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Authors: Kirchman, Jeremy J., and Schneider, Kathryn J.

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RANGE EXPANSION AND THE BREAKDOWN OF BERGMANN'S RULE IN RED-BELLIED WOODPECKERS (*MELANERPES CAROLINUS*)

JEREMY J. KIRCHMAN[1,3] AND KATHRYN J. SCHNEIDER[2]

ABSTRACT.—Previous studies of northward expansion of breeding ranges of North American bird species have focused on correlated changes in climate and land-use, but very few studies have examined patterns of morphological change within the context of range expansion. We used data from museum specimens to examine geographic and temporal variation in body size of the Red-bellied Woodpecker (*Melanerpes carolinus*), a species undergoing dramatic range expansion. We plotted georeferenced occurrence data from Christmas Bird Counts (winter distributions going back to the year 1900), USGS Breeding Bird Surveys (summer distributions since 1966), and the holdings of twenty-six natural history museums (year-round distributions since 1867) to document the historic range of *M. carolinus* in decade increments. Christmas Bird Counts, but not museum specimens, indicate a trend of slow northward expansion beginning as early as the 1910s, and all data sets show rapid expansion to the north and west since the 1950s (average of 0.85° N latitude per decade and 1.06° W longitude per decade). Geographic variation in body size of specimens collected prior to the period of rapid expansion follows Bergmann's rule, with larger birds occurring in northern latitudes. This pattern breaks down in the sample of birds collected after the onset of rapid expansion, suggesting that warming temperatures since the 1950s have enabled northward range expansion in a species previously limited by cold. Birds collected at the northern boundary of their range before 1940 were larger than birds collected in recent decades from the same latitudes, further supporting the hypothesis that Red-bellied Woodpeckers have been released from a former ecological or physiological constraint in the face of climate warming. *Received 31 May 2013. Accepted 20 December 2013.*

Key words: Bergmann's rule, Breeding Bird Survey, Christmas Bird Count, climate change, geographic variation, range expansion, Red-bellied Woodpecker.

Long-term data sets documenting bird distributions reveal decade-scale dynamics in the ranges of many species. Museum specimen collections and repeated scientific surveys (e.g., Tingley et al. 2009), as well as data from citizen-science projects such as repeated state breeding bird atlases, the Cornell Lab of Ornithology's Project Feeder Watch, National Audubon Society's Christmas Bird Count and the USGS Breeding Bird Survey, have been used to examine the patterns and potential causes of range shifts in birds (Root and Weckstein 1994; Hitch and Leberg 2007; Mehlman 1997; LaSorte and Thompson 2007; Zuckerburg et al. 2009, 2011). The majority of range shifts in diverse species assemblages are consistent with expected response to recent climate warming (Parmesan and Yohe 2003, Root et al. 2003), but some species have moved in the opposite direction and many species have not moved at all (McGowan and Zuckerberg 2008). The northward expansion of some elements of the ''Carolinian avifauna'' is a particularly compelling case of range shift in the face of climate warming. Northward movement of several presumably cold-limited species endemic to the southeastern United States has long been recognized (Beddall 1963, Robinson 1977, Kricher 1981, Stiles 1982, David et al. 1990, Ellison 1993, Jackson and Davis 1998). But whereas several studies have found that latitudinal and altitudinal range shifts can be explained by models that include climate variables, changes in land use, habitat structure, bird feeding, and interspecific competition are also important drivers of distributional changes in birds (Emlen et al. 1986, Root and Weckstein 1994, Hitch and Leberg 2007, Zuckerberg et al. 2009, Zuckerberg et al. 2011).

Distribution shifts are interesting, because they provide insights regarding the ecological and evolutionary factors that limit species ranges (Holt 2003). Root (1988a,b) found that the northern range boundaries of 148 bird species wintering in the United States were strongly associated with average minimum January temperature and that the northern limits of many species' ranges were restricted by metabolic rate. Selection for cold tolerance, in addition to determining range limits, is the likely basis for latitudinal clines in body size within species such as in Bergmann's rule, the observation that larger

[1] New York State Museum, 3140 Cultural Education Center, Albany, NY 12230, USA.

[2] Department of Biology, Chemistry and Physics, Hudson Valley Community College, 80 Vandenburgh Avenue, Troy, NY 12180, USA.

[3] Corresponding author; e-mail: jkirchma@mail.nysed.gov

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individuals are found in colder regions in geographically widespread species of birds and mammals (Bergmann 1847, James 1970). As organisms increase in size, they grow more rapidly in volume than surface area. Because heat loss depends on surface area, large animals with a smaller surface to volume ratio will be at an advantage in colder climates. The generality of Bergmann's rule has been disputed (Meiri et al. 2009), but Meiri and Dayan (2003) found it to be the pervasive pattern of geographic variation in a sample of 94 bird species, and Zink and Remsen (1986) and James (1970) showed that it fits the morphological patterns observed in many non-migratory bird species, and is especially prevalent in woodpeckers. Ramirez et al. (2008) used published and estimated mean body masses for >3800 bird species from North and South America to confirm that birds (species in this case, not individuals) are larger closer to the poles, and that the trend is stronger in winter than in summer because of seasonal range shifts of migratory species. They concluded that winter temperatures drive the latitudinal gradient of body size in birds.

The link between climate and body size in birds has led some researchers to investigate changes in body size over recent decades. McCoy (2012) measured museum specimens collected in Connecticut before and after the onset of rapidly warming temperatures (defined in that paper as 1955), and found significant reductions in wing length (a proxy for body size) over time in three species (Purple Finch *Haemorhous purpureus*, Blue Jay *Cyanocitta cristata*, and Common Grackle *Quiscalus quiscula*). Yom-Tov et al. (2006) found reductions in body weight of four species banded in England over a 30-year period, and Van Buskirk et al. (2010) found steady reductions in mass and wing-chord over a 45-year period for several species captured at a migration monitoring station in Pennsylvania. In these studies, declining body size was interpreted as evidence of weakening selection on body size because of climate warming. The trend of shrinking body size with climate warming at one geographic locality is consistent with predictions based on Bergmann's rule, but no study has examined recent changes in body size variation across latitude, or investigated how range dynamics might alter geographic patterns of body size or other morphological characters under apparent selection for cold-tolerance.

In this study we ask whether the period of northward range expansion by Carolinean bird species has been accompanied by morphological change consistent with easing of selection for cold-tolerance. To address this question we simultaneously examined range dynamics and morphological evolution of the Red-bellied Woodpecker (*Melanerpes carolinus*) in North America on decade to century time scales using three long term data sets: National Audubon Society North American Christmas Bird Counts (CBC), United States Geological Survey Breeding Bird Surveys (BBS), and specimen data from North American natural history museums. Red-bellied Woodpeckers are non-migratory and are currently considered monotypic (Short 1982, Shackelford et al. 2000), although four subspecies were recognized by the American Ornithologists' Union (AOU; 1957) based on the work of Burleigh and Lowery (1944) and Koelz (1954). These authors focused mostly on plumage differences but geographic variability in bill length and wing length is known to occur. Males average slightly larger than females, but Pyle (1997) describes the variation as ''broadly clinal and obscured by individual variation.'' Jackson and Davis (1998) suggested that range expansion in Red-bellied Woodpeckers began in the early 1900s, the result of a combination of reforestation, Dutch elm disease, climate change, and bird feeding. Emlen et al. (1986) identified latitude as the single most important environmental correlate of density of Red-bellied Woodpeckers surveyed along a latitudinal transect in the bottomland forests of the Mississippi River valley. The study by Zuckerberg et al. (2009) concluded that Red-bellied Woodpeckers were among the most climate restricted species, being strongly limited by the average minimum temperature throughout a winter season. Their analysis of winter-long changes in site occupancy also showed that Red-bellied Woodpeckers had a higher probability of extirpation at colder sites even though they regularly visited supplemental food sources.

We plotted occurrence data to document the historic range of the Red-bellied Woodpecker in decade increments. We then measured museum specimens collected throughout the species' range both before and after the onset of northward expansion. Our goals were to measure as many study skins as possible from newly colonized areas to see if the ''pioneers'' had physical characteristics that were different from others in

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TABLE 1. Museum holdings of specimens used to document historical occurrence of Red-bellied Woodpeckers. Institutions marked with * provided access to or loans of specimens used in morphological analyses.

Institution	Location	Approximate number of specimens
American Museum of Natural History*	New York, NY	227
Academy of Natural Sciences	Philadelphia, PA	87
Bell Museum of Natural History*	Minneapolis, MN	35
Columbia Greene Community College*	Hudson, NY	9
Carnegie Museum of Natural History*	Pittsburg, PA	83
Canadian Museum of Nature*	Ottawa, ON	12
Cleveland Museum of Natural History	Cleveland, OH	42
Cornell Museum of Vertebrates*	Ithaca, NY	66
Delaware Museum of Natural History*	Wilmington, DE	38
Denver Museum of Natural Science*	Denver, CO	32
Field Museum of Natural History*	Chicago, IL	317
Illinois State University	Normal, IL	12
University of Kansas*	Lawrence, KS	171
Museum of Comparative Zoology*	Cambridge, MA	352
Michigan State University Museum	Lansing, MI	15
New York State Museum*	Albany, NY	16
Royal Ontario Museum	Toronto, ON	88
Sam Noble Museum of Natural History*	Norman, OK	174
University of Michigan Museum of Zoology*	Ann Arbor, MI	183
University of Nebraska State Museum*	Lincoln, NE	15
US National Museum, Smithsonian Institution	Washington, DC	516
Yale Peabody Museum*	New Haven, CT	30

the population and to see if the recent colonization of more northern latitudes was accompanied by changes in body size. Climatological data clearly show that winter temperatures have risen steadily in North America (Intergovernmenatl Panel on Climate Change 2007). If temperature constraints influence body size, we would expect birds collected in recent decades, now freed from the restrictions of a cold climate, to be smaller than birds that occupied northern borders of the species range during colder times.

METHODS

In August–September 2010, we obtained occurrence records of *M. carolinus* by requesting data from the National Audubon Society for the North American Christmas Bird Count (CBC), the United States Geological Survey for the Breeding Bird Survey (BBS), and from North American natural history museums by searching the ORNIS data portal (www.ornisnet.org) and contacting museum curators and collections managers. For CBC data, we requested localities for all CBC ''circles'' and for all CBCs reporting at least one *M. carolinus* from the program's inception in 1900 to the present. Latitude and longitude correspond to the center of each 24-km diameter count circle. BBS data comprised all routes surveyed and all routes reporting at least one *M. carolinus* from the program's inception in 1966 to the present, with latitude and longitude corresponding to the start of the 40.23-km route. Not every CBC circle or BBS route was counted every year, and some were added over time while others were discontinued. In order to map the species' winter range (CBC) and summer range (BBS) over time, we pooled the data by decade, identifying and plotting any CBC circle or BBS route where *M. carolinus* was observed at least once during the decade. Over the 110+ year history of the CBC and the 40+ years of the BBS, these decade-long windows summarize *M. carolinus* sightings from 40 states, the District of Columbia and eight Canadian provinces.

We used ORNIS, searchable museum websites, and data provided by curators to compile date and locality information on more than 2,500 *M. carolinus* specimens held in the collections shown in Table 1. We did not include specimen records for which year of collection was not recorded, or for which locality information was less precise than county. Some museums (especially CMN, DMNS, FMNH, NYSM, ROM, UMMZ, YPM, listed in Table 1) provided latitude and longitude

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data for some or all of their specimens. For specimens without coordinate information we used GEOLocate version 3.22 (www.museum.tulane.edu/geolocate.html), BioGeomancer (Guralnick et al. 2006), or MaNIS Georeferencing Calculator (manisnet.org/gci2.html) to georeference the localities according to MaNIS/HerpNET/ORNIS Guidelines (Wieczorek et al. 2004, Chapman and Wieczorek 2006). In general we used GEOLocate if the locality was a place name, a street address or had single orthogonal offsets. If the locality was a county, we used BioGeomancer. For localities with two orthogonal offsets we used MaNIS Georeferencing Calculator. We were unable to georeference about 8% of museum specimens because of imprecise verbal locality descriptions, leaving us with 1997 specimens with useful date and locality information.

We plotted occurrences from all three data sets using Arc Map version 9.3. These maps allowed us to estimate the boundaries of the Red-bellied Woodpecker's summer and winter ranges for each decade. Plotting all CBC circles and BBS routes surveyed at least once each decade allowed us to verify that these survey programs had sufficient geographic coverage to delimit the boundaries of the species' range. We quantified the movement of the northern boundaries of the range over time in all three data sets by calculating the mean and standard deviation of the latitude of the ten northern-most occurrences in each decade and the most northern 5% of occurrences in each decade. We tracked movement of the western boundary in the same way using longitudes of the ten western-most occurrences and the most western 5% of occurrences in each decade. The southern and eastern boundaries were constrained by the Gulf of Mexico and Atlantic Ocean.

Although we were especially interested in measuring birds at the edge of the range and ''pioneers'' collected from the expanding front, we endeavored to measure adult individuals of both sexes throughout their range from all time periods to provide baseline estimates of geographic variation in body size and shape. We visited or received loans of specimens from the museums listed in Table 1 and measured a total of 406 study skins. Using digital calipers we took five measurements on each bird to the nearest 0.1 mm: 1) length of unflattened wing chord from the carpal joint of the right wing to the distal end of the outermost primary, 2) length of wing from the carpal joint of the right wing to the distal end of the outermost secondary, 3) exposed culmen from the non-feathered base of the upper mandible to its distal end, 4) tail length, from the point of insertion of the two central rectrices to the end of the longest rectrix, 5) tarsus length, from the posterior junction of the tibiotarsus and the tarsometatrsus to the junction of the latter with the middle toe. We measured only non-molting birds in adult plumage. In a few cases we measured the left wing or leg if the right one was damaged. All measurements were made by KJS and were determined to be statistically repeatable by a repeated measures ANOVA of 52 randomly chosen specimens that were measured twice.

To examine temporal changes to geographic patterns of body size, we first estimated body size as the loading on the first principal component of a principal components analysis performed in Statistica Version 6 (StatSoft Inc. 2001) on the correlation matrix of log transformed measurements. Because *M. carolinus* males are larger than females we performed separate PCAs for each sex. We also used raw wing chord as a measure of body size because it is highly correlated with other measures of size and widely accepted as a proxy for bird size (Aldrich and James 1991, Ashton 2002). In the first analysis we divided our morphological data set into a pre-expansion period (1867–1949) and post-expansion period (1952–2009) based on the results of our mapping of the species' range (described above), which identified the decade of the 1950s as the onset of rapid range expansion. The pre-expansion sample comprises 281 specimens collected prior to 1950, and the post expansion sample comprises 124 specimens collected after 1954 and a single specimen from 1952. Previous studies have identified the year 1955 as the onset of rapidly warming temperatures in the eastern United States (McCoy 2012), thus our choice of 1950 is conservative with respect to the onset of the expansion period. We used linear regression to detect changes in the relationship between body size and latitude between the two time periods, interpreting slopes significantly greater than zero to be support for Bergmann's rule.

In a second analysis we analyzed the entire morphological data set using a mixed-effect linear model implemented in the lme4 package for the program R, version 2.3.0 (R Development Core Team 2006). In the model, body size (from PC 1) was the response variable, with sex as a random

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effect, and latitude, year of specimen collection, and an interaction between latitude and year as covariates. We interpreted a significant contribution to the model of the ''year × latitude'' parameter to indicate that the relationship between body size and latitude was changing over the 105-year span of specimen data. Significance was tested in R with both a one-way ANOVA and by conducting a chi-squared likelihood ratio test that compared the full model with a model that did not include the year × latitude parameter.

We devised two methods for examining the evolution of body size at the expanding northern margin of the range of *M. carolinus*. In the first analysis, we used our plotted occurrence maps to identify the latitudinal range 41–44°N as the pre-expansion northern boundary. We then used a *t*-test to compare average body size of birds collected in that latitudinal range well before (1869–1939, $n = 33$ males and 32 females) and well after (1989–2009, $n = 13$ males and 15 females) the onset of the expansion period. We examined the residuals for these data to confirm the assumption of normality, and we eliminated the few specimens collected between 1940–1989 from this analysis so that there was a clear separation of the pre-expansion and post-expansion periods.

Our second analysis compared the body size of ''pioneers'' collected near the new northern front (north of 44.5°N, 1970–2009) to birds collected near the old northern front (41–44°N) to determine if larger birds predominate in the colonization of new areas. Unfortunately, there have been few museums actively salvaging and collecting specimens in the last few decades in the northeastern United States and southern Canada, and there are very few *M. carolinus* specimens from latitudes north of 44.5°N in collections. Therefore, this analysis was limited to males ($n = 14$) collected in the northwestern part of the species' range in Minnesota and Wisconsin.

RESULTS

Our graphical analysis of all three data sets reveals that the current range expansion began in the 1950s and has been characterized by expansion north and west, primarily following inland waterways and the Atlantic coast (Fig. 1). In the 19th century and early decades of the 20th century, an era prior to the advent of coordinated bird survey projects in which extralimital records were routinely documented by collecting specimens, our museum dataset documents the occasional occurrence of vagrant individuals well to the north and west of the core range. These records are primarily of males collected between April–September, including a male from September 1897 in North Dakota, a pair from April 1898 in Arizona, a male from Colorado in 1899, and a male from eastern Massachusetts in May 1915.

All three datasets clearly indicate rapid range expansion over the last several decades and also reveal a seasonal component to the expansion, such that winter records (CBC) occur farther north and west than summer records (BBS; Fig. 2). The average expansion from 1970s to 2000s is 0.8162 degrees north latitude/decade for CBC data versus 0.5186 degrees north latitude/decade for BBS data. The rate of western expansion over this same time interval is generally slower, but is still higher for winter birds (0.4963 degrees west longitude/decade) than summer birds (0.2652 degrees west longitude/decade). Areas that were newly occupied by winter birds become occupied by breeding birds in the following 1–2 decades, as for example in the Hudson River/Lake Champlain valley of New York, and later in the Red River valley of Minnesota and North Dakota and along the Atlantic coast of New England and Canada (Fig. 2).

Whereas we find little evidence from our maps of expansion in the first half of the 20th century, CBC data indicate steady expansion of the northern and western fronts as documented by the mean latitude and longitude of the northernmost and western-most records (Figs. 3, 4). This pattern could be a result of the greatly expanding number of CBC circles over this time period, but we consider this cause unlikely because the geographic coverage of count circles in these decades was always much greater than the known range of Red-bellied Woodpeckers.

We found a positive correlation between body size (PC 1) and degrees north latitude in our pre-expansion sample, consistent with Bergmann's rule (Fig. 5). Slopes of regression lines were significantly different from zero for both males ($r^2 = 0.1848$, $P = 1.134 \times 10^9$) and females ($r^2 = 0.2254$, $P = 4.018 \times 10^9$). This relationship breaks down in the post-expansion sample (Fig. 5) for both males ($r^2 = 0.0161$, $P = 0.371$) and females ($r^2 = 0.0256$, $P = 0.351$). In the mixed-effects linear model for the entire sample of specimens, sex accounted for 52.32% of the variance in body size. Latitude ($t = 2.126$, $P < 0.001$) and year of collection ($t = 1.532$,

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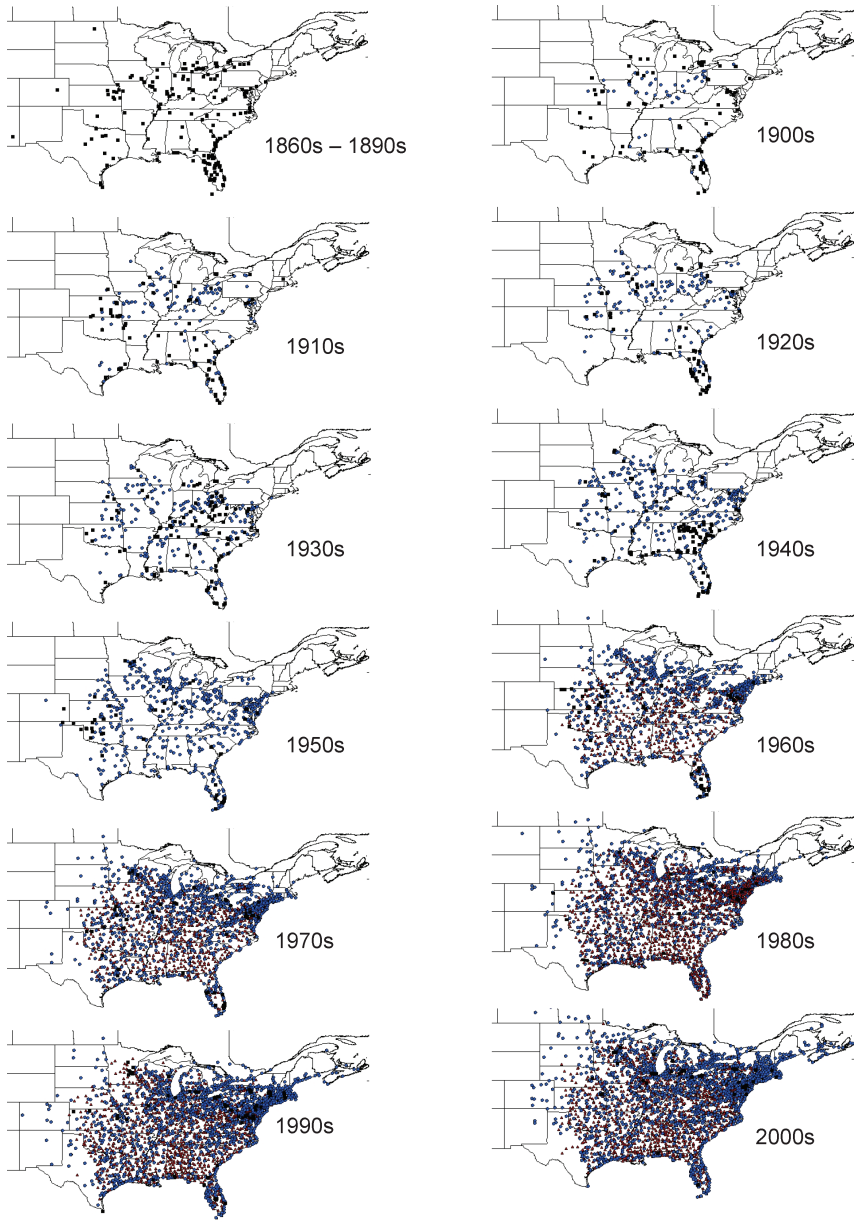


FIG. 1. Occurrence records by decade from museum specimens, Christmas Bird Counts (CBC), and Breeding Bird Surveys (BBS). Nineteenth century specimen records document wide ranging ''pioneers'' before a period of rapid range expansion to the north and west beginning in the 1950s. Expansion follows inland waterways and the Atlantic coast. The average rate of expansion from the 1970s to 2000s is slightly slower to the west (CBC 0.4963 degrees west longitude/decade; BBS 0.26517 degrees west longitude/decade) than to the north (CBC 0.8162 degrees north latitude/decade; BBS 0.5186 degrees north latitude/decade).

$P = 0.001$) had large effects on body size, and the interaction of latitude × year had a small but marginally significant effect on body size ($t = -1.970$, $P = 0.049$; $X^2 = 3.885$, $P = 0.048$), indicating a changing relationship between latitude and body size over the sampling period.

We also find evidence for breakdown of Bergmann's rule in our comparisons of body size

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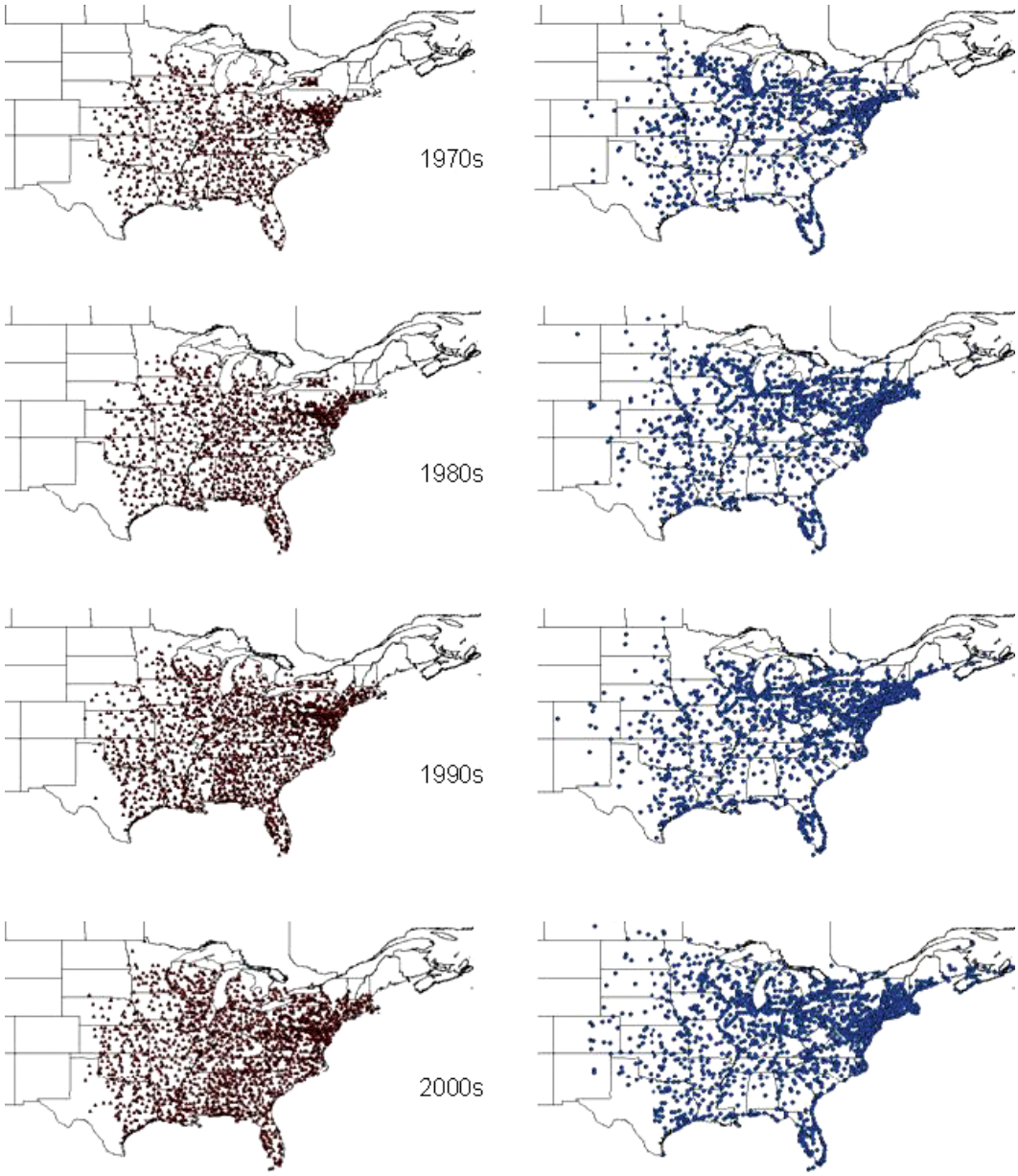


FIG. 2. Seasonality of range expansion. Plotting summer (left; BBS) and winter (right; CBC) occurrences from the expansion period shows that establishment of breeding in new areas lags behind colonization by non-breeders by about two decades.

of birds sampled before and after the onset of rapid range expansion at latitudes that correspond to the old northern periphery of the species' range. Birds collected near the old northern boundary (41–44°N in the period 1869–1939) were larger than birds collected from those same latitudes in recent decades (1989–2009) both in terms of wing chord (Females: mean wing chord = 127.87 mm pre-expansion and 125.71 mm post expansion; Males: mean wing chord = 131.52 mm pre-expansion and 130.08 mm post expansion) and PC 1 (Fig. 6). This difference was larger and significant in females ($P = 0.008$ for wing chord, $P = 0.004$ for PC 1), but not in males ($P = 0.083$ for wing chord, $P = 0.064$ for PC 1). Results of our second test indicate that ''pioneers'' (males

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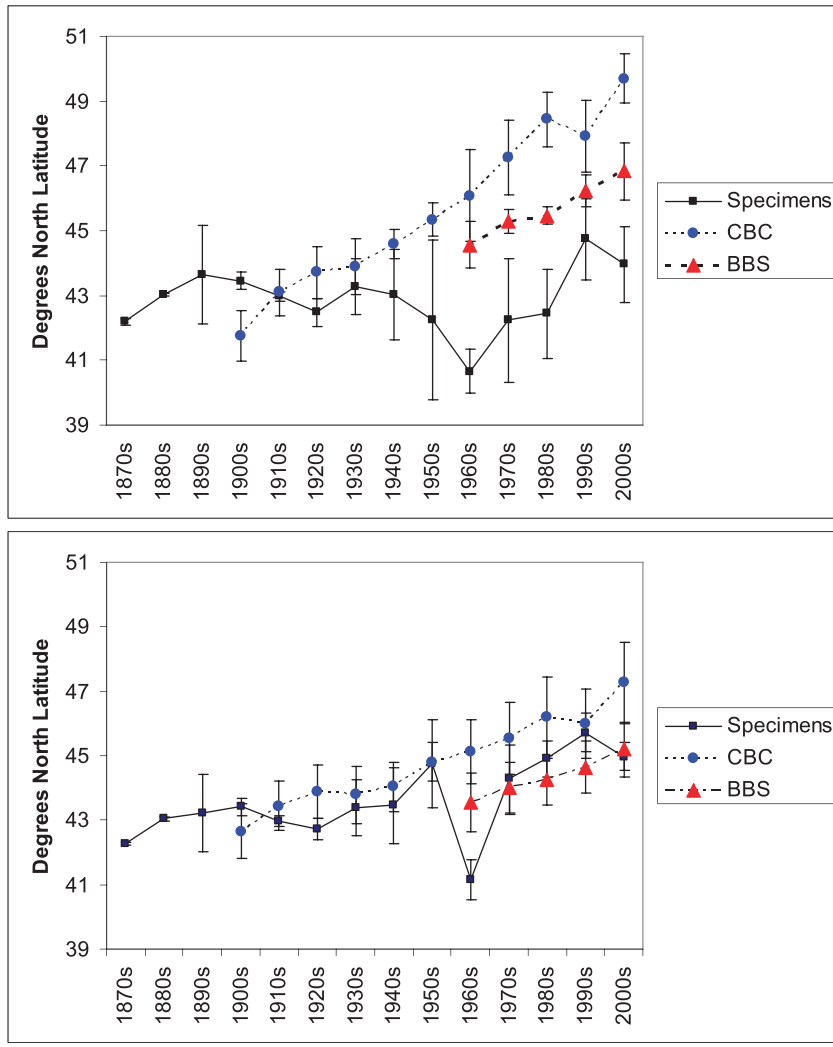


FIG. 3. Latitude of the northern edge of the range as determined by the (a) ten most northern occurrences and (b) the most northern 5% for each data set by decade has increased since 1950. Sample sizes for the most northern 5% graph (b) are as follows: Specimens n = 2–16, mean = 6.8; CBC n =52–1350, mean = 597.9; BBS n =625–1775, mean = 1209.4.

only) are not significantly larger than birds collected in the same time period near the old northern boundary (P = 0.69), and in fact are smaller than birds collected in the pre-expansion period near the old northern boundary (P = 0.019). This result is consistent with our finding that body size no longer correlates with latitude in the post-expansion sample of specimens.

DISCUSSION

Range Expansion.—Using three data sets, each with their own weaknesses and strengths allowed us to document the dynamics of the range of *M. carolinus* over the last 150 years. Museum specimens provide the longest history and document vagrants well, but the idiosyncratic and opportunistic nature of specimen collection, as well as the general waning of collecting effort beginning in the 1950s, has resulted in some decades with very few specimen records. Thus, mean latitudes of the northern-most 10 specimens or the northern-most 5% of specimens from a decade (Fig. 3) have large standard deviations, especially in the most recent decades. The large standard deviation of specimen latitudes in the 1890s results from the 1897 specimen from North

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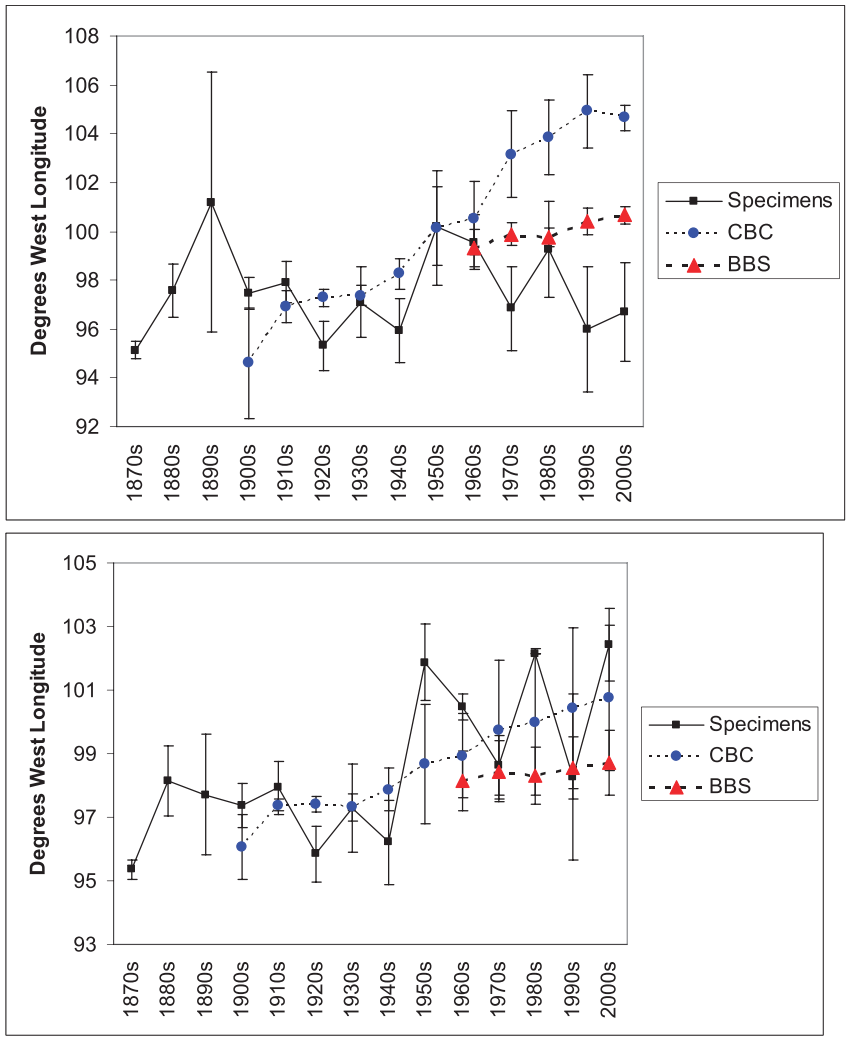


FIG. 4. Longitude of the western edge of the range as determined by the (a) ten most western occurrences and (b) the most western 5% for each data set by decade has increased since 1950. Sample sizes for the most western 5% graph (b) are as follows: Specimens n = 2–16, mean = 6.8; CBC n = 52–1,350, mean = 597.9; BBS n = 625–1,775, mean = 1209.4.

Dakota (UMMZ 53410), well to the north of the range at that time. Compared to coordinated survey projects like the CBC and BBS, museum collections do a poor job documenting the boundaries of ranges, but specimens uniquely document evolving phenotypes. In these times of rapid population dynamics and changing selective pressures, it is more important than ever that ornithologists judiciously collect specimens of even the most common bird species.

The CBC and BBS are more systematic surveys and document presence or absence throughout the range of Red-bellied Woodpeckers. CBC and BBS sampling effort has varied geographically over the years (Dunn et al. 2005), but even the first decades of these counts covered the known range of the Red-bellied Woodpecker, a vocal and conspicuous species that is not likely to be overlooked or confused with other species within its range. La Sorte and Thompson (2007) tracked latitudinal shifts in 254 species, including Red-bellied Woodpecker, by using CBC data to estimate the northern boundary (estimated as the latitude of the northernmost count circle reporting at least one individual), center of abundance (adjusted for survey effort by dividing the number

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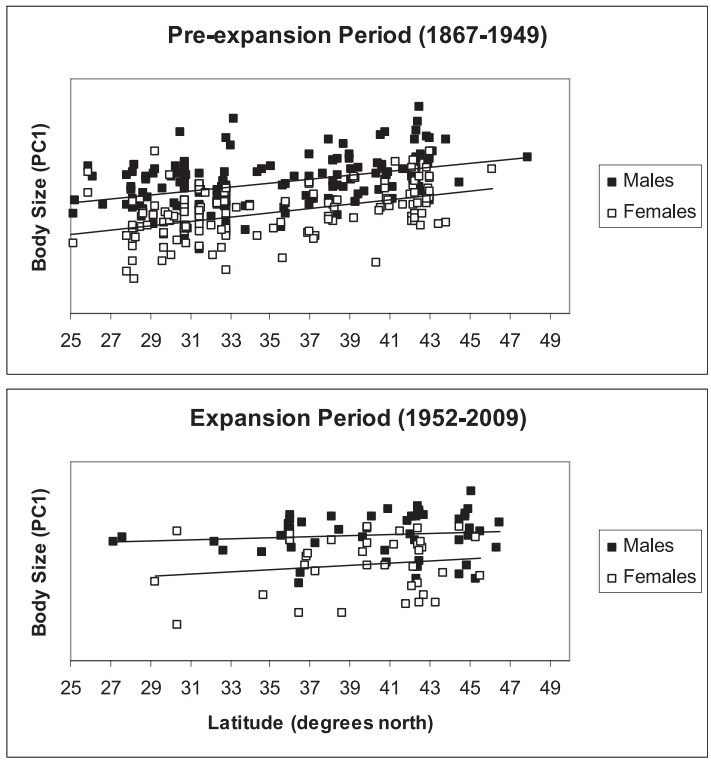


FIG. 5. Latitudinal variation in body size follows Bergmann's rule before 1950 (slope of regression line is greater than zero; males $r^2 = 0.1848$, $P < 0.0001$; females $r^2 = 0.2254$, $P < 0.0001$) but not after, during the expansion period from 1952–2000 (slope of regression line is not greater than zero, males $r^2 = 0.0161$, $P = 0.37$; females $r^2 = 0.0256$, $P = 0.35$).

of birds seen by party-hours), and center of occurrence of each species' winter range. For Red-bellied Woodpecker, they found northward movement in all three measures and that the rate of the latitudinal shift (measured as slopes from linear models) was faster at the northern boundary than the center of occurrence, but that the fastest movement was the center of abundance, hinting that a demographic population expansion over the last 40 years might be the driving force behind the expanding range of Red-bellied Woodpeckers, which we show has moved both north and west over the same time period.

Comparing data from winter (CBC) and summer (BBS) allowed us to identify a seasonal pattern of Red-bellied Woodpeckers' range expansion; new areas to the north and west are occupied first by winter birds and later by probable breeders. Counts conducted in the winter are likely to record the crop of new birds hatched the previous breeding season, some of which surely will not survive to breed. This pattern might be affected by the time-scale (decades) we chose for our analyses. Further study at shorter intervals or tracking of individual birds throughout the annual cycle might better resolve the lag time between colonization and the establishment of breeding sites.

The seasonal pattern we infer suggests a possible mechanism for Red-bellied Woodpeckers' range expansion. Whereas pairs defend territories during the breeding season, the territorial boundaries break down in the fall and the sexes occupy separate, largely non-overlapping foraging areas throughout the winter. Young of the year are driven away from the natal territory by the adults in late summer or early fall and can disperse large distances (Boone 1963). Both adults and juveniles have been observed to move into bottomland forest habitats in winter where mast is abundant (Kilham 1961). Since males are larger than females, those that disperse into areas with colder winters might be more likely to survive and establish territories the following spring. This hypothesis is consistent with our observations that vagrants collected far north or

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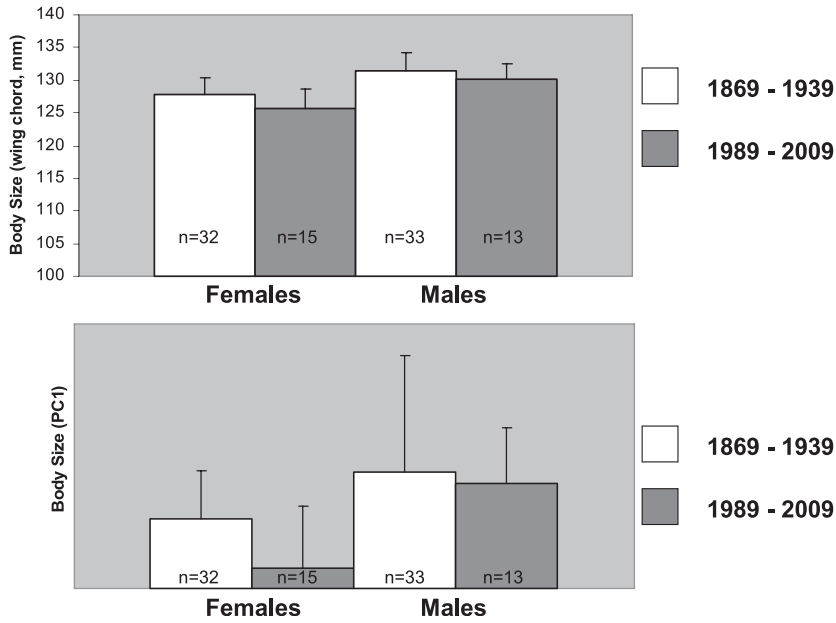


FIG. 6. Body size at the northern range boundary has changed as the front moves north. Birds collected between 41° N and 44°N were bigger in the pre-expansion era, both in overall body size (PC1) and wing chord. This difference is significant only for females (*t*-test results: females $P = 0.004$ for PC1, $P = 0.008$ for wing chord; males $P = 0.064$ for PC1, $P = 0.083$ for wing chord).

west of the core of the Red-bellied Woodpeckers' range tend to be non-breeding season males, and that expansion has proceeded west and north along river valleys. We predict that field surveys in late winter at the northern edge of the species' range would detect more males than females.

Bergmann's Rule.—We find evidence that prior to the onset of rapid range expansion, body size in Red-bellied Woodpeckers was positively correlated with latitude, a pattern of geographic variation known as Bergmann's rule. Both our regression analysis of pre- and post-expansion body sizes and our mixed-effects linear model of body size and latitude over a 105-year period indicate that the relationship between size and latitude in Red-bellied Woodpeckers has changed in recent decades. When ranges are stable and gene flow is low, populations may adapt to the prevailing local climate, resulting in a cline in body size such as we observed in Red-bellied Woodpeckers collected prior to 1950. To the extent that body size is a heritable genetic trait, latitudinal gene flow arising either from dispersal of individuals within a stable range or from range expansion will tend to disrupt the cline. We interpret the breakdown of Bergmann's rule to indicate that selection for large body size at the old northern boundary of the species' range has relaxed in recent decades, leading to an apparent shrinking in the average body size of birds at these latitudes. An alternative explanation is that northward expansion has been enabled by some factor other than climate, and that selection for increased body size is too weak to produce a detectable effect in our sample of birds from recent decades. Our small sample of pioneer specimens does a poor job of characterizing body size at the current northern boundary population, relative to our pre-expansion sample of specimens from the old northern front at 41–44°N. However, we do find that males from northern Wisconsin and Minnesota are significantly smaller than the specimens from the pre-expansion peripheral population there. For these reasons we interpret our results as support for the hypothesis of weakened selection for large body size at high latitudes, regardless of whether other factors, such as increased availability of bird feeders or decreased competition from other species, have facilitated the northward range expansion.

Bergmann's rule is thought to result from metabolic/morphological adaptation in response

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to selection for cold-tolerance, and there is some indication that Bergmann's rule (in birds) is easier to detect in data drawn from winter distributions (Ramirez et al. 2008). The fact that the latitudinal gradient in mean body mass of bird species is stronger in winter is primarily due to seasonal migrations of smaller bodied birds toward the equator (Ramirez et al. 2008). This highlights the fact that endotherms follow several adaptive pathways to cold-tolerance including entrance to torpor, and behavioral pathways such as food storage, and use of warm microclimates (McNabb 2002). In addition to the metabolic advantage, larger body size may also provide greater starvation endurance, further complicating the factors that contribute to body size. We found a seasonal pattern with respect to range expansion but did not investigate seasonal variation in Red-bellied Woodpecker body size. An interesting extension of our work might be to greatly increase the number of specimens measured to enable comparisons of body size in winter birds versus summer birds.

The question remains as to whether the population-level morphological change we have documented is an evolved trait or a developmental response to changed conditions (i.e., phenotypic plasticity). Other studies have documented instances of population-level morphological change on decade time scales, including the studies showing reduced body size in response to climate warming that are consistent with Bergmann's rule (Yom-Tov et al. 2006, Van Buskirk et al. 2010, McCoy 2012), and a study that documented changes in wing shape over a period of 100 years in response to changes in forest fragmentation (Desrochers 2010). The key to establishing that changes such as these are evolved responses is documentation of heritability of these traits, either through pedigree analyses or experimental relocation studies.

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