Biodivers Conserv (2016) 25:345–356
DOI 10.1007/s10531-016-1053-6

ORIGINAL PAPER

Informing conservation by identifying range shift patterns across breeding habitats and migration strategies

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Received: 5 August 2015 / Revised: 19 January 2016 / Accepted: 22 January 2016 /

Abstract A species distribution combines the resources and climatic tolerances that allow an individual or population to persist. As these conditions change, one mechanism to maintain favorable resources is for an organism to shift its range. Much of the research examining range shifts has focused on dynamic distribution boundaries wheras the role of species breeding habitat or migration strategies on shift tendencies has received less attention. We expand on previous research by using a large suite of avian species (i.e., 277), analyzing observed abundance-weighted average latitudes, and categorizing species by breeding environment and migration strategy. We used the North American Breeding Bird Survey dataset to address two questions: (1) Has the center of observed abundance for individual species shifted latitudinally? (2) Is there a relationship between migration strategy or breeding habitat and range shifts? Results indicate the majority of species have experienced poleward range shifts over the last 43 years, and birds breeding in all habitat showed trends of poleward shift but only those species breeding in scrub-shrub and grassland environments were different from zero. Additionally, species that are short distance migrants are experiencing significant poleward shifts while Neotropical and

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Communicated by Matts Lindbladh.

Electronic supplementary material The online version of this article (doi:10.1007/s10531-016-1053-6) contains supplementary material, which is available to authorized users.

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permanent residents had shifts that were not different from zero. Our findings do support the general trend expected from climate driven changes (i.e., > 52 % shifting poleward), however, the proportion of species exhibiting equatorial shifts (24 %) or no significant shifts (23 %) illustrates the complex interplay between land cover, climate, species interactions, and other forces that can interact to influence breeding ranges over time. Regardless of the mechanisms driving range shifts, our findings emphasize the need for connecting and expanding habitats for those species experiencing range shifts. This research describes the patterns of breeding birds through central North America and we encourage future research to focus on the mechanisms driving these patterns.

Keywords Breeding Bird Survey · Climate change · Global environmental change · Great Plains · Latitudinal shift · Migration

Introduction

Climate is an important determinant of the geographic range for a species, through species-specific physiological thresholds of temperature and precipitation tolerance (Davis and Shaw 2001; Warren et al. 2001; Hoffman and Parsons 1997; Angert et al. 2011). Given that (a) the global climate is changing at unprecedented rates, and (b) individual species vary greatly in their responses to change, understanding species' abilities to shift ranges has important implications for assessing extinction risk, predicting future community structure, and managing species of conservation concern (Chen et al. 2011; Stocker et al. 2013).

As a major contributor to climate change around the world, increased temperature is widely identified as a driver of range shifts. At a global scale, temperatures have increased by 0.74 °C, with a 1.1 °C increase in North America over the last five decades (Stocker et al. 2013). For comparison, in temperate zones, a 3 °C change in the mean annual temperature corresponds to a shift in isotherms of approximately 300–400 km in latitude or 500 m in elevation (Hughes 2000); not surprisingly, temperature increases have been implicated in poleward shifts in many species across several levels of ecological organization (McCarty 2001). Poleward shifts have been recorded in plants (Crumpacker et al. 2001; Grabherr et al. 1995), butterflies (Parmesan et al. 1999; Crozier 2004), marine bivalves (Roy et al. 2001), and birds (Thomas and Lennon 1999; Peterson 2003; Hitch and Leberg 2006; La Sorte and Thompson 2007; Zuckerburg et al. 2009). A complementary mechanism—upslope range shifts due to warming at lower elevations—has been described among montane birds (Gasner et al. 2010; La Sorte and Jetz 2010, 2012; Tingley et al. 2012), and plants (Kelly and Goulden 2008).

Species unable to alter their geographic range risk extinction (Veneir et al. 1999), but a successful range shift requires similar or substitutable resources in the new environment, including food and shelter in the short term, and mate availability in the long term. Anthropogenic landscape alterations (e.g., fragmentation through agriculture or urbanization; energy development such as oil and gas or wind energy) further restrict geographic ranges and potentially reduce the ability of many organisms to respond to climate change through range shifts (Brennan and Kuvlesky 2005; Lawler et al. 2013). Moreover, changes are not uniform across space or through time, and patterns are complicated by interactions between region-specific and species-specific factors (Tingley et al. 2012).

Elucidating the patterns of responses to global change and the mechanisms behind them can increase the capacity of conservationists and managers to prevent species decline and extinction, but detecting a causal relationship between range shifts and environmental change is difficult given the numerous confounding factors that exist in natural environments and the paucity of suitable data. As evidence of complex responses to climate change, up to 25 % of examined species have shifted their ranges equatorward or downslope while an additional 10–30 % of species have not shifted (Parmesan and Yohe 2003; Chen et al. 2011). Many potential mechanisms for non-poleward shifts have been suggested including adaptation of local populations to new climates (Parmesan et al. 2005), an inability to disperse (Davis et al. 1998), temporal lag in response to changes (Svenning et al. 2008), importance and intensity of species interactions (Lenoir et al. 2010) and habitat modification (Archaux 2004) to name a few. Nonetheless, the majority of species have exhibited shifts in the direction expected in a warming environment and describing range shift patterns in all directions has important ecological implications (McCarty 2001).

Because of their vagile nature, identifiability, and the long term citizen science data sets that occur in many countries, birds represent one of the best sources to examine range shift patterns, but most studies have focused on small geographic regions, few species, or investigated range dynamics outside of the breeding season (La Sorte and Thompson 2007; Zuckerburg et al. 2009; Albright et al. 2010; DesGranges and Morneau 2010). Few studies have examined North American breeding bird shifts among large suites of species across broad geographic regions or studied the influence of breeding environment and migration strategy to determine which bird species or groups are shifting—or not shifting—and in which direction (Hitch and Leberg 2006; La Sorte and Thompson 2007; Lehikoinen and Virkkala 2015).

In this paper, we advance and add to previous work done on range shifts by 1) including a broad suite of avian species, 2) using observed abundance-weighted average latitudes rather than northern range boundaries, which are more susceptible to observer biases and land use change (La Sorte and Thompson 2007; Kujala et al. 2013), and 3) classifying avian species by breeding habitat and migration strategy. We utilized North American Breeding Bird Survey data to examine range shift patterns and addressed two specific questions: (1) Has the center of observed abundance for individual species shifted latitudinally? (2) Is there a relationship between migration strategy or breeding habitat and range shifts? Our findings provide further insights into avian range shifts and help illustrate the dynamic patterns that are occurring across individuals, breeding habitats, and migration strategies.

Methods

Study area and timeframe

Initiated in 1966 with the aim of monitoring the status and trends of North American bird species, the Breeding Bird Survey (BBS) is cooperatively managed by the United States Geologic Survey and the Canadian Wildlife Service (Ziolowksi et al. 2010). BBS data are collected annually on randomly assigned, permanent routes spanning more than 4100 locations in Canada and the United States. Routes are 40 km long with 50 stops spaced 0.8 km apart. Observers start one half hour prior to sunrise and conduct a 3-min point count at each stop in which they record every bird heard and seen within a 400 m radius. The BBS has advantages over many long term data sets because data are collected in a systematic way following a strict protocol (Hitch and Leberg 2006). Hence, observer effort is the same for all routes across all years. However, we recognize that like all citizen science datasets, these BBS data have potential shortcomings such as changes in observers over time and their corresponding changes in skill level, and the potential temporal variation in observations across years (i.e., observation windows can be a couple months during the breeding season) which can affect species detection. Nonetheless, the BBS data of North America is a worthy citizen science dataset when the limitations are recognized. We obtained BBS data using the EcoData Retriever, which downloads, processes, and installs ecological datasets into database management systems (Morris and White 2012).

We used Environmental Protection Agency (EPA) level II ecoregion boundaries to delineate our study area across the central United States. For the purpose of this study, we limited our data to this region to avoid major longitudinal gradients affecting bird community composition and to exclude changes in altitude associated with mountain ranges that could confound latitudinal responses (Hitch and Leberg 2006). This spatial delineation of our study area does create a bias, making it more likely that bird movements will be greater from north/south (long axis) rather than east/west (short axis); however, longitudinal direction of shifts should not be influenced. Thus, we limited the study area from east to west to those routes that were within the longitudinal bounds of 95°E to 105°E. We used the median date for all routes conducted in our study region—1993—as a cutoff between early and late time period classification to limit bias from uneven sampling effort. Thus the early time period was classified as those routes conducted between 1967 and 1992 and the late time period was classified as routes done from 1993 through 2010. This late versus early approach is a more conservative analysis than other published research examining range boundaries that used BBS data (e.g. Hitch and Leberg 2006) and focuses on our primary research question of broad, climate change-driven trends in bird ranges.

Our study draws on data from 198 BBS routes that were sampled >7000 times. We only included routes that were sampled ten or more times during each sampling period (e.g., early and late) and species that were detected ten or more times during the entire period (1967–2010). Our liberal criterion for inclusion of species was to maximize the data used to make habitat and migration evaluations, and the inclusion of species with few detections did not create bias as there was no relationship between species abundance and shift magnitude ($R^2 = 0.0185$, $p > 0.05$). Additionally, we ensured included routes were well distributed across the sampling region to avoid spatial biases (Fig. 1).

Data analysis

Species were analyzed individually as well as by groups based on migration strategy and breeding habitat. We used the United States Patuxent Wildlife Research Center's classification for migration strategy and breeding habitat for each avian species. Migration strategy was divided into three classifications: permanent resident, short-distance, and Neotropical. Breeding environment was divided into five classifications: grassland, wetland, successional or scrub, woodland, and urban (https://www.pwrc.usgs.gov/bbs/).

We quantified range shifts for species and migration and breeding classifications by comparing the weighted latitudinal mean and standard deviation for each observed abundance across the two sampling periods. We refer to this as 'observed abundance' rather than 'abundance' because abundance is actually the product of a species true abundance and the individual detection probability and here we are using detections alone. We used the center of observed abundance because they are less problematic than the northern limits which can be very dynamic over time and subject to sampling biases (Doherty et al. 2003; Kujala et al. 2013).

We calculated weighted mean and weighted standard deviations with the wt.mean and wt.sd functions, respectively, in the SDMTools package for the R statistical environment

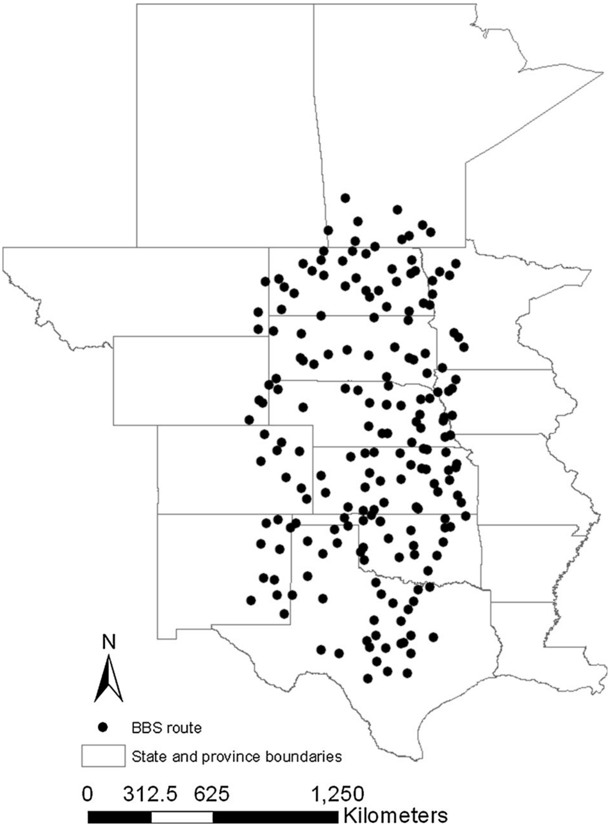

Fig. 1 Distribution of breeding bird survey locations used in analysis

(R Core Team 2014, VanDerWal et al. 2012). To determine meaningful (non-zero) range shifts for each species and migration/breeding group, we estimated 95 % confidence intervals with a simulation function that compared differences between periods based on 1000 simulated distributions derived from weighted means and standard deviations from each period. We calculated the overall shift across species as a mean and standard deviation of all 277 species' responses weighted by their frequency of occurrence in the dataset. Online Resource 1 includes R script for all analysis.

Results

We examined range shifts for 277 species inhabiting the central portion of the United States surveyed over a 43 year span. We used weighted latitudinal averages to calculate population centroids over 198 BBS routes. Despite a mean poleward shift of 28 km across all species, 95 % confidence intervals for the estimate overlap zero (95 % CI −29 to 84) due to considerable variation among species: ca. 52 % of species demonstrate poleward shifts but 23 and 24 % did not shift or shifted equatorward, respectively (Fig. 2).

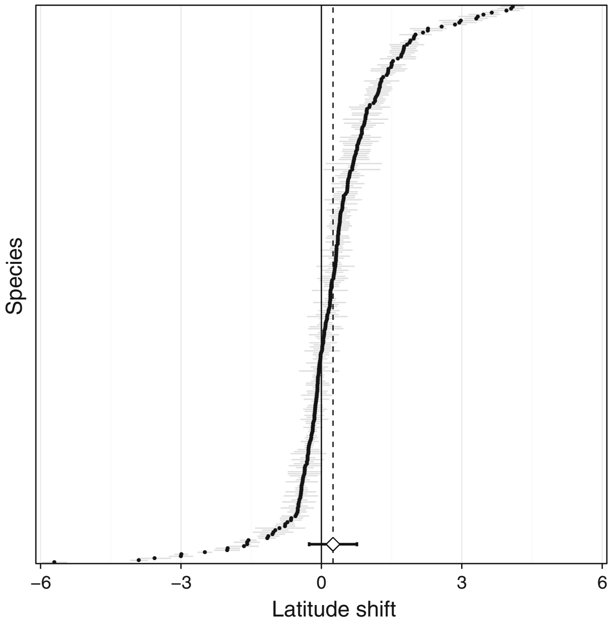

Fig. 2 Change in weighted latitudinal mean observed abundance (*dot*) and 95 % confidence interval (*gray horizontal lines*) calculated as the difference of the weighted observed abundance from the early period (1967–1992) to the late period (1993–2010) for each of the 277 North American breeding birds. The *dashed vertical line* and *diamond* represent the overall weighted mean change for the avian community and the corresponding weighted standard deviation (*bold horizontal line*) for the entire avian community. (Color figure online)

Examined by breeding habitat, birds in scrub-shrub and grasslands exhibited poleward shifts that are substantially different than zero, while wetland, woodland, and urban species are all exhibiting poleward shift trends but these shifts are not different from zero (Fig. 3). On average, birds in scrub-shrub habitats have shifted poleward by 127 km (95 % CI 79–177) and grassland breeding birds have shifted poleward by 65 km (95 % CI 23–104). Among different migration strategies, ranges of short-distance migrants shifted poleward by an average of 86 km (95 % CI 43–128) but trends in Neotropical migrants and resident species did not differ from zero (Fig. 4).

Discussion

Our examination of range shift patterns in North American breeding birds showed multi-directional shifts for individual species and across breeding and migration groups. Generally, the patterns we observed support a climate change signature (i.e., poleward shifts). While the overall poleward trend for the 277 species did not differ from zero, no breeding or migration group showed equatorward shifts and three groups—birds breeding in shrub-scrub, grassland habitats, and short-distance migrants—demonstrated substantial poleward shifts. Previous work across multiple taxa showed a proportion of species exhibit multi-directional shifts, and several mechanisms have been proposed to explain these patterns (Table 1). For birds, it is likely that multiple drivers influence the direction of range shifts

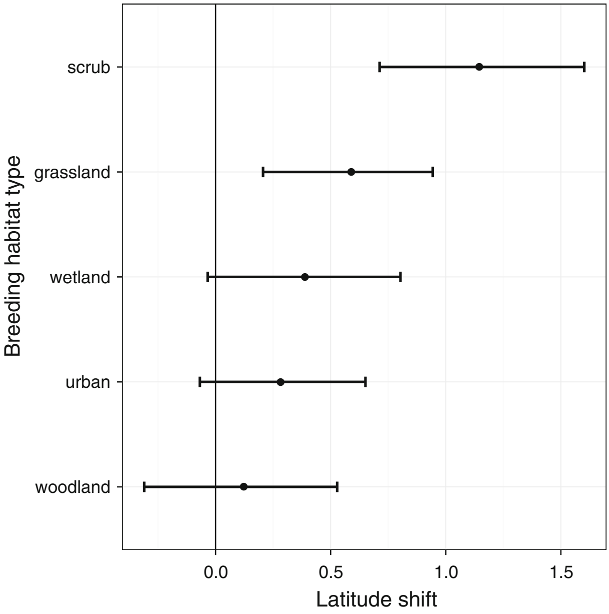

Fig. 3 Change in weighted latitudinal mean observed abundance (*dot*) and 95 % confidence interval (*horizontal lines*) weighted by species abundance for birds breeding in scrub-shrub ($n = 58$), grassland ($n = 29$), wetland ($n = 73$), urban ($n = 12$), and woodland ($n = 105$) environments. Breeding environments were classified using the United State Geologic Service Patuxent Wildlife Center breeding bird survey webpage (https://www.pwrc.usgs.gov/bbs/)

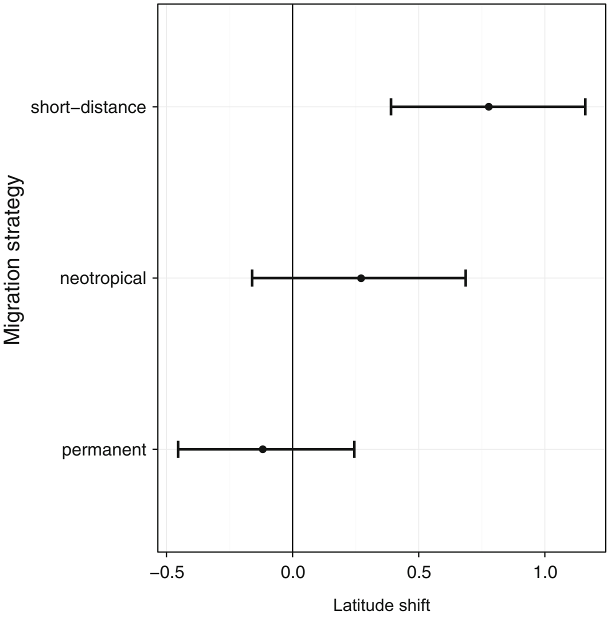

Fig. 4 Change in weighted latitudinal mean observed abundance (*dot*) and 95 % confidence interval (*horizontal lines*) weighted by species abundance for short-distance ($n = 130$), Neotropical ($n = 99$), and permanent resident ($n = 48$) migration strategies. Migration strategies were classified using the United State Geologic Service Patuxent Wildlife Center breeding bird survey webpage (https://www.pwrc.usgs.gov/bbs/)

Table 1 Mechanisms proposed by previous research to explain varied organismal responses to range shifts expected as a consequence of climate change

Direction	Proposed mechanism (driver)	Citation
Poleward/ Upslope	Increases in early winter temperatures	Lehikoinen et al. (2013)
	Period of climatic warming	Thomas and Lennon (1999), Parmesan and Yohe (2003), Hitch and Leberg 2006), Chen et al. (2011), Tayleur et al. (2015)
	Interaction between climate change and regional factors	La Sorte and Thompson (2007)
	Colonization event	La Sorte and Thompson (2007), Tayleur et al. (2015)
	Southern range retraction	VanDerWal et al. (2012)
Neutral	Adaptation of local populations to new climate	Rodrigues-Trelles and Rodriguez (1998), Parmesan et al. (2005)
	Inability to disperse	Davis et al. (1998)
	Insufficient amount of climate change	Tingely et al. (2009)
	Generalized species switching prey base	Both and Visser (2001)
	Temporal lag in movement response	Svenning et al. (2008)
	Lack of availability (e.g., limited elevational range, continental limit)	Hickling et al. (2006); VanDerWal et al. (2012)
Equatorward/ Downslope	Stochastic fluctuations in population size	Lenoir et al. (2010)
	Measurement error.	Lenoir et al. (2010)
	Habitat modification (natural disturbances, human-induced disturbance, permanent changes of land use)	Archaux (2004)
	Importance and intensity of species interactions (facilitation, predation, competition)	Hughes (2000), Lenoir et al. (2010)
	Changes in non-temperature environmental gradients (e.g., precipitation)	Tingley et al. 2009, Zuckerburg et al. (2009), Crimmins et al. (2011)
	Uneven warming (i.e., areas of cooling)	Parmesan and Yohe (2003), VanDerWal et al. (2012)
	Parasite outbreak	Tayleur et al. (2015)

with land use and land cover changes being two primary examples (Archaux 2004). Additionally, there is evidence of uneven warming across the central portion of the United States so it is conceivable that species are seeking ideal thermal environments by moving equatorward or that temperatures have not reached a point that causes individual physiological constraint (Chen et al. 2011; Stocker et al. 2013). Moreover, even when abiotic conditions on breeding grounds change, not all species possess the traits necessary to shift ranges which may lead to population declines (Davis et al. 1998).

Trends among all breeding habitat groups showed mean poleward shifts in their range with scrub-shrub and grassland exhibiting the greatest shifts. Scrub-shrub breeding birds might shift to match advanced phenology in breeding areas that drive earlier leaf flush, flowering, hatching of insect eggs, and seed production as a result of climatic changes (Thomas et al. 2001; Bertin 2008). Although similar phenomena likely occur in wetland and woodland habitats, corresponding patterns in bird range shifts might be obscured from our data by less-pronounced phenological changes or greater generalization of birds in these habitats. Alternatively, spatial limitations of available habitat might constrain the ability of these species to adapt through range shifts (VanDerWal et al. 2012), or changes in non-temperature environmental gradients such as precipitation may be the driving force of current ranges (Tingley et al. 2009). Observation of shifts in grassland species is somewhat more predictable because grassland environments occur throughout much of the central United States, making shifts possible, and these species are likely more adaptable to changes because of their long evolutionary history of living in heterogeneous habitats that experience frequent disturbance (Knopf 1994). Moreover, grassland species are generally multi-brooded and vagile meaning they possess several key traits allowing them to be adaptable to change through range shifts (Lenoir et al. 2010; Chen et al. 2011).

Short-distance migrants exhibited the greatest poleward range shifts. This suite of species, more so than permanent residents or Neotropical migrants, generally possess the traits desired to adapt to change through range shifts (Angert et al. 2011). For example, short-distance migrants have greater dispersal ability than permanent residents as they are adept at making migration events each year; they have reproductive rates that are generally greater than or equal to Neotropical migrants due to their ability to arrive on the breeding grounds earlier in the season and many species in this group are multi-brooded. Moreover, short-distance migrants are the most ecologically generalized based on their ability to migrate intermediate distances as opposed to the other strategies (i.e., permanent residents or Neotropical migrants) that require large movements or no movements at all. We speculate that short-distance migrants react more rapidly to changes in food resources and nesting cover when compared to Neotropical migrants which would have difficulty tracking these events from distant wintering grounds (Both and Visser 2001). Additionally, short-distance migrants may be responding to changes in winter environments that Neotropical migrants do not experience and permanent residents may lack the dispersal ability to avoid (La Sorte and Thompson 2007). On a positive note, the large range shift we documented for short-distance migrants likely means that resources exist to make shifting possible and that this suite of species has the capacity to cope with a changing climate.

We used the center of observed abundance rather than range boundaries to investigate range shifts. This method has advantages over the use of range boundaries (Doherty et al. 2003; La Sorte and Thompson 2007; Kujala et al. 2013), but it could also lead to erroneous speculation of a climate signature when in fact the shift may be driven by a non-climate retraction at a portion of the species' distribution. Nonetheless, our all-inclusive approach shows that while the majority of species are moving poleward there are many species experiencing equatorial shifts, which further illustrates the complexity of climate change and land use/land cover interactions (Kampichler et al. 2012) and illustrates that some avian species may respond positively through increases in population to future climate change (Matthews et al. 2004). Furthermore, it could be evidence of climate change events that are not directly related to temperature change or are a combination of temperature and other factors, such as precipitation, that mask the expected signature of climate induced shifts (VanDerWal et al. 2012).

There are many potential mechanisms that could be contributing to range shifts in the avian community (Table 1). The generality of climate-induced shifts in bird distributions has to be taken with caution, as shown by La Sorte and Thompson (2007) that highlighted possible confounding effects, especially anthropogenic environmental changes. At large extents, landscape structure (e.g. patch size, shape, and orientation) and composition can effect bird distribution and movements (Gutzwiller et al. 2010; Rittenhouse et al. 2012). At finer scales, changes in land use and management are known to influence bird communities, especially factors that have a homogenizing effect on plant community structure

(Archaux 2004; Fuhlendorf et al. 2006). As habitat patches become sparser due to anthropogenically induced land change, the potential for species-shifts increases in all directions. However, the use of long term data sets over large landscapes may be the best attempt to reduce noise that could generate misleading results, and the absence of range shift "result" should not immediately be discounted as a lack of a response to global changes.

Our observations of range shift patterns and those on other taxa throughout the world promote the idea that land managers and researchers should place the most emphasis on species and populations that are indeed shifting their ranges. However, we would like to point out that species that are not shifting their ranges could be those in the greatest need of conservation action. A lack of range shift could be the result of many different, not mutually exclusive, circumstances. For example, individuals that are able to adapt to local changes (Parmesan et al. 2005), have an inability to disperse (Davis et al. 1998), are generalized enough to switch prey bases (Both and Visser 2001), or have a lack of available area to shift to as a result of geographic or land use limitations (Hickling et al. 2006), may all exhibit non-shifting range patterns. Emphasis on dynamics within the previous or existing range fails to consider the availability of suitable habitat or resources beyond the current range. To assess the threat of global changes such as shifts in land use and climate change, greater focus should be placed on which resources are limiting and where sufficient substitutes exist if we are to fully understanding range shift patterns (or a lack thereof). Understanding the causes of variation in these patterns is imperative for making predictions about species distributions so we may have efficient and targeted future conservation efforts (Lehikoinen and Virkkala 2015).

The potential impacts of global change are of increasing concern both in terms of general influences on biodiversity and specifically on the potential of future species extinctions. Given the fragmentation and human alteration of the landscape, adapting to a changing world through range shifts will be challenging, especially for species inhabiting the most altered ecosystems and those with limited dispersal abilities (e.g., resident birds). Continued further analysis of existing long term data sets will improve our identification of vulnerable species, and we recommend using inclusive approaches when doing so, even if the results are less dramatic and consequentially less publishable (Harrington et al. 1999). Furthermore, future research needs to try and identify mechanisms driving range shifts, but perhaps more importantly, research also needs to focus on resource availability and accessibility for those species that have not undergone range shifts but may still be affected by climate change.

Acknowledgments This work was supported by funding from USDA-AFRI Managed Ecosystems Grant #2010-85101-20457 and by the Oklahoma and North Dakota Agricultural Experiment Stations.

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