

Connecticut Birds and Climate Change: Bergmann's Rule in the Fourth Dimension

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Abstract - Bergmann's Rule notes a correlation between animal size reduction and geographical temperature increase in three dimensions. This study examines bird size change in the context of temperature change in a fourth dimension: time. The body size of six passerine bird species found year-round in Connecticut was measured using museum specimens collected between 1874 and 2009, during which time mean temperature in Connecticut increased by 0.94 °C (SD = 0.71). Mean wing length significantly decreased from a pre-1955 period (1874-1952) to a post-1955 period (1958-2010) for all species combined ($P < 0.0025$) and for three of the six species ($P < 0.025$), suggesting that some Connecticut passerines exhibit an evolved size decrease since 1874. This study joins a growing body of research suggesting a causal relationship between climate change and animal morphological change, and it demonstrates the importance of museum specimens in documenting such global trends.

Introduction

Karl Bergmann (1847) observed geographic variation in body size of birds and mammals and noted that smaller animals live in warmer climates, while larger animals inhabit colder regions. He interpreted this correlation to derive from a scaling relationship. Surface area increases as the square of the radius while volume increases as the cube, so a smaller body is proportionally better at externally heating or cooling (Hamilton 1961, James 1970, Olson et al. 2009). Until recently, studies examining such correlations between body size and temperature were concerned almost entirely with three-dimensional temperature gradients based on variation in latitude and altitude (e.g., Meiri and Dayan 2003). However, recent studies have introduced a fourth dimension—namely, time—to examine body size variation in the context of climate change (reviewed in Millien et al. 2006). Given climate warming, it is logical to expect that studies examining species from one region, such as Connecticut, would find trends of decreasing body size over time. A group of such studies have examined birds specifically: those analyzing multiple bird species predominantly show a decrease in body size over time (Gardner et al. 2009, Koontz et al. 2001, Salewski et al. 2010, Van Buskirk et al. 2010, Yom-Tov 2001), while those reporting on one or two species have had mixed results, with some showing a decrease (Teplitsky et al. 2008, Yom-Tov et al. 2006) and some no change or an increase (Guillemain et al. 2010, Kanuscak et al. 2004).

No compilation of body size measurements is available for North American birds spanning a century or more. Using museum specimens, I here report the

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trends in body size of birds in the state of Connecticut over the last 136 years and find significant decreases in a standard measure of body size for three of six species and for the aggregate combined data from all six species.

Methods

Connecticut bird specimens were studied from the collections of the Yale University Peabody Museum (YPM) and the University of Connecticut (UConn). The study focused on songbirds (order Passeriformes) from six different families. I limited analysis to birds that were year-round residents in Connecticut and for which 15 or more specimens were available in both of two time intervals (1874–1952 and 1958–2010). These intervals were chosen with midpoint 1955, a year in which temperature began to increase steeply (Brohan et al. 2006, Garnaut 2008, Hansen et al. 2010, NCDC 2010). To test for sensitivity, three different midpoints were tested—1945, 1955, and 1965—in each case, with a five-year gap separating the two resulting time periods (for example, for midpoint 1945, the two time periods were 1874–1942 and 1948–2010).

Connecticut temperature data were obtained from the National Climatic Data Center of the United States Department of Commerce (NCDC 2010). Measured temperature data for Connecticut were not available for years 1874–1894, a time period during which 158 of the 574 total bird specimens were collected. Therefore, the temperature change trend during that time interval was approximated from global and United States temperature data, which uniformly report minimal temperature change between 1874 and 1894 (Brohan et al. 2006, Garnaut 2008, Hansen et al. 2010). The average Connecticut temperature for the first ten years for which such data exist, 1895–1904, was $8.62\text{ }^{\circ}\text{C} \pm 0.62$. Because this was a figure that remained fairly constant over this period, it was assumed to have been the constant temperature during the unknown interval. With this approximation, mean annual temperature in Connecticut increased significantly ($P < 0.0025$) from the 1874–1952 period ($8.89\text{ }^{\circ}\text{C}$) to the 1958–2010 period ($9.38\text{ }^{\circ}\text{C}$) (Fig. 1H). Second, to control for the possibility that this assumption impacted the results, analyses of significance were also run with a later cutoff date of 1895 rather than 1874. Therefore, taking into account both sensitivity analyses, six analyses were performed with midpoints 1945, 1955, or 1965 and cutoff dates of 1874 or 1895.

Six species were included: *Cyanocitta cristata* L. (Blue Jay, family Corvidae); *Poecile atricapillus* L. (Black-capped Chickadee, Paridae); *Sitta carolinensis* Latham (White-breasted Nuthatch, Sittidae); *Passer domesticus* L. (House Sparrow, Passeridae); *Carpodacus purpureus* Gmelin (Purple Finch, Fringillidae), and *Quiscalus quiscula* L. (Common Grackle, Icteridae). Measurements were taken for approximately equal numbers of males and females except for the Common Grackle, which exhibits relatively strong sexual dimorphism in size (Peer and Bollinger 1997) and for which the available sample size was sufficient only for males. Only breeding-season specimens were used for the Blue Jay and Common Grackle, which are considered migrants (Peer

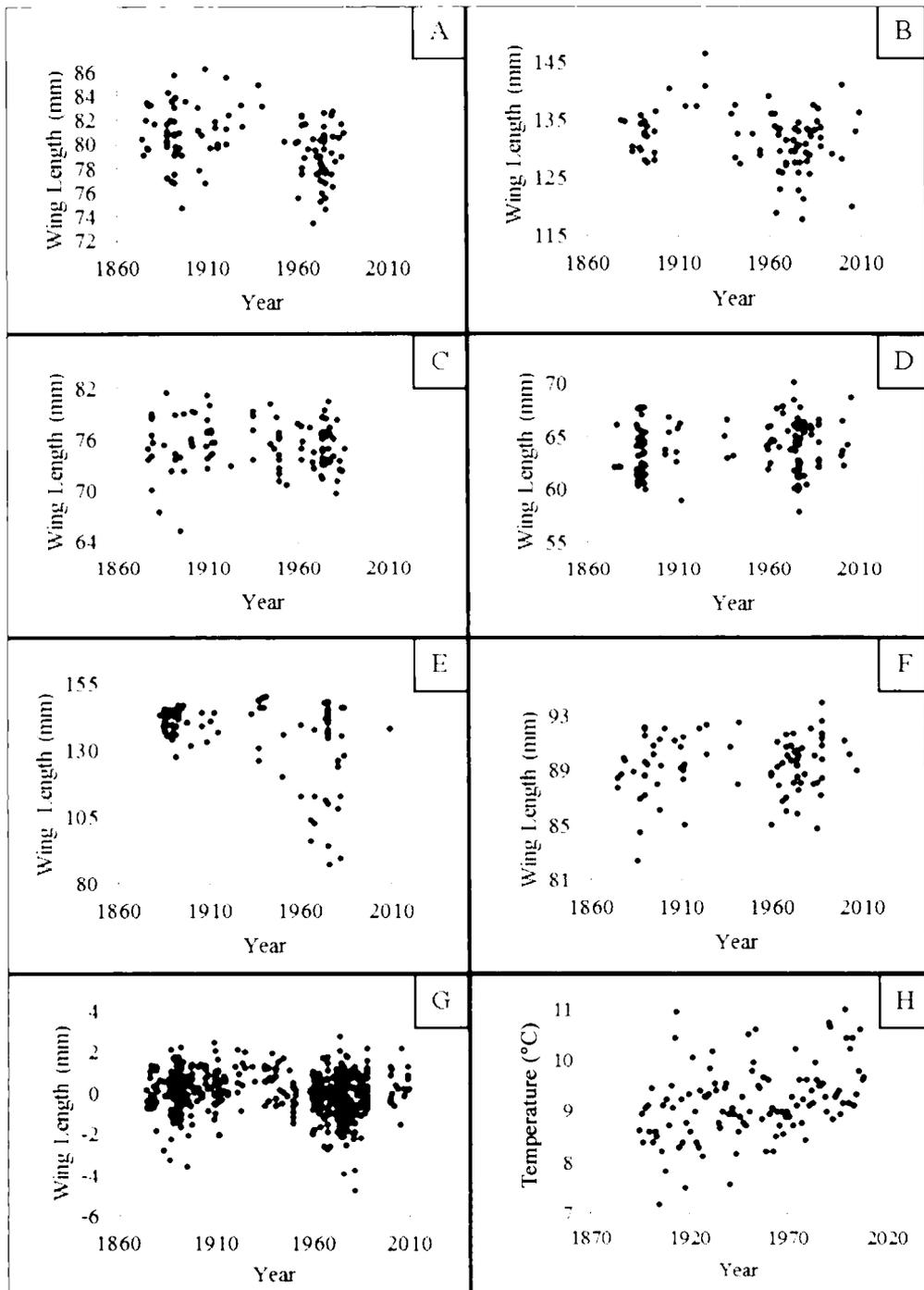


Figure 1. Wing chord length (mm) versus year for each species and combined data. A. Purple Finch (*Carpodacus purpureus*); B. Blue Jay (*Cyanocitta cristata*); C. House Sparrow (*Passer domesticus*); D. Black-capped Chickadee (*Parus atricapillus*); E. Common Grackle (*Quiscalus quiscula*); F. White-breasted Nuthatch (*Sitta carolinensis*); G. Combined standardized data; H. Mean annual temperature in the state of Connecticut from 1895 to 2009 (NCDC 2010).

and Bollinger 1997, Tarvin and Woolfenden 1999). For the remaining three species, specimens were collected in approximately even numbers throughout the year. The Purple Finch is irruptive and experiences cycles of migration in Canada and the southern United States, but the Purple Finch's summer and winter ranges overlap in the northern United States, where Purple Finches are banded year-round (Kennard 1977, Wootton 1996). Specimens of Purple Finch from all seasons were included; however, it is possible that birds collected in the winter were from different latitudes than those collected in the summer. Therefore, inferences drawn from Purple Finch data are tentative.

Wing length was used as an indicator of bird size, following prior studies (see Ashton 2002 for discussion). This metric has been criticized because wing length can be affected by migratory tendencies, habitat occupied, and age (Aldrich 1984, Hamilton 1961, Meiri and Dayan 2003, Merom et al. 1999, Zink and Remsen 1986), but it is the most frequently used proxy for body size in birds (Ashton 2002), is commonly used in studies of birds and climate change (e.g., Guillemain et al. 2010, Van Buskirk et al. 2010), and is significantly related to other measurements of body size (e.g., Graves 1991, Power 1969, Rand 1936). Unflattened wing chord length was measured to the nearest 0.1 mm using digital calipers (Pyle et al. 1987). Only adult, non-molting individuals with undamaged primaries and mature plumage were measured, with maturity being determined based on relevant species-specific characteristics (Pyle et al. 1987). Individual measurements were standardized within each species by subtracting the species mean from each individual measurement and dividing the resulting difference by the species standard deviation, producing a distribution with a mean of 0 and a variance of 1 for each species. This procedure allows combined analysis across species because each standardized data point represents the number of standard deviations away from the mean.

The statistical significance of difference between groups was tested using the two-sample *t*-test. Significance was tested for each species and the overall standardized data, and is reported in detail for the intervals 1874–1952 and 1958–2010 (Table 1). A *t*-test was performed for the slope of regression line for wing length versus year for each species. The Bonferroni correction for multiple testing was applied to establish significance levels. With two comparison groups, the usual significance threshold of 0.05 was divided by 2 to arrive at an adjusted threshold of 0.025. The same significance tests were performed for the 5 alternative scenarios described above used to test for sensitivity (Table 2).

Results

Wing length measurements were obtained for 574 specimens, with 276 assigned to the 1874–1952 group and 298 to the 1958–2010 group (Table 1). The percent change in mean wing length ranged from -6.7% to 0.95%. Table 1 presents the mean wing length values for each species for 1874–1952 and 1958–2010, along with the percent decrease between the means. Between those two time periods, mean annual temperature in Connecticut increased significantly from 8.89 °C to 9.38 °C ($P < 0.0025$); further, all six analyses showed significant

temperature increase between the earlier and later time periods (Table 2), indicating that the selection of the 1955 midpoint and the use of an assumed constant temperature prior to 1895 did not bias the results. A significant ($P < 0.025$) temporal decline in body size was detected for three species, Purple Finch, Common Grackle, and Blue Jay, with a fourth, House Sparrow, showing a non-significant trend in the same direction (Table 1). Further, the standardized data for all six species combined show a statistically significant decrease in mean wing length ($P < 0.0025$; Table 1).

The analyses of the five additional sensitivity scenarios showed that the above results were not biased by the choice of midpoint and the temperature assumptions. All scenarios included the same qualitative results and retained significance in 19 of 20 instances (Table 2). The sole exception was the Common Grackle for the interval with midpoint 1965 and cutoff 1895 (1895-1962 and 1968-2010), a loss of significance that was probably due to highly reduced sample size. Additionally, the significance levels with the 1955 midpoint were greater than or equal to those of the other two midpoints in 7 of 8 instances for the 1874 cutoff and 5 of 8 instances for the 1895 cutoff (Table 2).

Individual wing length measurements were plotted against time for each species (Fig. 1) and a linear regression calculated. This procedure was also used to examine the overall combined species data (Fig. 1G). Negative slopes were detected in four of six species (Blue Jay, Purple Finch, Common Grackle, and House Sparrow), but none of the linear regressions were statistically significant.

Discussion

To my knowledge, this is the first study examining climate change and body size in North American birds over a century-long interval. The aggregate combined data for all species demonstrated a significant decrease in mean wing length from 1874-1952 to 1958-2010. Additionally, three of the six studied Connecticut passerine species demonstrated a statistically significant decrease; no statistically

Table 1. Comparison of mean wing chord length values from 1874-1952 to 1958-2010, with percent change and significance levels. * indicates significant difference. The bottom row (total) represents the standardized pan-species data (see Methods section for more details); the values represent the number of standard deviations away from the mean, not wing length per se. Thus, negative values are possible and the percent change is not meaningful.

| Species | Total | Number of Individuals | | Mean wing length (mm) | | Percent change | <i>P</i> |
|-------------------------|-------|-----------------------|-----------|-----------------------|-----------|----------------|------------|
| | | 1874-1952 | 1958-2010 | 1874-1952 | 1958-2010 | | |
| Purple Finch | 104 | 55 | 49 | 81.0 | 79.0 | -2.4% | < 0.00025* |
| Blue Jay | 55 | 18 | 37 | 134.3 | 130.0 | -3.2% | < 0.025* |
| House Sparrow | 103 | 58 | 45 | 75.6 | 75.1 | -0.79% | 0.4 |
| Black-capped Chickadee | 131 | 61 | 70 | 63.4 | 64.0 | 0.95% | 0.1 |
| Common Grackle | 97 | 45 | 52 | 141.8 | 132.4 | -6.7% | < 0.0025* |
| White-breasted Nuthatch | 84 | 39 | 45 | 89.3 | 89.3 | 0% | N/A |
| Total (standardized) | 574 | 276 | 298 | 0.149 | -0.139 | N/A | < 0.0025* |

Table 2. Sensitivity test showing significance levels (*P*-values) from the analysis of 6 different time intervals varying in midpoint and cutoff dates.

| Tested time period intervals | Midpoint | Cutoff | Purple Finch | Blue Jay | House Sparrow | | Black-capped Chickadee | | Common Grackle | White-breasted Nuthatch | | Overall Standardized Data | | Temperature |
|------------------------------|----------|--------|--------------|-----------|---------------|-----------|------------------------|------|----------------|-------------------------|-----------|---------------------------|-----------|-------------|
| | | | | | Sparrow | Chickadee | Nuthatch | Data | | | | | | |
| 1874-1952; 1958-2010 | 1955 | 1874 | <0.00025* | <0.0025* | 0.4 | 0.1 | 0.1 | 0.1 | <0.00025* | 1.0 | <0.0025* | <0.00025* | <0.00025* | |
| 1895-1952; 1958-2010 | 1955 | 1895 | <0.0025* | <0.025* | 0.3 | 0.9 | 0.9 | 0.3 | <0.0025* | 0.3 | <0.00025* | <0.025* | <0.025* | |
| 1874-1942; 1948-2010 | 1945 | 1874 | <0.00025* | <0.0025* | 0.3 | 0.1 | 0.1 | 0.1 | <0.00025* | 1.0 | <0.00025* | <0.00025* | <0.00025* | |
| 1895-1942; 1948-2010 | 1945 | 1895 | <0.0025* | <0.00025* | 0.2 | 0.9 | 0.9 | 0.3 | <0.00025* | 0.3 | <0.00025* | <0.0025* | <0.0025* | |
| 1874-1962; 1968-2010 | 1965 | 1874 | <0.00025* | <0.025* | 0.3 | 0.3 | 0.3 | 0.4 | <0.0025* | 0.4 | <0.0025* | <0.00025* | <0.00025* | |
| 1895-1962; 1968-2010 | 1965 | 1895 | <0.0025* | <0.0025* | 0.2 | 0.8 | 0.8 | 0.08 | 0.08 | 1.0 | <0.0025* | <0.00025* | <0.00025* | |

significant effect was observed for the other three species. Although the linear regressions did not have statistically significant slopes, there is no a priori basis for contending that the response need be linear (Nevoux et al. 2008). Moreover, the temperature record is variable, and birds may be responding to features of the variability as opposed to trends. Nonetheless, the data demonstrate that some Connecticut passerines have decreased in size over the last century.

As discussed in the prior section, the sensitivity tests confirmed that the above results were not biased by our time period selections and assumptions. However, it is worth noting that for the three species that demonstrated significant decreases and for the standardized data, the significance levels with the 1955 midpoint were greater than or equal to those of the other two midpoints in 13 of 16 instances (Table 2). Since the 1955 midpoint represents the time at which temperature began to increase steeply (Brohan et al. 2006, Garnaut 2008, Hansen et al. 2010, NCDC 2010), this trend supports the hypothesis that temperature change may be directly or indirectly related to bird body size change in Connecticut.

These results mirror similar outcomes reported for multiple bird species over a range of time intervals. Studies reporting decreasing body size over time include examinations of Israeli passerines since 1950 (Yom-Tov 2001), British passerines since 1968 (Yom-Tov et al. 2006), Australian passerines over the last century (Gardner et al. 2009), central European passerines since 1971 (Salewski et al. 2010), a phylogenetically diverse assemblage of western Pennsylvanian birds since 1961 (Van Buskirk et al. 2010), goshawks from Denmark over the last century (Yom-Tov and Yom-Tov 2006), and gulls from New Zealand since 1958 (Teplitsky et al. 2008). Strong support for the effect of climate change on mammalian body size is also available for woodrats (Brown 1968; Brown and Lee 1969; Smith and Betancourt 2006; Smith et al. 1995, 1998). The pattern of decreasing body size is well established, but the underlying cause remains to be determined.

Temperature differences may directly drive the body size effect. Ambient temperature imposes physiological limits upon birds regardless of their body size, diet, or habitat, and there is evidence that winter survivorship is a key selective pressure for body size change (Root 1988). Support for this hypothesis comes from the lifestyle of the three species that did not demonstrate significant body size decreases in this study: the Black-capped Chickadee, White-breasted Nuthatch, and House Sparrow. Since these three species are cavity nesters and roosters (Foote et al. 2010, Grubb and Pravosudov 2008, Lowther and Cink 2006), their shelters may protect them from direct effects of very hot (or very cold) temperature. Cavity nesting would be particularly advantageous if winter survivorship (see Root 1988) is in this case a strong selective factor.

Moreover, all of the species that failed to exhibit a size decrease live in association with human dwellings. Data from Project FeederWatch (PFW) in Connecticut reveal that these three species are seen at a higher percentage of human dwellings (Black-capped chickadee, 87.5%; White-breasted Nuthatch, 74%; House Sparrow, 45%) than two of the remaining three species (Common Grackle, 19%; Purple Finch, 11%; see Wells et al. 1998 for details of PFW protocol).

While the Blue Jay also commonly frequents human dwellings (76%), it is larger than the other three species and is not a cavity nester, two characteristics that may have prevented the Blue Jay from benefiting from an advantage conferred upon the White-breasted Nuthatch, House Sparrow, and Black-capped Chickadee. It is possible that association with humans may have ameliorated a direct temperature effect through access to ready-made high-quality shelters which the Blue Jay could not use. Thus, temperature change may directly drive body size changes in Connecticut passerines.

It is possible that birds are responding to features of the environment rather than mean temperature change. Environmental productivity, a factor that depends on temperature (e.g., Boisvenue and Running 2006), is known to affect body size (Boyce 1978, Lindsey 1966, Olson et al. 2009, Rosenzweig 1968). Primary productivity controls net food availability, so a decrease in productivity, causing less food to be available, may select for smaller-sized individuals. Further, access to bird feeders, with readily available food regardless of productivity, may have conferred an advantage upon the species which did not demonstrate a size decrease, since those three live in close association with humans (Project Feeder Watch data, see Wells et al. 1998 for details of protocol). It should also be noted that the three large-bodied species decreased in size significantly; perhaps they are more susceptible to general environmental selection for small individuals. Other factors that are correlated with body size change include species richness (Brown and Nicoletto 1991, Olson et al. 2009), predator-prey interactions and competition (McNab 1971), and altitudinal variation (Blackburn and Ruggiero 2001, Rand 1936, Traylor 1950). Of these, my focus on a narrow geographic region, Connecticut, likely removes any effect of altitudinal (or latitudinal) variation in body size. However, it is possible that one of the other environmental factors, rather than mean temperature change, drove the body size effect.

Temperature and environmental change also affect patterns of migration and range boundaries (Blackburn et al. 1999, Root 1988). For example, minimum January temperatures have been shown to be related to range expansion (Root 1988). Therefore, environmental factors leading to migratory shifts and range expansion may have driven the effect found herein, perhaps through a tendency of smaller birds to expand farther north. However, our sample deliberately included only breeding-season specimens of migratory birds, and all of the studied species for which data are available have not demonstrably changed their ranges or migratory habits (Hitch and Leberg 2007, Poole 2005, Sage 1913). Nevertheless, it is still possible that poorly understood range dynamics, especially of irruptive or partially migratory species, could affect inferred patterns of body size evolution.

Finally, this pattern may not be associated with temperature or climate, but rather may be driven by other long-term trends over the past century, notably the increased density of humans in Connecticut. Human activity unquestionably alters habitat and food availability. However, the species were selected to represent a variety of different diets and habitats, a selection process that may be expected to limit the influence of specific habitat and diet requirements.

Moreover, it is not obvious why human density should unidirectionally select for smaller size. Rather, the more parsimonious explanation is that the Connecticut data reported here reflect the effect of a larger (regional or global) trend, such as climate change. If so, this study joins a growing body of support for a causal relationship between climate change and changes in animal phenology, physiology, distribution, and morphology (reviewed by Hughes 2000, McCarthy 2001, Millien et al. 2006), highlights the importance of museum specimens in documenting such historical trends, and supports the application of Bergmann's rule into the fourth dimension.

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