Breeding Distributions of North American Bird Species Moving North as a Result of Climate Change

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Abstract: *Geographic changes in species distributions toward traditionally cooler climes is one hypothesized indicator of recent global climate change. We examined distribution data on 56 bird species. If global warming is affecting species distributions across the temperate northern hemisphere, these data should show the same northward range expansions of birds that have been reported for Great Britain. Because a northward shift of distributions might be due to multidirectional range expansions for multiple species, we also examined the possibility that birds with northern distributions may be expanding their ranges southward. There was no southward expansion of birds with a northern distribution, indicating that there is no evidence of overall range expansion of insectivorous and granivorous birds in North America. As predicted, the northern limit of birds with a southern distribution showed a significant shift northward (2.35 km/year). This northward shift is similar to that observed in previous work conducted in Great Britain: the widespread nature of this shift in species distributions over two distinct geographical regions and its coincidence with a period of global warming suggests a connection with global climate change.*

Keywords: avian distributions, breeding distributions, climate change, global warming, North American birds, range shifts

Distribución Reproductiva de Especies de Aves Norte Americanas en Movimiento Hacia el Norte como Resultado del Cambio Climático

Resumen: *Los cambios en la distribución de las especies hacia climas tradicionalmente más frescos es un indicador hipotético del cambio climático global reciente. Examinamos los datos de distribución de 56 especies de aves. Si el calentamiento global está afectando la distribución de especies en el Hemisferio Norte templado, estos datos deberían mostrar la misma expansión en la distribución hacia el norte de aves que se han reportado para Gran Bretaña. Debido a que un cambio hacia el norte en las distribuciones puede deberse a expansiones multidireccionales en la distribución de múltiples especies, también examinamos la posibilidad de que aves con distribuciones norteñas estén expandiendo sus distribuciones hacia el sur. No hubo expansión hacia el sur de aves con una distribución norteña, lo que indica que no hay evidencia de una expansión de distribución general de aves insectívoras y granívoras en Norte América. Como se predijo, el límite norteño de aves con distribución sureña mostró un cambio significativo hacia el norte (2.35 km/año). Esta expansión hacia el norte es similar a la observada en trabajos previos realizados en Gran Bretaña: el carácter generalizado de este cambio en las distribuciones de especies en dos regiones geográficas distintas y su coincidencia con un período de calentamiento global sugiere una conexión con el cambio climático global.*

Palabras Clave: aves de Norteamérica, calentamiento global, cambio climático, cambios de distribución, distribución de aves, distribución reproductiva

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Introduction

Global mean surface air temperatures have increased between 0.4 and 0.8° C since the late nineteenth century. Most of this increase has occurred in two distinct periods, 1910–1945 and since 1976 (IPCC 2001). In the northern hemisphere spring maximum temperatures increased 1.1° C between 1950 and 2004 (Vose et al. 2005). Seasonally, the greatest warming since 1976 over land has occurred during the northern hemisphere winter and spring and the largest rates of warming continue to be found in the mid- and high-latitudinal continental regions of the northern hemisphere (IPCC 2001). Although one expects to see shifts in biological phenomena in response to global warming, it is difficult to establish causal links (McCarty 2001) and to differentiate between trends and stochastic events (Fleishman & Mac Nally 2003). In spite of these difficulties, there is at least some evidence that changes in physiology, adaptation, phenology, and distribution are associated with climate change (Hughes 2000; Root et al. 2003). Shifts in distributional ranges have been documented in a number of various taxa: Florida plants (Crumpacker et al. 2001), butterflies (Crozier 2004), Mexican birds (Peterson et al. 2002), and marine bivalves (Roy et al. 2001).

In the northern hemisphere one biological phenomenon that could be affected by global temperature is the northern limit of the distribution of a species. A recent global meta-analysis that included a wide range of taxa demonstrated significant shifts in species distributions toward the poles (Parmesan & Yohe 2003). Birds might be especially good subjects for investigations into trends in species distributions because their ranges are strongly associated with temperature (Root 1988) and because of the availability of long-term data sets. For example, survey data collected by volunteers has been useful in demonstrating extensive changes in wintering ranges and abundance patterns observed in North America over the last century (Root & Weckstein 1995).

In one of the few comparisons of multiple species to date, birds in Great Britain exhibited a northward range expansion that closely followed a period of global warming (Thomas & Lennon 1999). If this trend is due to global climate change, we expect the breeding bird distributions elsewhere in the northern hemisphere to exhibit a similar pattern. Furthermore, because of the moderating effect of oceans on the climate of small landmasses, we predict that any trend observed in Great Britain will be more dramatic in North America if it is due to global warming. With the exception of studies focusing on a small subset of species (Peterson 2003), we are aware of no large-scale multispecies analysis of distributional changes of breeding bird ranges in North America. We are also aware of no studies that utilize the North American Breeding Bird Survey (BBS) to test for the effects of global warming. To determine whether northward shifts in the range of birds observed in Great Britain is a global phenomenon as predicted under a global climate change scenario, we used BBS data to test the null hypothesis that breeding distributions of North American bird species are not moving northward.

Methods

We used data from the BBS (USGS 2001) to analyze geographic changes in breeding distributions of North American bird species. The BBS is a large landscape-level survey of birds in North America. Currently, BBS participants collect standardized data on an annual basis at over 3500 roadside survey routes in the continental United States, southern Canada, and northern Mexico. The BBS has an advantage over other large surveys in that it is conducted in a systematic fashion with highly trained observers. The BBS is a valuable scientific tool that has been used in environmental assessment to examine spatial and temporal trends over long time periods (Peakall 2000; Gaston & Blackburn 2002). It also has been used to examine distributional changes in bird species and community assemblages (Falardeau & Desgranges 1991; Cade & Woods 1997; Fortin et al. 2005; La Sorte & Boeklen 2005).

To exclude possible confounding geographical and climatic effects associated with large elevational shifts, we restricted our evaluation of distributional shifts to the two BBS regions (Central and East) east of the Rocky Mountains. After reviewing the list of potential species, we restricted the analysis to arboreal and semiarboreal insectivores and granivores of the orders Passeriformes, Columbiformes, Cuculiformes, Caprimulgiformes, and Piciformes. Birds in these groups make up the majority of species detected on BBS routes. Other potential candidate species, such as game birds, were excluded because their distributions have been influenced by documented human introductions and releases. Birds dependent on aquatic habitats were excluded because they have very different habitat and dietary requirements than more terrestrial species and breeding populations of many waterbirds may not be well sampled in roadside surveys.

Following Thomas and Lennon (1999), we divided the birds into species that had southern and northern breeding distributions. Birds with a southern range margin that was not south of approximately 34° N were classified as having a northern distribution (Fig. 1). Birds with a northern range margin that was not north of approximately 44° N were classified as having a southern distribution. These southern and northern limits of distributions were roughly 200 km north or south of the boundaries of the area sampled by the BBS (Fig. 1). This buffer was chosen to allow for the detection of range shifts to the north for species with a southern distribution and to the south for species with a northern distribution. Although it

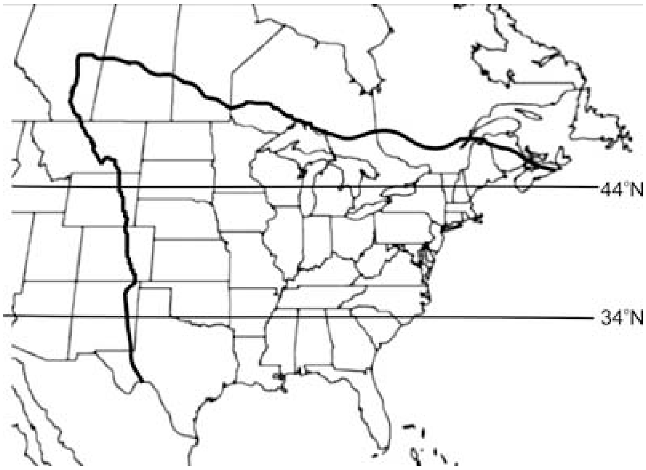

Figure 1. Sampling area (dark, solid line) for breeding bird distributions in North America.

would have been interesting to look for northward shifts of species with northern distributions, this analysis was not possible because of the lack of BBS routes in southern Canada.

If a group of species is experiencing overall range expansion, sampling only northward shifts of the northern extent of distributions would result in the appearance of a response to climate change when ranges are expanding for other reasons, such as changing patterns of land use or increased supplemental feeding. Likewise, if BBS routes are run more frequently or by more-skilled observers now than when the survey was initiated, probability of detection of individual species may have increased with time. This could result in increased detections at distributional margins in latter surveys, resulting in the appearance of range expansions. Following Thomas and Lennon (1999), we examined these possibilities by evaluating whether birds with northerly distributions were expanding their ranges southward. Such a pattern could not be explained by climatic warming but might be explained by land-use changes, supplemental feeding, or improvements in the detection of birds during surveys.

We evaluated shifts in species distributions between 1967 and 1971 and between 1998 and 2002. We did not include the first year the BBS was conducted (1966) because of the small number of routes that were surveyed. Routes used in the analysis were run three or more times within each time period to provide a reasonable chance of detecting the selected bird species. By analyzing only routes run in both time periods, we excluded the possibility that changes in distribution of routes could bias our results. For species with southern distributions, we identified the 10 northernmost routes in which the species was detected in each sampling period (following Thomas & Lennon 1999).

To analyze patterns across species, we tested the null hypothesis that the mean latitude of species with a southern distribution had not shifted northward between the two sampling periods. For this analysis, species was the unit of replication, and we averaged the 10 northernmost latitudes of routes on which the species was observed to obtain an average northern latitude for the extent of the species distribution. We tested the hypothesis that the average northern latitude for the years 1998–2002 was not greater than for the years 1967–1971, with a paired one-tailed t test. We used a paired t test because species was the unit of replication and each species had one mean average northern latitude for each time period. For analysis of distributional shifts of each individual species, we used an unpaired two-tailed t test to test the null hypothesis that the mean latitude of the 10 northernmost observations had not changed between the first and second sampling periods. We used a two-tailed test here because we were interested in determining how many individual species were experiencing range shifts in either direction. This comparison required the use of an unpaired t test because this analysis did not necessarily compare the same 10 routes in each period. These same procedures were used to identify the 10 southernmost routes where each species with a northern distribution was detected, and to test hypotheses related to shifts in the southern extent of their distributions.

We chose 10 routes to estimate the latitude of the species distributional margins so that our analysis would be as comparable as possible to the study conducted in Great Britain (Thomas & Lennon 1999). Increasing the number of sample routes would have increased the power to detect shifts in individual species ranges but it also would have include routes well into the core of the distribution of many species, which would not be useful for detecting distributional shifts. Replications of the analyses with 5, 10, and 20 routes yielded similar conclusions, aside from some increased ability to detect shifts of individual sizes with sample size. We present results based on only 10 routes. All statistical analyses and data manipulations were conducted with SAS (SAS Institute 2003).

Results

We identified 26 species with southern distributions and 29 species with northern distributions (Table 1) that satisfied our criteria for inclusion in the study. The northern margin of the southern birds showed a significant northward shift ($t = -2.67$, df $= 26$, $p = 0.0128$). Nine of the 27 bird species exhibited a significant northward shift in the northern extent of their distributions over the 26-year period between our samples (Table 1). Only two species that shifted the northern margin of their range had shifted southward (Table 1). The average shift northward of all southern birds was 2.35 km/year.

Table 1. Latitudinal shifts (km) of the margins of the breeding ranges of species with southern and northern distributions in central and eastern North America over a 26-year period.

Species	*Common name*	t	p	*Mean shift north*
Southern distribution				
Columbidae				
Columbina passerina	Common Ground-dove	0.51	0.617	−20.41 ± 40.82
Columbina inca	Inca dove	−4.62	0.0002[a]	254.18 ± 57.51
Picidae				
Melanerpes aurifrons	Golden-fronted Woodpecker	−0.33	0.747	33.40 ± 96.48
Caprimulgidae				
Caprimulgus carolinensis	Chuck-will's-widow	−0.98	0.341	14.84 ± 16.70
Tyrannidae				
Tyrannus forficatus	Scissor-tailed Flycatcher	0.50	0.621	−14.84 ± 29.69
Corvidae				
Corvus ossifragus	Fish Crow	−2.93	0.009[a]	131.73 ± 22.26
Icteridae				
Quiscalus mexicanus	Great-tailed Grackle	−4.71	0.0002[a]	333.96 ± 70.50
Quiscalus major	Boat-tailed Grackle	−0.50	0.623	94.62 ± 191.10
Emberizidae				
Aimophila aestivalis	Bachman's Sparrow	2.12	0.048[b]	−176.25 ± 83.49
Cardinalidae				
Passerina ciris	Painted Bunting	0.08	0.934	−1.86 ± 27.83
Thraupidae				
Piranga rubra	Summer Tanager	−2.42	0.026[a]	42.67 ± 16.70
Vireonidae				
Vireo griseus	White-eyed Vireo	−1.99	0.062	59.37 ± 29.69
Parulidae				
Limnothlypis swainsonii	Swainson's Warbler	−1.14	0.270	79.92 ± 68.65
Helmitheros vermivorus	Worm-eating Warbler	−1.69	0.108	48.24 ± 27.83
Vermivora pinus	Blue-winged Warbler	−4.92	0.0002[a]	85.34 ± 18.55
Dendroica dominica	Yellow-throated Warbler	0.35	0.731	−12.99 ± 33.40
Dendroica discolor	Prairie Warbler	−0.51	0.614	16.70 ± 33.40
Seiurus motacilla	Louisiana Water thrush	−0.95	0.355	25.97 ± 27.83
Oporornis formosus	Kentucky Warbler	−2.51	0.022[a]	148.43 ± 59.37
Icteria virens	Yellow-breasted Chat	1.27	0.220	−77.92 ± 61.23
Wilsonia citrina	Hooded Warbler	−3.12	0.006[a]	115.03 ± 40.82
Mimidae				
Mimus polyglottos	Northern Mockingbird	−1.67	0.112	94.62 ± 55.66
Troglodytidae				
Thryomanes bewickii	Bewick's Wren	3.72	0.002[b]	−111.32 ± 29.69
Paridae				
Baeolophus bicolor	Tufted Titmouse	−1.51	0.149	51.95 ± 35.25
Poecile carolinensis	Carolina Chickadee	−2.10	0.050[a]	53.80 ± 25.97
Sylviidae				
Polioptila caerulea	Blue-gray Gnatcatcher	−13.83	<0.0001[a]	313.55 ± 22.26
Northern distribution				
Cuculidae				
Coccyzus erythropthalmus	Black-billed Cuckoo	−3.75	0.002[a]	276.44 ± 72.36
Picidae				
Sphyrapicus varius	Yellow-bellied Sapsucker	3.49	0.003[b]	−57.51 ± 14.84
Tyrannidae				
Empidonax flaviventris	Yellow-bellied Flycatcher	−1.48	0.157	40.82 ± 27.83
Empidonax alnorum	Alder Flycatcher	7.56	<0.0001[b]	−192.95 ± 24.12
Empidonax trailii	Willow Flycatcher	−2.23	0.039[a]	135.44 ± 59.37
Corvidae				
Perisoreus canadensis	Gray Jay	−1.28	0.217	18.55 ± 48.28
Icteridae				
Dolichonyx oryzivorous	Bobolink	3.22	0.005[b]	−87.20 ± 27.83
Fringillidae				
Carpodacus purpureus	Purple Finch	0.58	0.566	−24.12 ± 38.96
Loxia leucoptera	White-winged Crossbill	3.53	0.002[b]	−159.56 ± 44.53
Carduelis pinus	Pine Siskin	2.17	0.044[b]	−185.53 ± 85.34

continued

Table 1. (continued)

Species	*Common name*	t	p	*Mean shift north*
Emberizidae				
Pooecetes gramineus	Vesper Sparrow	−1.12	0.277	76.07 ± 68.65
Passerculus sandwichensis	Savannah Sparrow	0.00	1.000	0 ± 98.33
Zonotrichia albicollis	White-throated Sparrow	−2.01	0.060	51.95 ± 25.97
Melospiza lincolnii	Lincoln's Sparrow	1.11	0.281	−22.26 ± 20.41
Melospiza georgiana	Swamp Sparrow	−0.56	0.585	24.12 ± 44.53
Cardinalidae				
Pheuticus ludovicianus	Rose-breasted Grosbeak	0.54	0.595	−20.41 ± 37.11
Parulidae				
Vermivora chrysoptera	Golden-winged Warbler	−2.74	0.013[a]	218.93 ± 81.63
Vermivora ruficapilla	Nashville Warbler	−0.67	0.510	18.55 ± 25.97
Vermivora peregrina	Tennessee Warbler	−1.58	0.131	51.95 ± 33.40
Dendroica tigrina	Cape May Warbler	−0.68	0.508	29.69 ± 42.67
Dendroica coronata	Yellow-rumped Warbler	3.98	0.001[b]	−90.91 ± 22.26
Dendroica magnolia	Magnolia Warbler	0.55	0.590	−22.26 ± 42.67
Dendroica cerulea	Cerulean Warbler	−0.15	0.885	14.84 ± 96.47
Dendroica castanea	Bay-breasted Warbler	−0.11	0.917	3.71 ± 25.97
Seiurus noveboracensis	Northern Waterthrush	−0.23	0.821	9.28 ± 42.67
Oporornis philadelphia	Mourning Warbler	2.08	0.053	−37.11 ± 16.70
Paridae				
Poecile atricapillus	Black-capped Chickadee	−0.03	0.978	0 ± 24.11
Poecile hudsonica	Boreal Chickadee	−1.21	0.244	42.67 ± 35.25
Turdidae				
Catharus ustulatus	Swainson's Thrush	−2.39	0.028[a]	141.00 ± 57.51

[a] *Indicates species that exhibited a significant ($p < 0.05$) distributional shift north.*
[b] *Indicates species that exhibited a significant ($p < 0.05$) distributional shift south.*

The southern distributional limits of the species with northern distributions showed no significant shift to the south ($t = -0.52$, df $= 28$, $p = 0.6076$). Although the distributional limit of six species exhibited a significant shift south, the distributional margin of four species shifted northwards (Table 1), confirming that there was no general trend in distributional shifts across species.

Discussion

Our results suggest that the northern margins of breeding birds in North America have been shifting northward over recent decades. This observation is consistent with the results of Thomas and Lennon (1999) from Great Britain. The observation of two independent northward expansions of distributions of multispecies groups supports the contention of Thomas and Lennon (1999) that the northward expansions are due to climatic warming. It is difficult to identify other factors that would be expected to cause the distributions of so many species to shift northward on two continents.

The northward shift in the distributions of North American and British avian species does not appear to be multidirectional shifts in ranges due to population expansions, land-use changes, or improvements in species detection during surveys. If land-use changes or growing population were causing an overall range expansion, one would expect to see species with northern distributions shifting southward (Thomas & Lennon 1999). Likewise, the impression of a range expansion, caused by better censusing of birds at their range margins in the latter sampling period, should have resulted in southward shift of species with northern distributions. Such a southward shift of distributions was not observed in our study or in Great Britain (Thomas & Lennon 1999). It is important to acknowledge that although our and Thomas and Lennon's (1999) use of species with northern distributions as a control for the possibility of overall range expansions might explain northward range expansions, this represents an imperfect control. This use assumes that as a group, species with northern and southern distributions have similar biological requirements aside from those associated with climate; the relativity of this assumption is difficult to evaluate.

We expect that some of the northward range expansions of individual species are due to factors other than climate change. Even though some of the results of individual species might be due to other factors, there is a clear tendency across species for a northward expansion of species with southern distributions. This trend is remarkably similar to a comparable study conducted in Great Britain and is difficult to explain without invoking climatic change.

Across species, northern distributions were expanded northward an average 2.35 km/year. In Britain the northern margins of bird species were shifting northward at an average of 0.945 km/year over roughly the same period of time (Thomas & Lennon 1999). Given that recent warming is greatest over continents (IPCC 2001), one would expect to see more rapid shifts over North America then Great Britain.

Although the northward shifts in the observations of birds in North America and Great Britain appear to provide evidence that climate change is affecting the distributions of avian species, the implications for the viability of these species is unclear. Birds are extremely mobile that allows them to move in response to climatic conditions; thus, they could certainly adjust their locations in response to warming trends. Furthermore, the levels of warming do not appear to be so great they are forcing birds to abandon the southernmost portions of their distributions. Nevertheless, the ability of a species to rapidly shift distributions may not be as important as the degree to which it is dependent on other species that are not capable of rapid distributional shifts (Root et al. 2003). Mobile species dependent on habitat types that have become fragmented are prone to extinctions associated with changing climate (McLaughlin et al. 2002). It is difficult to predict when or if the forces behind the distributional shifts of birds we report here may lead to extinctions of local populations.

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