

Pervasive poleward shifts among North American bird species

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Abstract. Climate change is expected to influence species' geographic distributions in the form of poleward and upward range expansion combined with extirpations from the equatorial and downslope sides of the distribution, but such shifts observed to date have been relatively subtle. Such shifts would be driven by changing patterns of fitness under changing conditions, producing population responses that would then be followed by range expansions and retractions. Here, we demonstrate pervasive population trends across the North American avifauna, reflected in the mean latitudinal position across all individuals of each species, conservatively estimated as affecting nearly half of the species in the avifauna. This result appears to constitute an intermediate step that would likely translate into concrete range shifts in numerous species over coming decades. We take this bellwether as a signal that climate change processes are affecting a significant proportion of North American bird species, and that biodiversity conservation and protected areas planning and management strategies in the region will need reexamination and re-planning in light of likely population trends and range shifts.

INTRODUCTION

The reality of present-day climate change processes is in little doubt, notwithstanding debates regarding human roles in their causation (IPCC 2007): global temperatures are rising precipitously, patterns of precipitation are rearranging, and sea level is rising. Given that elements of biodiversity are known to respond intimately to climate in terms of distribution and phenology (Grinnell 1917, 1924; Brown and Lomolino 1998), these climatic changes have long been expected to translate into several predictable sets of distributional effects (poleward and upslope range expansions, equatorial-side and downslope retractions) (Dobson *et al.* 1989; Holt 1990; Visser *et al.* 1998; Crozier 2003; Perfors *et al.* 2003; Lovejoy and

Hannah 2005). Several studies have documented shifts fitting these expectations (Holt 1990; Root *et al.* 2003; Lovejoy and Hannah 2005), suggesting that elements of biodiversity are beginning to respond to warming climates (Parmesan 1996; Visser *et al.* 1998; Parmesan *et al.* 1999; Chapin *et al.* 2000; Walther *et al.* 2002; Crozier 2003; Parmesan and Yohe 2003; Perfors *et al.* 2003; Huntley *et al.* 2007), but the ubiquity of these responses is unclear.

The process of manifesting these shifts, particularly in terms of geographic distributions, can be conceptualized as a process of temporal differentials in fitness causing population swells and lows in different portions of the geographic distribution, followed by eventual extirpation of equatorial-side populations and colonization of new areas along the poleward side of the distribution (Fig. 1). Under this scheme, actual distributional shifts would be the last signal of climate change effects on species, and would not be detectable until late in the process, but would be preceded by population shifts within the original distributional area. Indeed, several analyses of distributional shifts as a function of climate change have detected only subtle distributional shifts (Parmesan 1996; Parmesan *et al.* 1999; Cresswell and McCleery 2003; Crozier 2003; Parmesan and Yohe 2003; Conti Nunes *et al.* 2007). In contrast, population shifts have not been analyzed on continental scales—the focus of this contribution—we show that numbers in about half of North American bird species are swelling poleward and declining on the equatorial sides of species' distributional areas, a trend that will eventually translate into real range shifts.

MATERIALS AND METHODS

Data for these analyses were obtained from the U.S. Breeding Bird Survey (BBS), drawing on survey results from the entire span of the survey (1966-present). We included only breeding bird species, and eliminated nonnative species from all analyses. We further reduced the working dataset by focusing on only those species for which ≥ 5 occurrence localities were available, so as to analyze only those species for which sampling was sufficient for assessment of trends.

For each species in each year, we calculated the average latitude across all individuals as \bar{x}_i , where x_{ij} is the number of individuals of species i at site j , and L_j is the latitude of site j .

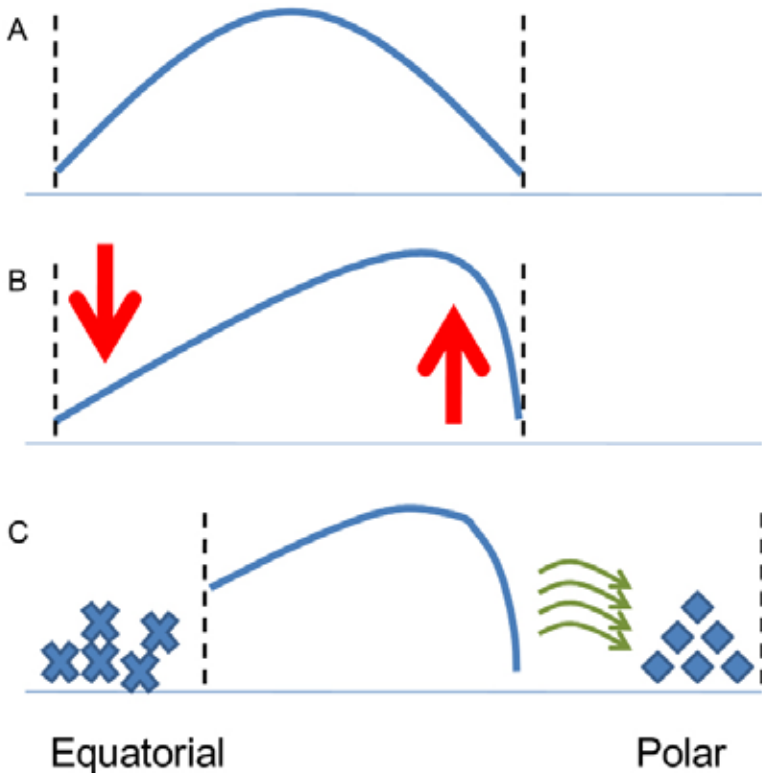


Figure 1. Hypothesized process of climate change effects on species' geographic distributions. Curved blue lines summarize approximate abundance of the species; black dashed lines indicate range limits; arrows indicate increases and decreases in fitness; and diamonds and X's indicate colonizing populations and extirpated populations, respectively. (A) "Normal" condition; (B) intermediate stage, in which numbers swell along poleward margin of species range, but reduce along equatorial margin; and (C) actual range shifts, consisting of poleward colonization, and equatorial-side extirpation.

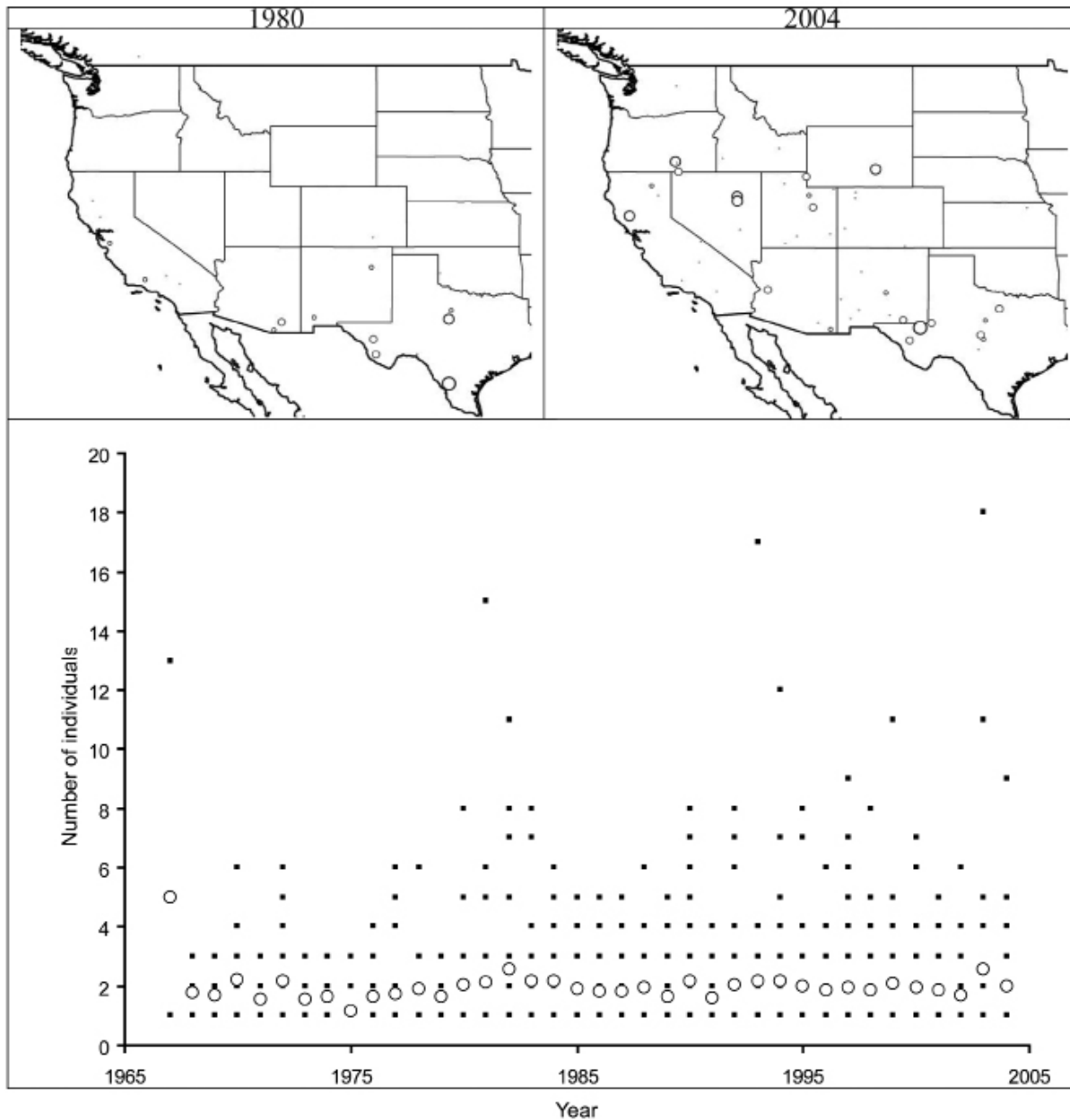


Figure 2. Example map of a species (Common Poorwill, *Phalaenoptilus nuttallii*), showing strong northward shifts in distribution over the Breeding Bird Survey sampling period: (top left) distribution of individuals of the species in 1980; (top right) distribution of individuals of the species in 2004; (bottom) graph of numbers of individuals of the same species across all sampling transects in the BBS, showing individual transects (small black squares) and average latitude (L_{avg} ; large white circles) through 1967-2004. Circles on maps indicate numbers of individuals detected, with successive sizes (small to large) representing 1, 2, 3, 4-5, and 6-9 individuals detected. The high 1967 L_{avg} value is based on only 3 occurrences detected that year, as opposed to much larger sample sizes in succeeding years.

we then developed a simple linear regression for each species, with L_{avg} as the dependent variable, and year as the independent variable, taking probability values of ≤ 0.05 as statistically significant. Finally, we were concerned that shifting patterns of coverage in the BBS effort could be producing the shifts in L_{avg} that were observed in initial analyses. As a consequence, we restricted a second iteration of our analyses to only those survey routes for which ≥ 20 yr of survey data were available, and repeated the analyses described above. Clearly, however, because numbers of routes are smaller in the 20-year data set, fewer species meet the sample size requirements.

RESULTS

Calculating the average latitude across all individuals tallied on 4726 U.S. Breeding Bird Survey (BBS 2006) routes in each year during 1960-2006, we regressed average yearly latitude on year to search for poleward population swells (Fig. 2; see methods below and summary table in Supplementary Information). Of 572 species tested, 261 showed significant northward population

shifts, whereas only 74 showed significant southward population shifts and 237 showed no significant shifts. The imbalance between positive and negative shifts was statistically significantly different from expectations ($P < 10^{-15}$).

To guard against possible biases from historical shifts in distribution of survey routes, we repeated the analysis over 1829 survey routes for which time series of ≥ 20 yr were available, and results were similar: 180 species increasing versus 33 species decreasing in average latitude, out of 378 species, with an associated probability of $P < 10^{-14}$. Hence, even controlling for potential bias resulting from uneven spatial distribution of additions of routes to the BBS, the poleward population swell is clear across almost half of North American bird species. Results were similar when species were divided into terrestrial (193 increasing and 59 decreasing in latitude, out of 419 species) versus aquatic (34 increasing and 15 decreasing in latitude, out of 153 species), again indicating the widespread nature of the population shifts.

DISCUSSION

The pervasive poleward population swells documented herein among North American bird species have several important implications for conservation. First, as can be appreciated in Fig. 1, population shifts will likely be *followed by* distributional shifts. This situation will have myriad implications for conservation efforts: presently well-situated reserves may no longer contain populations of the species that they were designed to protect, and discords among appropriate climate conditions and appropriate land cover types may arise (Peters and Darling 1985; Lovejoy and Hannah 2005). As such, we suggest serious reconsideration of the configuration of both current and planned protected natural areas to take into account ongoing climate change and the likely future configuration of distributional areas (Papeš 2006; Hannah *et al.* 2007)—clearly, this recommendation has serious implications, but the frequency with which we have observed species' numbers shifting northward strongly suggests dramatic range shifts in years to come.

More subtly, these results indicate the need for caution in interpreting estimates of overall trends in species' numbers, which has become a popular means of summarizing results of long-term monitoring data sets (Robbins *et al.* 1989; Butcher and Niven 2007; Butcher *et al.* 2007). Certainly, given our results, an overall 'species trend' would oversimplify the population processes that may differ in different sectors of species' distributions. Of particular note are species that are shifting in the northernmost tier of Breeding Bird Survey routes may *appear to be* in decline, when they are simply shifting out of the survey region populationwise—recent high-profile press releases and proposals for priority conservation status (Hamel 2000; Hunter *et al.* 2001) should be reconsidered in this light. In general, though, this study serves to indicate that the poleward, upward, and earlier shifts that have been documented in recent years (Parmesan 1996; Visser *et al.* 1998; Parmesan *et al.* 1999; Inouye *et al.* 2000; Crozier 2003; Parmesan and Yohe 2003; Nakazawa *et al.* 2007) are but the tip of the (melting?) iceberg. That is to say, we readily publish on the observed distributional or phenological shifts, and perhaps do not publish so readily on negative evidence (Peterson 2003; Archaux 2004). Nonetheless, among the large majority of species not as yet showing distributional responses to warming climates, based on the results of this study, many more are undergoing population shifts probably based on differential fitness across latitudinal gradients that will eventually manifest as real distributional shifts.

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