

Population trends for North American winter birds based on hierarchical models

CANDAN U. SOYKAN,^{1,†} JOHN SAUER,² JUSTIN G. SCHUETZ,¹
GEOFFREY S. LeBARON,³ KATHY DALE,³ AND GARY M. LANGHAM⁴

¹Conservation Science, National Audubon Society, 220 Montgomery St., Suite 1000, San Francisco, California 94104 USA

²Patuxent Wildlife Research Center, U.S. Geological Survey, 12100 Beech Forest Road, Laurel, Maryland 20708 USA

³Citizen Science, National Audubon Society, 2300 Computer Avenue, I-49, Willow Grove, Pennsylvania 19090 USA

⁴National Audubon Society, 1200 18th Street, NW, Suite 500, Washington, D.C. 20036 USA

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Abstract. Managing widespread and persistent threats to birds requires knowledge of population dynamics at large spatial and temporal scales. For over 100 yrs, the Audubon Christmas Bird Count (CBC) has enlisted volunteers in bird monitoring efforts that span the Americas, especially southern Canada and the United States. We employed a Bayesian hierarchical model to control for variation in survey effort among CBC circles and, using CBC data from 1966 to 2013, generated early-winter population trend estimates for 551 species of birds. Selecting a subset of species that do not frequent bird feeders and have $\geq 25\%$ range overlap with the distribution of CBC circles (228 species) we further estimated aggregate (i.e., across species) trends for the entire study region and at the level of states/provinces, Bird Conservation Regions, and Landscape Conservation Cooperatives. Moreover, we examined the relationship between ten biological traits—range size, population size, migratory strategy, habitat affiliation, body size, diet, number of eggs per clutch, age at sexual maturity, lifespan, and tolerance of urban/suburban settings—and CBC trend estimates. Our results indicate that 68% of the 551 species had increasing trends within the study area over the interval 1966–2013. When trends were examined across the subset of 228 species, the median population trend for the group was 0.9% per year at the continental level. At the regional level, aggregate trends were positive in all but a few areas. Negative population trends were evident in lower latitudes, whereas the largest increases were at higher latitudes, a pattern consistent with range shifts due to climate change. Nine of 10 biological traits were significantly associated with median population trend; however, none of the traits explained $>34\%$ of the deviance in the data, reflecting the indirect relationships between population trend estimates and species traits. Trend estimates based on the CBC are broadly congruent with estimates based on the North American Breeding Bird Survey, another large-scale monitoring program. Both of these efforts, conducted by citizen scientists, will be required going forward to ensure robust inference about population dynamics in the face of climate and land cover changes.

Key words: Audubon; Bayesian hierarchical modeling; bird conservation; Christmas Bird Count; citizen science; monitoring; North America; North American Breeding Bird Survey; population trend.

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† **E-mail:** cbc@audubon.org

INTRODUCTION

Long-term, large-scale monitoring studies, often carried out by citizen scientists, provide invaluable data on bird and other wildlife populations for

conservation and management activities (Lindenmayer and Likens 2009, Dickinson et al. 2010, Hochachka et al. 2012). The Christmas Bird Count (CBC), conducted annually since 1900 and managed by the National Audubon Society since the

formation of the organization in 1905, constitutes the longest-running, and is among the geographically most widespread, surveys of bird life in the world (Dunn et al. 2005). The program now includes >2400 count circles and involves >70,000 observers each year (LeBaron 2014). Each CBC consists of a tally of all birds detected by groups of counters within a circle 24.1 km (15 miles) in diameter, on a single day within a few weeks around Christmas (fixed dates of the count period are 14 December through 5 January). Although participation in the CBC has increased in Latin America and the Caribbean, the majority of circles (and most historical data) are from the United States and southern Canada, hereafter called North America.

In spite of its vast potential, variation in survey effort among circles and across years as well as the nonrandom selection of circle locations has complicated inference about bird populations (Dunn et al. 2005, Link et al. 2006). These factors can bias conclusions drawn without appropriate methods to control for them (Hochachka et al. 2012). Recognizing the potential value of the CBC, researchers have adapted Bayesian hierarchical models, developed for the North American Breeding Bird Survey (BBS) (Link and Sauer 2002), to control for nuisance factors that affect the CBC (Link et al. 2006). However, the results of these analyses—for the majority of birds in North America—are not readily available to the scientific community or public (but see Niven et al. 2004, Link et al. 2006, Sauer et al. 2009).

Hierarchical models treat the parameters of interest (e.g., trend) as random effects and include hyperparameters to describe the probability distributions of the parameters (Link and Sauer 2002). This structure is more efficient and powerful than standard linear modeling approaches, and provides a coherent and flexible method for modeling the effects of sampling variation. Moreover, the hierarchical structure of the model mirrors the hierarchical structure of the data and allows effects to be modeled at the appropriate scale (Smith et al. 2014). Hierarchical models are naturally handled using Bayesian methods, which provide intuitive and direct estimates of uncertainty around parameter estimates (Link and Sauer 2002). Sauer and Link (2011) showed that Bayesian hierarchical models better portrayed patterns of species population change over time than a prior approach based on route-regression.

Knowledge of species-specific trends will enable more informed conservation and management by highlighting those species most in need of attention. Although trends, on their own, do not reveal the causes of population change (Krebs 1991), they can be combined with information on species' ecological and life history traits to identify associations that may underlie observed trends (Yoccoz et al. 2001, North American Bird Conservation Initiative 2014). An examination of relationships between traits and population trends allows for generalization across multiple species and provides the foundation for hypotheses about causes of population decline that can be explicitly tested in more focused studies (Julliard et al. 2003). Research has linked bird population trends with a host of ecological and life history traits including range size, population size, migratory strategy, habitat affiliation, mass, diet, number of eggs per clutch, age at sexual maturity, lifespan, and tolerance of urban/suburban settings (e.g., Gaston and Blackburn 1995, Owens and Bennett 2000, Julliard et al. 2003—we highlight additional relevant studies in the *Methods* section). By identifying which traits are most strongly associated with trends in North American birds we can gain insight into the mechanisms driving changes in species' abundances. Hierarchical models facilitate this process by providing robust trend estimates of population change and an overall framework for modeling the effects of covariates (i.e., mechanistic drivers) on population change.

Hierarchical models thus promote a more integrated use of monitoring data. Not only do the data permit estimation of trends, they can be combined with covariates to predict the effectiveness of management efforts. Monitoring, analysis, and management join together in an iterative cycle in which scientists use monitoring data to build models that link population responses to relevant covariates. These results are, in turn, used to guide management decisions. Ongoing monitoring then allows researchers to re-evaluate the associations based on population responses to management activities, and revise the models. Monitoring in this framework has two active roles: developing associative models and providing future population status information that allows researchers to test the validity of those models.

Our specific goals were to: (1) identify population trends for species of North American birds during

the winter season for the period 1966–2013 while accounting for variation in survey effort among CBC circles; (2) aggregate results across individual species at regional and North American scales; and (3) examine ecological and life history correlates of population trends across species. To address the first goal, we estimated population trends using a Bayesian hierarchical model. For the second goal we generated aggregate trend estimates for the region as a whole and for individual states/provinces, Bird Conservation Regions (BCRs), and Landscape Conservation Cooperatives (LCCs). To address the third goal, we examined the relationship between individual species CBC trend estimates and the aforementioned traits.

METHODS

Christmas Bird Count

The CBC consists of bird counts made on 24.1 km diameter circles on a single calendar day within the December 14–January 5 time-frame. Participants join groups that survey sub-units of the circle during the course of the day using a variety of transportation methods (mostly on foot, in a car, or watching at a feeder, but can include boat, ski, or snowmobile). The number of individuals participating and the duration of counts vary among circles and through time (see Butcher et al. 1990 for details of the CBC). In recent decades, the number of party-hours has been recorded as a covariate to account for the variable duration of, and participation in, the count. We refer to this covariate as effort.

Strata delineation

Dividing North America into strata facilitates analysis with hierarchical models, which—by accounting for variation in quality of information over circles and time—provide more efficient and robust estimates of trend (Sauer et al. 2004a, b). Strata should be designed to: (1) accommodate varying sample intensity among regions over which population trends can be estimated (see Eqs. 1–4 below); and (2) provide an opportunity to summarize population change at scales and for geographies relevant to regional management agencies (Sauer et al. 2003). With respect to the former purpose, a tradeoff exists between smaller strata being more uniform in habitat type and other potential drivers of population dynamics,

and containing too few bird counts to allow for reliable trend estimation. With respect to the latter purpose, a tradeoff exists between summarizing data using geographies relevant to political boundaries (e.g., states and provinces), and geographies relevant to birds (e.g., BCRs).

Past CBC trend analyses have reported their results at the BCR level (Niven et al. 2004, Link et al. 2006, Sauer et al. 2009). BCRs were developed for regional avian conservation by a team of migratory bird biologists from Canada, the United States, and Mexico (Sauer et al. 2003). They are based on Commission for Environmental Cooperation ecoregions covering North America. Using BCRs as strata allows for comparison of winter trend estimates generated using CBC data with breeding season trend estimates generated using BBS data (Sauer and Link 2011). Unlike BCRs, which are specific to birds, LCCs provide a forum for States, Tribes, Federal agencies, non-governmental organizations, universities and other groups to work together toward landscape-scale conservation (<http://lccnetwork.org/>). This makes them important for cross-taxonomic conservation and management efforts. Moreover, since LCC boundaries were developed by aggregating BCRs, LCC-level trends can be estimated using the strata developed for BCRs. Given our desire to remain consistent with past studies and the BBS while also allowing for trend estimation at other scales (e.g., states/provinces, LCCs) we settled on strata formed by the intersection of states/provinces and BCRs (Fig. 1). These are small enough to be fairly uniform biologically, but can be readily combined to make larger strata in the form of states/provinces, BCRs, or LCCs. Moreover, preliminary analyses using 10 test species suggested that our selected strata were sufficiently large to allow for reliable trend estimation (see Appendix S1 for a description of the preliminary results).

The number of CBC circles and the start year for the CBC in each stratum are provided along with the aggregate trend estimates reported in Supplement S1: Tables S4–S7. To ensure that these two factors did not unduly influence aggregate trend estimates, we examined the relationship between two response variables (the median and standard deviation in trend estimates) for each state/province, BCR, and LCC and two predictor variables (the number of CBC circles and the start year for the CBC in each stratum) using multiple linear

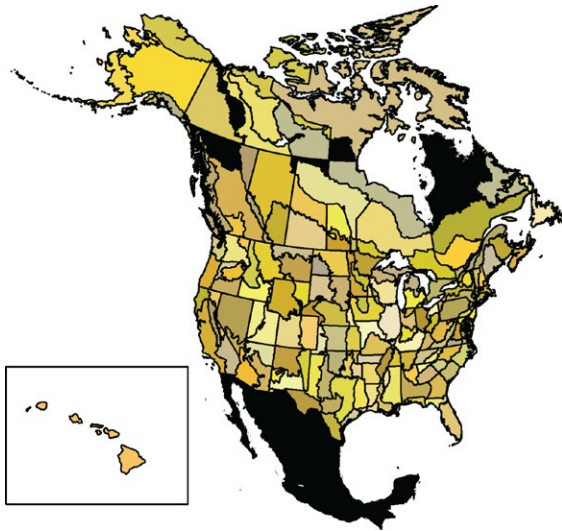


Fig. 1. Strata used to estimate North American bird population trends based on CBC data from 1966 to 2013. The strata represent the intersection of States/Provinces and Bird Conservation Regions. Areas in black were outside the scope of the analysis (Mexico) or did not meet the threshold criteria for inclusion as strata (see Appendix S1 for details on the criteria).

regression (one regression for each stratum-type, response variable combination for a total of six models).

Modeling population change

We estimated species population change using a Bayesian log-linear hierarchical model. We modeled counts, $Y_{ij,t}$ for a given circle (j), in a given year (t) and stratum (i) as overdispersed Poisson random variables. The logarithm of the expected value of the counts, $\lambda_{ij,t}$, is assumed to be a function of stratum, circle, year, temporal change, and effort effects:

$$\log(\lambda_{ij,t}) = S_i + \omega_j + \gamma_{i,t} + \beta_i(t - t^*) + \frac{B_i(\xi_{ij,t}^{p_i} - 1)}{p_i} + \varepsilon_{ij,t} \quad (1)$$

S_i denotes a stratum-specific intercept, ω_j is a circle effect, $\gamma_{i,t}$ is a stratum-specific year effect, and β_i is a stratum-specific temporal change effect indexed relative to a base year (the midpoint of the time series, $t^* = 1989$). Our model also includes stratum-specific slope B_i and exponent p_i effects

of effort ($\xi_{ij,t}$), and an overdispersion parameter, $\varepsilon_{ij,t}$. The parameters B_i and p_i govern the shape of the relationship of effort to count, ranging from a straight line to a saturating curve; for $P < 0$, the model specifies diminishing returns as effort increases (Link et al. 2006).

Link et al. (2006) describe the distributional assumptions and prior distributions associated with this model. Circle, year, and overdispersion effects are assumed to be distributed as independent normal random variables with mean 0 and variances $\sigma_{\omega_j}^2$, $\sigma_{\gamma_i}^2$, and σ_{ε}^2 , respectively. Note that the variances of year effects are stratum-specific. The means of the normal distributions are all zero, except for effort parameters p_i and B_i , which are independent normal random variables with means μ_p and μ_B and variances σ_p^2 and σ_B^2 . Variances are assigned diffuse inverse gamma distributions with scale and shape parameters set to 0.001. Parameters μ_p and μ_B , β_i and S_i are given diffuse normal distributions with mean 0 and variance 10^6 .

We defined annual population indices for each stratum in terms of model parameters β_i , S_i , and $\gamma_{i,t}$ (Link and Sauer 2002), adjusted for the area of the stratum (A_i), and for proportion of circles in the stratum in which the species occurs (z_i):

$$N_{i,t} = A_i z_i \exp(S_i + \beta_i(t - t^*) + \gamma_{i,t}) \quad (2)$$

We note that Sauer and Link (2011) include variance components in the computation of $N_{i,t}$ to scale the indices to levels consistent with historical BBS analyses. Trend, defined as an interval specific measure of change, for stratum i is calculated as the geometric mean rate of change in $N_{i,t}$ between two times (t_a and t_b):

$$T_i = \left\{ \frac{N_{i,t_b}}{N_{i,t_a}} \right\}^{1/(t_b - t_a)} \quad (3)$$

We converted these trend estimates to percent change per year by subtracting 1 from T_i and multiplying by 100%. We calculated composite indices that summarize population change over >1 stratum by summing indices from component strata:

$$N_t = \sum_{i=1}^I N_{i,t} \quad (4)$$

Analogous to T_i , composite trend is defined as the geometric mean rate of change in the composite index for specified t_a and t_b .

We fit the model using the Bayesian methods described in Link et al. (2006), with the exception that we used OpenBUGS (Lunn et al. 2009), called from the R statistical program with the package R2OpenBUGS (Sturtz et al. 2005, R Development Core Team 2015), to implement the Markov chain Monte Carlo technique for estimating the posterior distributions of parameters. In Bayesian inference, the posterior distributions of the parameters are used to compute summary statistics such as means and credible intervals.

Species included in the analysis

We generated population trend estimates for all species that met the criteria identified in our preliminary analyses (see Appendix S1), resulting in a total of 551 individual species population trend estimates. Recognizing that some of these species have only a fraction of their total population in the United States and Canada during the winter, we considered two subsets of the total species list in our initial aggregate analyses (see Appendix S2): birds with $\geq 25\%$ of their winter range, as defined by BirdLife, intersected by the area covered by the CBC (293 species); and birds with $\geq 50\%$ of their winter range intersected (207 species).

In the early 1970s, the CBC was amended to include counts made while observing birds at a feeder. The time and effort spent observing feeders, termed feeder-hours, is recorded, but not included in the total hours used to model effort. Nevertheless, it has increased to $\sim 15\%$ of the hours spent counting birds via traditional methods. To highlight birds whose trends might be influenced by this effect, we used Dunn and Tessaglia-Hymes (1999) to classify all 551 species as frequent visitors (78 species), occasional visitors (108 species), or nonvisitors (365 species) to bird feeders. As above, we considered these different groupings in our initial aggregate analyses (see Appendix S2).

Precision of individual species trend estimates

The precision of a species trend estimate is a measure of survey quality. The one-half width of the 95% credible interval (CI) provides a simple and intuitive measure of precision (e.g.,

the smaller the one-half width the more precise a trend estimate). Using the one-half width of the 95% CI we calculated how many of the estimated trends were precise enough to detect a 3-, 2-, and 1% per year change in population size.

Sampling theory predicts that precision (one-half width of the CI) should be inversely related to the number of samples. For empirical results to match this pattern, sampling must be consistent across survey units. To examine this prediction for the CBC, we used Spearman rank correlation to compare the precision of the trend estimates with the number of circles in which a species was detected as well as the number of strata for which the species' trend was modeled. A strong relationship between precision and both sets of factors would suggest that the CBC is consistent in its sampling of species among circles and across strata.

Population trends across species

In addition to single-species trend estimates, we generated aggregate trends for suites of species. To estimate trends across a suite of species, we constructed a composite summary of population change using the CBC trend estimates for individual species as input, following the approach of Gregory et al. (2005), as implemented by Sauer and Link (2011). Gregory et al. (2005) estimated composite change as a time series showing change from a base year (usually the first year of the interval, scaled to 1) to all successive years. In the analysis, estimated total change is computed for each species from a base year to each successive year, and geometric mean of trends for each year is used as the composite measure of change for that year. Sauer and Link (2011) suggested that because population trend estimates for individual species vary in quality, the simple averages of the estimated changes do not provide a valid summary of change for the group of species. They developed a hierarchical model to summarize groups of trend estimates that preserves the geometric-mean approach but imposes hierarchical structure on the estimated trends. As in the Gregory et al. (2005) approach, the data are trend estimates for each species, calculated from a base year (1966, in this case) to all successive years. To model species trends

by year, the logarithm of the change estimates $\ln(\beta_s)$ for each species ($s = 1, \dots, n$ species in the group) is assumed to be normally distributed, with mean $\ln(\beta_s)$ and variance σ_s^2 . The collection of parameters $\ln(\beta_s)$ is normally distributed with mean μ and variance τ^2 . Diffuse priors (as defined above) were provided for μ (normal distributions with means 0, variances 10^6) and τ^2 (inverse gamma distributions with scale and shape parameters set to 0.001). We implemented this model using Bayesian methods for the trend estimates for each year and calculated the median and percentile CIs of the posterior distribution of $\exp(\mu)$.

Based on the results of our continental population trends estimates for different aggregates of species (Appendix S2), we included in our regional aggregate analyses those 228 species that are not frequent visitors to feeders and have $\geq 25\%$ of their BirdLife winter range intersected by the CBC. In addition to aggregate trend estimates, we used the method of Sauer and Link (2002) to estimate the median number of species with positive population trend estimates for each group, along with 95% CIs. We ran aggregate analyses for the entire survey area and for the three regional groupings described above (states/provinces, BCRs, and LCCs).

To assess whether the regional results might be biased by differences in temporal or spatial sampling of birds, we developed multiple regression models relating median aggregate trend estimates for the states/provinces, BCRs, and LCCs to the year the CBC was initiated in each region and the number of CBC circles each contains. Likewise, to assess whether the inclusion of certain regions increases the variance around trend estimates, we used multiple regression models to relate the standard deviation of aggregate trend estimates for the states/provinces, BCRs, and LCCs to the year the CBC was initiated and the number of CBC circles it contains. Thus, in total we built six models (three regional summaries by two trend metrics).

Relating population trends to biological traits

We selected ten factors relating to bird ecology and life history that have been linked to population dynamics: range size, population size, migratory strategy, habitat affiliation, body size, diet, number of eggs per clutch, age at

sexual maturity, lifespan, and tolerance of urban/suburban settings (Supplement S1: Table S1). Range size is considered to be one of the main correlates of extinction risk (Lee and Jetz 2010); species with smaller ranges tend to be more at risk. Population size has been linked with recent continent-wide declines of birds in Europe, with more common species declining more than their less-abundant kin (Inger et al. 2015). Past research has shown a link between migration strategy and population trends, with those species that migrate further declining more, presumably as a result of threats on their wintering grounds and/or along migratory routes (Robbins et al. 1989, Sauer and Link 2011). Given that major habitat categories face different types and levels of threat, assigning birds to a primary habitat provides a means to assess the status of birds as a whole in that habitat (North American Bird Conservation Initiative 2014). Body size has been shown to influence threat status for birds, with larger bodied taxa being at greater risk (Gaston and Blackburn 1995). Diet also affects extinction risk (Purvis et al. 2000, Lee and Jetz 2010), with taxa that occupy higher trophic levels facing elevated risk. Life history traits have been linked to threat status (Bennett and Owens 1997, Purvis et al. 2000, Reynolds 2003) with increased risk being associated with slower life histories (e.g., fewer eggs per clutch, later age at sexual maturity, and longer lifespan). Finally, we considered tolerance of urban/suburban settings, since synanthropic species are expected to thrive in an increasingly human-dominated world while their less tolerant kin decline (McKinney and Lockwood 1999). Data were gathered from online databases (Supplement S1: Table S2) and are summarized in Supplement S1: Table S3; in the rare instance where a datum was not available for a particular species, a value was assigned based on the median value given for its nearest relatives (normally congeners).

Since the aforementioned factors are not independent, examining their associations with population trends can be challenging (Sauer et al. 1996). Given that our purpose was to document patterns, we elected to use general linear models to highlight the effects of individual covariates, recognizing that our results might omit important interactions and ignore collinearity

among variables (which we address in the discussion). For the continuous covariates, we centered and scaled all covariates by subtracting the mean and dividing by the standard deviation so that the coefficients could be compared with each other. To better control for the influence of poorly estimated trends on these cross-species analyses, we used precision-weighted models analogous to those described in Smith et al. (2014).

Comparison with trends based on the Breeding Bird Survey

The North American Breeding Bird Survey (BBS) is continent-wide bird monitoring effort conducted between May and July each year, comparable in both spatial and temporal extent to the CBC (Sauer and Link 2011). As with the CBC, bird population trend estimates can be calculated with the BBS. It therefore provides a logical comparison for the trend estimates generated in this study. BBS trend estimates analyzed at the survey-wide scale for the period 1966–2012 were downloaded from the USGS Patuxent Wildlife Research Center BBS website (<http://www.mbr-pwrc.usgs.gov/bbs/bbs2012.html>). We first identified species with population trend estimates for both the CBC and the BBS. Then, using Spearman rank correlation we examined the relationship between CBC and BBS trends (percent change per year) using: (1) all species that had trend estimates in both surveys; (2) only resident species; and (3) only resident species that had a statistically significant trend estimate in the CBC (Dunn and Sauer 1997). We used Wilcoxon sign rank tests (for the three subsets described above) to determine if CBC trends differed systematically from BBS trends.

We ran boosted regression trees (BRTs), implemented in R using the *dismo* package (Hijmans et al. 2015, R Development Core Team 2015), to examine what factors might cause CBC and BBS trends to differ. We used the difference between CBC and BBS trend estimates as the response variable; as predictors we used the ten factors described above, along with four additional variables: (1) the number of CBC circles included in each species' CBC trend analysis; (2) the number of BBS routes included in each species' BBS trend analysis; (3) the percent range overlap between each species' BirdLife winter range map and the

distribution of CBC circles in North America; and (4) whether the species was a frequent, occasional, or nonvisitor to bird feeders. We built the initial BRT model using the function *gbm.step*, and dropped unimportant variables using the *gbm.simplify* function.

RESULTS

Individual species trends

Individual species trend results are presented in Supplement S1: Table S4. Of the 551 species analyzed, we estimated that 377 (68.4%) had positive population trends from 1966 to 2013. The trend estimates based on the CBC were precise enough to detect a 3% per year change for 383 species (70%). A 2% per year change could be detected for 287 species (52%), and a 1% per year change for 134 species (24%). The precision of the trend estimates (measured as the half width of the 95% CI) was correlated with the number of circles in which a species was detected (Spearman rank correlation coefficient = -0.61 , $P < 0.001$), as well as the number of strata for which the species' trend was modeled (Spearman rank correlation coefficient = -0.52 , $P < 0.001$).

Population trends across species

The median North American winter bird population trend across the 228 species selected for inclusion in the aggregate analysis was 0.9% per year for the period 1966–2013; the 95% CIs did not overlap zero (0.7–1.0% per year). Aggregate regional trend estimates from 1966 to 2013 were likewise largely positive. Fifty-nine of 62 states/provinces had positive population trends across species, all but three of which (Alabama, Saskatchewan, and Yukon Territory) had 95% CIs that did not overlap zero (Fig. 2; Supplement S1: Table S5). Three states (Hawaii, Florida, and Vermont) had negative population trends across species; the latter two had 95% CIs that did not overlap zero. A similar geographic pattern in trend estimates held true for LCCs and BCRs (Figs. 3, 4). For LCCs, 20 of 22 had positive population trend estimates; for all of these the 95% CIs did not overlap zero (Fig. 3; Supplement S1: Table S6). Of the two LCCs that had negative median trend estimates (the Pacific Islands and Peninsular Florida), only

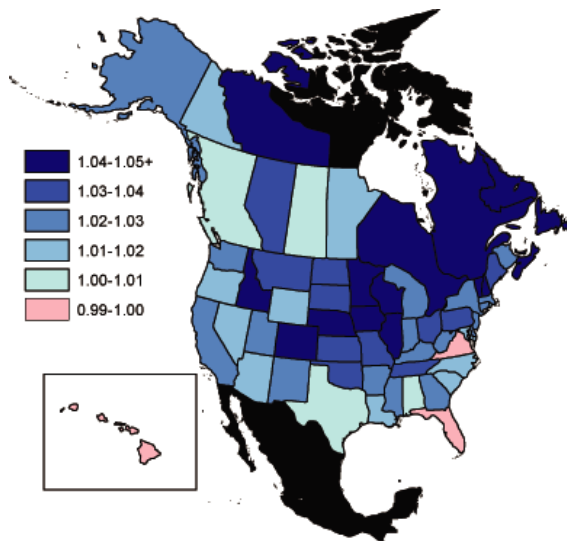


Fig. 2. Median trend estimates at the state/province level. Species included in this analysis were those which do not frequent bird feeders and which have $\geq 25\%$ of their winter range in the CBC area (228 species total).

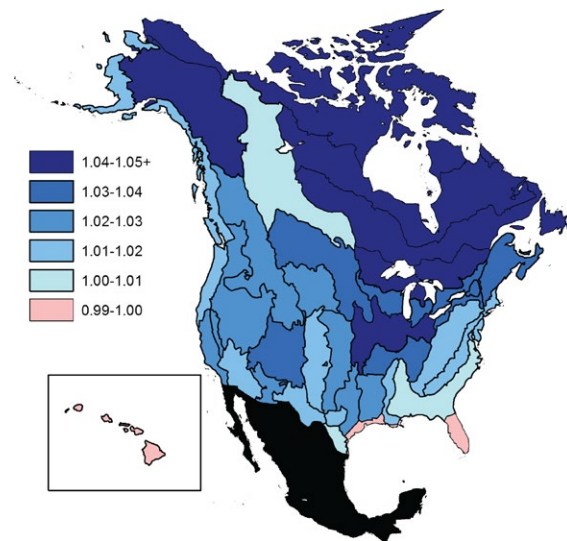


Fig. 4. Median trend estimates at the BCR level. Species included in this analysis were those which do not frequent bird feeders and which have $\geq 25\%$ of their winter range in the CBC area (228 species total).

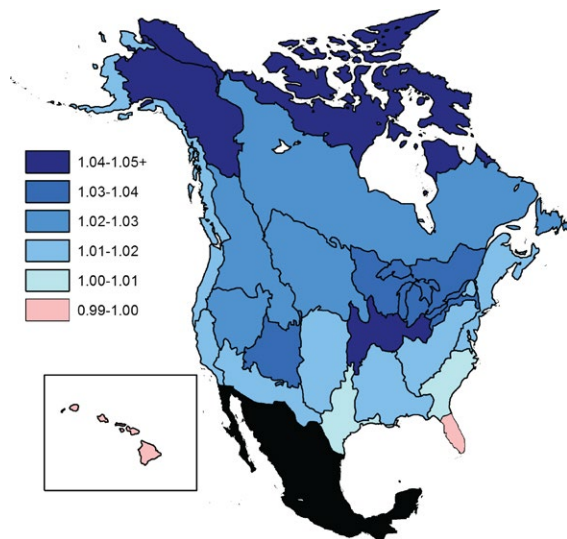


Fig. 3. Median trend estimates at the LCC level. Species included in this analysis were those which do not frequent bird feeders and which have $\geq 25\%$ of their winter range in the CBC area (228 species total).

the latter had 95% CIs that did not overlap zero. For BCRs, 35 of 38 strata had positive population trend estimates; for all but one of these (Boreal Taiga Plains) the 95% CIs did not overlap zero (Fig. 4, Supplement S1: Table

S7). Of the three BCRs that had negative median trend estimates (Hawaii, the Gulf Coastal Prairie, and Peninsular Florida), only the latter had 95% CIs that did not overlap zero.

Strata with a longer history of CBC involvement and more CBC circles had more precise trend estimates, but their accuracy was not affected. Multivariate models suggest a significant relationship with the standard deviation in trend estimates for states/provinces ($R^2 = 0.14$, $P = 0.01$) and BCRs ($R^2 = 0.36$, $P < 0.001$), but not for LCCs ($R^2 = 0.15$, $P = 0.21$) (Supplement S1: Table S8). For the states/provinces and BCRs, the standard deviation was positively associated with year when the CBC was initiated and negatively (though not significantly) associated with the number of CBC circles. Models relating median trend estimates to the year the CBC was initiated and the number of CBC circles showed no association when run at the level of states/provinces ($R^2 = 0.001$, $P = 0.97$), LCCs ($R^2 = 0.003$, $P = 0.97$), or BCRs ($R^2 = 0.031$, $P = 0.57$); see Supplement S1: Table S8 for coefficient estimates and confidence intervals. As only three of 38 BCRs and four of 62 states/provinces had not initiated CBC counts by 1966, we decided that the slight increase in uncertainty caused by including those strata was

not enough to warrant dropping them from the overall analysis.

Relating population trends to biological traits

Of the 10 precision-weighted linear models that examined the association between biological traits and population trend, only one (winter range size) did not have a statistically significant effect at an alpha level of 0.05 (Table 1, Figs. 5, 6). The deviance explained by the various models, a statistical measure analogous to R^2 , ranged from -17.2% (effectively 0%) to 33.7% (Table 1). With respect to diet, all groups had trend estimates that differed significantly from zero (Fig. 5). Seed eaters were the only group with a negative trend, whereas birds that eat vertebrates, fruit, and vegetation had trend estimates >1% per year. For lifespan, trend estimates increased significantly from short- to intermediate categories, and then increased

significantly again from intermediate- to long categories (Fig. 5). With respect to migratory strategy, residents, short-, and moderate-distance migrants had significantly positive trend estimates, whereas withdrawal migrants had significantly negative estimates (Fig. 5). Birds affiliated with urban environments increased significantly more than birds not affiliated with urban areas, although both were significantly greater than zero (Fig. 5). As for habitat type, woodland-associated species had the largest increase of any group; wetland species and those birds associated with multiple habitat types also increased significantly (Fig. 5). In contrast, shrubland and grassland species decreased significantly. There was a significant positive effect of body size and age at sexual maturity on population trends, and a significant negative effect of the number of eggs per clutch and population size (Fig. 6).

Table 1. Results of precision-weighted general linear models examining the relationships between the 10 ecological and life history traits and CBC population trends from 1966 to 2013.

Trait	Category	Lower 95% CI	Median estimate	Upper 95% CI	Deviance explained (%)
Diet	Fruit	0.701	1.651	2.597	12.5
	Invertebrates	0.629	0.730	0.832	
	Omnivore	0.295	0.427	0.558	
	Seed	-0.861	-0.573	-0.283	
	Vegetation	1.138	1.523	1.916	
	Vertebrates	1.643	1.733	1.821	
Life expectancy	Short	0.417	0.507	0.597	7.1
	Intermediate	1.292	1.378	1.464	
	Long	1.602	1.766	1.931	
Habitat	Grassland	-0.727	-0.493	-0.258	33.7
	Ocean	-0.035	0.749	1.556	
	Shrubland	-0.531	-0.404	-0.278	
	Various	0.577	0.726	0.875	
	Wetland	0.927	1.056	1.184	
	Woodland	2.072	2.163	2.254	
Urban affiliate	No	0.527	0.599	0.671	12.7
	Yes	1.807	1.904	2.002	
Migratory strategy	Long	-1.446	-0.410	0.672	10.3
	Irruptive	-0.655	0.290	1.252	
	Moderate	0.918	1.205	1.491	
	Resident	0.733	0.876	1.016	
	Short	1.254	1.324	1.393	
	Withdrawal	-0.930	-0.736	-0.540	
log10(mass)		0.457	0.518	0.579	7.7
Mean eggs per clutch		-0.408	-0.326	-0.245	1.7
Mean age at sexual maturity		0.635	0.710	0.785	9.7
Population size		-0.155	-0.085	-0.014	-17.2
Winter range area		-0.055	-0.016	0.023	0.0

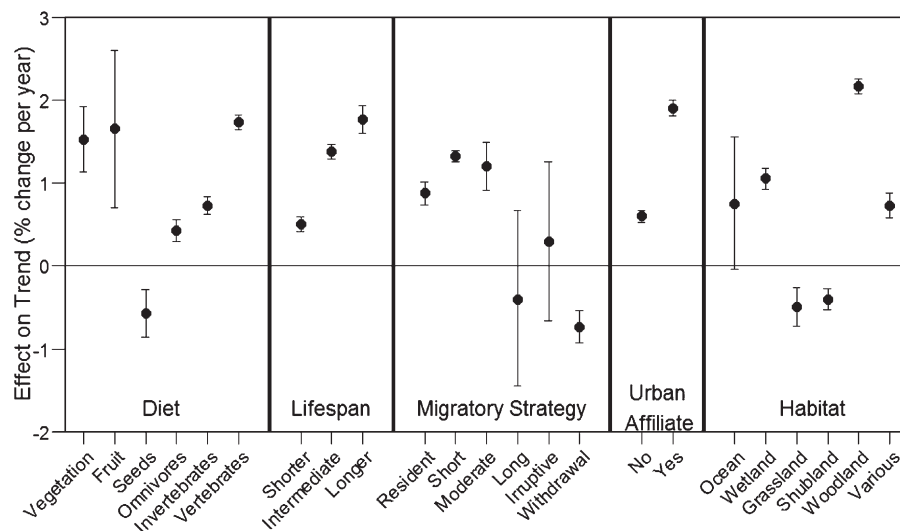


Fig. 5. Precision-weighted group means and 95% confidence intervals for the five categorical covariates examined in this study. Species included in this analysis were those which do not frequent bird feeders and which have $\geq 25\%$ of their winter range in the CBC area (228 species total).

Comparison with trends based on the BBS

Overall, 359 of 551 species were monitored by both the CBC and BBS; Spearman rank correlation of these species' trends revealed a significant positive association between trend estimates in the two surveys (Fig. 7a, Spearman rank correlation coefficient = 0.51, $P < 0.001$). The correlation grew stronger if only the 79 resident species were included (Fig. 7b, Spearman rank correlation coefficient = 0.61, $P < 0.001$). It grew even stronger if only the 44 resident species with a significant trend in the CBC were included (Spearman rank correlation coefficient = 0.7, $P < 0.001$). Wilcoxon sign rank tests suggest that the CBC trends are significantly greater than the BBS trends for all three subsets of species described above ($P < 0.001$, $V = 14,235$ for the full set of 359 species; $P = 0.014$, $V = 1074.5$ for the 79 resident species; and $P = 0.013$, $V = 280.5$ for 44 resident species with a significant trend in the CBC).

Of the 359 species monitored by both surveys, 172 trend estimates (48%) had the same statistical interpretation (e.g., statistically significant increase, decrease, or no significant trend in both surveys). An additional 152 trend estimates (42%) suggested a significant trend for one survey, but not the other; of these 152, 125 (82%) had a more positive trend for the CBC estimate than the BBS

(e.g., significant increase in the CBC, no trend in the BBS or no trend in the CBC, significant decrease in the BBS). Finally, there were 35 trend estimates (~10% of the total) where the CBC and BBS suggested significant trends in opposite directions (e.g., significant increase in the CBC, significant decrease in the BBS; Supplement S1: Table S9); of these 35, 33 (94%) had a more positive trend for the CBC than the BBS. The similarity between CBC and BBS trend estimates is stronger if only resident birds are compared. Of the 79 species that are monitored by both surveys and are classified as residents, 49 (62%) had the same statistical interpretation and only six (8%) had significant trends in opposite directions.

Boosted regression tree models suggest that two factors are most strongly associated with differences in trend estimates between the two surveys: (1) the number of CBC circles included in each species' CBC trend analysis (variable importance = 59.3); and (2) the species' winter range area (variable importance = 40.7). Both of these relationships display an exponential decline in difference between trend estimates with increasing values of the predictor variable (Fig. 8a, b), implying that the discrepancies between surveys are greatest for those species that are poorly sampled by the CBC and/or have small winter ranges.

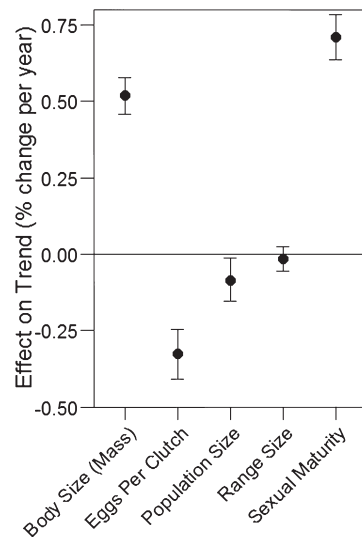


Fig. 6. Precision-weighted regression coefficients and 95% confidence intervals for the five continuous covariates examined in this study. Species included in this analysis were those which do not frequent bird feeders and which have $\geq 25\%$ of their winter range in the CBC area (228 species total).

DISCUSSION

Our models suggest that 68% of the 551 bird species included in this study experienced population increases in the study area between 1966 and 2013. When only those birds that do not frequent feeders and have $>25\%$ of their winter range in North America are considered, the overall trend is slightly less positive, but still significantly greater than zero. These trends have manifested across the continental US and Canada, with estimated trends generally being greater in more northerly regions. Diet, lifespan, migratory strategy, tolerance of urban/suburban settings, habitat affiliation, mass, number of eggs per clutch, population size, and age at sexual maturity were associated with median population trend estimates across species, although not necessarily in the directions predicted by past studies.

Disproportionate increases in species with $<25\%$ of their winter range in North America, combined with the geographic distribution of trend estimates, suggests that warming winter climates may account for the marked increases in winter bird population estimates. Indeed, data

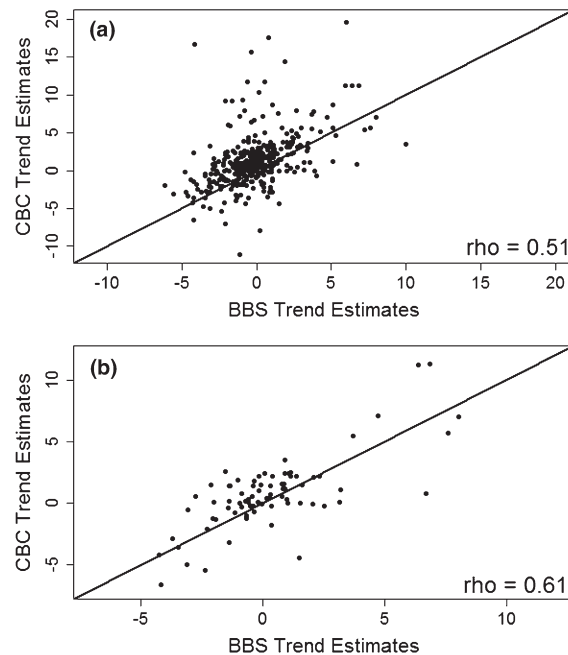


Fig. 7. BBS median trend estimates vs. CBC median trend estimates. (a) Species monitored by both surveys (359 species); (b) species monitored by both surveys that are classified as residents (79 species). A 1:1 line was added to both figures to help visualize the difference in trend estimates between the CBC and BBS.

for a subset of 305 species that are widely distributed in North America suggest a northward shift in the wintertime center of abundance (U.S. Environmental Protection Agency 2014). In addition to range shifts, warming winters might result in population increases due to enhanced overwinter survival, particularly in more northerly strata (e.g., Mehlman 1997, Link and Sauer 2007). Further support for these mechanisms is the fact that CBC trend estimates were significantly greater than BBS trend estimates for the three subsets of species considered in the comparison analyses. Nevertheless, the population gains in the study area may not merely be due to redistribution (i.e., bird range centers shifting northward).

Several lines of evidence suggest that the gains reported above represent true changes in wintering bird populations within the study area, at least for a subset of species. First, for species such as the Bald Eagle, Peregrine Falcon, and Brown Pelican that were decimated by direct and

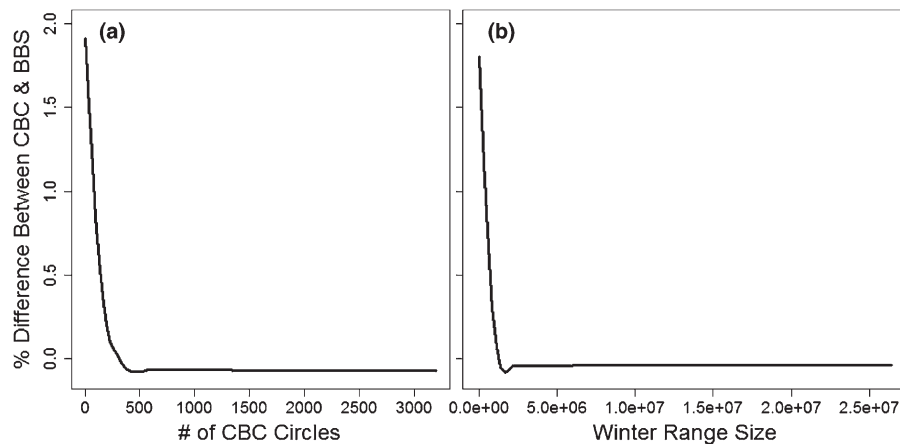


Fig. 8. Partial dependence plots depicting the modeled difference between CBC and BBS trend estimates as a function of (a) the number of CBC circles included in each species' CBC trend analysis; and (b) each species' winter range area (in km²). The plots are based on the results of the boosted regression tree analysis.

indirect effects of human activity, these gains reflect the success of focused conservation efforts, environmental regulations, and Endangered Species Act protection/management (Schwartz 2008). Second, numerous species of birds tolerate and/or benefit from human activity (Johnston 2001, Marzluff 2001), resulting in often large population increases for synanthropic species such as Canada Goose, Common Raven, and Red-tailed Hawk. Finally, a number of non-native species have established and spread during the past five decades, often accounting for the most dramatic population increases documented in this study (e.g., Eurasian Collared-Dove, Rose-ringed Parakeet).

Approximately one-third of the species included in this study have declined over the past five decades, some of them quite dramatically. For example, ~8% (45 of 551) of species had median trend estimates $\leq -3\%$ per year, indicating a decline of $>75\%$ over the past 48 years. Certain at-risk groups highlighted by our analyses of the association between trend estimates and biological traits have already been identified by other researchers. The decline in grassland bird populations is well-documented (Mineau and Whiteside 2013, North American Bird Conservation Initiative 2014) and correlates with both agricultural pesticide use and changes in land use practices across North America (as well as on wintering grounds in Latin America). Like-

wise, declines in shrubland (i.e., arid-land) birds were noted in the State of the Birds report (North American Bird Conservation Initiative 2014), although a clear mechanism is not obvious. A number of major threats face Hawaiian birds (North American Bird Conservation Initiative 2014), and likely account for the overall decline noted in this region. The decline in withdrawal migrants is somewhat surprising. It may reflect shifting migration patterns due to warming winters (e.g., few individuals returning to more temperate strata than in the past), but merits further scrutiny.

The negative relationship between population size and trend estimates may reflect the success of conservation efforts, which may also account for some of the other patterns identified by the trait analyses. Lifespan, body size, eggs per clutch, and age at sexual maturity results contradict past studies (Gaston and Blackburn 1995, Reynolds 2003), with larger, longer lived, slower reproducing species increasing more than their smaller, shorter lived, faster reproducing counterparts (but see Amano and Yamaura 2007, Pocock 2011). Likewise, higher trophic level consumers fared better, on average, than seed eaters and omnivores, a result at odds with ecological theory (Purvis et al. 2000, Lee and Jetz 2010). Given that large-bodied, upper trophic level species that mature later in life were often the first species to be affected by human disturbance (e.g., hunting, pesticide use, habitat loss)

these patterns may simply reflect the stabilization and/or recovery of such species due to environmental regulations and management efforts. However, interpretation of associations is risky when multiple factors are influencing groups (Sauer et al. 1996), and we acknowledge that the present analysis is not controlling for correlated features among species. For example, these patterns may reflect differential range shifts among taxa (though the two hypotheses are not mutually exclusive). Lifespan, body size, age at sexual maturity, eggs per clutch, and trophic position are associated with mobility; thus, the perceived increases in these species populations may reflect greater northward movement of mobile species populations. Another plausible explanation is physiological: increases in temperature variability due to climate change might favor species with larger body size (Gardner et al. 2011).

Consistent with Pocock (2011), the predictive ability of the trait analyses was modest in this study. Still, these findings are worthy of further investigation to confirm which mechanisms account for the unanticipated patterns. Importantly, correlations between the traits examined in this study complicate interpretation of these univariate results. Stronger insight could be achieved using independent contrasts to control for collinearity among factors (along with phylogeny), but can only be done with a small subset of species (e.g., those which have most traits in common, but differ in the covariate of interest).

Continued monitoring into the future will provide tests of some of the proposed causes of population decline/increase (e.g., ESA listing/delisting, fluctuations in farmland conservation funding, drought, and individual species management efforts). The ensuing results will clarify the driving mechanisms, enabling managers to make more informed decisions. Continuity in survey effort will also help tease apart the relative influence of climate change and other factors on bird population dynamics.

Although warming temperatures may have contributed to increases in overwintering bird populations within the study area, future climate change may have an opposite effect. First, increases in warm-adapted species (Princé and Zuckerberg 2015) result in novel species interactions, potentially harming cold-tolerant birds that are competitively inferior. Second, climate

change is expected to alter species' breeding distributions more than their winter distributions (Distler et al. 2015); thus, future range contraction during the breeding season may overwhelm more favorable conditions during the winter. Third, historical climate change has been fairly modest in comparison with the changes forecast for the next century (IPCC 2013, Langham et al. 2015); further change may push birds over a threshold where their populations no longer respond positively to changing conditions (e.g., precipitation may increase past a point where it benefits a given species). Fourth, as the rate of climate change accelerates in the future, its pace may exceed many bird species' capacities to shift and/or adapt (Devictor et al. 2008). Finally, severe weather episodes (major storms, cold snaps), are predicted to increase in frequency; these can have major impacts bird populations (Mehlman 1997, Butler 2000, Link and Sauer 2007).

Population trends estimated using the CBC were generally congruent with those based on the BBS. The greatest discrepancies occurred between species that are not well-sampled by the CBC, either because their winter ranges do not overlap many CBC circles, or because they have small winter ranges. This underscores the need to be cautious in interpreting CBC trend estimates for those birds sampled by fewer than 300 CBC circles and/or with winter ranges <2.5 million km².

That residents showed stronger congruence between CBC and BBS trend estimates than migrants suggests that some of the disparity between trend estimates may be due to the fact different portions of each species population are monitored by the two surveys. For widely distributed species, the BBS captures the south-central part of their breeding distribution, whereas the CBC captures the northern part of their winter distribution. If species ranges are shifting northward due to climate change, one would expect a slight positive bias in the CBC trend estimates and no change (or a slight negative bias) in the BBS estimates. This is because the species core range (where density is highest) is either shifting out of (BBS) or into (CBC) the survey area. Where the core range is shifting out of (into) the survey area, one would expect a decline (increase) in counts, even if the global population were unchanged. This pattern is indeed what we observe,

with more points falling above the 1:1 line than below it (Fig. 7a, b).

Observer effects might also account for the positive bias in CBC relative to BBS trends. Research suggests that BBS trends estimates generated without modeling observer effects are more positive than trends modeled with observer effects (Sauer et al. 2004a, b). Since observer effects cannot be modeled for the CBC, and there has been a general improvement in observer ability over time, some of the differences between CBC and BBS trend estimates might be due to the explicit incorporation of observer effects into the latter, but not the former.

Observer effects notwithstanding, the analytical methods used to estimate CBC trend for this study are similar to those used to estimate BBS trends. In both cases, a Bayesian hierarchical model is used to calculate relative abundance while accounting for variation in year, circle (route), and observer (BBS) or effort (CBC) effects. The modest differences described above notwithstanding, the similarity in trend estimates between surveys suggest similar realities on the ground (although the CBC and BBS have very different sampling methods and spatial designs). Moreover, given that the BBS is often cited as the standard against which other larger scale surveys are measured (in terms of scientific value), the similarity in trend estimates suggests that the CBC provides reliable information on North American bird population dynamics.

The trends we report provide some reason for optimism. Increasing population sizes for certain species likely reflect the success of conservation measures enacted over the past five decades, such as the Clean Air and Water Acts, regulations on pesticide use, and the Endangered Species Act. There are, however, numerous exceptions to the overall trend introducing a note of caution. Moreover, the specter of climate change belies the population increases reported herein (Langham et al. 2015). It is imperative that monitoring efforts such as the CBC and BBS continue; their spatial and temporal scope provide population information at scales needed for tracking bird responses to climate.

The most immediate question raised by these results is the relative contributions of range shifts and in situ population growth to the trends estimated in this study. A number of approaches

could leverage existing data sources (e.g., grouping species according to range boundaries and comparing the group trends; examining the effect of latitude on trends within species). The CBC, BBS, and eBird provide invaluable information for these sorts of analyses. Other approaches would require increased monitoring in Latin America and winter surveys along southern range boundaries (e.g., full life-cycle analyses of bird species populations). The relative influence of each mechanism will shape interpretation of the trend results and management response. Evidence of in situ population growth would support the effectiveness of conservation efforts over the past half century, whereas evidence of range shifts would highlight the need for climate change adaptation strategies to buffer species against the threats posed by future climate change.

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