DRAFT

Northward Shifts in the Abundance of North American Birds in Early Winter: A Response to Warmer Winter Temperatures?

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INTRODUCTION

Distributions of birds are determined by a complex array of short- and long-term climatic and environmental conditions, vegetation composition, and a variety of interspecific interactions. In particular, the associations between birds and their habitats have been well studied (Cody 1985, Verner et al. 1986, Morrison et al. 1992). However, the primary factors that underlie these distributional patterns may often be the prevailing climatic conditions that support these habitats. Moreover, distributional range boundaries may be determined at least in part by climatic conditions independent of specific habitat boundaries (Root 1988a,b,c).

In the face of growing concern about rapid global changes in climatic conditions, much of it due at least in part to human activities (Intergovernmental Panel on Climate Change 2007), there has been speculation about what impacts these changes may have on various ecological communities (McCarty 2001, Huntley et al. 2006, Jetz et al. 2007, Intergovernmental Panel on Climate Change 2007, BirdLife International 2008). Among vertebrates, birds provide unique opportunities for investigation of these questions. They are generally easy to detect, identify, and count relative to other classes of organisms, and as a result we possess a wealth of information about their distribution, habitat selection, and abundance. They are speciose and ubiquitously distributed both geographically and among habitats. They include within their ranks both widespread and geographically restricted species, extreme habitat specialists and adaptable generalists, and both sedentary species with little ability to disperse and migrants whose individual movements may span ten thousand kilometers. As a result, they are an ideal class of organisms with which to investigate current and predicted impacts of climate change.

A number of studies have investigated local and/or regional level effects of climate change on phenomena such as changes in the timing of spring arrival and breeding of migrants (Butler 2003, Torti & Dunn 2005, Macmynowski et al 2007) or potential extinctions of endemics from local biodiversity hotspots or isolated alpine areas (Malcolm et al 2006, Sekercioglu et al. 2007). Many of these studies make a strong case suggesting potentially catastrophic ecological consequences as a result of long-term climate change, on at least a subset of species with specialized ecological requirements. Other studies have predicted, for a large number of species, the impacts climatic change may have on future avian distributions and abundance (Matthews et al. 2004, Huntley et al. 2007) using survey data or atlas maps of current distributions and habitat associations in conjunction with models of predicted climate change. Only a few studies, however, have attempted to assess long-term changes in distribution across a large geographic scale that may be attributable to climate change (Hitch & Leberg 2007, La Sorte & Thompson 2007).

The focus of this paper is to (1) determine if birds have exhibited continent-wide latitudinal shifts in their distribution within a relatively short ecological time period of 40 years (which likely outpaces most changes in vegetation communities), (2) investigate the possibility that changes in climatic conditions may be partially responsible for any such distributional changes, and (3) investigate guild-specific changes in distribution. We also discuss additional possible causes of distributional shifts, such as changes in human-provisioned supplemental food.

METHODS

Climate data and analysis

Monthly average temperature estimates were available for each of the lower forty-eight contiguous states and the continental aggregate of these states (NOAA, US Climate Divisions dataset 2007). For each month we used least squares regression to assess the extent and significance of change in continental temperatures over a 40-year time period from 1966 through 2005. For January temperatures, which we found to exhibit the greatest change (see results), we also assessed the rate of change in each U.S. state.

Avian data, survey area, and time period covered

The Christmas Bird Count may be the largest, and longest running wildlife survey used to assess continental patterns of distribution and abundance, of any class of animals in the world. Currently, more than 2000 counts are conducted annually during a three-week period between mid-December and early January, with the participation of over 30,000 volunteer observers.

Each local count is conducted once annually during a 24-hour period in a 24.14-km (15 mile) diameter circle. A variable number of observers divide into separate field “parties” who each survey a different region of the circle and tally the total number of individuals of each species detected. An attempt is made to detect all species, but cryptic and/or rare species, as well as some nocturnal species, may be under-sampled. Nonetheless, the CBC is applicable to assess continental change in the abundance and distribution of most species of relatively common birds in the continental U.S. and southern Canada.

We based our analysis on the 40-year time period from the winter of 1966-67 through the winter of 2005-06. Although the CBC began in 1900, we choose 1966-67 as a starting point because by that year we believed the CBC survey methods had become standardized and sample sizes, particularly in the western part of the survey area, were sufficient for statistical analyses.

The survey area was defined as the contiguous lower 48 U.S. states and the southern portions of Alaska and the Canadian provinces. The northern portions of Alaska and Canadian provinces were too poorly covered to provide meaningful data; therefore the northern extent of coverage was defined based on the ecological boundaries of Bird Conservation Regions 5, 10, 11, 12, and 14 as defined by the North American Bird Conservation Initiative (1999; Fig 1).

The primary sampling units (strata) for our analyses are the portions of the 55 states and provinces occurring within the survey area as defined above.

Preliminary data analysis and choice of species

For 305 North American species, 40-year population trends and annual indices of abundance were estimated, both continentally and for each state and province (called strata from here), with hierarchical models in a Bayesian analysis using Markov chain Monte Carlo techniques (Link et al. 2006, Sauer & Niven, in press). Because the number of observers and amount of time devoted to each survey varies among CBCs, differences in effort among circles were accounted for in the model based on the number of "party hours" devoted to each survey (Link & Sauer 1999a,b). This method estimates the best non-linear effort adjustment appropriate for each species in each stratum and applies those adjustments to each circle in the strata.

To address the differences in the reliability of the estimates among species, the 305 species included in these analyses all met the following criteria: the minimum number of CBC circles in the analysis was at least 25, the precision estimate [measured as 1.96*sqrt(variance)] was sufficient to detect a trend of 10% per year or less, the mean relative abundance was at least 0.01 (approximately equal to the average number of birds detected per circle with the average amount of effort), and the percentage of the species' hemispheric early-winter range included within the CBC survey area was at least 1.0%. In addition, to assure that each species was sufficiently widespread in our survey area to detect distributional change by use of our methods, no species was included in the analysis unless the species was found in at least five strata and occurred in at least 5 CBC circles in each of these strata. Moreover, we also required minimum relative abundance of at least 0.01 and the precision to detect a trend of 10% per year in each stratum as well. The list of 305 species that met these criteria is included in Appendix 1.

Definitions of guilds and other classifications used

Each of the 305 species was classified into one of the following ecological guilds based on their distribution and habitat use during early winter (Appendix 1):

"Coastally-restricted Species" – species whose distributions are largely restricted to the immediate coast or offshore waters. The 33 species in this guild are exclusively waterfowl, shorebirds, seabirds, or wading birds, with the exception of two passerines restricted to coastal salt marshes.

"Inland/Mixed Waterbirds" not restricted to the coast – this guild was comprised of all species primarily dependent on aquatic habitats for feeding and/or roosting, including some found only in freshwater and others that use both fresh and saltwater. While the majority of species are members of families typically considered waterbirds by the North American Waterbird Conservation Plan (Kushlan et al. 2002), twelve landbirds (passerines or members of other families not considered to be waterbirds taxonomically) are included in this guild due to their dependence on aquatic habitats.

"Landbirds" – species primarily dependent upon terrestrial habitats. We further subdivided this guild as follows:

Grassland birds – occurring primarily in natural or artificial grassland habitats in winter

Shrubland birds – occupying natural shrubland or rangeland habitat, as well as species characteristic of edge and young second-growth habitats

Woodland birds – species characteristic of mature or late-successional deciduous or coniferous forests, savannahs, open woodlands, or gallery or riparian woodlands.

Generalists – species not easily classified within one of the other guilds due to approximately equal use of two or more habitat types during winter. We also included in this guild species often associated with urban or suburban environments.

We further subdivided landbirds based on their use of supplemental food provided at feeding stations. Our classification generally follows that of Dunn and Tessaglia-Hymes (1999), but has been expanded and modified based on our personal experience and consideration of species accounts from the Birds of North America series (Poole 2005) as follows:

Regular feeder users – species that make regular use of human-supplemented food, and as a result may at times become partially reliant upon these food sources

Occasional feeder users – Species that may use supplemental food sources when they are available, but are unlikely to develop any dependence upon these sources

Non-feeder users – Species that rarely or never visit feeding stations

Estimation of annual change in latitudinal center of abundance

Year-specific latitudinal centers of abundance within our survey area were estimated for each species as the mean centroid latitude among all strata (states and provinces) included in the analysis, weighted by the species' strata-specific indices of abundance and the area (in km^2) of each stratum. In the population trend analyses, discussed above, data for a species in a stratum were only included if the species occurred at least once in four or more CBCs over the 40-year sampling period. Smaller sample sizes were assumed to reflect observations that were peripheral to the species' early-winter range and/or records from species that were too rare to provide meaningful data.

To facilitate the comparison of annual changes in latitudinal distribution among species, for each species we subtracted the estimated value of the centroid latitude in year one (winter 1966-67) from each of the 40 yearly estimates. By doing so this defined the 'change in latitude' value as zero for year one (1966-67) and all subsequent years reflected a change from this standard starting point. For each species, and for the median aggregate values among all species in each guild of interest, standard least squares linear regression was used to determine if the change in mean centroid latitude (center of abundance) over 40 years differed significantly from zero.

Estimation of geographic variation in population trends:

To explore geographic variation in population trends, for each species and each stratum (state or province) in which it occurred, we calculated the deviation of the stratum trend estimate from the continental trend estimate (which for simplicity we will refer to as the "Stratum Trend Deviation") by subtracting the 40-year continental population trend estimate from the 40-year stratum population trend estimate. A positive stratum trend deviation indicates that the population trend in that state or province was higher than the overall continental average and vice versa. For each guild of interest we estimated the median stratum trend deviation among all the species that met sample size requirements within each stratum. We then regressed the

median stratum trend deviations against the latitudinal center of each stratum using least squares regression to assess the relationship between strata trend deviation and latitude.

For mapping purposes we also determined, for each guild, if more than 50% of the species in each stratum exhibited positive or negative stratum trend deviations, or if an equal number of species had stratum-specific trends above and below their continental trends.

Estimation of change in relative abundance between coastal and inland strata

For the 272 species that regularly occur at inland locations, we calculated the mean relative abundance within the inland strata (inland R.A.) and within coastal strata (coastal R.A.) from the weighted relative abundance estimates in each of the 31 inland strata (strata with no coastal border) and 24 coastal strata for the first and last 10-year periods of the study. For each species we calculated the proportional relative abundance inland [inland R.A. /(inland R.A. + coastal R.A.)] for the two ten-year periods

Southern tier species not included in other analyses

Our list of 305 species used for the majority of the analyses included only those widespread enough to detect latitudinal patterns of change (sufficient data in 5 or more strata). We also assessed the continental trends of an additional suite of species that met our criteria in one or more state but may not have occurred in a sufficient number of states to be included above. From these we selected those which primarily occurred in the southern U.S. states bordering Mexico or the Gulf of Mexico. We assessed the mean population trends of these species in comparison to the population trends of the 305 species used for our primary analysis. We considered positive and negative continental trends to be those where the credible intervals did not overlap zero.

RESULTS

Temperature patterns

Regression analysis showed a positive increase in monthly temperature over the 40-year study period for six of the 12 months (Table 1). The greatest rate of change occurred in January (slope=0.117) showing a more than 4.5 degree Fahrenheit increase over the 40-year period. The rate of change in average January temperatures during the 40 years of this study was significantly greater at higher latitudes (Fig.2a). This latitudinal gradient of temperature change, however, was primarily a result of patterns among the inland strata (Fig. 2b).

All 305 North American species

Among the 305 bird species in our study, there was a strong northern shift in latitudinal center of abundance over the past 40 years. Of the 305 species in the analysis, 177 showed a significant shift north and 79 showed a significant shift south. Overall, the average latitudinal center of abundance significantly shifted to the north ($F=233.4$, $n=40$, $p<0.0001$, $R^2=0.86$; Fig. 3) by a distance of 34.8 miles based on the difference between the predicted estimate in year 40 and the predicted Y intercept at year zero from the regression analysis.

The latitudinal center of abundance differed considerably from year to year, so there was not a steady march north (Fig. 3). However, when the residuals from the predicted annual distance moved were compared to the residuals from the predicted annual change in temperature for the November/December period preceding and during the CBC survey period, the relationship was significant ($F=8.79$, $p=0.0052$, $R^2=0.19$) indicating that in warm early winters birds were found further north than in cold early winters (Fig. 4).

Among the 305 species in our analysis, Canadian provinces and northern U.S. states are dominated by species that have positive stratum trend deviations (average 40-year population trends above their respective 40-year continental trends), whereas the majority of species in most southern states have negative stratum trend deviations (Fig. 5). Moreover, we found that the median stratum trend deviations among the species present in each stratum were significantly correlated with the latitude of the strata ($F=31.78$, $p<0.0001$, $R^2=0.37$, Fig. 6), indicating that population trends were relatively more positive (higher) in northern strata.

Because the rate of temperature change in January increased significantly with latitude over the same 40-year time period (Fig. 2a), we also examined the relationship between the median stratum trend deviations and the rate of January temperature change (Fig 7). The relationship was significant ($F=10.48$, $p=0.0023$, $R^2=0.19$; Fig. 7).

As well as shifting their centers of abundance within the CBC survey area to the north, the 305 species in our analysis also significantly shifted their distributions inland from the coast ($F=410.9$, $p<0.0001$, $R^2=0.92$; Fig. 8). The average distance shifted was 20.5 miles (the difference between the predicted estimate in year 40 and the predicted Y intercept at year zero from the regression analysis). Moreover, the proportional relative abundance of the 305 species among the inland versus coastal strata increased from 0.31 in the first decade to 0.35 in the forth (recent) decade.

<u>Three broadly-defined guilds:</u>

When the 305 species were separated into guilds, we found that average centers of abundance shifted north for each of the three broadly-defined guilds: landbirds, inland/mixed waterbirds, and coastally-restricted species (Fig. 9). Among these guilds, landbirds showed the greatest change in their centers of abundance, with an average northern movement of approximately 50 miles. Of the 179 landbird species, 114 (64%) shifted significantly north and 33 (18%) shifted significantly south. Of the 93 waterbird species, 48 (52%) shifted significantly north and 33 (35%) shifted significantly south. Of the 33 coastally restricted species, 15 (45%) shifted significantly north and 13 (18%) shifted significantly south.

Although the annual indices reveal significant northward shifts in the centers of abundance for all three guilds (Fig. 9), the median stratum trend deviations were significantly correlated with latitude for landbirds (Fig. 10a) but not for waterbirds or coastal birds (Fig. 10b, 10c). In other words, population trends showed a positive increase with latitude for landbirds but showed no latitudinal relationship for waterbirds or coastally-restricted species.

Both landbirds and inland/mixed waterbirds significantly shifted their distributions inland (Fig. 11) although waterbirds shifted inland by a considerably larger distance than landbirds. [By definition coastally-restricted species are not included in this analysis.] This pattern of shifting distributions is apparent from the stratum-specific estimates of relative abundance as well. The proportional relative abundance inland for landbirds increased by only 0.025 (from 0.41 to 0.43 or 4.9%) between the first and last 10 years of the study, whereas for waterbirds, while considerably more abundant in coastal strata, the proportional abundance inland increased 5.9% from 0.13 to 0.19.

Habitat guilds

Because landbirds represent a large and diverse guild, we separated them into additional habitat guilds. Among the four guilds we investigated, woodland birds, shrubland birds and generalists each showed significant shifts of their centers of distribution to the north, but grassland birds did not (Fig 12). Woodland birds shifted their ranges the farthest north; more than twice as far as the other guilds, at an average distance of more than 70 miles in 40 years. Of the 88 woodland species, 62 (70%) shifted significantly north and 10 (11%) shifted significantly south. Of the 39 shrub species, 26 (67%) shifted significantly north and 7 (18%) shifted significantly south. Of the 26 grassland species, 10 (38%) shifted significantly north and 9 (35%) shifted significantly south. Of the 26 generalist species, 16 (61%) shifted significantly north and 7 (27%) shifted significantly south.

In terms of movement inland from the coasts, each of the four landbird guilds shifted significantly inland of the 40 year study (Fig. 13). Patterns among grassland and woodland birds were opposite of those found for latitudinal movement: grassland birds exhibited the strongest movement inland whereas forest birds showed only modest (but significant) movement inland.

Feeder use among landbirds

We divided the landbird guild into those that regularly use, occasionally use, or seldom/never use supplemental food provided at bird feeders. All three of these groups of landbirds shifted their centers of abundance significantly to the north (Fig. 14). However, in an analysis of variance we found differences among the three groups in the slopes of change in center of abundance with year ($F=6.04$, $p=0.0029$). A pairwise Ryan-Einot-Gabriel-Welsch Multiple Range test revealed that the mean slope of 0.030 for regular feeder users was significantly steeper than the slopes for occasional feeder users or non-feeder users, whose slopes (0.014 and 0.008, respectively) did not differ from one another.

Because feeder users and woodland landbirds both show the strongest patterns of northward shifts, and many of the feeder users are also woodland birds, we divided woodland birds by feeder use status. Each group of woodland species showed highly significant northward shifts in the center of their ranges (Fig. 15), and the mean slopes of change in latitude during the 40-year sample period for regular feeder users (0.039), occasional feeder users (0.020) and non-feeder users (0.018) did not differ from one another in pairwise comparison test. Therefore, the northward shifts in the distribution of woodland birds occurred independently of their feeder-use.

Species from southern tier states

Among the southern species in the CBC dataset that were not included among the 305 species in the primary analyses, 33 had population trends that differed from zero (based on credible intervals that did not overlap zero), and among those 23 (69.7%) had positive trends. Among the 305 species 107 had population trends that differed from zero and 64 (59.8%) had positive trends.