

Full annual cycle climate change vulnerability assessment for migratory birds

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Abstract. Climate change is a serious challenge faced by all plant and animal species. Climate change vulnerability assessments (CCVAs) are one method to assess risk and are increasingly used as a tool to inform management plans. Migratory animals move across regions and continents during their annual cycles where they are exposed to diverse climatic conditions. Climate change during any period and in any region of the annual cycle could influence survival, reproduction, or the cues used to optimize timing of migration. Therefore, CCVAs for migratory animals best estimate risk when they include climate exposure during the entire annual cycle. We developed a CCVA incorporating the full annual cycle and applied this method to 46 species of migratory birds breeding in the Upper Midwest and Great Lakes (UMGL) region of the United States. Our methodology included background risk, climate change exposure × climate sensitivity, adaptive capacity to climate change, and indirect effects of climate change. We compiled information about migratory connectivity between breeding and stationary non-breeding areas using literature searches and U.S. Geological Survey banding and re-encounter data. Climate change exposure (temperature and moisture) was assessed using UMGL breeding season climate and winter climate from non-breeding regions for each species. Where possible, we focused on non-breeding regions known to be linked through migratory connectivity. We ranked 10 species as highly vulnerable to climate change and two as having low vulnerability. The remaining 34 species were ranked as moderately vulnerable. In general, including non-breeding data provided more robust results that were highly individualistic by species. Two species were found to be highly vulnerable throughout their annual cycle. Projected drying will have the greatest effect during the non-breeding season for species overwintering in Mexico and the Caribbean. Projected temperature increases will have the greatest effect during the breeding season in UMGL as well as during the non-breeding season for species overwintering in South America. We provide a model for adaptive management of migratory animals in the face of projected climate change, including identification of priority species, research needs, and regions within non-breeding ranges for potential conservation partnerships.

Key words: adaptive capacity; annual cycle; climate change exposure; climate change vulnerability; climate sensitivity; migratory birds; migratory connectivity; non-breeding season.

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INTRODUCTION

Climate has played a key role in shaping the life histories of species (Parmesan 2006). Rapid human-induced climate changes, such as those experienced today, and the effects this will have on the evolution and ecology of wildlife species are not well understood (Parmesan 2006, Dawson et al. 2011). Migratory animals, for example, are highly mobile, which could make them more resilient to climate change if they are able to shift their ranges or their phenology to track suitable climate. In fact, long-distance migration may have evolved in response to prehistoric climate change (Louchart 2008). On the other hand, migrants may be more vulnerable because their annual climatic and ecological requirements are complex and span vast distances. They are exposed to a wide range of climatic conditions, and climate changes at migratory, winter, or summer locations could influence survival, reproductive success, or ecological cues used to optimize migratory timing (e.g., Studds and Marra 2007, Gienapp et al. 2012, Cohen et al. 2015). If necessary resources do not track the changing climate, even highly mobile animals, such as migratory birds, may suffer reduced fitness (Root and Schneider 2006). Migratory animals may be more reliant on predictable resources (Mettke-Hofmann 2016), which will become less predictable under climate change, thus making phenological mismatch more likely.

Climate change vulnerability assessments (CCVAs) are one of several tools used to help inform management and conservation decisions such as selecting species or habitats to target for conservation, prioritizing land acquisition, directing monitoring efforts, and identifying specific factors that may contribute to vulnerability (Glick et al. 2011). Other tools in use include species distribution modeling, which can be extremely data heavy (e.g., Stralberg et al. 2015). Climate change vulnerability assessments, however, can integrate quantitative as well as qualitative data to quickly and efficiently measure the vulnerability of species and their environments to climate change. They tend to incorporate exposure, sensitivity, adaptive capacity, and indirect biotic interactions (e.g., Dawson et al. 2011, Cahill et al. 2012, IPCC 2014).

Climate change vulnerability assessments to date have not accounted for climate change exposure throughout the annual cycle. If we hope to

understand vulnerability of migratory animals to climate change, however, incorporating year-round climate data may be necessary (Small-Lorenz et al. 2013). North American CCVAs have focused almost exclusively on the breeding season (e.g., Young et al. 2011, Gardali et al. 2012, Foden et al. 2013, but see Bagne et al. 2014) and ignored the complex annual cycles of migratory animals. None have incorporated data from linked populations, which may be why they tend to conclude migratory animals are less vulnerable than other taxa. For example, seven CCVAs, which included a combined total of 95 North American breeding migratory bird species, classified 2% as highly vulnerable, 16% as moderately vulnerable, and 82% as not vulnerable (either stable or likely to increase; NatureServe v.2.1, connect.natureserve.org/science/climate-change/ccvi). This result is surprising, given considerable evidence suggests migratory bird populations may be vulnerable to climate change (e.g., altered phenology, population declines, and extirpation; Parmesan 2006, Jiguet et al. 2007, Moussus et al. 2011). Although these CCVAs may have multiple flaws, a critical one to consider is that only breeding season data were used. At worst, assessments of migratory species that do not consider risk throughout the full annual cycle could lead to incorrect conclusions and inefficient allocation of resources, decreasing our ability to design conservation efforts that will most improve habitat and reduce threats to species that actually may be vulnerable. At best, including full annual cycle data could result in better CCVAs with stronger arguments for action or inaction.

For migratory birds, climate at breeding (e.g., Skagen and Yackel Adams 2012, García-Pérez et al. 2014, Öberg et al. 2015) and non-breeding locations, for both sedentary (Studds and Marra 2007, Wilson et al. 2011) and migratory periods (Marra et al. 2005, Paxton et al. 2014, Cohen et al. 2015), can influence fitness. During breeding, temperature and rainfall can influence survival (García-Pérez et al. 2014, Öberg et al. 2015) as well as reproductive success (Dreitz et al. 2012, Skagen and Yackel Adams 2012, Öberg et al. 2015). In addition, an increasing number of studies are finding that events between periods of the annual cycle are inextricably linked (Marra et al. 1998, 2015) so that the annual cycle can be thought of as a continuous series of linked events rather than discrete periods. For example, higher rainfall on

the sedentary non-breeding grounds has been correlated with improved body condition as well as advanced spring arrival and laying dates on the breeding grounds (e.g., Saino et al. 2007, Studds and Marra 2007, 2011), both of which affect reproductive success (Reudink et al. 2009). Although less is known about the influence of climate during migration, temperature has been correlated with the speed of spring migration (Marra et al. 2005) while temperature and rainfall have been shown to influence timing of migration (Cohen et al. 2015) and body condition during migration (Paxton et al. 2014). Assessing climate change seasonally is also critical because we do not expect climate perturbations to be uniform throughout the year. For example, mid-century drying effects in the Upper Midwest and Great Lakes are expected to be 14 times greater during summer than during winter (see also Karl et al. 2009). Due to carryover effects, exposure during one season could affect vulnerability during another. The complex relationship between climate and fitness throughout the annual cycle of migratory animals complicates our ability to infer the impacts of future climate change and emphasizes the need to consider risk seasonally throughout the full annual cycle in CCVAs.

Ideally, quantifying climate risk throughout the full annual cycle of migratory animals should incorporate how populations are connected between breeding and non-breeding periods. Migratory connectivity, or the extent to which individuals and populations are linked across phases of the annual cycle (Webster and Marra 2005), can have important implications for understanding complex population dynamics driven by annual climatic variability (e.g., summer vs. winter climate change; Webster and Marra 2005, Wilson et al. 2011, Small-Lorenz et al. 2013). Unfortunately, while we know basic breeding and stationary non-breeding ranges of most North American breeding birds, information on how populations are linked between these areas is rudimentary. Telemetry tools to track long-distance movements are expensive and, until recently, were too heavy to use on small species <20 g (Hallworth and Marra 2015). However, the USGS North American Bird Banding Laboratory (BBL) can also provide movement data and may be the largest inventory of tagged vertebrates in the Western Hemisphere (>1.2 million individuals banded annually, >74 million total

banding records, >4.8 million total re-encounter records, and >750 species represented, dating back to 1914). Banding and re-encounter data are a spatially accurate source of information on migratory connectivity for many species and are the only long-term data set available for most Nearctic breeding bird species. For example, analysis of BBL data for Gray Catbirds (*Dumetalla carolinensis*) suggests two geographically distinct breeding populations (Midwest and Northeast United States) that each winter in distinct geographic areas (southern Mexico and Florida, respectively; Ryder et al. 2011). Differences in projected climate change between southern Mexico vs. Florida could impact our understanding of vulnerability of the breeding populations and subsequent management strategies. Including migratory connectivity makes it possible to link the appropriate breeding and non-breeding climate exposure into vulnerability assessments. Although migratory connectivity research is in its infancy for some species, our knowledge continues to improve making vulnerability assessments more precise and informative.

Here, we present a CCVA that incorporates climate and life-history data from the full annual cycle and uses migratory connectivity where possible. We demonstrate our approach by quantifying climate change vulnerability for 46 species of migratory birds that breed in the Upper Midwest and Great Lakes region and spend the stationary non-breeding season in North America, Latin America, the Caribbean, and South America. For each species, we determine where and when they are most likely to be affected, assess which factors contribute most to vulnerability, and identify potential intrinsic or management-based adaptation strategies that could be adopted by management agencies. This is the first effort to separate and evaluate multiseason and spatially explicit components of climate change vulnerability.

METHODS

Vulnerability assessment framework

We define vulnerability as the evidence that climate change or other anthropogenic factors will negatively affect a regional population of a species. This could manifest as range contraction, local or widespread population decline, or extirpation. Mechanisms for changes in population trends include reduced survival during the breeding or

non-breeding seasons, reduced reproductive output during the breeding season, or range shift out of the region. The central aspect of our approach is incorporation of data from the full annual cycle, particularly climate change exposure data. As such, it is a better alternative for assessing vulnerability of migratory species than other CCVAs currently in use (Small-Lorenz et al. 2013). Details of how we included full annual cycle data in vulnerability calculations should be considered a flexible framework that should be modified depending on the data at hand as well as priorities.

We selected criteria for the vulnerability framework based on two workshops (held October 2012 and January 2013 at the Smithsonian Conservation Biology Institute, Washington, D.C., USA) and expert consultation, including five governmental and non-governmental agencies (Environmental Defense Fund, The Nature Conservancy, Smithsonian Conservation Biology Institute, USFWS, USGS). We used information from climate models, literature review, and migratory connectivity to calculate total vulnerability as an average of five categories for 46 migratory bird species (Appendix S1): (1) background risk (factors unrelated to future climate change); (2) climate change exposure; (3) climate sensitivity; (4) adaptive capacity to climate change; and (5) indirect effects of climate change. We integrated climate change-related factors and background risk to provide a more comprehensive vulnerability assessment that theoretically includes all threats. Although the migratory period plays a substantial role in annual survival (Sillelt and Holmes 2002), and exposure to climate change may be important during these periods (Ewert et al. 2015), we did not include it here because migration routes and stopover sites are generally not fixed locations. Rather, sites may shift from year to year, making it hard to assess climate exposure. In addition,

migration routes and important stopover sites are often unknown for individual species. We did not want lack of information to prevent us from presenting a full annual cycle approach. Therefore, we proceeded with the best data at hand and restricted our analysis to the breeding and sedentary non-breeding periods of the annual cycle. Hereafter, we refer to these periods as breeding and non-breeding. We scored each category separately on the same 5-point scale with 5 being most vulnerable (<1: no vulnerability or positive response, 1–1.9: low vulnerability, 2–2.9: moderate vulnerability, 3–3.9: high vulnerability, and 4–5: very high vulnerability). We calculated total vulnerability as seen in Eq. 1 below.

Because a species' climate sensitivity can interact with climate change exposure and buffer or compound its effects, we used it as a modifier of climate change exposure (Young et al. 2011). To compare the independent influences of background and climate change risk, we also calculated vulnerability to climate change-related factors alone as seen in Eq. 2 below.

We summarized median scores across all species because the median is robust to outliers and skewed data. To compare scores between categories and groups of species, we used the non-parametric Mann–Whitney *U* test. See Appendix S2 for details on the vulnerability assessment framework and Appendix S3 for vulnerability scores by category for individual species.

Background risk

Species that are already at risk of extinction due to other anthropogenic stressors such as habitat loss may be less resilient and thus more vulnerable to climate change (e.g., species with small or declining populations; McLaughlin et al. 2002). We used data from the Partner's in Flight regional conservation assessment (PIF, Panjabi et al. 2012),

$$\text{Total vulnerability} = \frac{\sum [\text{background risk} + (\text{climate change exposure} \times \text{climate sensitivity})^{1/2} + \text{adaptive capacity to climate change} + \text{indirect effects of climate change}]}{4} \quad (1)$$

Climate change specific vulnerability

$$= \frac{\sum [(\text{climate change exposure} \times \text{climate sensitivity})^{1/2} + \text{adaptive capacity to climate change} + \text{indirect effects of climate change}]}{3} \quad (2)$$

Upper Mississippi River and Great Lakes Region Joint Venture (Potter et al. 2007), the Upper Mississippi Valley/Great Lakes Waterbird Conservation Plan (Wires et al. 2010), and population trend data from the Breeding Bird Survey (BBS, www.pwrc.usgs.gov/bbs) to calculate background risk. We used PIF data because it is the most comprehensive regional listing of conservation status for avian taxa, does not include climate change as a risk factor, incorporates both breeding and non-breeding data, is revised every five years, and is scored on a 5-point scale similar to ours (Panjabi et al. 2012). For taxa not listed by PIF, we used the Upper Mississippi River and Great Lakes Region Joint Venture (Potter et al. 2007) and the Upper Mississippi Valley/Great Lakes Waterbird Conservation Plan (Wires et al. 2010), which use PIF methods and cover the focal region.

The PIF assessment uses population abundance, population trend, breeding range size, non-breeding range size, breeding threats, and stationary non-breeding threats to rate conservation status (Potter et al. 2007, Wires et al. 2010, Panjabi et al. 2012). Where possible, we replaced population abundance and population trend scores with estimates of probability of quasi-extinction derived from regional BBS counts. Quasi-extinction was first termed by Ludwig (1999) and is defined as a drop in population abundance below a specified level (Semmens et al. 2016). To estimate risk of quasi-extinction, we used a count-based population viability analysis developed to estimate extinction risk of rare species of concern (e.g., Thogmartin et al. 2006, Bronte et al. 2010, Stanton et al. 2016). Population viability was predicted to be at levels above those where demographic stochasticity and Allee effects may become important (Lande et al. 2003, Fagan and Holmes 2006). As such, we did not estimate absolute risk of extinction per se, but rather the potential for quasi-extinction, a drop in the population below some subjective level in which small-population processes begin to dominate dynamics. Quasi-extinction is used by the World Conservation Union's International Union for the Conservation of Nature (Mace and Lande 1991) and the U.S. Endangered Species Act (DeMaster et al. 2004). Setting a quasi-extinction level can be subjective and value-laden (Fagan and Holmes 2006). To overcome uncertainty in minimum detection with BBS data, we calculated

quasi-extinction for a relative abundance index of 10% of the year 2000 estimate. This, in effect, calculates the probability of obtaining an additional 90% decline from the year 2000 population. We converted probability of quasi-extinction to a 5-point scale (see Appendix S2).

For species with robust quasi-extinction probabilities from BBS counts (67% of our focal species), we calculated background risk from PIF range size scores, PIF threat scores, and quasi-extinction risk score (in lieu of PIF population abundance and population trend scores; see Appendix S2). For species with unreliable BBS counts, we did not include quasi-extinction risk but instead used population abundance, population trend, range size, and threat scores from PIF, Upper Mississippi River and Great Lakes Region Joint Venture, or Upper Mississippi Valley/Great Lakes Waterbird Conservation Plan, which all use the same methods (see Appendix S2).

Climate change exposure

Exposure is determined by extrinsic environmental factors (Williams et al. 2008, Dawson et al. 2011). Here, we specifically included climate-related exposure due to predicted mid-century (2040–2069) changes in mean temperature and mean moisture, where moisture is defined as the actual vs. potential evapotranspiration ratio (Aridity Index Plus from www.climatewizard.org). We used this moisture index instead of precipitation because it accounts for the drying effects of reduced precipitation combined with higher temperatures and increased evaporation (www.climatewizard.org). Although moisture does not capture some negative effects of increased precipitation (e.g., damage that severe storms may have on nest survival), it is a better reflection of general moisture requirements for birds and can account for the net loss of available moisture that is possible even in regions with increased precipitation (Brooks 2009). We quantified exposure to temperature and moisture change separately for breeding and non-breeding periods of the annual cycle. For migratory birds, this meant determining exposure for two or more disjointed locations.

We used the Nature Conservancy's online tool, Climate Wizard, to quantify mid-century (2040–2069) change in mean temperature and mean moisture (www.climatewizard.org). Climate

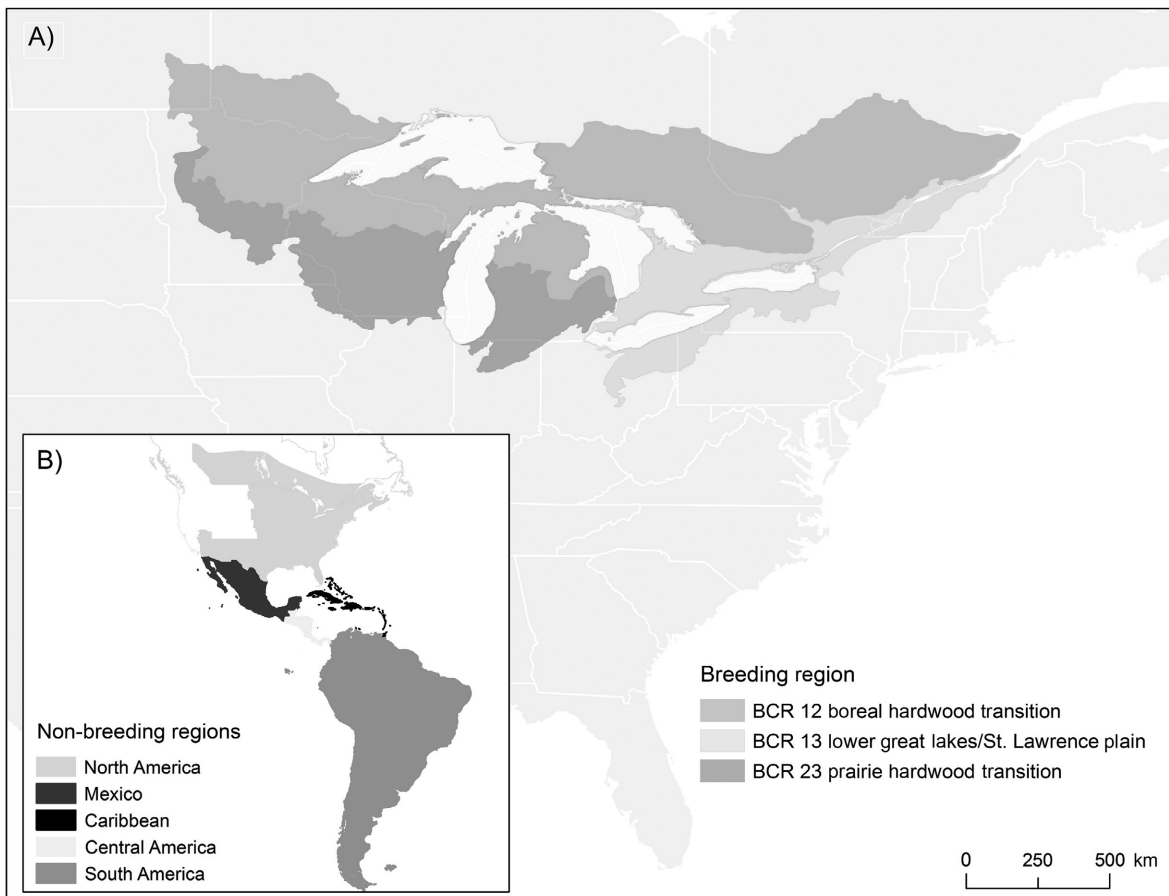


Fig. 1. Map of the study areas. (A) Upper Midwest and Great Lakes breeding region in relation to state boundaries and Bird Conservation Regions. (B) Delineation of the five non-breeding regions used for analysis. The North America region included all plausible non-breeding locations in United States and Canada (i.e., northwestern United States and most of Canada were excluded).

data originated from an ensemble of 16 general circulation models downscaled by the Nature Conservancy into fine-scaled ArcGIS (ESRI 2010) raster grids (1/8-degree grid cells, www.climatewizard.org). We used the high-emissions scenario, A2 (IPCC SRES 2000), to present maximum estimates of vulnerability and provide a more realistic assessment—current trends in greenhouse gas emissions exceed most worst case scenarios outlined in the Intergovernmental Panel on Climate Change 4th Assessment Report (IPCC 2007). We measured breeding season exposure (June–August) for areas where breeding ranges overlapped with the Upper Midwest and Great Lakes region (UMGL, Fig. 1). This varied slightly for each species according to breeding range boundaries. We obtained range maps

from NatureServe (www.birdlife.org/datazone/info/spcdownload). We measured non-breeding season exposure (December–February) for non-breeding ranges. For each species, we separated non-breeding ranges into five general regions (North America, Mexico, Caribbean, Central America, and South America, Fig. 1) and assessed exposure separately for each region. For species with known migratory connectivity (see *Migratory connectivity* below), we focused our calculation of non-breeding exposure on the appropriate region or regions. For the remaining species, we determined non-breeding exposure for all regions in the non-breeding range. Thus, for species with large non-breeding ranges, we calculated multiple estimates of non-breeding climate change exposure, one for each

non-breeding region. We did this because climate change is expected to vary widely geographically and we wanted to be able to compare exposure in each region and determine where species would be most vulnerable.

We converted predicted changes in climate to a 5-point scale (see Appendix S2) and obtained temperature and moisture exposure scores separately for each region and season: breeding temperature change in UMGL, breeding moisture change in UMGL, overall non-breeding temperature change (all relevant, species-specific non-breeding regions, identified through migratory connectivity where possible), regional non-breeding temperature change (i.e., North America, Mexico, Caribbean, Central America, and South America), overall non-breeding moisture change, and regional non-breeding moisture change. We combined breeding and non-breeding temperature and moisture exposure scores into a total climate change exposure score (i.e., breeding temperature exposure, breeding moisture exposure, non-breeding temperature exposure, and non-breeding moisture exposure; see Appendix S2).

Climate sensitivity

We defined sensitivity as the ability of a species to physiologically tolerate change. Because birds generally have high metabolisms and body temperatures (Gill 1995), they can be particularly sensitive to temperature extremes (Wolf 2000, McKechnie and Wolf 2010). Although they have behavioral strategies to tolerate high temperatures, such as avoiding sun exposure and activity during the hottest part of the day, as temperatures increase, evaporative heat loss becomes essential, particularly for small bird species (Wolf 2000). Here, we treat sensitivity as an intrinsically determined trait that can modify the effects of climate change exposure (Young et al. 2011). In a hypothetical example, highly sensitive species may not be as vulnerable if they occur in regions buffered from climate change. Conversely, insensitive species may not be vulnerable even if they occur in regions expected to change rapidly. For this reason, climate change exposure and climate sensitivity were multiplicative in our calculation of total vulnerability.

Climate sensitivity is determined by physiological thresholds that are not well understood

for birds. However, there is support for using historic climate patterns overlaid with species distributions to predict avian response to climate change (e.g., Jiguet et al. 2007, Moussus et al. 2011, Hurlbert and Liang 2012). Distributional data are widely available for most avian species and can be consistently accessed (www.birdlife.org/datazone/info/spcdownload). Thus, we used distribution maps to determine historic thermal tolerance as a measurement of sensitivity to future temperature change (for details, see Jiguet et al. 2006, 2007, Moussus et al. 2011). We adapted these methods to calculate historic precipitation tolerance as an index of sensitivity to future moisture change. We used Climate Wizard to gather historical climate data (seasonal mean temperature and precipitation, 1951–2001) from each species' entire breeding (June–August) and non-breeding ranges (December–February). We calculated tolerance as the weighted mean from the 50 hottest (or driest) cells minus the weighted mean from the 50 coldest (or wettest) cells using ArcGIS (ESRI 2010).

We calculated temperature and moisture sensitivity separately by season (breeding season thermal tolerance on the breeding grounds, breeding season precipitation tolerance on the breeding grounds, non-breeding thermal tolerance on the non-breeding grounds, and non-breeding precipitation tolerance on the non-breeding grounds) and converted tolerance values to a 5-point sensitivity scale (see Appendix S2).

Adaptive capacity to climate change

We defined adaptive capacity as the ability of a species to adjust to change. It is determined by intrinsic traits of evolutionary potential and phenotypic plasticity (Williams et al. 2008, Dawson et al. 2011, Nicotra et al. 2015). For most avian taxa, evolutionary potential is largely unknown. However, paleontological evidence suggests phenotypic plasticity may be more important than evolutionary capacity in regard to climate change (Dawson et al. 2011). Species with more flexibility are more likely to take advantage of changing ecosystems, regardless of how the environment is changing. Observational and correlational evidence suggests that flexible avian species are more likely to use novel combinations of resources in situ or may be able to move and track changing resources more quickly (e.g.,

Végvári et al. 2010, Dawson et al. 2011, Salido et al. 2011).

We used the Birds of North America (Poole 2005) and species range maps (www.birdlife.org/datazone/info/spcdownload) to determine plasticity of relevant life-history traits that we considered to be the most reliable indices of flexible behavior in unpredictable environments: (1) migration strategy: short-, medium-, long-, or ultra-long-distant migrant; (2) breeding and non-breeding habitat niche specialization: diversity of general and microhabitat types used; (3) breeding and non-breeding diet niche specialization: diversity of general and specific food groups taken and diversity of foraging strategies used; and (4) breeding site fidelity: probability to return to a particular location within and between breeding seasons.

There is evidence that short-distance migratory birds may be less vulnerable because they are better able to adjust to phenological changes (e.g., Both and Visser 2001, Moussus et al. 2011, Hurlbert and Liang 2012). In addition, a review of avian cognitive ability by Mettke-Hofmann (2016) concludes that long-distance migrants are less flexible than short-distance and facultative migrants. We treated migratory distance similar to Galbraith et al. (2014). Studies suggest that generalist species may be less vulnerable because it is less likely that all habitat or food types will disappear or be otherwise negatively affected due to climate change (Jiguet et al. 2007, Végvári et al. 2010, Angert et al. 2011, Moussus et al. 2011). We included both habitat and diet specialization variables because both are important to species survival and exploratory analyses showed them to be uncorrelated (breeding habitat ~ breeding diet: $r = 0.24$, $t(44) = 1.7$, $P = 0.1$; non-breeding habitat ~ non-breeding diet: $r = 0.16$, $t(44) = 1.1$, $P = 0.28$). Strategies of high fidelity work well in stable environments while nomadic or transient strategies are better suited to unpredictable environments (Dean 1997, Mettke-Hofmann 2016).

We converted life-history information to a 5-point scale for each component, with 5 representing the least adaptive species. We calculated total adaptive capacity to climate change from migration strategy, breeding and non-breeding habitat specialization, breeding and non-breeding diet specialization, and breeding site fidelity (see Appendix S2). Some species (9%) had

no information on diet during the non-breeding season, while 11% had limited information on breeding site fidelity (Appendix S3). For these species, we calculated adaptive capacity to climate change without these data. Because adaptive capacity data were more subjective than the above categories, we assessed data uncertainty for each component and scored uncertainty on a 5-point scale with 5 being the most uncertain.

Indirect effects of climate change

Correlational studies suggest climate change will have its greatest effect on species survival through indirect biotic interactions rather than direct physiological stressors (Parmesan 2006, Cahill et al. 2012). Indirect effects due to climate change have been quantified by others under sensitivity, or adaptive capacity (e.g., Young et al. 2011, Foden et al. 2013), but we assessed them separately because they are primarily determined by extrinsic factors, whereas sensitivity and adaptive capacity are determined by intrinsic factors.

We included habitat vulnerability and evidence for changes in biotic interactions due to climate change. For species using more than one habitat, we averaged vulnerability of all relevant habitats. Possible biotic interactions we considered included changes in prey or other resources, predators, disease, parasites, and competitors. For example, warming of lakes and other water bodies is expected to make aquatic toxins more prevalent (Finch 2012), which would decrease prey quality for aquatic foraging species, thus increasing vulnerability. We conducted a literature review using Google Scholar to search for peer-reviewed papers and government-issued reports on habitat vulnerability and biotic interactions in North America, Mexico, the Caribbean, Central America, and South America (Appendix S3: Table S3.9).

We assessed four aspects of indirect effects of climate change: habitat vulnerability on the breeding grounds, vulnerability of biotic interactions on the breeding grounds, habitat vulnerability on the non-breeding grounds, and vulnerability of biotic interactions on the non-breeding grounds. We converted each of these to a 5-point scale and then calculated total indirect effects of climate change (see Appendix S2). Because of information gaps in non-breeding diet and in future prey status in

the tropics, we were unable to determine non-breeding biotic interactions for 26% of our focal species (Appendix S3). Nevertheless, we used information that was available and calculated indirect effects of climate change without the non-breeding biotic interactions data. As with adaptive capacity, indirect effects data were more subjective than climate change exposure and climate sensitivity. Thus, we assessed data uncertainty for each component and scored uncertainty on a 5-point scale with 5 being the most uncertain.

Focal area and species

We applied our CCVA to avian taxa breeding in the UMGL Landscape Conservation Cooperative (LCC), including parts of Illinois, Indiana, Iowa, Michigan, Minnesota, Missouri, Ohio, and Wisconsin, and three Bird Conservation Regions (boreal hardwood transition, lower Great Lakes/St. Lawrence plain, and prairie hardwood transition, www.nabci.net/International/English/bird_conservation_regions.html, Fig. 1). The diversity of habitats and ecosystems found in the UMGL reflects the region's importance to migratory birds. For example, the largest freshwater resource in North America, coastal wetlands, major rivers, boreal forests, and prairie-hardwoods are in the UMGL. Numerous challenges threaten the ecological integrity of the region, including a history of intensive land conversion, energy development, water limitations, invasive species, population growth, and climate change. Necessarily, conservation biologists and agencies must work together to manage this important region, and the UMGL LCC brings more than 30 agencies and organizations together, connecting science, conservation, and management.

We assessed vulnerability of 46 nongame migratory bird species (Appendix S1) breeding within the UMGL region. We chose diverse taxa representing a variety of habitats and life-history characteristics, pairing taxonomically similar species common in the region with those of conservation concern in the UMGL.

Migratory connectivity

For each species, we summarized all migratory connectivity information between the UMGL and five non-breeding regions (North America, Mexico, Caribbean, Central America,

and South America). We used this broadscale approach because local-scale data were not available or were inconsistent among species. We used the BBL banding and re-encounter database to map and determine migratory connectivity (Appendix S4). This database describes bird movement from original banding location to re-encounter locations and includes both spatial and temporal information. We limited breeding season locations (May–August) to those from Bird Conservation Regions 12, 13, and 23 (boreal hardwood transition, lower Great Lakes/St. Lawrence plain, and prairie hardwood transition). We plotted all non-breeding locations but categorized them according to sedentary non-breeding period (November–March), fall migration (September–October), and spring migration (April–May). We plotted original capture and re-encounter locations >18 km (10-min block) from the original capture location (using ArcGIS) to create migratory connectivity maps for each species (Appendix S4). For determination of migratory connectivity and climate change vulnerability analysis, we used only locations from the sedentary periods. For most species, we summarized migratory connectivity in general terms because we lacked data to account for spatial variation in detectability. For two species (Caspian Tern and Common Tern), however, we had sufficient data to quantify migratory connectivity more precisely and used multistate mark–re-encounter models to estimate geographic linkages. These models estimate the probability that populations from the UMGL region spend the winter in specific non-breeding regions (see Cohen et al. 2014 for methods).

In addition to the BBL re-encounter database and migratory connectivity models, we conducted literature reviews for each species and summarized all migratory connectivity data relevant to the UMGL. We searched for peer-reviewed literature and government-issued reports using Google Scholar and key words: migratory connectivity, connectivity, migration, tracking, telemetry, stable isotope, genetic marker, geolocator, satellite telemetry, GPS, and the common and Latin names of each species.

When calculating climate change exposure, we used only those non-breeding regions identified as having a possible link with the UMGL (based on BBL data and/or literature review). For species where we were unable to identify possible

Table 1. Vulnerability scores for 46 migratory species breeding in the Upper Midwest Great Lakes.

Species	Total vulnerability	Background risk	Climate change vulnerability	Exposure × sensitivity	Adaptive capacity	Indirect effects
Pied-billed Grebe (<i>Podilymbus podiceps</i>)†	2.9	3.9‡	2.5	0.7	3.6	3.3
Red-necked Grebe (<i>Podiceps grisegena</i>)	3.1	3.3	3.1	1.6	4.0	3.8
Green Heron (<i>Butorides virescens</i>)	2.7	3.0	2.6	1.4	3.3	3.0
Black-crowned night heron (<i>Nycticorax nycticorax</i>)†	2.4	3.3‡	2.1	0.7	2.8	2.7
American Kestrel (<i>Falco sparverius</i>)	2.1	3.6‡	1.6	0.7	2.8	1.2
Peregrine Falcon (<i>Falco peregrinus</i>)†	2.1	3.1‡	1.8	0.6	3.1	1.8
Killdeer (<i>Charadrius vociferus</i>)	1.8	1.7	1.9	1.1	3.0	1.3
Upland Sandpiper (<i>Bartramia longicauda</i>)†	2.4	2.0	2.5§	2.1	4.1	1.3
Caspian Tern (<i>Hydroprogne caspia</i>)	3.2	2.8	3.3§	2.6	3.5	3.9
Black Tern (<i>Chlidonias niger</i>)†	3.6	3.9	3.5	2.9	4.1	3.6
Common Tern (<i>Sterna hirundo</i>)†	3.2	3.9‡	3.0	1.4	3.9	3.6
Forster's Tern (<i>Sterna forsteri</i>)	3.3	3.0	3.4	2.5	3.5	4.2
Yellow-billed Cuckoo (<i>Coccyzus americanus</i>)	2.3	2.0	2.4	2.0	3.6	1.5
Black-billed Cuckoo (<i>Coccyzus erythrophthalmus</i>)†	2.5	2.7	2.4	2.1	3.6	1.6
Short-eared Owl (<i>Asio flammeus</i>)†	2.1	3.0‡	1.8	0.8	2.9	1.7
Northern Saw-whet Owl (<i>Aegolius acadicus</i>)	2.2	2.8‡	1.9	1.2	3.0	1.7
Common Nighthawk (<i>Chordeiles minor</i>)	2.2	2.9‡	1.9	1.1	3.6	1.0
Eastern Whip-poor-will (<i>Antrostomus vociferus</i>)†	3.2	3.7‡	3.1	2.9	4.3	2.0
Red-headed Woodpecker (<i>Melanerpes erythrocephalus</i>)†	2.0	2.1	1.9	1.4	3.0	1.4
Yellow-bellied Sapsucker (<i>Sphyrapicus varius</i>)	2.3	2.4	2.3	2.0	3.3	1.7
Yellow-bellied Flycatcher (<i>Empidonax flaviventris</i>)	3.2	3.7	3.1	2.6	3.9	2.8
Acadian Flycatcher (<i>Empidonax virescens</i>)†	2.8	2.3	2.9§	2.4	3.9	2.5
Swainson's Thrush (<i>Catharus ustulatus</i>)	2.8	3.3‡	2.6	1.8	3.7	2.3
Wood Thrush (<i>Hylocichla mustelina</i>)†	2.7	2.7	2.7	2.9	3.3	2.0
Worm-eating Warbler (<i>Helminthos vermivorum</i>)†	3.2	3.3	3.1	3.1	3.8	2.4
Golden-winged Warbler (<i>Vermivora chrysoptera</i>)†	2.8	2.7	2.9	2.8	3.7	2.0
Blue-winged Warbler (<i>Vermivora cyanoptera</i>)†	2.7	2.3	2.9§	3.2	3.8	1.7
Black-and-white Warbler (<i>Mniotilta varia</i>)	2.5	1.9	2.7§	2.1	3.8	2.3
Tennessee Warbler (<i>Oreothlypis peregrina</i>)	2.8	3.2‡	2.6	2.5	3.3	2.0
Nashville Warbler (<i>Oreothlypis ruficapilla</i>)	2.8	2.2	3.0§	3.1	3.7	2.1
American Redstart (<i>Setophaga ruticilla</i>)	2.3	1.8	2.5§	2.0	3.1	2.4
Cerulean Warbler (<i>Setophaga cerulea</i>)†	2.8	2.7	2.9	2.4	3.9	2.3
Yellow Warbler (<i>Setophaga petechia</i>)	2.2	1.3	2.5§	1.6	3.1	2.8
Black-throated Blue Warbler (<i>Setophaga caerulescens</i>)	3.1	3.8‡	2.8	2.9	3.5	2.1
Prairie Warbler (<i>Setophaga discolor</i>)†	2.7	2.6	2.7	3.1	3.2	1.9
Canada Warbler (<i>Cardellina canadensis</i>)†	2.8	2.3	3.0§	2.5	3.9	2.6
Field Sparrow (<i>Spizella pusilla</i>)†	2.2	2.1	2.2	2.4	3.3	1.0
Vesper Sparrow (<i>Pooecetes gramineus</i>)	2.2	2.1	2.2	2.5	3.2	1.0
Savannah Sparrow (<i>Passerculus sandwichensis</i>)	2.0	1.4	2.2§	1.4	3.4	1.8
Indigo Bunting (<i>Passerina cyanea</i>)	2.0	1.7	2.1§	2.6	2.7	1.0
Dickcissel (<i>Spiza americana</i>)†	2.6	3.0‡	2.5	3.1	3.4	0.9
Bobolink (<i>Dolichonyx oryzivorus</i>)†	2.5	2.3	2.6	2.5	4.1	1.2
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	1.5	1.3	1.6	0.5	2.5	1.7
Rusty Blackbird (<i>Euphagus carolinus</i>)†	3.0	3.3	2.9	1.5	4.0	3.1
Orchard Oriole (<i>Icterus spurius</i>)†	2.3	2.0	2.4§	2.9	3.0	1.3
Baltimore Oriole (<i>Icterus galbula</i>)	2.1	1.8	2.2§	2.7	2.9	1.2

Notes: Total vulnerability includes background risk and climate change vulnerability. Climate change vulnerability includes exposure × sensitivity, adaptive capacity, and indirect effects. Maximum score is 5 for all columns. Scores <2.0 are considered low vulnerability, while scores ≥3.0 are considered high vulnerability.

† Species of conservation concern in USGS Region 3.

‡ Background risk at least 20% > climate change vulnerability.

§ Climate change vulnerability at least 20% > background risk.

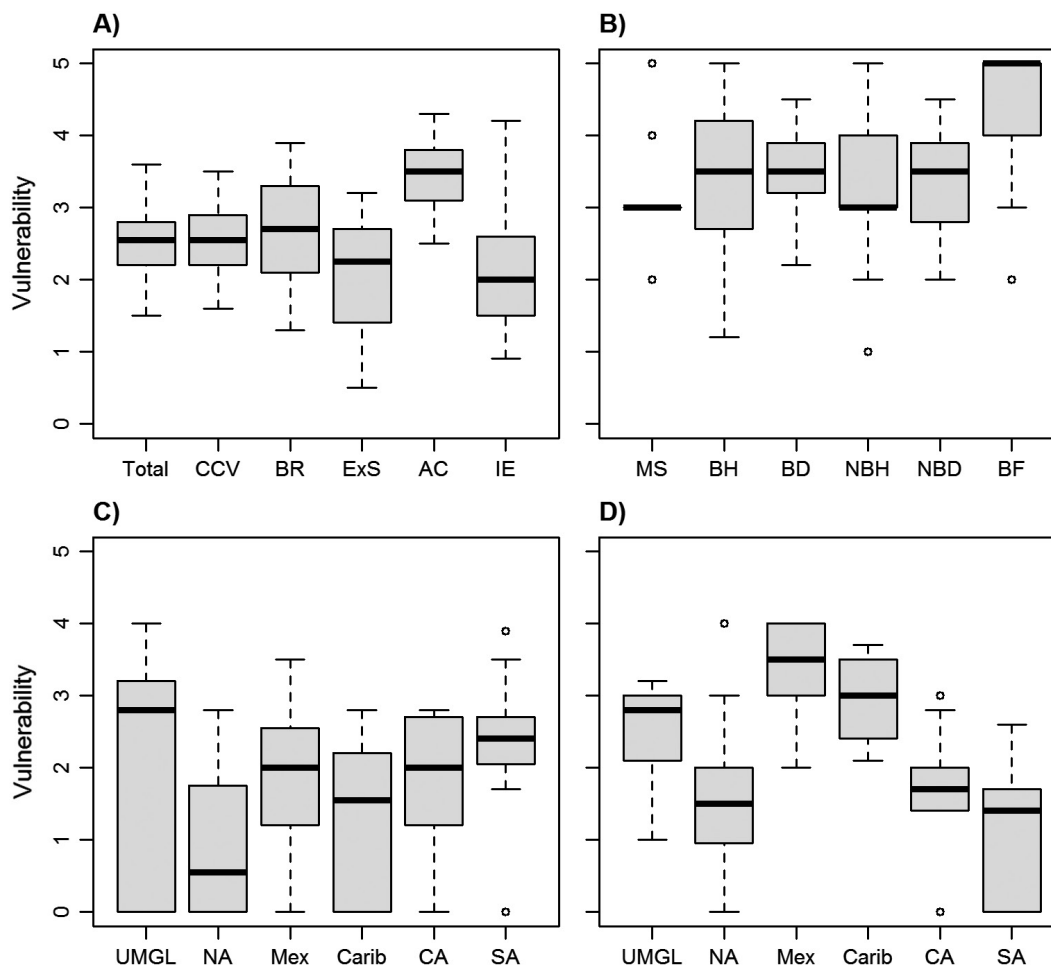


Fig. 2. Distribution of climate change vulnerability scores for 46 migratory species breeding in the Upper Midwest Great Lakes region (maximum vulnerability = 5). (A) Total vulnerability (“Total”; includes background risk, climate change exposure \times climate sensitivity, adaptive capacity to climate change, and indirect effects of climate change), vulnerability due to climate change-related factors only (“CCV”; i.e., excludes background risk), background risk (“BR”), climate change exposure \times climate sensitivity (“E \times S”), adaptive capacity to climate change (“AC”), and indirect effects of climate change (“IE”). (B) Adaptive capacity to climate change scores, including migration strategy (“MS”), breeding habitat specialization (“BH”), breeding diet specialization (“BD”), non-breeding habitat specialization (“NBH”), non-breeding diet specialization (“NBD”), and breeding site fidelity (“BF”). (C) Temperature change exposure \times temperature sensitivity scores by region and season, including Upper Midwest Great Lakes during breeding (“UMGL”), North America during non-breeding (“NA”), Mexico during non-breeding (“Mex”), Caribbean during non-breeding (“Carib”), Central America during non-breeding (“CA”), and South America during non-breeding (“SA”). (D) Moisture change exposure \times moisture sensitivity scores by region and season, including UMGL during breeding, NA during non-breeding, Mex during non-breeding, Carib during non-breeding, CA during non-breeding, and SA during non-breeding.

migratory connectivity, we included all non-breeding regions within the species range. For the two species with mark–re-encounter models, we included all non-breeding regions with $\geq 10\%$ probability of migratory connectivity.

RESULTS

We assessed climate change vulnerability for 46 migratory bird species breeding in the UMGL (Table 1; Appendix S3). Total vulnerability

included background risk, climate change exposure \times climate sensitivity, adaptive capacity to climate change, and indirect effects of climate change. Two species were ranked as having relatively low vulnerability, 10 were ranked highly vulnerable, and the remainder were categorized with moderate levels of vulnerability (median score = 2.6 of 5.0, Fig. 2A, Table 1). We compared background risk to climate change-only vulnerability and found seven species ranked highly vulnerable in both (Table 1). To understand how the full-cycle CCVA performed against breeding-only data, we compared breeding-only with full-cycle vulnerability results. In general, there was a significant decrease in overall CCVA scores when non-breeding data were included (breeding-only median score = 2.8, full-cycle median score = 2.5; $W = 1338$, $P = 0.03$; no species saw an increase). However, when we looked more closely at individual species and categories, we found nuances that may be useful for conservation management. For example, although Black and Forster's terns had no change between breeding-only and full-cycle CCVA scores, they were ranked highly vulnerable during both breeding and non-breeding seasons. In addition, when we focused on the temperature change exposure \times sensitivity combined effect, vulnerability scores increased for 17% of species when non-breeding data were included, decreased for 39%, and were unchanged for 44%. Likewise, comparing breeding-only moisture change exposure \times sensitivity combined effect vs. full-cycle found vulnerability scores increased for 15% of species, decreased for 44%, and were unchanged for 41%.

The climate change exposure \times sensitivity combined effect on avian vulnerability was significantly different among regions and seasons. On average, temperature increases on the UMGL breeding grounds were expected to have a larger effect on vulnerability compared with most non-breeding locations (UMGL median score = 2.9; North America median score = 0.6, $W = 854$, $P < 0.001$; Mexico median score = 2.0, $W = 828$, $P = 0.017$; Caribbean median score = 1.6, $W = 726$, $P = 0.003$; and Central America median score = 2.0, $W = 860$, $P = 0.15$; Fig. 2C). The exception was South America where the effect of temperature was expected to be as great as in the UMGL (South America median score = 2.4, $W = 620$, $P = 0.25$; Fig. 2C). In contrast, moisture

changes (i.e., drying) in Mexican and Caribbean non-breeding regions were expected to have a greater effect on vulnerability compared with moisture change anywhere else, including the UMGL breeding grounds (UMGL median score = 2.8; Mexico median score = 3.5, $W = 1042$, $P < 0.001$; Caribbean median score = 3.0, $W = 742$, $P = 0.002$; Fig. 2D).

We ranked nine species as highly vulnerable to temperature and/or moisture change throughout the annual cycle: Upland Sandpiper, Black Tern, Eastern Whip-poor-will, Acadian Flycatcher, Nashville Warbler, Prairie Warbler, Dickcissel, Bobolink, and Orchard Oriole. For these species, we expect high exposure to climate change during summer in the UMGL region will be compounded by high exposure during winter on the non-breeding grounds. All of these species except the Nashville Warbler are already considered species of conservation concern.

For most species, the adaptive capacity category (including migration strategy, breeding and non-breeding habitat specialization, breeding and non-breeding diet specialization, and breeding site fidelity) was the leading contributor to total vulnerability, relative to background risk, climate change exposure \times climate sensitivity, and indirect effects of climate change (Table 1, Fig. 2A). Within adaptive capacity, species with high scores had high breeding site fidelity on average and were less likely to move to new breeding locations between years (breeding site fidelity median score = 5.0). They were also fairly specialized in their breeding habitat use and breeding diet (breeding habitat and diet specialization median scores both = 3.5, Fig. 2B).

Despite its importance, little information was available about migratory connectivity of North American birds. We used all available resources to determine migratory connectivity for UMGL populations of the 46 migratory species included in our analysis (Table 2). Of these, 13% had >100 breeding to non-breeding band encounters in the USGS Bird Banding Lab database, 2% had 10–100, 30% had <10, and 54% had none. We used mark–re-encounter models to determine migratory connectivity for Caspian and Common terns, Appendix S4). Our literature search found migratory connectivity information on 11 species and included data from stable isotope analysis, genetic analysis, morphology, light-level

Table 2. Summary of migratory connectivity data, including number of data points from USGS Bird Banding Laboratory (breeding to stationary non-breeding banding encounters originating from the Upper Midwest Great Lakes), relevant literature, and which stationary non-breeding regions were included (Yes) and excluded (×) from the vulnerability analysis.

Species	Banding data	Literature review	Non-breeding region				
			NA	MEX	CAR	CA	SA
Pied-billed Grebe†	0		Yes	Yes	Yes	Yes	Yes
Red-necked Grebe	0		Yes				
Green Heron	0		Yes	Yes	Yes	Yes	Yes
Black-crowned night heron†,‡	114		Yes¶	×	Yes	Yes	×
American Kestrel‡	125	Hobson et al. (2009)	Yes	×	×	×	×
Peregrine Falcon†,§	165	Fuller et al. (1998)	Yes	×	Yes	Yes	Yes¶
Killdeer	8		Yes	Yes	Yes	Yes	Yes
Upland Sandpiper†	0						Yes
Caspian Tern‡	266†		Yes	×	Yes	×	×
Black Tern†	2			Yes		Yes	Yes
Common Tern†,§	279†		Yes		Yes	Yes	Yes
Forster's Tern	31		Yes	Yes	Yes		
Yellow-billed Cuckoo	1						Yes
Black-billed Cuckoo†	0						Yes
Short-eared Owl†	0		Yes	Yes	Yes		Yes
Northern Saw-whet Owl	6		Yes	Yes			
Common Nighthawk	0				Yes		Yes
Eastern Whip-poor-will†	0		Yes	Yes		Yes	
Red-headed Woodpecker†	3		Yes				
Yellow-bellied Sapsucker	3		Yes	Yes	Yes	Yes	
Yellow-bellied Flycatcher	0			Yes		Yes	
Acadian Flycatcher†	0					Yes	Yes
Swainson's Thrush	0	Kelly et al. (2005)		Yes		Yes	Yes
Wood Thrush†,§	0	Stutchbury et al. (2011), Stanley et al. (2012), Rushing et al. (2014)		Yes		Yes	
Worm-eating Warbler†	0			Yes	Yes	Yes	
Golden-winged Warbler†	0					Yes	Yes
Blue-winged Warbler†	1			Yes	Yes	Yes	
Black-and-white Warbler	1	Dugger et al. (2004)	Yes	Yes	Yes	Yes	Yes
Tennessee Warbler	0			Yes	Yes	Yes	Yes
Nashville Warbler	0	Lovette et al. (2004)	Yes	Yes	Yes		
American Redstart§	0	Norris et al. (2006)		Yes	Yes	Yes	×
Cerulean Warbler†,§	0	Jones et al. (2008)					Yes
Yellow Warbler§	0	Boulet et al. (2006)		Yes¶	×	Yes	Yes
Black-throated Blue Warbler	0	Rubenstein et al. (2002), Royle and Rubenstein (2004)			Yes	Yes	
Prairie Warbler†	0		Yes		Yes	Yes	
Canada Warbler†	0					Yes	Yes
Field Sparrow†	3		Yes	Yes			
Vesper Sparrow	1		Yes	Yes			
Savannah Sparrow	3		Yes	Yes	Yes		
Indigo Bunting	3			Yes	Yes	Yes	
Dickcissel†	0			Yes		Yes	Yes
Bobolink†	0						Yes
Red-winged Blackbird‡	325		Yes¶	×	×		
Rusty Blackbird†	2	Hobson et al. (2010)	Yes¶				
Orchard Oriole†	0			Yes		Yes	Yes

(Continued)

Table 2. Continued.

Species	Banding data	Literature review	Non-breeding region				
			NA	MEX	CAR	CA	SA
Baltimore Oriole	6		Yes	Yes	Yes	Yes	Yes

Notes: NA, North America; MEX, Mexico; CAR, Caribbean; CA, Central America; SA, South America; UMGL, Upper Midwest and Great Lakes. Regions left blank are not in the species range. For Caspian and Common terns, we also used multi-state mark-re-encounter models to estimate migratory connectivity.

† Species of conservation concern in USGS Region 3.

‡ Evidence for strong migratory connectivity with UMGL.

§ Evidence for weak migratory connectivity with UMGL.

¶ Only part of the non-breeding range in this region was included.

geolocators, and satellite telemetry. From the combined results (banding, modeling, and literature search), we were able to draw conclusions regarding migratory connectivity between UMGL breeding to specific non-breeding regions for 10 species (Table 2). Patterns of migratory connectivity varied greatly among species with some showing evidence of strong connectivity (i.e., UMGL-breeding populations migrate primarily to one non-breeding region, Table 2), while others showed evidence of weak connectivity patterns (i.e., UMGL-breeding populations migrate to many non-breeding regions, Table 2). For these 10 species, we excluded from our vulnerability analysis climate change exposure scores for non-breeding regions that had little evidence of migratory connectivity with UMGL populations. For the remaining 36 species, we included all non-breeding regions that were within each species range (Table 2).

Uncertainty was greater for the indirect effects category compared with adaptive capacity (Fig. 3). Overall, indirect effects data tended to be poorly documented (median uncertainty score = 2.9 of 5.0), while adaptive capacity data tended to be well documented on average (median score = 1.0). Within the indirect effects category, data on non-breeding biotic interactions were least certain (median score = 4.0). Within the adaptive capacity category, breeding site fidelity was least uncertain (median uncertainty score = 3.0). In contrast, our knowledge of migration strategy and breeding ecology was excellent for all of these species.

DISCUSSION

Effective conservation and management of migratory animals benefits from a full annual

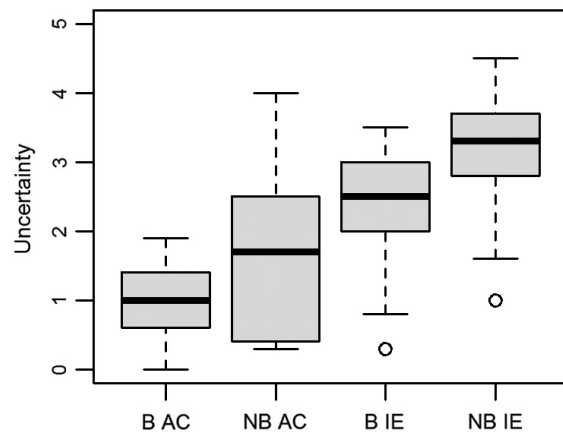


Fig. 3. Uncertainty of adaptive capacity and indirect effects categories, separated by breeding and non-breeding (maximum uncertainty = 5). Breeding adaptive capacity (B AC) includes migration strategy, breeding habitat specialization, breeding diet specialization, and breeding site fidelity. Non-breeding adaptive capacity (NB AC) includes non-breeding habitat specialization and non-breeding diet specialization. Breeding indirect effects (B IE) include breeding habitat vulnerability and breeding biotic interactions. Non-breeding indirect effects (NB IE) include non-breeding habitat vulnerability and non-breeding.

cycle approach (Marra et al. 2015). The methods presented here assess vulnerability of migratory birds to mid-century climate change using species-specific seasonal and geographic data. To date, several climate vulnerability assessments have been developed (e.g., Young et al. 2011, Gardali et al. 2012, Foden et al. 2013), but none have attempted to account for the full annual cycle climate change exposure that birds are exposed to across the globe. Focusing solely on

climate change during the breeding season ignores the majority of an animal's annual cycle. For all 46 species, including non-breeding data either did not change overall vulnerability status or decreased it. Yet the value of including non-breeding data was apparent when we looked at individual species. For example, we predicted high overall vulnerability during both breeding and non-breeding seasons for two species (Black and Forster's terns). The potential for year-round vulnerability strengthens the case for management action for such species. In addition, when we focused exclusively on the climate change exposure \times sensitivity combined effect, including non-breeding data increased vulnerability for some species (eight species when temperature change was analyzed, seven when moisture change was analyzed). These results accentuate how nuanced vulnerability to climate change can be and demonstrate that broad summaries across taxa may not be as informative. A one-size-fits-all approach to managing and conserving species under climate change may not be appropriate. Rather, it may be better to assess how individual traits and breeding and wintering locations might increase or decrease vulnerability. Including non-breeding data result in better and more robust CCVAs with stronger arguments for when and where action is needed or not needed. Indeed, comprehensive evaluation of climate exposure throughout the annual cycle is likely important for non-migratory species as well because patterns of climate change will not be consistent or in the same direction across seasons.

Migratory connectivity is an important component to the study of migratory species and a full annual cycle approach, whether the subject is the impact of climate change or the drivers of population dynamics. Knowing where birds from the UMGL region spend the non-breeding season allows one to focus on the most relevant non-breeding regions. For most animals, migratory connectivity research is still in its infancy and much remains to be discovered. Our analysis of BBL re-encounter database adds to a growing body of data, and we found at least some breeding to non-breeding encounters for 46% of our focal species with several of these having >100 encounters. We were able to do extensive mark-re-encounter models for Caspian and Common terns and found very different patterns

of migratory connectivity (Appendix S4). For example, land managers in the UMGL now know that most Caspian terns breeding around the Great Lakes spend the winter in the southeastern United States and the Caribbean. Using these data, we predicted that Caspian terns from the UMGL may be more vulnerable than previously thought because of high exposure to moisture change in the Caribbean. Such information will enable a more targeted conservation strategy for this species and may foster collaborative management between the UMGL and the southeastern United States and/or Caribbean nations. Nevertheless, although migratory connectivity is important, lack of these data should not prevent full-cycle analyses. We demonstrate how non-breeding data can be included even without migratory connectivity information. Including non-breeding climate change exposure in distinct regions allows managers to conservatively evaluate where vulnerability might be greatest, while understanding the uncertainty regarding actual strength of connectivity with each region. As more information becomes available, full life cycle CCVAs should be adapted to include these data and thus become more precise.

Of the 46 species we analyzed, 20% were ranked as highly vulnerable whereas none were ranked as very highly vulnerable. Only two species (4%) had low vulnerability, leaving the majority, 76%, in the moderately vulnerable category (Table 1). These results are markedly different from other climate change vulnerability assessments that include migratory birds. For example, while seven assessments from NatureServe also found no species to be extremely vulnerable (equivalent to very highly vulnerable) to climate change, they categorized just 2% as highly vulnerable and 16% to be moderately vulnerable. Most species (82%) were either not vulnerable or were likely to benefit (connect.natureserve.org/science/climate-change/ccvi). Another CCVA by Foden et al. (2013) assessed all avian taxa worldwide. Of the 364 migratory species that breed in the contiguous United States, they ranked 90% as "least vulnerable." These CCVAs were not targeted toward migratory animals or birds and excluded potentially important variables from their analyses. Without information on migration strategy, breeding site fidelity, non-breeding ecology, and non-breeding climate change exposure, they may

be unable to recognize vulnerability of some species even when it is there.

More quantitative methods used to investigate vulnerability to climate change include species distribution models (e.g., Langham et al. 2015, Stralberg et al. 2015). Although these methods are very different from CCVAs such as ours, and factors other than climate (e.g., habitat use) likely play an important role in current and historic species distributions, thus influencing results of species distribution models, we did see some similar patterns. When it came to gauging number of vulnerable species, Stralberg et al. (2015) and Langham et al. (2015) predicted 19–21% of bird species would be vulnerable to population declines and range contraction; we rated 22% of species as highly vulnerable to climate change (background risk was not included for comparison). However, we did not have similar results when it came to determining low or no vulnerability. Langham et al. (2015) and Stralberg et al. (2015) projected 32–44% of species will experience no net loss in range size or will increase in abundance; we rated only 17% of species with low climate change vulnerability. It may be prudent for managers to use multiple methods to determine which species are vulnerable to climate change and hedge their bets using the more conservative estimate.

When we separated our vulnerability assessment into climate change-specific vulnerability vs. background risk, we found five species were highly vulnerable to both (Table 1). In some cases, the combined effect of background risk factors like habitat loss and fragmentation has been shown to additively or synergistically exacerbate the effects of climate change and speed rates of extirpation (e.g., McLaughlin et al. 2002). For these species, heightened conservation management would be prudent. For ten species, background risk appeared to be the main factor driving vulnerability, whereas for 12 species, climate change-related variables appeared to be most important (Table 1). In general, vulnerability scores were highly individualistic by species. Species-specific information can be valuable for targeting conservation strategies, and we hope assessments like ours will improve these efforts.

When we isolated the effect of temperature change, we found that 37% of the 46 species analyzed were highly vulnerable to temperature

change on the UMGL breeding grounds, whereas 13% were highly vulnerable to temperature change on the non-breeding grounds (Appendix S3: Table S3.5). Four of these species were highly vulnerable to temperature change on both the breeding and non-breeding grounds, thus compounding their overall vulnerability throughout the annual cycle. Vulnerability to temperature change on the non-breeding grounds was driven in part by exposure in South America, where some regions are expected to experience large increases in winter temperature. Conservationists in North America should be aware of which species might overwinter in South America and whether their ranges overlap with those regions of high temperature change exposure.

Unfortunately, there is much uncertainty among general circulation climate change models predicting moisture change, and some in the 16-model ensemble used here predict opposite patterns for the same locations. Even with this complication, however, we consistently found that bird species in Mexico are expected to experience a 6–11% decrease in winter moisture. The magnitude of this effect suggests that it is a real drying trend and perhaps a conservative estimate. Our results may also underestimate the magnitude of moisture loss in other non-breeding regions (Neelin et al. 2006), and it would be beneficial to assess exposure to moisture change in a more nuanced way by analyzing wet and dry general circulation models separately. The flexibility of our full life cycle method is conducive to such modifications, and we encourage others to adjust our methods to their priorities. Nevertheless, the effect of moisture change showed a similar pattern to the effect of temperature change. We found that 33% of species analyzed were highly vulnerable to moisture change on the UMGL breeding grounds, while 9% were highly vulnerable to moisture change on the non-breeding grounds (Appendix S3: Table S3.6). One of these species was highly vulnerable to moisture change during both. Vulnerability to moisture change on the non-breeding grounds was primarily driven by exposure in Mexico and the Caribbean, which are expected to become much drier. All of the species that were highly vulnerable to non-breeding moisture change winter primarily in Mexico and the Caribbean. There were some Mexican- and Caribbean-wintering species,

however, that were less sensitive to moisture change and may be able to withstand the drying climate expected in those areas.

These results illustrate the value of conducting comprehensive CCVAs throughout the annual cycle. Some species that appeared to be resilient to temperature and moisture change during one season were actually highly vulnerable at other times of the year. In addition, it is important to know which species could be vulnerable throughout the year. Making things more complicated is the fact that carryover effects of climate between seasons are possible. For example, we know that for some warblers, moisture on the non-breeding grounds can influence breeding ground abundance (Wilson et al. 2011) as well as timing of arrival to breeding areas (Saino et al. 2007, Studds and Marra 2007), which can in turn influence the number of young fledged. We found that 58% the warbler species in our analysis were most vulnerable to changes in moisture during the non-breeding season, particularly moisture change in Mexico and the Caribbean. For species spending the non-breeding season in Mexico and the Caribbean, there may be indirect consequences of climate change that do not manifest until arrival upon the breeding grounds. It is critical for us to understand how factors on the non-breeding grounds influence timing, condition, and survival during spring (Paxton et al. 2014, Cohen et al. 2015) so that we can make sense of trends seen in North America during the breeding season (Wilson et al. 2011).

We designed this CCVA to be flexible tool for use by anyone with access to Climate Wizard, peer-reviewed literature, and conservation status for birds of North America. It is broadly applicable to species of many regions and needs and could be adapted to other scenarios, particularly as migratory connectivity and climate change science continue to advance and evolve. For example, results here apply to mid-century (2040–2069) climate change under an A2 high-emissions scenario (IPCC SRES 2000). However, it may be more appropriate to use a different time frame, emissions scenario, or ensemble of models, depending on management location and priority. In addition, scoring thresholds and details of how each category were calculated into final vulnerability scores could be modified depending on research and management assumptions and goals. For

example, our evaluation of climate exposure used predicted change in mean temperature and moisture. However, some studies predict that climatic variability will also increase under climate change and that it may be equally important to population viability (Stakhiv 2011). Mean temperature may increase slowly over the decades, while temperatures of extreme heat waves may increase much more quickly. The ability of species to survive extreme events will depend on several compounding factors, some of which were used in our CCVA. We did not, however, include climatic stochasticity here because we did not have ready access to data on number and magnitude of future extreme events for individual regions. Including stochasticity would improve this CCVA, however, and we encourage others to do so.

We assessed uncertainty for the most subjective categories: adaptive capacity and indirect effects. We found many gaps in our knowledge of indirect effects, and our understanding of what will happen to habitats and species used by migratory birds due to climate change is relatively limited, particularly non-breeding biotic interactions. This result was not surprising because much of the research in this field is still in its infancy and continues to develop. Breeding site fidelity was also uncertain for many species, which was somewhat surprising given the amount of research devoted to the breeding season. In general, results regarding the indirect effects category and breeding site fidelity should be interpreted with caution.

Conducting a CCVA is the first step toward managing species under the threat of climate change. The next step is to use this information to develop adaptive management strategies and conservation plans (AFWA 2009). Such planning can help reduce or mitigate future vulnerability, in both the short term and long term (IPCC 2014). Strategies may include measures designed to increase resistance to climate change, make a population or species more resilient, or assist adaptation. We have identified a few areas that may help focus adaptive management strategies, including upgrading conservation status of some species, prioritizing conservation of species that overwinter in Mexico and the Caribbean, establishing partnerships with conservation managers in those regions, and focusing research on determining where UMGL populations spend the

non-breeding season. These strategic points are also supported by goals outlined by the National Fish, Wildlife, and Plants Climate Adaptation Partnership (e.g., enhance management capacity across jurisdictions and increase knowledge and information, 2012).

Species currently not listed as a conservation concern but having a high vulnerability to climate change may warrant increased observation and management (e.g., Red-necked Grebe, Caspian Tern, Forster's Tern, Yellow-bellied Flycatcher, and Nashville Warbler). In addition, species highly vulnerable to both background risk and climate change may warrant heightened conservation status (e.g., Eastern Whip-poor-will and Worm-eating Warbler).

Not only is climate change occurring at a vast scale, but migratory animals operate over broad regions that can span multiple continents. Conservation organizations and governmental agencies would be wise to adapt and work across these large spatial scales to effectively manage species and populations (Runge et al. 2015). This includes creating both domestic and international partnerships. One way to facilitate cooperation is through networking and increased communication regarding monitoring, data sharing, data development, and adaptive management (NFWPCAS 2012), especially for shared species and populations. Organizations and cooperatives such as the LCC, Habitat Joint Ventures, and PIF already work across broad regions and may be models for expanding cooperation and communication across geopolitical boundaries and to help protect species from climate change throughout their annual cycle.

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