found in Hayhoe et al. (2007).

Different groups of birds will be differentially affected by the projected habitat shifts. The abundance of neotropical and temperate migrants, that compose the majority of birds breeding in the Northeast, may undergo major change with either high or low emissions scenarios (Table 2). For these two groups of migrants under both high emission scenarios, over 44% of the species are projected to decline and an additional 33% are projected to increase in incidence by more than 25% as a result of climate change. If these changes are realized, they would constitute a dramatic alteration of the composition of bird communities throughout the region (Figure 2). Surprisingly, as a group, temperate migrants show the potential for the greatest overall losses in incidence as a result of shifting habitat. This is in part due to a greater proportion of losses compared to gains, while the neotropical migrants show substantial losses of current occupants as well as substantial gains of more southern species, resulting in a lower net change in total incidence across this group (Table 2, Figure 2).

Migratory birds will be affected by climate change during all phases of their seasonal cycle: in wintering areas and during migration and breeding. In winter, habitat quality is reduced by drought associated with the El Niño-Southern Oscillation (Sillett et al. 2000). Projected drying of the islands within the Caribbean Basin due to climate change (Neelin et al. 2006) can therefore be expected to reduce winter habitat quality for neotropical migrants. Increasing climate variability and extremes will increase mortality risk during migration, when up to 85% of annual adult mortality can occur (Sillett and Holmes 2002).

Resident birds might be expected to benefit from climate warming (Figure 2), particularly winter warming, as the abundance of these species is commonly thought to be limited by winter conditions (Newton 1998). In fact, 15 of the 25 resident species for which data are available increased significantly during 1966 – 2005 (Rodenhouse et al., *in press*). However, the cause of most range expansions of residents in the Northeast is not clear. Climate warming, urbanization, winter bird feeding by homeowners, vegetation change, and changes in interactions among bird species have all been hypothesized as causes. Our projections suggest that residents in general will be favored in both range and incidence under the climate change scenarios (Figure 2, Table 2). Yet, a notable number of residents are also projected to decrease in incidence or range, including Ruffed Grouse (*Bonasa umbellus*) and Black-capped Chickadee (*Poecile atricapilla*).

Table 2. Number of species of neotropical migrants, temperate migrants or residents projected to increase, remain stable or decrease in incidence or range. Only bird species that currently occupy at least 2% of the Northeast (i.e., 20 grid squares) were included. Species were counted as declining or increasing only when the projected change exceeded 25% of current incidence or range.

	<u>Neotropical migrants (n=63)</u>			<u>Temperate migrants (n=41)</u>			<u>Residents (n=16)</u>		
	<u>Decline</u>	<u>Stable</u>	<u>Increase</u>	<u>Decline</u>	<u>Stable</u>	<u>Increase</u>	<u>Decline</u>	<u>Stable</u>	<u>Increase</u>
<i>Incidence</i>									
HAD-hi	30	8	25	21	11	9	4	3	9
GCM3-hi	26	12	25	20	12	9	3	4	9
GCM3-lo	19	21	23	17	19	5	2	5	9
PCM-lo	15	27	21	17	21	3	1	9	6
<i>Range</i>									
HAD-hi	15	25	23	14	20	7	1	10	5
GCM3-hi	14	26	23	14	20	7	1	10	5
GCM3-lo	9	33	21	10	26	5	1	11	5
PCM-lo	6	40	17	9	29	3	0	12	4

Over 53% of wetland bird species could experience losses in incidence as a result of habitat changes (Table 3). Under all four general circulation model GCM scenarios, American Bittern (*Botaurus lentiginosus*), Common Loon (*Gavia immer*), and Sora (*Porzana carolina*) are projected to decrease by at least 50% in their Northeastern abundance, while species such as Green Heron (*Butorides virescens*), Great Egret (*Ardea albus*), and Cattle Egret (*Bubulcus ibis*) are projected to increase. Coastal wetlands are projected to decline in quality and area due to rising sea levels and damage by storms (Galbraith et al. 2002; Ashton et al., this issue), negatively affecting birds breeding in these wetlands (e.g., waterfowl), using them as migratory stopover sites (e.g., shorebirds) or wintering there, e.g., Common Loons are dependent on fish populations sustained by coastal estuaries. Inland wetlands will experience increased frequency of drought by mid century, particularly short-term drought (1 – 3 months duration) during summer under both low and high emissions scenarios (41% and 57% increases, respectively), and flooding will increase as rainfall patterns shift to fewer, but more intense events (Hayhoe et al. 2007). Floods will be a direct threat during the nesting period for some species (Desgranges et al. 2006) and can damage wetland vegetation. Summer drought will potentially reduce food supplies for nesting wetland birds (Batzer and Wissinger 1996) and increase rates of nest predation as water barriers protecting nests from terrestrial predators evaporate (e.g., Picman 1988). Although it might seem counter intuitive to use climate, elevation and tree species variables to project changes in wetland habitats for birds; in fact, these variables can define the ecological contexts in which wetlands occur. For example, black spruce, a tree species only found in wetlands, was the strongest correlate of the incidence of Common Loon, and Iverson et al. (this issue) project dramatic declines in the abundance of this tree species.

Table 3. Number of breeding bird species projected to change in incidence in four different habitat types. Species that currently occupy less than 2% of grid cells (i.e., < 20) were not included in the table. Species were counted as declining or increasing only when the projected change exceeded 25% of current incidence or range.

Scenario	Forest species (n = 50)			Wetland species (n = 17)		
	Declining	Stable	Increasing	Declining	Stable	Increasing
HAD-hi	27	4	19	9	2	6
GCM3-hi	24	7	19	10	2	5
GCM3-lo	22	12	16	10	4	3
PCM-lo	18	19	13	11	4	2
Scenario	Shrubland species (n = 26)			Grassland species (n = 11)		
	Declining	Stable	Increasing	Declining	Stable	Increasing
HAD-hi	11	6	9	6	1	4
GCM3-hi	10	6	10	6	2	3
GCM3-lo	5	12	9	5	3	3
PCM-lo	5	13	8	6	2	3

Some bird species are projected to increase their presence greatly in the Northeast as habitats and climates shift. These include many of the predominately southern species that our models predict currently occupy no more than 2% of the Northeast, such as Brown-headed Nuthatch (*Sitta pusilla*), Chuck-will's-widow (*Caprimulgus carolinensis*) and Loggerhead Shrike (*Lanius ludovicianus*). All analyzed climate change scenarios project an increase of suitable conditions for these southern species, allowing them to occupy at least 25% of the Northeast, provided that land uses are compatible in areas where they may expand. In addition, most species thriving in urban areas are unlikely to be affected because they are already coping well with warmer conditions than those experienced in the surrounding suburbs and rural areas. However, some species using suburban areas, e.g., Wood Thrush, may be sustained by immigration (Roth and Johnson 1993). These populations may decline in abundance as the quality of their habitat in rural source areas diminishes. Warming may aid some suburban species, but these are species that typically benefit from anthropogenic habitats and are not of conservation concern. Examples of these species include: introduced species such as the House Finch (*Carpodacus mexicanus*), native species with expanding ranges in the Northeast such as the Tufted Titmouse, and species that have adapted behaviorally to suburban habitats such as the Canada Goose (*Branta canadensis*).

3. High-elevation forest birds

The assessment of common bird species of the Northeast, although extensive, is methodologically limited to relatively widespread species and could not include bird species that are found only in relatively inaccessible areas, in particular, high-elevation areas where few BBS survey routes occur. High-elevation areas are likely to be among the habitats most affected by climate change (Hodkinson 2005). To assess the impact of climate change on high-elevation bird species of the Northeast, we focus on Bicknell's Thrush (BITH) (*Catharus bicknelli*) that breeds in high-elevation spruce-fir forest and has been the subject of long-term study (Rimmer et al. 2001).

In the Northeast, montane spruce-fir forest covers less than 1% of the landscape and is restricted to upper elevations (Cogbill and White 1991). Despite its rarity, montane spruce-fir makes a major contribution to the region's avian diversity. It is a primary habitat for several breeding birds that occur here at the southern edge of their boreal distributions, including Spruce Grouse (*Falcipecten canadensis*), Three-toed Woodpecker (*Picoides tridactylus*), Black-backed Woodpecker (*Picoides arcticus*), Yellow-bellied Flycatcher (*Empidonax flaviventris*), Gray Jay (*Perisoreus canadensis*), Boreal Chickadee (*Poecile hudsonica*), Ruby-crowned Kinglet (*Regulus calendula*), Blackpoll Warbler (*Dendroica striata*), and White-winged Crossbill (*Loxia leucoptera*) (Laughlin and Kibbe 1985; Foss et al. 1994). All but two members of this group, Boreal Chickadee and Ruby-crowned Kinglet, are listed by one or more northeastern states as species in greatest need of conservation.

Montane spruce-fir forests of New York and northern New England provide over 90% of the world's nesting habitat for BITH (Rimmer et al. 2001). Bicknell's Thrush is a rare, neotropical migrant, and the only bird species that breeds exclusively in northeastern U.S. and adjacent areas of Quebec, New Brunswick, and Nova Scotia (Lambert et al. 2005). Its specialized habitat requirements, limited and fragmented range, and low abundance make it vulnerable to extinction (Rich et al. 2004). Because the extent of BITH habitat is primarily controlled by climate, projected warming has the potential to alter the distribution and abundance of this species.

Vegetational zonation along elevational gradients in the Northeast is strongly influenced by temperature (Spear 1989; Botkin et al. 1972). Air heat sums form a near-perfect linear relationship with elevation in the northern Appalachian region (Richardson et al. 2004), and Cogbill and White (1991) report that mean July temperature correlates well with forest ecotones in the Appalachian Mountains. Mean growing season temperature (May-September) was the highest ranked of 36 climatic, soil, elevation, and land-use variables in an assessment of balsam fir importance values in forest inventory plots across the region (Iverson et al., *this issue*).

Warmer growing seasons could gradually elevate mountain ecotones and confine high-elevation plant and animal communities to progressively higher, smaller, and more isolated patches. Indeed, an upward shift in the lower spruce-fir ecotone may be underway on Northeastern mountains (Hamburg and Cogbill 1988), where warming enables northern hardwoods to encroach on red spruce (*Picea rubra*) and balsam fir (*Abies balsamea*) (Lee et al. 2005). Such shifts in ecotones have occurred in the past. Pollen and macrofossils from a high elevation lake on Mt. Washington, NH provide evidence that treeline moved upslope during warming in the early and middle Holocene (to about 3,500 y BP), possibly to the current tree species limit (1700 m) (Spear 1989; Miller and Spear 1999). Neoglacial cooling began in the White Mountains about 2,500 years ago lowering treeline to present levels (Miller and Spear 1999).

That treeline currently remains lower than expected from temperature alone is an indicator of recent warming (Richardson et al. 2004). Treeline represents the long-term average climatic history of a site (decades to centuries), and when there is an upward trend in temperature, treeline should be

found at an elevation lower (i.e., warmer) than expected, because the upslope movement of trees cannot take place instantaneously (Richardson et al. 2004). In addition, the upslope movement of treeline is not simply a response to temperature; the damaging effects of wind and ice also influence the distribution of woody vegetation (Kimball and Weihrauch 2000).

3.1. Methods

To project effects of climate change on Bicknell's Thrush habitat, we first modeled mean July temperature in mountainous areas of New York and northern New England. Next, we identified a temperature range that corresponds with the species' current distribution. We then simulated warming, in one-degree increments, and measured changes in the availability of suitable habitat. Finally, we used predicted future changes in mean July temperature to assess potential impacts on the amount of suitable habitat available under different climate-change scenarios.

Temperature equations were derived from a regression analysis of long-term monthly weather data (1950 – 1980; $n = 164$) against latitude, longitude and elevation (Ollinger et al. 1995). Elevation data were obtained from a digital elevation model of New York, Vermont, New Hampshire, and Maine (USGS 1999). A raster of mean July temperature was created for each 30-m cell, using the raster calculator in the Spatial Analyst extension of ArcGIS 9.1 (ESRI 2005). Calculations were constrained to areas over 600 m in elevation, encompassing the entire U.S. breeding range of BITH (Lambert et al. 2005).

We compared the model of mean July temperature with a validated model of BITH distribution (Lambert et al. 2005) and determined that over 99% of potential habitat occurred in areas where July temperatures averaged 9.3 – 15.6 °C. The proportion of thrush-positive cells for each modeled temperature followed a quadratic curve ($R^2 = 0.90$). The corresponding equation ($y = -0.0747x^2 + 1.8693x - 10.918$) allowed us to estimate the proportion of thrush-positive cells for all mean July temperatures between 9.3 and 15.6 °C.

We simulated the effects of warming by: a) adding one degree to each cell in the mean July temperature model; b) calculating the area for each adjusted temperature between 9.3 and 15.6 °C; c) estimating the extent of potential habitat for each adjusted temperature by entering each of these values into the quadratic equation; and d) summing the results within the 9.3 -15.6 degree range. We repeated these steps for each 1-degree increase until all mean July temperatures in the model exceeded 15.6 °C.

We further assessed the vulnerability of BITH habitat, by using the same simulation procedures, but this time incorporating predicted changes in mean July temperature rather than simple 1-degree increments. This approach adds a temporal component and accounts for geographic variability in temperature change. Predicted changes were derived from three atmosphere-ocean general circulation models (AOGCMs): NOAA/GFDL CM2.1 (Delworth et al. 2005), UKMO HadCM3 (Pope et al. 2000), and DOE/NCAR PCM (Washington et al. 2000). Simulations were forced by the IPCC Special Report on Emission Scenarios (SRES) (Nakićenović et al. 2000) higher (A1fi) and lower (B1) emissions scenarios. These scenarios describe internally consistent pathways of future societal development and corresponding greenhouse gas emissions, and cover a wide range of alternative futures based on projections of economic growth, technology, energy intensity, and population size.

We assumed no change in treeline, because ice damage, snow depth, and wind may reduce the importance of temperature in controlling this limit (Spear 1989; Kimball and Weihrauch 2000). It is possible that warming will merely fragment unforested alpine habitat on the highest peaks, as occurred in the early to middle Holocene (Miller and Spear 1999). However, if more extreme

climatic models prove correct, even the highest peaks would probably support at least *krummholtz* vegetation. In any case, expansion of spruce-fir forest into present unforested alpine habitats would make only a small contribution to spruce-fir forest area, as unforested alpine areas represent only a small fraction of the Northeast's high elevation zone.

3.2. Results

Regional warming of even 1 °C will reduce potential BITH habitat by more than half and an increase of 2 °C may be sufficient to eliminate all breeding sites from the Catskill Mountains of New York and most of Vermont (Figure 3). A 3 °C increase in growing season temperatures has the potential to nearly eliminate the habitat of BITH in the Northeast. Remnant patches of suitable habitat may persist in New Hampshire's Presidential Range (55 ha) and on Mount Katahdin in Maine (20 ha) after 5 °C of summer warming; however, no habitat for BITH is projected to exist in the Northeast following an increase of 6 °C. Summer temperatures are projected to rise on average by 2.8 °C under the lower-emissions scenario and 5.9 °C under the higher-emission scenario compared with the 1961 to 1990 average (UCS 2006).

In general, greater projected habitat loss was associated with the higher temperature changes projected by the HadCM3 and GFDL models as compared with PCM (Figure 4), and with the higher emissions scenario (A1fi) compared with the lower scenario (B1; scenarios as in Hayhoe et al. 2007). All models and scenarios projected the loss of more than 50% of BITH habitat during the next 30 years, and only the PCM model with a low emissions scenario projects more than 10% of thrush habitat remaining after warming predicted for this century.

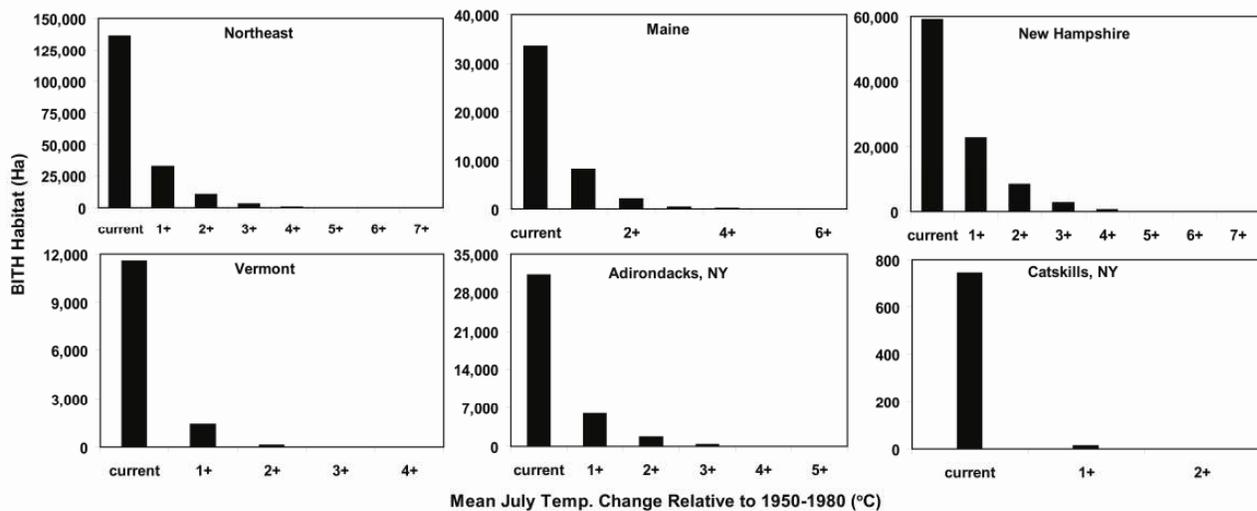


Figure 3. Projected reductions in Bicknell's Thrush (*Catharus bicknelli*) (BITH) habitat (in hectares) in the northeastern US as a whole and in selected regions that include most of the habitat for this species. Simulations raised mean July temperature in 1°C increments and assumed even warming.

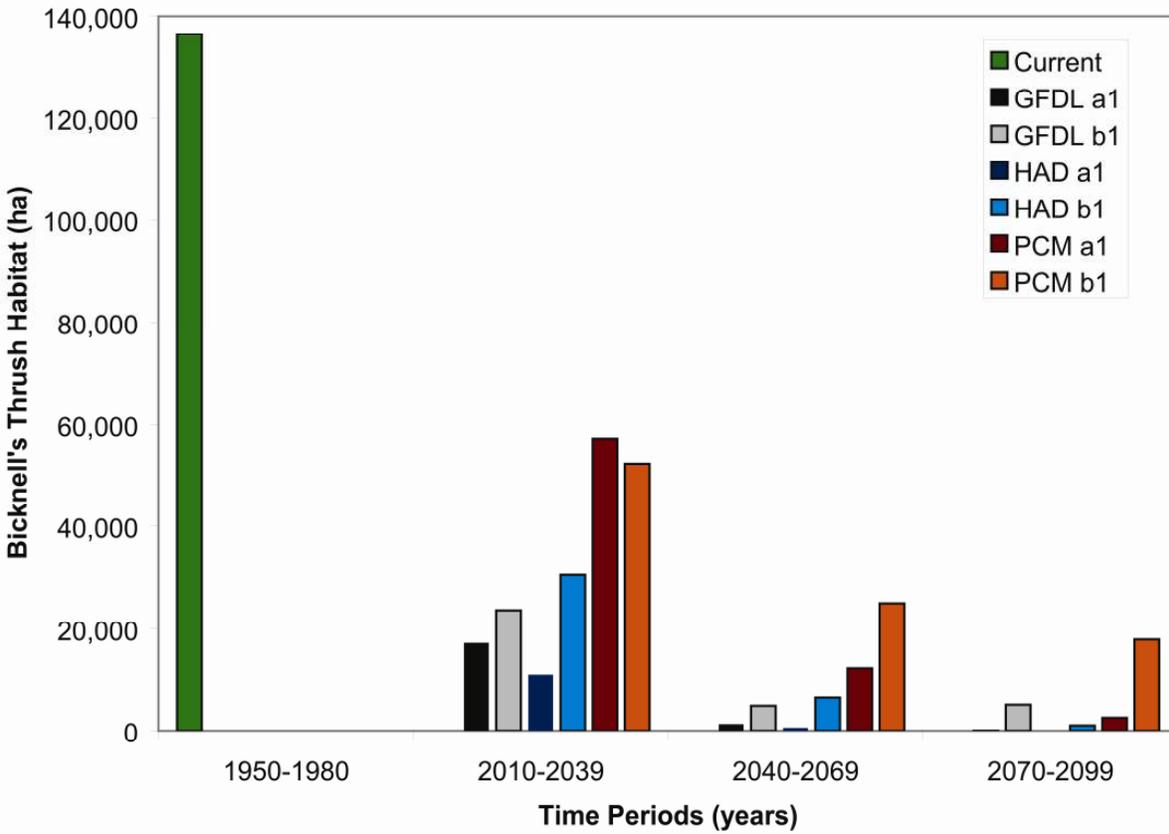


Figure 4. Amount of suitable habitat (in hectares) available to Bicknell's Thrush (*Catharus bicknelli*) in the Northeast based on projected increases in mean July temperature made by three atmosphere-ocean general circulation models: Geophysical Fluid Dynamics laboratory (GFDL), Hadley Center Coupled Model (HAD), and Parallel Climate Model (PCM), under two different CO₂ emissions scenarios: higher (A1) and lower (B1).

Rising treelines around the world (Kullman 2001) suggest that the spatial location of the ecotones delimiting spruce-fir habitat can shift measurably within decades; however, the precise amount of warming required to shift ecotones is controversial (Spear 1989), and it is highly likely that ecotonal shifts will lag at least decades behind climate changes (Kullman 2001). Lag times may be as long as 100 to 200 years (Woodward 1992). Such lags occur due to slowly changing soil characteristics, interactions among tree species and the disturbance required for one habitat type to invade and replace an adjacent one under variable climate conditions (Hamburg and Cogbill 1988). Our model projects the amount of habitat that will be available *after* habitat changes have reached equilibrium with climate changes. The temperature envelope approach we take here, therefore, should be interpreted to present that range of possible changes in spruce-fir habitat during the coming century, ranging from little to no change in the amount of spruce-fir habitat to a nearly complete shift in ecotonal boundaries as temperatures warm.

Predicting how montane forest will change is further complicated by incomplete understanding of the effects of new climate on patterns of natural disturbance (e.g., fire and hurricanes) and the spread of introduced and native insect pests (e.g., balsam woolly adelgid, *Adelges piceae* and spruce budworm, *Choristoneura fumiferana*) (Dale et al. 2001). Balsam fir is the least fire-resistant conifer in the northeastern United States, and this species is generally slow to reestablish after fire. It is usually rare or absent for the first 30 to 50 years after fire, and it typically establishes gradually from seed under the canopy of other tree species. With climate change, such regeneration may not be possible.

The loss of montane spruce-fir forest habitat is projected to be greatest for the first degree of warming with proportionally less loss with each additional increment of warming. Although one might interpret this as a hopeful sign--that some habitat will be resistant to climate change--in fact, the interpretation is not that clear. Much of the habitat lost with the first degree of warming occurs in sparsely occupied areas near the transition zone between northern hardwoods and spruce-fir forest (i.e., habitat at the lower ecotonal boundary of spruce-fir forest). The effect on population sizes and dynamics of this loss may not be as great as the size of the area lost would suggest, in part, because this is probably low-quality habitat for BITH. On the other hand, low quality habitat can play an important role in population dynamics and population viability (Donovan et al. 1995). In addition, this marginal habitat may contribute a significant number of individuals to total population size (Hale 2006).

Loss of montane spruce-fir forest habitat can be expected to reduce the distribution and abundance of BITH and of essentially all other bird species using largely or exclusively this habitat type (examples of other species listed above). In fact, BITH has been disappearing from mountains along the southern edge of its range in recent decades (Rimmer et al. 2001), although the extent to which these recorded losses are due to climate change is unknown. Southern areas are most vulnerable to local extirpations, e.g., the Catskills (NY) and southern Green Mountains (VT) for BITH and for montane, spruce-fir bird communities in general. In the Berkshire Mountains (MA) and Allegheny Plateau (PA), encroachment of hardwoods into mountaintop habitats will threaten the small populations of such species as Blackpoll Warbler and Yellow-bellied Flycatcher that occur in remnant patches of montane, spruce-fir forest. Northern populations of birds are less susceptible to such shifts because avian species of spruce-fir forest in these areas occur in both high and low elevation spruce-fir forests.

We foresee no potential benefits associated with climate change for mountain-breeding species. Although the prospect for retaining these species throughout most of the Northeast is not good under any of the projected scenarios, we also cannot predict with any precision when population declines and losses will occur. Predicting the pattern and timing of such losses would require knowing precisely how much temperature will change and where, the effects of site-specific factors such as slope and aspect, how disturbance regimes within spruce-fir forest may change, and last, the effects of climate change on montane food webs. We simply do not yet know enough about the ecology of montane biological communities to make more than qualitative projections of change for most species of this habitat type. Furthermore, few measures could be taken now or in the near-term to adapt to or minimize the severity of projected impacts on high-elevation, spruce-fir forest birds. Active management of this high-elevation habitat is impractical because of its size, widespread and patchy spatial distribution and inaccessibility.

4. Habitat quality

In addition to the amount of habitat available to birds, the quality of the habitat available may be altered by climate change. Habitat features determining quality for avian reproduction and survival can be classified generally as vegetation characteristics, food availability, abundance of predators (influencing the probability that eggs, nestlings or adults survive), and weather. Few studies have investigated each of these features of habitat quality under a range of climatic conditions, but such studies have been carried out for Black-throated Blue Warblers (BTBW). This species has been studied on plots distributed across a 600-m range in elevation within the Hubbard Brook Experimental Forest (HBEF), New Hampshire. This gradient spans approximately 2 °C in mean annual temperature, with about 35 mm more precipitation falling on the middle and high-elevation areas compared with the lower areas.

The BTBW is a common species of northern hardwoods forest that has sustained relatively stable abundance during the past 30 years (Holmes and Sherry 2001; Sillett and Holmes 2005). It is a foliage-gleaning neotropical migrant that feeds heavily on Lepidoptera larvae during the breeding season, builds an open cup nest and is multibrooded (Holmes et al. 2005). In addition to intensive monitoring of this species' demography (Sillett and Holmes 2005), experimental studies have examined its relationships with vegetation structure (Steele 1992), nest predators (Reitsma et al. 1990) and food supplies via food reduction (Rodenhouse and Holmes 1992) and food supplementation (Nagy and Holmes 2005). Study of this species is unique in the Northeast in its breadth, duration and intensity.

Studies of BTBW have revealed that its stable abundance is likely due to regulation of annual fecundity by processes occurring in breeding areas, specifically by local crowding effects occurring among neighboring breeding pairs and by site dependence occurring at a regional spatial scale (Rodenhouse et al. 2003). Site dependence occurs as individuals preemptively use territory sites that differ in suitability for reproduction and survival. This mechanism assumes that the best sites are always used and that sites of progressively poorer quality are used as the population grows (Rodenhouse et al. 1997). This mechanism can promote the growth of small populations, because when population size is small, only the best territories are used and reproductive output is high (McPeck et al. 2001). However, the operation of this mechanism depends critically on the maintenance of high quality habitat.

In New Hampshire's White Mountains, high quality habitat for BTBW occurs above mid elevation (above about 500 m), although breeding pairs can be found throughout the full elevational range of northern hardwoods, i.e., from about 200 to 900 m. At higher elevations, BTBW have a greater area of foraging substrate and higher food abundance. The density of deciduous leaves in the shrub layer, where BTBW nest and forage, is about 50% greater at high than at low elevation (Rodenhouse et al. *In prep*), and the biomass of Lepidoptera larvae is more than two times greater on leaves at mid and high than at low elevation. In addition, flying insects (primarily adult Lepidoptera and Diptera that are also consumed by BTBW) are significantly more abundant at high than at mid and low elevations. This abundance of food at higher elevations is paired with significantly lower nest predator density at mid and high elevations than at low elevation (Rodenhouse et al. *In prep*).

Greater territory quality for BTBW at mid and high elevation is matched by greater annual fecundity (number of young produced per pair per season) and greater apparent survival (as indicated by year-to-year return rates of adults) at mid and high elevations than at low elevation (Rodenhouse et al. *In prep*). It is not surprising then that recruiting BTBW settle at the highest elevation allowed by leaf expansion at the time of arrival (Rodenhouse et al. *Unpubl data*). In fact,

BTBW have a significantly clumped distribution within the HBEF with major aggregations occurring only at mid and high elevations (Doran 2003). The upper elevation (and probably latitude) at which BTBW settle is determined by the transition from northern hardwoods to unsuitable spruce-fir forest that begins at about 900 m.

Climate warming will reduce the area within which high quality territories for BTBW occur, as warming extends the distribution of low quality habitat up slope (and farther north). The net effect will be lowering of the average quality of territories available to this species. Indeed a 2 °C rise in mean annual temperature would degrade habitat quality within our entire study area that extends from 250 to 850 m--nearly the entire elevational range used by BTBW. Reductions in habitat quality will result in lower annual fecundity and likely in smaller population size because of the significant correlation between annual fecundity and recruitment in the subsequent year (Sillett and Holmes 2000). Although a quantitative comparison cannot be made, reductions in population size as a consequence of lower habitat quality corresponds qualitatively with the reduction in incidence projected for northern neotropical migrants by using bioclimatic envelope modeling (see section 2 above).

Changes in habitat quality for Black-throated Blue Warblers are likely to occur rapidly, because they do not depend on changes in long-lived species such as trees. Furthermore, food availability is the critical feature for habitat quality of BTBW (Rodenhouse and Holmes 1992; Nagy and Holmes 2005), and food abundance (particularly the abundance of Lepidoptera larvae) is strongly dependent upon food web interactions. These interactions seem linked to climatic conditions as they shift across environmental gradients (Hodkinson 2005).

5. Can bird species respond adaptively to rapid climate change?

Responses to climate change by the resident and migrant birds of the Northeast might be expected because they have experienced climate changes in their evolutionary history, and because they encounter a wide range of conditions in their strongly seasonal environment. The most flexible type of response would be behavioral shifts, e.g., in foraging methods, the timing of migration and breeding, etc. to take advantage of favorable weather or to mitigate the negative effects of inclement weather. Such behavioral plasticity in response to weather is well documented (Elkins 1988; Walther 2001) as are climate-related shifts in the timing of migration (Strode 2003) and the onset of breeding (Both et al. 2006). The extent to which behavioral plasticity can enhance the benefits of favorable weather or mitigate inclement conditions is unknown. Even less clear are the effects of such behavioral responses on demography.

Evolutionary adaptation to climate change, i.e., that associated with heritable variation in morphological or physiological traits, is also possible (Pulido and Berthold 2004). Such evolutionary adaptation of morphology is well documented for some species such as the House Sparrow (*Passer domesticus*) (Johnston and Selander 1971) and Galapagos finches (*Geospiza spp.*) (Grant and Grant 1995). In a recent review of such effects, Yom Tov et al. (2006), conclude the reductions in the body mass of some bird species (4 of 14 species tested) over the past 30 years can be attributed to climate warming, but they found no evidence of recent change in wing length among the species tested. These data are intriguing, and the hypothesis of evolutionary adaptation to climate change therefore merits further testing; however, at present there seems to be no strong signal that birds in general are adapting morphologically as climate is changing.

Most bird populations may not adapt evolutionarily to rapid climate change for several reasons. First, most bird species of the Northeast have broad distributions and extensive gene flow (Webster

et al. 2002), making local or even regional adaptation unlikely as selection pressures probably differ in kind and intensity over species' ranges. Second, for migrants, changing selection pressures in breeding areas may counter or mask adaptation to changing conditions in wintering areas. Third, in a more variable environment, the direction of selection may shift frequently, resulting in no consistent directional change. Last, extreme events may cause the loss of genetic variation required for adaptive shifts (Pulido and Berthold 2004).

6. Dealing with uncertainty

Much about the future effects of climate change on birds is still uncertain. Chiefly: (1) We do not know how rapidly vegetation composition and structure will respond to changes in climate. Because birds will respond to changes in the distribution of their habitat, the extent of effects on birds will depend in part on how rapidly their habitat changes, and this may depend critically on stochastic disturbances (e.g., fire, drought, insect, disease) that provide opportunity for habitat change. In addition, the degree to which individual species are specialized on certain habitat or vegetation features will likely influence how and how much they respond to habitat shifts. (2) The dynamics of species populations during the transition to new habitat structures and locations is not clear. As the composition of biological communities changes, so will interactions among species (i.e., predator-prey, host-parasite, mutualisms, competition) as species respond individually to climate change. In consequence, species interactions and population fluctuations will be destabilized, benefiting some species and putting others at risk. (3) Surprises—dramatic and unexpected changes in species populations—will happen due to the multiple indirect effects of climate within food webs and due to time-lags in the propagation of those effects. For example, predators and parasitoids of forest Lepidoptera larvae may significantly alter the dynamics of food available to birds (Hodkinson 2005; Stireman 2005). (4) How climate change will interact with other global and regional disturbances (e.g., habitat fragmentation and loss, nitrogen deposition, acid deposition, invasive species, etc.) is also unclear. However, we are unaware of any scenarios in which the effects of such interacting disturbances on the biological communities of the Northeast will promote the stability and viability of bird populations.

Acknowledgements

This work was supported by grants from Wellesley College, the U.S. National Science Foundation to Wellesley College and Dartmouth College, the Smithsonian Institution, the Trustees and members of the Vermont Institute of Natural Science, the Thomas Marshall Foundation, Stone House Farm Fund of the Upper Valley Community Foundation, the U.S. Fish and Wildlife Service Migratory Bird Division, and the Northern Global Change Program of the U.S. Forest Service. We are indebted to our wonderful colleague, the late Raymond O'Connor, for all his early work in spatial assessments of bird distributions.

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