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Using value of information to prioritize research needs for migratory bird management under climate change: a case study using federal land acquisition in the United States

Clark S. Rushing^{1,2*}, Madeleine Rubenstein³, James E. Lyons² and Michael C. Runge²

ABSTRACT

In response to global habitat loss, many governmental and non-governmental organizations have implemented land acquisition programs to protect critical habitats permanently for priority species. The ability of these protected areas to meet future management objectives may be compromised if the effects of climate change are not considered in acquisition decisions. Unfortunately, the effects of climate change on ecological systems are complex and plagued by uncertainty, making it difficult for organizations to prioritize research needs to improve decision-making. Herein, we demonstrate the use of qualitative value of information analysis to identify and prioritize which sources of uncertainty should be reduced to improve land acquisition decisions to protect migratory birds in the face of climate change. The qualitative value of information analysis process involves four steps: (i) articulating alternative hypotheses; (ii) determining the magnitude of uncertainty regarding each hypothesis; (iii) evaluating the relevance of each hypothesis to acquisition decision-making; and (iv) assessing the feasibility of reducing the uncertainty surrounding each hypothesis through research and monitoring. We demonstrate this approach using the objectives of 3 U.S. federal land acquisition programs that focus on migratory bird management. We used a comprehensive literature review, expert elicitation, and professional judgement to evaluate 11 hypotheses about the effect of climate change on migratory birds. Based on our results, we provide a list of priorities for future research and monitoring to reduce uncertainty and improve land acquisition decisions for the programs considered in our case study. Reducing uncertainty about how climate change will influence the spatial distribution of priority species and biotic homogenization were identified as the highest priorities for future research due to both the value of this information for improving land acquisition decisions and the feasibility of reducing uncertainty through research and monitoring. Research on how changes in precipitation patterns and winter severity will influence migratory bird abundance is also expected to benefit land acquisition decisions. By contrast, hypotheses about phenology and migration distance were identified as low priorities for research. By providing a rigorous and transparent approach to prioritizing research, we demonstrate that qualitative value of information is a valuable tool for prioritizing research and improving management decisions in other complex, high-uncertainty cases where traditional quantitative value of information analysis is not possible. Given the inherent complexity of ecological systems under climate change, and the difficulty of identifying management-relevant research priorities, we expect this approach to have wide applications within the field of natural resource management.

Key words: climate change, land acquisition, migration, migratory birds, protected areas, structured decision-making, value of information

¹Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT, 84322, U.S.A.

²Patuxent Wildlife Research Center, U.S. Geological Survey, Laurel, MD, 20708, U.S.A.

³National Climate Adaptation Science Center, U.S. Geological Survey, Reston, VA, 20192, U.S.A.

^{*} Author for correspondence (Tel: +1 435 797 0337; E-mail: clark.rushing@usu.edu)

CONTENTS

I.	Introduction	
	(1) Identifying research priorities to inform acquisition decision-making	.1111
	(2) Expected value of information (EVI)	.1112
II.	Methods	.1113
	(1) Literature review and expert elicitation	.1113
	(2) Hypothesis evaluation	.1113
	(3) Hypothesis ranking	
III.	Results	.1116
	(1) Highest priority	.1117
	(a) Hypothesis 1a: breeding distributions will shift poleward due to warming temperatures	
	(b) Hypothesis 4b: climate change will lead to more homogeneous bird communities that are dominated that are dominated to the communities are dominated to the commun	ted by
	a small number of generalist species	
	(c) Hypothesis 1b: non-breeding distributions will shift poleward due to warming temperatures	1118
	(2) High priority	
	(a) Hypothesis 2b: decreased precipitation during the breeding season will lower abundance	1119
	(b) Hypothesis 2a: warmer temperatures on temperate non-breeding grounds will increase	
	abundance	
	(3) Medium priority	
	(a) Hypothesis 1c: distributions will shift towards higher elevations due to warming temperatures .	
	(b) Hypothesis 3c: climate-driven phenological mismatches will lower abundance of migratory birds	
	through their effects on reproductive success or survival	
	(4) Low priority	
	(a) Hypothesis 3b: migration distances will lengthen for long-distance migrants	
	(b) Hypothesis 4a: climate change will result in a lower proportion of migratory species in temperate	
	communities due to increased competition with resident species	1123
	(c) Hypothesis 2c: reduced precipitation on the non-breeding grounds will decrease abundance of s	
	that overwinter in tropical areas	
	(d) Hypothesis 3a: migration distances will shorten for short-distance migrants	
	Conclusions	
	Acknowledgements	
	Author contributions	
V.	References	. 1126

I. INTRODUCTION

Over the past century, habitat loss and fragmentation have been the primary threats to biodiversity across the globe (Fahrig, 1997; Owens & Bennett, 2000; Brooks et al., 2002). In response to this threat, many governments and nongovernmental organizations have established land acquisition (LA) programs to protect critical habitats in perpetuity (Noss et al., 2002; Brooks et al., 2006). Although these programs currently protect millions of acres of habitat from development and conversion (Balmford et al., 2002), global climate change threatens to diminish the conservation value of LA programs by altering the distribution and demography of priority species and the location of critical habitats on which they depend (Araújo et al., 2004; but see Johnston et al., 2013).

Existing LA programs prioritize different combinations of geography, scale, and taxonomic focus (e.g. Csuti et al., 1997; Howard et al., 1998; Noss et al., 2002; Brooks et al., 2006) and each program uses a distinct set of criteria to prioritize which available parcels to acquire for protection, including the presence or abundance of priority species, cost, and risk of loss (Wilson et al., 2006). Despite acknowledging the risk that

climate change poses to the efficacy of protected areas, most acquisition decisions are based on the current state of the biological and anthropocentric systems rather than the potential future states (Araújo *et al.*, 2004). In the face of climate change, selection criteria that do not account for uncertainty about the future state of both the land and the species risk reducing the conservation value of acquisition decisions by protecting parcels that meet current criteria but fail to meet long-term objectives (Virkkala *et al.*, 2013).

The challenges associated with establishing protected areas in the face of climate change are particularly complicated when the focus is conservation and management of migratory birds. To complete their annual journeys and maintain viable populations, migratory birds require intact breeding, non-breeding, and stopover habitats; loss or degradation of habitat at any stage of the annual cycle can lead to population declines (Sherry & Holmes, 1995; Sutherland, 1996). However, the population-level consequences of habitat loss are not necessarily equivalent at different stages of the annual cycle. Instead, changes in population size due to habitat loss will be greatest in whichever season has the largest influence on *per capita* survival and fecundity (Newton, 2004). Unfortunately, the

relative influence of breeding *versus* non-breeding habitat loss on population limitation is poorly understood for most species, making it difficult to prioritize LA decisions across the annual cycle. Because climate change may alter both the location and quality of habitats as well as the behaviour and physiology of migratory birds, predicting which locations will protect species both now and in the future is a pressing issue.

(1) Identifying research priorities to inform acquisition decision-making

The primary objective of most LA programs is to acquire the subset of available parcels that maximizes future persistence of one or more priority species over a defined spatial scale. The motivation for our case study is to help prioritize research needs to support three LA programs used by the United States Fish & Wildlife Service (FWS) to conserve habitat for migratory birds (Table 1). Although our focus is the programs described in Table 1, we emphasize that the approach developed herein is broadly relevant to natural resource decisions that may be affected by climate change.

LA decisions may be constrained by multiple factors, including costs and competing objectives (Conroy *et al.*, 2011). As described in Table 1, the primary LA programs we assessed for this analysis have different objectives, processes, taxonomic focus, and jurisdictions. However, all three programs share a number of common characteristics and, more importantly, share a fundamental objective (i.e. the primary ecological objective of the programs; Lyons *et al.*, 2008) of maximizing the long-term abundance or viability of migratory bird populations.

Despite sharing the same fundamental objective, each LA program makes specific decisions about which parcels to

Table 1. Primary federal land acquisition (LA) programs utilized by the U.S. Fish & Wildlife Service (FWS)

	MBCF	LWCF	NAWCA
Program description	Created in 1934 as part of the Migratory Bird Hunting and Conservation Stamp Act to provide funds for the protection of migratory bird habitat. The MBCF is financed primarily through the sale of Migratory Bird Hunting and Conservation Stamps ('duck stamps'). Funds are used to protect critical habitat within the FWS Refuge System for priority waterfowl.	Established in 1964 to protect public lands and waters, financed by earnings from offshore oil and gas leasing. LWCF funds are used across Department of Interior Agencies for conservation. Within the FWS, the LWCF is used to protect migratory waterfowl habitat within the Refuge System.	Established in 1989 to protect wetland habitats across North America. This program focuses primarily on migratory waterfowl, but protection of critical habitat for wetland-associated migratory birds and T&E species is also considered. Funds can be used for conservation within Mexico, Canada, and the United States.
Focal species	Primary: waterfowl Secondary: T&E species	Primary: waterfowl Secondary: migratory birds of conservation concern; T&E species	Primary: waterfowl Secondary: wetland-associated migratory birds; T&E species
Decision maker	FWS leadership FWS refuge & regional managers States	FWS leadership FWS refuge & regional managers	NAWCA council: FWS leadership; State representatives; NFWF; NGOs
Jurisdiction	U.S. (Refuge or WPA)	U.S. (Refuge)	North America (U.S., Mexico and Canada)
Foundational plan	NAWMP	NAWMP Landbird, Waterbird, & Shorebird Conservation Plans T&E species listings	NAWMP Landbird, Waterbird, & Shorebird Conservation Plans T&E species listings SWAPs
Criteria	Limiting factor mitigation Relative abundance for priority species Limiting factor and relative abundance for secondary species WPAs: risk of loss/conversion	Limiting factor mitigation Relative abundance for priority species Relative abundance for secondary species Priority geography T&E Species Recovery Plan Directive	Abundance for priority species Abundance for secondary species Priority geography Wetland status and trend Long-term conservation and climate change benefit Partnerships
Climate change	Not explicitly considered	Not explicitly considered	Considered in evaluation of long-term benefit and whether actions are adaptive for climate change impacts

LWCF, Land and Water Conservation Fund; MBCF, Migratory Bird Conservation Fund; NAWCA, North American Wetland Conservation Act; NAWMP, North American Waterfowl Management Plan; NFWF, National Fish and Wildlife Foundation; NGO, non-governmental organization; SWAP, State Wildlife Action Plan; T&E, Threatened and Endangered species; WPA, Waterfowl Production Area.

conserve based on the degree to which available parcels meet program-specific criteria that serve as a proxy for habitat importance (Table 2). Under stationary conditions, these criteria, also known as means objectives (Lyons *et al.*, 2008), are assumed to serve as direct proxies for the program's fundamental objective of maximizing long-term viability of migratory bird populations. In other words, parcels that currently score highly based on the criteria described in Table 2 are assumed to be those that will be most effective for achieving long-term persistence of priority species. The success of federal LA programs is therefore predicated on the assumption that means objectives, as currently expressed through program criteria, are sufficient proxies for meeting fundamental objectives. The focus of our analysis is to determine whether and how climate change may challenge this assumption.

Although previous reviews have identified important knowledge gaps regarding the effects of climate change on migratory birds (Robinson et al., 2009; Knudsen et al., 2011; Guillemain et al., 2013), few studies have placed these priorities within the context of real-world decision-making. In the face of uncertain future conditions, there is an understandable desire to reduce uncertainty through research and monitoring. Reducing all sources of uncertainty is not feasible, however, and not all sources of uncertainty have the same effect on conservation and management decisions (Grantham et al., 2008; Runting, Wilson, & Rhodes, 2013). Within a specific decision context, investing resources to reduce uncertainty is only worthwhile if it is feasible to reduce the uncertainty through research and monitoring and the new information will potentially change the decision (Runge, Converse, & Lyons, 2011). In other words, investing resources to reduce uncertainty about the effects of climate change should only be undertaken if that investment is expected to yield a significant improvement in management outcomes compared to the current state of uncertainty (Felli & Hazen, 1998). In the case of protecting land in the face of climate change, a critical first step to prioritizing

research needs is understanding which sources of uncertainty are relevant to improving LA decisions.

(2) Expected value of information (EVI)

In other areas of natural resource management, the concept of EVI has been used successfully to identify sources of uncertainty that are relevant to decisions (Felli & Hazen, 1998). Conceptually, the EVI is defined as the 'difference between the expected value of an optimal action after new information has been collected and the expected value of an optimal action before the new information has been collected' (Runge et al., 2011, p. 1215). Value of information (VoI) and its variants (e.g. value of perfect information, value of sample information) provide a formal means of assessing the improvement in performance that can be expected by reducing uncertainty about a specific hypothesis. An anticipated EVI greater than 0 is necessary for investing resources in research and monitoring to reduce uncertainty. In the context of climate change, which involves a complex set of nonmutually exclusive hypotheses, the expected value of partial information (EVPXI), which measures the value of reducing individual sources of uncertainty, is particularly relevant to identifying targets for research (Runge et al., 2011).

However, conducting a formal EVI analysis requires quantifying alternative hypotheses of system behaviour, the prior probability that each hypothesis is correct, and predictions of the outcomes of each management action under each hypothesis. This may not be feasible for complex problems with broad scope like acquiring habitats to protect migratory birds under climate change. Nevertheless, improving LA decisions in the face of climate change requires rigorous application of VoI concepts.

Herein, we demonstrate the use of qualitative value of information (QVoI; M.C. Runge, C.S. Rushing, M. Rubenstein & J.E. Lyons, in preparation) to determine which sources of uncertainty regarding the effects of climate

Table 2. Common program criteria shared by federal land acquisition (LA) programs that focus on migratory bird conservation

Criteria	Description	Example from a specific program
Current distribution	Is the focal species currently distributed on the parcel?	Decision tree used in evaluating parcels for the LWCF asks whether a priority species (e.g. bird of conservation concern) is present on the land.
Current abundance	Is the focal species currently abundant on the parcel?	Decision tree used in evaluating parcels for MBCF acquisition asks whether refuge in question overlaps with high abundance areas for a priority species.
Limiting habitat	Does the parcel represent limiting habitat for the species? Does the parcel provide high-quality habitat for the focal species?	Evaluation criteria for LWCF program ask whether the parcel would mitigate a population-limiting factor for a priority species, as determined by subject matter experts.
Risk/threat of loss	Is the parcel at risk of being converted, lost, or otherwise degraded if not acquired?	Decision tree used in the WPA program of the MBCF asks whether the parcel is at risk of being converted to agriculture if not acquired. Evaluation criteria for NAWCA grants ask whether the parcel represents a type of wetland generally in decline.

LWCF, Land and Water Conservation Fund; MBCF, Migratory Bird Conservation Fund; NAWCA, North American Wetland Conservation Act; WPA, Waterfowl Production Area.

change on migratory birds will have the greatest effect on improving LA decisions. As in any VoI analysis, our analysis requires a specific and well-defined objective, which was defined by the stated objectives, jurisdictions, and taxonomic scope of the programs listed in Table 1. Specifically, we defined the objective of our analysis to be maximizing longterm viability of migratory waterfowl and landbird populations within the United States. The QVoI process involves four steps: (i) articulating alternative hypotheses about how climate change will affect migratory birds; (ii) determining the magnitude of uncertainty regarding each hypothesis; (iii) evaluating the relevance of each hypothesis to acquisition decision-making; and (iv) assessing feasibility of reducing the uncertainty surrounding each hypothesis through research and monitoring. We start by describing the methods and qualitative metrics used to carry out the QVoI analysis. We then evaluate a series of hypotheses about the effects of climate change on migratory birds to identify which hypotheses are likely to have the highest VoI for the focal LA programs. Finally, we provide a list of priorities for future research and monitoring to reduce uncertainty and improve LA decisions for migratory birds.

II. METHODS

(1) Literature review and expert elicitation

Our analysis used a combination of expert elicitation and a review of the literature on climate change effects on migratory birds to identify which sources of uncertainty have the highest relevance to LA decision-making. To identify major hypotheses related to climate change effects on migratory birds, we first convened a workshop of LA program managers from FWS as well as researchers with expertise in migratory bird ecology, biology, and conservation science. During this workshop, we created a conceptual model of climate change on migratory bird populations and their habitats, and made initial descriptions of the ways in which these changes might alter LA decision-making.

Following the workshop, we used *Google Scholar* and the ISI Web of Science to finalize our articulation of major hypotheses about the effects of climate change on migratory birds, and to assess the state of the science regarding the uncertainty surrounding each hypothesis. We searched for published papers using the phrase 'migratory bird*' combined with the following terms: 'climate', 'climate change', 'temperature', 'precipitation', or 'phenology'. We also reviewed the citations within the papers located *via* these searches to find additional papers that the searches missed. Given the extensive literature on certain topics, our review was not meant to be exhaustive; instead, our objective was to review a representative sample of published papers to draw general conclusions about the current state of knowledge regarding climate change effects on migratory birds. Although there are a virtually unlimited number of specific hypotheses about climate change effects to migratory birds expressed in the literature, many of which

are specific to particular species, regions, and types of climate effects, we identified a set of specific hypotheses that fall into four major categories:

Distribution: as far back as the early 20th century (Grinnell, 1917a, 1917b), ecologists have hypothesized that climatic conditions, especially temperature, play an important role in determining species distributions. Numerous hypotheses have been proposed to predict how species distributions may shift in response to climate change.

Abundance: numerous studies have demonstrated that the demographic rates of migratory birds are influenced by both precipitation and temperature. Climate change therefore has the potential to influence the future abundance of migratory birds, although changes are expected to vary across season (breeding *versus* non-breeding) and region (temperate *versus* tropical).

Migration and phenology: migrating annually between breeding and wintering grounds allows migratory birds to take advantage of seasonally abundant resources. Although migratory birds are adapted to a life on the move, this strategy requires individuals to time their movements to coincide with spatial and temporal resource peaks. As climate change influences the phenology of these resource peaks, the distance and timing of seasonal migrations may also change.

Community responses: climate-driven changes to distribution, abundance, and phenology will likely combine to alter the spatial and temporal overlap of interacting species. Climate-driven changes to community composition may therefore have complex effects on competitive dominance, exposure to novel predators or pathogens, and ecosystem services.

To make our qualitative assessment of the specific hypotheses associated with these categories more tractable, we assumed a null hypothesis (H_0) that climate change will not influence the ecological or demographic process of interest (i.e. the current state of the system will not be altered by climate change). These null hypotheses are consistent with many current LA decision criteria, which implicitly assume stationarity. Each proposed hypothesis is thus treated as an alternative (H_1) to the null.

(2) Hypothesis evaluation

Once the hypotheses were identified and the literature compiled, we used three criteria and a standard rubric (Table 3) to evaluate each hypothesis:

Magnitude of uncertainty (hereafter uncertainty): all else being equal, research and monitoring will have a larger effect on improving management outcomes when focused on hypotheses that are more uncertain (i.e. larger uncertainty regarding whether H_0 or H_1 is true). We used the results of the literature review to score each hypothesis based on the current magnitude of uncertainty. Hypotheses that had a theoretical foundation based on demographic mechanisms and support from a large (>10) number of empirical studies were considered the most certain, whereas hypotheses that lacked either a theoretical foundation or consistent empirical support were

Table 3. Description of scoring rubric used to assess each hypothesis

Score	Uncertainty	Relevance	Reducibility
0	Firm theoretical foundation and a large number of empirical studies (> 10) that support theoretical predictions	Preferred management action will be favoured regardless of whether hypothesis is true	Data necessary to reduce uncertainty do not currently exist and will be prohibitively difficult/expensive to collect given current technologies
1	Firm theoretical foundation with robust empirical support; OR large number (> 10) of consistent empirical studies	Reducing uncertainty is predicted to improve management outcomes but range of outcomes will be swamped by natural variability and other uncertainties	Data to reduce uncertainty exist but only for a limited taxonomic, geographic, or temporal scope but cannot resolve the specific mechanisms; collection of additional data needed to discriminate among alternative mechanisms will be difficult/expensive or cannot be collected in the time frame relevant to decision
2	Firm theoretical foundation with moderate empirical support; OR moderate number (5–10) of consistent empirical studies	Reducing uncertainty is predicted to improve management outcomes; range of outcomes will be small to moderate compared to natural variability and other uncertainties	Data to reduce uncertainty exist but only for a limited taxonomic, geographic, or temporal scope OR data only allow weak inference about mechanisms; collection of additional data needed to discriminate among alternative mechanisms is feasible given current technologies
3	Firm theoretical foundation with no empirical support; OR small number (< 5) of consistent empirical studies	Reducing uncertainty is predicted to improve management outcomes and range of outcomes will be of the same order of magnitude as natural variability and other uncertainties	Data to reduce uncertainty exist across a large taxonomic, geographic, or temporal scope AND credible inference can be made from these data
4	Large disagreement between theory and empirical studies; OR no theoretical basis and inconsistent empirical studies	_	_

considered less certain (Table 3). Hypotheses that were scored as the most uncertain either had a large disagreement between theoretical predictions and empirical results or lacked a theoretical basis and had been the subject of few empirical studies.

Relevance of resolving uncertainty to meeting fundamental objectives (hereafter relevance): a key principle of decision analysis is that reducing uncertainty is only valuable if increased understanding of the system will lead to different decisions and the potential for better outcomes (Runge et al., 2011). Based on this principle, we scored each hypothesis based on the degree to which resolving uncertainty is expected to alter the outcomes of LA decisions by the focal programs. In some cases, it is possible that resolving uncertainty about climate change effects will not change which parcels of land should be protected because the preferred action will be favoured regardless of whether the null or alternative hypothesis is true (Fig. 1; Table 3). In other cases, resolving uncertainty might change which parcels of land are favoured under the null or alternative hypothesis, but the difference in performance among alternative actions would be swamped by natural variability in the system. Hypotheses in this category were scored as either 1 or 2 depending on whether we judged the difference in performance to be small or moderate relative to natural variability. Finally, reducing uncertainty about whether the null or alternative hypothesis is true may lead to

differences in performance that are similar to or greater than natural variability in the system. Hypotheses in this category were given a score of 3.

Degree to which uncertainty could be reduced through research and monitoring (hereafter reducibility): all else being equal, sources of uncertainty that can be reduced with existing data and analytical methods are easier to resolve than sources of uncertainty that will require additional long-term data collection. In extreme cases, some sources of uncertainty cannot be reduced without the development of new technological or analytical methods. We ranked hypotheses based on the degree to which uncertainty can be resolved in time frames relevant to LA decision makers (generally, <5-7 years). Hypotheses that can be resolved using currently available data or methodologies were scored higher than hypotheses for which current data are either insufficient to discriminate among alternative hypotheses or do not currently exist (Table 3). In cases where data do not currently exist and would be prohibitively expensive to collect given current technologies, we as assigned a reducibility score of 0.

The four authors served as an expert panel to score the hypotheses, following a formal process of expert judgment (Hanea *et al.*, 2017). Each author first independently scored the hypotheses using the rubrics described in Table 3. We then compared and discussed our scores, using the differences to reveal insights. The individual experts then

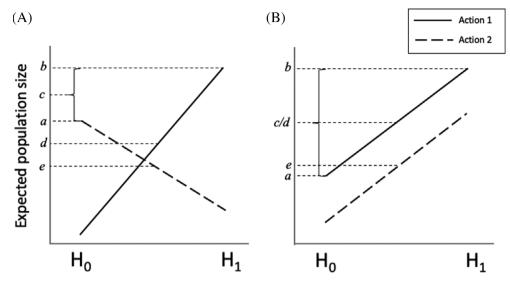


Fig. 1. Expected benefits of two alternative actions under different hypotheses about the future state of the system. The dashed lines a and b show the maximum possible outcomes assuming H0 or H1 is true, respectively. Because decision makers must make a decision prior to knowing which hypothesis is true, the expected outcome once uncertainty has been resolved must be averaged across alternative models. Assuming each hypothesis has equal probability of being true, this outcome is represented by the dashed line c = (a + b)/2. The dashed lines d and e show the average expected outcome of each action in the face of uncertainty; that is, the average outcomes assuming either H0 or H1 is true. In scenario A, action 1 has the higher expected outcome before uncertainty is resolved (d > e) and therefore would be the preferred action in the face of uncertainty. However, because resolving uncertainty is expected to lead to better outcomes (c > d), decision makers should seek to reduce uncertainty through research and monitoring. In scenario B, action 1 is still preferred in the face of uncertainty (d > e) but in this scenario, reducing uncertainty does not produce better outcomes because action 1 leads to better outcomes regardless of which hypothesis is true (c = d). As a result, research and monitoring will not change the decision about which action to take and therefore should not be pursued.

independently revised their scores. To gather further insight, we convened a subset of FWS LA managers for a second inperson meeting, to discuss how the various hypotheses either were, or were not, likely to alter LA decision-making. We described the list of specific hypotheses to the managers and asked them to discuss the relevance of each hypothesis to their decisions. After hearing those discussions, the authors reviewed their scores for each hypothesis. Finally, individual scores across experts were aggregated by finding a consensus score.

(3) Hypothesis ranking

In conventional decision analyses, the EVI is the expected outcome of the optimal action after uncertainty has been reduced minus the expected outcome of the optimal action based on the current knowledge of the system (Schlaifer & Raiffa, 1961). When multiple sources of uncertainty are being considered, the EVPXI can be used to rank individual sources of uncertainty. Although a formal evaluation of EVPXI is not possible using our qualitative criteria, the quantitative EVI is equivalent to the product of our uncertainty and relevance scores (M.C. Runge, C.S. Rushing, M. Rubenstein & J.E. Lyons, in preparation). For each hypothesis i, we therefore defined the QVoI as:

 $QVoI_i = uncertainty_i \times relevance_i$

Taking the product of the scores ensured that any hypothesis that was scored 0 in either of these categories automatically received a QVoI score of 0. This property is desirable because if, for example, a hypothesis was judged to be irrelevant to management decisions (score of 0 for relevance criteria), even a high degree of uncertainty would not make the hypothesis a high priority for additional research. QVoI scores therefore provide a principled method to rank hypotheses that is consistent with formal decision theory.

Our additional criterion (reducibility) captures the degree to which uncertainty can be reduced through research and monitoring, which is an important consideration for prioritizing research needs. Reducibility is not directly incorporated in the quantitative VoI analysis and we therefore included these scores into our ranking as a second axis along which hypotheses were ranked. Hypotheses that rank highly for both QVoI and reducibility are obvious priorities for future research, while hypotheses that rank poorly in both categories should not be priorities for research that aims to improve LA decisions. To create our final prioritization of research topics, we placed hypotheses into four categories, based on natural breaks in the final QVoI and reducibility scores (Fig. 2):

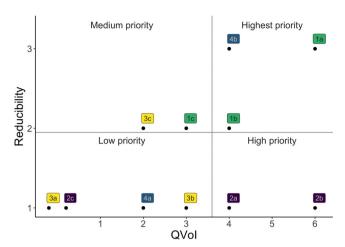


Fig. 2. Qualitative value of information (QVoI) and reducibility scores for 11 hypotheses about the impacts of climate change on migratory birds. Hypothesis category 1 (green boxes) = distribution; category 2 (purple boxes) = abundance; category 3 (yellow boxes) = migration and phenology; category 4 (blue boxes) = community responses. Note that a small jitter has been added to the QVoI scores of hypotheses 2c and 3a to avoid overlapping points.

Highest priority hypotheses are those that rank highly both in terms of QVoI and reducibility. These hypotheses are highly relevant to managers, have substantial uncertainty that needs to be reduced, and rank relatively highly in terms of reducibility. We define these as having a QVoI of ≥ 4 , and a reducibility of ≥ 2 .

High priority hypotheses are those that rank highly in QVoI, but have low reducibility. Resolving these uncertainties would be valuable to management decision-making, but the challenges associated with reducibility would render this task onerous. We define these as having a QVoI of ≥ 4 , with a reducibility of <2.

Medium priority hypotheses have a relatively low QVoI, but high reducibility. These are uncertainties that may not be of highest priority to management, or may have only a small uncertainty surrounding their likelihood of being true, but could be resolved easily. If reducibility is a high priority, these might be appealing candidate hypotheses. We define these as having a QVoI <4, with a reducibility ≥2.

Low priority hypotheses have a low QVoI, indicating that they are not particularly valuable to LA management decisions, or have low remaining uncertainty based on the literature. In addition, they will be difficult to reduce. Therefore, these are not high-priority topics. We define these as having a QVoI <4, and a reducibility <2.

III. RESULTS

Below we describe the major hypotheses about how climate change will affect migratory birds, along with the uncertainty, relevance and reducibility score for each hypothesis. We present them according to our final priority rankings, which reflect the results of our literature review as well as input from expert elicitation (Table 4).

Table 4. Evaluated and ranked hypotheses

Hypothesis	Uncertainty	Relevance	Reducibility	Priority ranking
1. Species distribution				
1a. Breeding distributions will shift poleward due to warming temperatures	2	3	3	Highest
1b. Non-breeding distributions will shift poleward due to warming temperatures	2	2	2	Highest
1c. Distributions will shift towards higher elevations due to warming	3	1	2	Medium
temperatures				
2. Abundance				
2a. Warmer temperatures on temperate non-breeding grounds will increase	4	1	1	High
abundance				
2b. Decreased precipitation during the breeding season will lower abundance	2	3	1	High
2c. Reduced precipitation on the non-breeding grounds will decrease	3	0	1	Low
abundance of species that overwinter in tropical areas				
3. Migration and phenology				
3a. Migration distances will shorten for short-distance migrants	3	0	1	Low
3b. Migration distances will lengthen for long-distance migrants	3	1	1	Low
3c. Climate-driven phenological mismatches will lower abundance of migratory	2	1	2	Medium
birds through their effects on reproductive success or survival				
4. Community responses				
4a: Climate change will result in a lower proportion of migratory species in temperate avian breeding communities due to increased competition with resident species	2	1	1	Low
4b: Climate change will lead to more homogeneous bird communities that are dominated by a small number of generalist species	2	2	3	Highest

(1) Highest priority

- (a) Hypothesis 1a: breeding distributions will shift poleward due to warming temperatures
- (i) Uncertainty score 2. Documenting and predicting climatedriven range shifts has been a major area of research for over two decades, and evidence of poleward range shifts have been documented in a variety of taxa (Parmesan & Yohe, 2003; Chen et al., 2011). Thanks to a wealth of long-term distributional data for many bird species, there are numerous examples of poleward distributional shifts in the breeding season. Researchers have documented poleward shifts of 0.8–2.35 km per year in the northern breeding limits of British (Thomas & Lennon, 1999; Massimino, Johnston, & Pearce-Higgins, 2015), Finnish (Brommer, 2004), and North American birds (Hitch & Leberg, 2007) over the past half century. Mean breeding latitudes have also shifted north in many species and geographic regions, including songbirds native to the North American Great Plains (4.4–6.6 km per year; Peterson, 2003), western United States (1.27 km per year on average; Auer & King, 2014), and New York State, U.S.A. (0.2 km per year; Zuckerberg, Woods, & Porter, 2009). Southern range limits are less well-studied than northern limits but are generally believed to be less sensitive to climate change (Parmesan, 1996; Parmesan et al., 1999). Consistent with this hypothesis, Massimino et al. (2015) found that southern range limits had not moved significantly in 80 species of British birds between 1994 and 2009.

In large multi-species studies, not all species have shifted equally or even at all. Brommer (2008) found that smallerbodied species showed larger northward range shifts than larger-bodied species and that terrestrial herbivores and wetland-dependent species shifted more than insectivores, granivores, and birds of prey. Angert et al. (2011) found that diet breadth, migratory status, and reliance on open water were positively correlated with range shifts in North American birds but that these traits had relatively low power to predict which species showed the largest shifts. Contrary to Angert et al. (2011), Auer & King (2014) found that the rate of northward expansion was negatively correlated with diet breadth and clutch size. Ralston et al. (2017) found that North American birds with increasing population trends were better able to expand into suitable habitat whereas species with decreasing trends were not.

Overall, the theoretical links between temperature and species distributions (Root, 1988) combined with the large number of studies that have documented northward range shifts across many avian species results in relatively high certainty that northern range limits will continue to shift northwards. But high interspecific variability in rates of range shift suggests that considerable uncertainty remains. Additionally, because there is less theoretical and empirical consensus about whether southern range limits are determined by temperature, there remains a moderate degree of uncertainty regarding this hypothesis.

(ii) Relevance score 3. The presence of one or more priority species is a key criterion for LA decisions by the three

programs that are the focus of this analysis. Given the current state of understanding, it is clear that future range shifts are likely for many species. Climate-envelope models predict that North American birds could shift 322 km northward on average by 2080 (Langham et al., 2015) and European species could shift by 258-882 km (Huntley et al., 2008), which could dramatically change the ability of parcels to meet fundamental objectives, especially for species with small range sizes. Parcels that are currently important due to the presence or abundance of priority species may no longer support those species in the future. Likewise, parcels that are currently uninhabited or support low-density populations may become critical to the maintenance of priority species under future climate conditions. Because the rate, direction, and magnitude of distributional shifts will vary across space, time, and species, the ability to identify parcels that will or will not support long-term management objectives prior to making LA decisions are expected to have high value.

(iii) Reducibility score 3. The ability to quantify breeding distribution shifts has been facilitated by the availability of largescale monitoring data for many species. For example, the North American Breeding Bird Survey (BBS; Sauer et al., 2015) and the Audubon Christmas Bird Count (CBC; Niven et al., 2004) provide over half a century of distributional data for 100 of breeding species. These structured monitoring programs are increasingly being supplemented by unstructured citizen-science initiatives (e.g. eBird; Sullivan et al., 2009), which provide millions of additional observations from across the globe each year. These programs provide a rich source of information for further investigation and prediction about how species distributions shift in response to climate change. Recent advances in species distribution modelling have provided new methods for estimating range shifts that improve upon earlier methods by taking into account imperfect detection (Guillera-Arroita, 2017), nonequilibrium dynamics (Clement et al., 2016; Rushing et al., 2019), and spatial autocorrelation (Johnson et al., 2013). Species distribution models (SDMs) that consider both the direct biological effects of climate change as well as the indirect effects of climate change on land-use decisions (Dale, 1997; Voldseth et al., 2009; Rashford et al., 2016) will be particularly useful for predicting future distributions of priority species. Given the quantity of existing data, the large temporal, spatial and taxonomic scope of these data, and increasingly powerful SDMs, reducing uncertainty about how breeding distributions will respond to future climate change should be highly feasible.

- (b) Hypothesis 4b: climate change will lead to more homogeneous bird communities that are dominated by a small number of generalist species
- (i) Uncertainty score 2. Ecological specialization is known to influence many processes and characteristics that relate to the adaptive capacity of species in the face of climate change, including range size (Slatyer, Hirst, & Sexton, 2013), dispersal dynamics (Kisdi, 2002), and population viability (Kotiaho et al., 2005). In general, specialists are thought to

favour stable environments and be poor colonizers of new habitat, whereas generalists are able to thrive in disturbed and newly created habitat (Levins, 1968). Thus, as the climate changes, ecological communities are predicted to become more homogeneous as generalist species flourish and specialists dwindle (McKinney & Lockwood, 1999). Understanding the relationships between ecological specialization and range size, dispersal, and population viability has a strong tradition in the theoretical literature (McKinney, 1997; Büchi & Vuilleumier, 2014), providing a firm theoretical foundation for predicting how climate change will influence biotic homogenization. A growing body of empirical studies have also found evidence that avian communities have become more homogeneous due to the increase of generalist species and decline of specialists. Davey et al. (2012) found that average community specialization of British birds decreased 3-5% over a 13-year period between 1994 and 2006. These results were directly linked to changes in breeding-season temperature, which favoured increases in generalist abundance rather than the replacement of specialist species (Sullivan, Newson, & Pearce-Higgins, 2016). Viol et al. (2012) found similar rates of homogenization across European bird communities between 1990 and 2008. Similar homogenization levels have been documented in France (Godet et al., 2015) and the Czech Republic (Reif et al., 2013). Despite consistent evidence of homogenization of European bird communities, few studies have documented concurrent changes in North America. Additionally, although changes in community composition have coincided with changes in several climate variables, the role of climate versus land-use change has not been fully explored in the existing literature.

(ii) Relevance score 2. Because many of the priority species for LA programs are range-restricted or low in abundance, loss of these species due to climate-driven homogenization is potentially relevant to LA decisions. Reducing uncertainty about this hypothesis could allow researchers to predict better which priority species may be unable to adapt to future conditions and where these species may remain present or abundant in the face of climate disruptions. Additionally, because community homogenization is also driven by non-climate drivers, such as urbanization and land-use change, LA program managers could potentially take these other drivers into account during acquisition decision-making as a buffer against climate-driven homogenization.

(iii) Reducibility score 3. The widespread availability of monitoring data from programs like the North American BBS, CBC, and eBird provide ample opportunities to estimate changes in community composition of North American birds over long timescales and across multiple spatial scales. When combined with SDMs that can account for dispersal ability (Bateman et al., 2013), these data sets may provide opportunities to predict how individual species and entire communities may be disrupted by changing patterns of abundance between generalists versus specialists.

(c) Hypothesis 1b: non-breeding distributions will shift poleward due to warming temperatures

(i) Uncertainty score 2. The environmental processes that limit non-breeding distributions have received less theoretical attention than breeding season processes. There is, however, evidence that winter temperature plays an important role in determining temperate winter distributions through its direct physiological effects and its indirect effects on food availability (Swanson & Olmstead, 1999; Canterbury, 2002). Empirical evidence that winter distributional limits are determined by temperature has been found for a number of year-round residents and temperate-wintering migrants (Root, 1988; Butler et al., 2007). Several studies have also found evidence that species' winter distributions have shifted northward. Hestbeck, Nichols, & Malecki (1991) found that between 1983 and 1988, Canada geese (Branta canadensis) increased in abundance in mid-latitudes and correspondingly decreased in southern latitudes. These shifts closely tracked winter severity in the mid-Atlantic U.S.A. Using counts of 254 species of wintering North American birds, La Sorte & Thompson III (2007) found that, on average, northern winter range limits had shifted northward by 1.48 km/year and centres of abundance shifted northward by 1.03 km/year. Similarly, Maclean et al. (2008) found that the range centre of seven European shorebird species shifted to the northeast by 30-119 km between 1981 and 2000 and Lehikoinen & Virkkala (2016) found that between 1980 and 2010 the centre of distribution of three European ducks moved northeast. Several intensive single-species studies have also found evidence of northward winter range shifts. For example, Ambrosini et al. (2011) found that the mean wintering latitude of Africanwintering barn swallows (Hirundo rustica) moved northward by 3-9 km/year over nearly a century (1912-2008). Ward et al. (2009) found that between 1963 and 2004 Pacific brant (Branta bernicla nigricans) shifted their winter distribution northward from primarily temperate areas along the Pacific U.S. coast to sub-Arctic areas on the Alaskan Peninsula. As in other studies, this shift coincided with warming temperatures and decreasing winter severity in the northern portion of the historic range.

The relatively large number of studies documenting northward winter range shifts in a wide variety of taxonomic groups, the consistency among studies, and the theoretical basis for predicting these shifts lead to relatively high certainty about how climate change will affect winter distributions of migratory birds. Some questions remain regarding the role of abiotic factors other than temperature and how climate change will affect the non-breeding ranges of species that winter in the tropics, but overall there is moderate uncertainty regarding this hypothesis.

(ii) Relevance score 2. Spatial changes in the winter distributions of priority species have the potential to significantly alter the ability of LA decisions to meet fundamental objectives in the future. However, predicted range shifts are smaller during winter than during the breeding season — one

analysis found that on average species winter distributions will shift by about 116 km by 2080 (Langham *et al.*, 2015), approximately one third of the predicted breeding season shift. Additionally, because many non-breeding distributions of U.S. migratory birds occur outside the jurisdiction of the programs considered here, shifts in non-breeding distributions will have limited effects on acquisition decisions in the U.S. The smaller scale of predicted winter shifts, the number of species that winter outside of the jurisdiction of federal LA programs, and the more natural variability in the winter distribution of temperate migrants, makes this hypothesis less relevant than hypothesis 1a.

(iii) Reducibility score 2. Several large-scale monitoring programs have been documenting the winter distribution of many bird species for decades, although these data sets are typically less extensive than their breeding season counterparts. The CBC in particular provides nearly a century of distributional data for 100 of wintering species (Niven et al., 2004). Augmenting these data with unstructured citizenscience initiatives like eBird within SDMs will further reduce uncertainty about how winter distributions will respond to future climate change.

(2) High priority

(a) Hypothesis 2b: decreased precipitation during the breeding season will lower abundance

(i) Uncertainty score 2. Over the past century, precipitation patterns in North America have undergone substantial changes (summarized by Wuebbles, Fahey, & Hibbard, 2017). In general, precipitation has decreased in the west, southwest, and southeast and increased in the southern Great Plains, midwest, and northeast. Changes in total precipitation, as well as changes in the frequency and severity of precipitation extremes, have the potential to affect the productivity of many terrestrial and aquatic habitats with important demographic consequences for the survival and reproductive success of migratory birds. This is particularly true for the billions of waterfowl and other wetland-dependent species that rely on permanent and ephemeral wetlands for successful breeding (Johnson et al., 2005; Millett, Johnson, & Guntenspergen, 2009). The relationship between wetland productivity and recruitment and abundance of wetlanddependent migratory birds is well established from both first principles (Johnson, Sparling, & Cowardin, 1987) and decades of long-term empirical studies (Markham, 1982; Walker et al., 2013; Zhao et al., 2016; Specht & Arnold, 2018). The effects of precipitation on non-wetland species are less certain but there is evidence that decreased precipitation can lead to lower reproductive success (Dybala et al., 2013; Öberg et al., 2015; Conrey et al., 2016), juvenile survival (Yackel Adams, Skagen, & Savidge, 2006; Vernasco et al., 2017), and adult survival (Oberg et al., 2015) in landbirds. There is therefore little uncertainty that reductions in breeding season precipitation will negatively affect these species.

However, substantial uncertainty remains about spatial and temporal changes in precipitation patterns. Although most climate models agree that the frequency and severity of extreme precipitation events will increase throughout North America, there is substantial disagreement among models about regional changes in the amount of annual precipitation and the seasonal timing of precipitation events (Stephens & Hu, 2010; Pierce et al., 2013; Wuebbles et al., 2017). The northeastern U.S. is expected to receive more winter precipitation (Rawlins, Bradley, & Diaz, 2012; Fan, Bradley, & Rawlins, 2014), although this precipitation is expected to come in the form of more extreme rain events punctuated by more frequent drought (Ning, Riddle, & Bradley, 2015). Regions of importance to North America's wetland-dependent species, in particular the Prairie Pothole region (PPR), show particularly large variation in precipitation patterns (Millett et al., 2009; Niemuth, Wangler, & Reynolds, 2010; Rashford et al., 2016) and predictions about changes to precipitation in the PPR are conflicting (Rashford et al., 2016; Sofaer et al., 2016) Thus, despite well-understood relationships between precipitation and the demography of migratory birds, the lack of certainty about spatial variation in the amount, timing, and frequency of future precipitation creates substantial uncertainty regarding this hypothesis.

(ii) Relevance score 3. Given the centrality of waterfowl to many of the federal LA programs, future reductions in precipitation and increasing droughts have the potential dramatically to alter abundances of the priority species that drive LA decisions in North America (Bethke & Nudds, 1995; Sorenson et al., 1998; Haig et al., 2019). The spatially heterogenous nature of projected precipitation changes renders this hypothesis particularly relevant to U.S. LA decisions – while some regions will receive less precipitation, some will receive more, and understanding this spatial variation will have important consequences for predicting which areas will provide high-quality habitat for priority species in the future, rendering this hypothesis highly relevant to meeting the objectives of LA programs.

(iii) Reducibility score 1. Although the relationships between precipitation, wetland quality, and breeding success of wetland-dependent species are relatively well understood, improving management actions in the face of future precipitation changes will require improving predictions of future precipitation changes at high spatial resolutions. Although climatologists are developing a better understanding of the physical processes that influence variation in precipitation patterns (Meehl, Arblaster, & Tebaldi, 2005; Stephens & Hu, 2010; Muller, O'Gorman, & Back, 2011), the predictive ability of precipitation models is still relatively low (Chen & Knutson, 2008; Wehner et al., 2010). Reducing uncertainty about this hypothesis will therefore fall heavily on the ability of climatologists to improve the predictive ability of climate models. For organizations and agencies that have both earth sciences and natural resource missions (e.g. U.S. Geological Survey), supporting research on precipitation models would be an important priority for improving migratory bird LA decisions. However, due to the inherent complexity of precipitation modelling, reducing uncertainty about this hypothesis will require continued long-term data collection and model development, both of which render this source of uncertainty difficult to reduce.

(b) Hypothesis 2a: warmer temperatures on temperate non-breeding grounds will increase abundance

(i) Uncertainty score 4. Climate conditions experienced during the non-breeding season can influence the survival and reproductive success of both resident and migratory birds (Harrison et al., 2011). For residents and migrants that overwinter in temperate areas, adverse winter weather (e.g. low temperatures, duration of frost/snow) has been shown to lower survival through direct thermoregulatory costs (Swanson & Olmstead, 1999) or food limitation (Jansson, Ekman, & von Brömssen, 1981) and to lower subsequent reproductive success via carry-over effects on body condition or phenology (Robb et al., 2008). Increasingly mild winter temperatures in temperate areas could therefore result in higher survival and reproductive success of species that winter in these areas, potentially resulting in higher abundance if species were previously limited in the non-breeding season. Although numerous studies have linked winter climate to survival, phenology, and reproductive success, studies linking winter climate to overall changes in abundance are rarer. A number of studies have found that annual changes in breeding abundance of migratory birds are correlated with weather conditions experienced during the non-breeding periods. Population increases of barnacle geese (Branta leucopsis) in Norway were attributed to increased winter survival (Owen, 1984) and increases in two colonies of thick-billed murres (Uria lomvia) in Canada were inferred to be the result of warming temperatures and improved foraging conditions on the shared wintering grounds (Gaston, 2003). Schummer et al. (2010) found that annual variation in the abundance of wintering mallards (Anas platyrhynchos) in Missouri was significantly correlated with cumulative weather severity. Pearce-Higgins et al. (2015) found that short-distance migrants and residents in England increased over a 45-year period between 1966 and 2000 due to increasing winter temperatures. Collectively, the studies linking improved demographic rates to warmer winter temperature and the studies linking increases in abundance to warmer winter temperatures provide support for this hypothesis.

However, the validity of this hypothesis is conditional on winter limitation – abundance of migratory bird populations will only increase in response to warming winters if winter temperature limits population growth. The degree to which populations of migratory birds are winter limited is poorly understood for the vast majority of species. Furthermore, there is currently no theoretical basis for predicting the degree to which populations are limited by winter processes. Collectively the lack of theory, combined with the lack of empirical evidence regarding winter limitation and the small number of studies that have directly linked changes in

abundance to winter temperature, leads to a large degree of uncertainty regarding this hypothesis.

(ii) Relevance score 1. If populations are currently winter limited, parcels that support high-abundance wintering populations of priority species will likely remain important sites in the future regardless of whether this hypothesis is true. As a result, management decisions based on current winter abundance are unlikely to be detrimental under this hypothesis as long as winter remains the limiting season. Therefore, reducing uncertainty about this hypothesis is not likely to change which LA actions produce the highest benefits, which would lead to a relevance score of 0 using our rubric. However, it is possible that warming temperatures may relax winter limitation enough that breeding-season processes become more limiting in the future. In this case, current objectives used by LA decisions may become unreliable predictors of the parcels that are most likely to meet fundamental objectives in the long term. Under this scenario, acquiring parcels that protect the most vulnerable breeding populations in the future would produce better results, although which parcels meet this criterion depends on patterns of migratory connectivity between breeding and winter populations (Webster & Marra, 2005; Cohen et al., 2018). However, populations are unlikely to become completely released from winter limitation, so protecting land that currently supports a high abundance of individuals is unlikely to have major downsides under future climate scenarios (unless distributions shift, see hypotheses 1a and 1b).

(iii) Reducibility score 1. Measuring breeding versus winter limitation has been a central focus of avian population ecology for decades (Newton, 2004). Despite this focus, researchers still lack a solid theoretical or empirical understanding of this issue because linking population processes to seasonal vital rates and environmental processes is exceedingly difficult, especially for migratory populations where density dependence, migratory connectivity, and seasonal interactions can play subtle but crucial roles in determining which season is more limiting (Sherry & Holmes, 1995; Sutherland, 1996; Runge & Marra, 2005). Nonetheless, the same monitoring programs that have proved useful for modelling species distributions, including the BBS, CBC, and eBird, provide data that can be used to quantify changes in abundance across space and time (Niven et al., 2004; Link & Sauer, 2007: Robinson et al., 2018). Combined with large-scale remote sensing data, these data can be used to model the relationship between abundance and winter climate for many species (Wilson et al., 2011; Rushing, Ryder, & Marra, 2016). In cases where demographic data are also available, integrated population models could provide a powerful method to link climate variation to changes in abundance via demographic vital rates (Weegman et al., 2017), which should improve predictions about future dynamics (Zipkin & Saunders, 2018). The ability to implement these methods, however, depends on a firm understanding of migratory connectivity, underscoring the need to document these patterns for priority species (Webster & Marra, 2005). Continued development of these data sources and analytical methods may provide important insights into this hypothesis in the future but progress will likely be limited by the intrinsic difficulty of the questions.

(3) Medium priority

- (a) Hypothesis 1c: distributions will shift towards higher elevations due to warming temperatures
- (i) Uncertainty score 3. In general, elevational shifts have been less well studied than latitudinal range shifts. Theoretical studies linking latitudinal distributional shifts to temperature should apply to elevation as well, but the role of non-climaterelated factors is not well understood for elevation (Chamberlain et al., 2012) and relatively few empirical studies have documented altitudinal range shifts. Tingley et al. (2012) quantified elevational shifts in breeding songbirds in the Sierra Nevada Mountains, U.S.A. and found that species shifted upslope 160-2500 m between 1911 and 2009, although only about half of the species included in their analysis shifted upslope. DeLuca & King (2017) found that the upper elevational limit of low-elevation species shifted upslope by 99 m over a 16-year period, although highelevation species shifted their lower elevational limit nearly 20 m downslope, contrary to predictions. Maggini et al. (2011) found that 35% of 95 Swiss birds show significant upward shifts in their upper elevational limit. Auer & King (2014) found that 40 species of western North American songbirds moved to higher elevation by an average of 65.8 m over a 30-year period (1981-2011). Given the weaker theoretical understanding of the factors that govern altitudinal limits and limited and inconsistent empirical results, there is a larger degree of uncertainty regarding this hypothesis than there is regarding latitudinal changes.
- (ii) Relevance score 1. Although altitudinal shifts may result in the spatial reconfiguration of important breeding habitat for some species, these changes are not likely to change LA decisions or outcomes. Across North America, much of the highelevation habitat is already under federal protection and therefore unlikely to be a high priority for LA programs even if species' ranges move upslope, though this may not be true in other countries. Furthermore, observed altitudinal shifts over the past 2-3 decades are on the magnitude of 10s to 100 s of metres, much smaller than the scale of most acquisition decisions and much smaller than documented or projected latitudinal shifts. Additionally, some species may not shift at all or may even shift downslope due to the influence of climate variables other than temperature (Tingley et al., 2012). Thus, even if future altitudinal shifts are on the high end of predicted shifts, these changes are likely to occur within current or proposed protected areas and would not therefore change decisions about priority parcels for acquisition relative to other sources of uncertainty.
- (iii) Reducibility score 2. Unlike latitudinal range shifts, documented elevational shifts of 20–100 m are likely too small to be detected by the 25-mile roadside survey routes used by the BBS. Finer-scale observations, such as those provided by

- eBird observations or more focused monitoring programs (e.g. many European monitoring schemes), are likely better suited for detecting altitudinal shifts but these programs are either limited in their temporal scope (eBird) or their spatial scale (focused monitoring programs). Therefore, meaningful reduction of uncertainty about altitudinal range shifts would likely require development of mechanistic simulations models or new monitoring programs specifically designed to track altitudinal limits.
- (b) Hypothesis 3c: climate-driven phenological mismatches will lower abundance of migratory birds through their effects on reproductive success or survival
- (i) Uncertainty score 2. Migratory bird species time their annual arrival on the breeding grounds to coincide with seasonally abundant resources needed to produce and raise offspring. In recent decades, warming temperatures in these regions have caused earlier emergence of the plant and insect resources that migrant birds require for successful reproduction (Walther et al., 2002). Because the phenology of spring migration is primarily driven by endogenous factors and environmental conditions on the wintering grounds, migrants may not be able to shift their arrival phenology to keep pace with earlier resource peaks, resulting in so-called 'phenological mismatches' (Both & Visser, 2001). Phenological mismatches may reduce reproductive output and survival, potentially resulting in reduced recruitment and large-scale declines in abundance.

There is a well-established body of research on the causes, magnitude, and consequences of phenological mismatches (Visser et al., 1998; Both & Visser, 2001), leaving little doubt that the phenology of temperate breeding resources used by migratory birds has advanced in recent decades (Parmesan & Yohe, 2003). Many species of migratory birds have undoubtedly shifted their phenologies in response, often at rates that fail to track advancing phenology in their food sources. Over the past 50 years, tree leaf-out dates in temperate regions have advanced by 5–10 days (Menzel, 2000; Chmielewski & Rötzer, 2001; Richardson et al., 2006; Ibáñez et al., 2010; Polgar & Primack, 2011) and hatching and emergence of insects has advanced by 8–15 days (Roy & Sparks, 2000; Walther et al., 2002; Both et al., 2009), yet numerous studies have found that arrival dates of migratory birds have not kept pace with advancing spring temperatures and food resources. These studies have documented phenologically driven reductions in reproductive success or survival in a range of taxa, including waterfowl (Clausen & Clausen, 2013; Brook et al., 2015; Lameris et al., 2017), shorebirds (Reneerkens et al., 2016), seabirds (Regular et al., 2014), and passerines (Visser et al., 1998; Thomas et al., 2001; Kullberg et al., 2015; Arlt & Pärt, 2017; Mallord et al., 2017; Mayor et al., 2017). Most current evidence suggests that longdistance migrants are more likely to exhibit phenological mismatches than short-distance migrants or residents (Miller-Rushing et al., 2010), as are insectivores (Dunn & Møller, 2014), and single-brooded species (Jiguet et al.,

2007; Dunn & Møller, 2014). Not all species have experienced phenological mismatches, however (Drever & Clark, 2007; Dunn et al., 2011: Kullberg et al., 2015: Valtonen et al., 2017: Meller et al., 2018). For example, Drever & Clark (2007) found little evidence that mismatches between spring temperature and clutch initiation affected the probability of nest success in five North American ducks. Dunn et al. (2011) found no evidence that mismatches between laying date and peak insect abundance influenced the reproductive success of North American tree swallows (Tachycineta bicolor), likely because insect abundance remains relatively high throughout the breeding season.

Despite the empirical focus on phenological mismatches, there is substantial uncertainty regarding the degree to which phenological mismatches are causing population declines. Møller, Rubolini, & Lehikoinen (2008) and Saino et al. (2011) found that the rates of population decline of over 100 European birds were correlated with changes in spring migration phenology, but subsequent studies found no evidence that mismatches between laying date and resource phenology were related to the rate of population decline (Dunn & Møller, 2014). At present, few studies have directly linked population declines to the demographic consequences of phenological mismatches. In addition, some studies have found that density-dependent mechanisms (reduced competition, multiple brood attempts) and altered foraging behaviour can counteract the negative reproductive effects of phenological mismatch (Thomas et al., 2001; Dunn et al., 2011; Reed, Jenouvrier, & Visser, 2013; Reneerkens et al., 2016; Mallord et al., 2017), resulting in overall stable population growth rates. Thus, although there is clear evidence that phenological mismatches are occurring and affecting the reproductive success of many migratory birds, the degree to which these mismatches influence population declines remains unclear.

(ii) Relevance score 1. Unlike distributional changes, which result in a mix of sites that will become more important or less important for supporting priority species in the future, most current evidence suggests that, when they occur, phenological changes are widespread across regions and habitats (Burgess et al., 2018). Thus, even if phenological mismatches have negative effects on abundance of priority species, these effects will likely occur across large spatial scales. If true, most parcels available for acquisition would be equally (or nearly so) affected by mismatches and LA decisions would not change even if uncertainty about the magnitude of phenological mismatches was reduced. It is possible that the magnitude of phenological mismatches will vary across space and therefore some sites may be less vulnerable to phenology shifts under future climate scenarios. For example, breeding resources may exhibit less seasonality at low latitudes or elevations, making sites in these areas less vulnerable to phenological mismatches than high-latitude or high-elevation sites that have shorter, more pronounced resource peaks. In this case, low-latitude/elevation sites may serve as refugia under future climate conditions (Keppel et al., 2012) and therefore would be prioritized for acquisition.

(iii) Reducibility score 2. Reducing uncertainty regarding the effect of phenological mismatches requires moving beyond documenting phenological mismatches and correlations between the rate of population declines and metrics of migration/breeding phenology. In particular, more studies are needed that explicitly link annual changes in abundance or population growth rate to phenological mismatches via their effect on demographic rates. To isolate the effects of phenological mismatches from the effects of other biotic and abiotic processes, studies should be based on long-term data on the phenology of avian migration and reproduction, the phenology of critical breeding resources, and estimates of demographic rates and/or abundance. For some well-studied species, these data may currently exist from long-term monitoring programs. Advances in population modelling, particularly the development of integrated population models (Schaub & Abadi, 2011; Arnold et al., 2018) that allow researchers to combine different types of data better to understand the demographic drivers of population dynamics, provide novel avenues for leveraging historical data sets to explore the population-level effects of phenological mismatches.

Given their limited geographic and taxonomic scope, long-term historical data sets are unlikely to provide sufficient information to understand how the effects of phenological mismatches differ across species and locations. However, citizen-science-based monitoring programs are increasingly providing new methods to quantify phenology and population-level processes across large scales (e.g. Bell et al., 2019). The temporal resolution, geographic scope, and taxonomic breadth of these observations allows researchers to quantify and predict abundance and phenology of migrating birds at unprecedented scales (Hurlbert & Liang, 2012). Similar programs exist to document the phenology of plants and insects, and advances in remote sensing are providing new ways to quantify resource phenology across large spatial scales (Cleland et al., 2007; White, Pontius, & Schaberg, 2014). Together, these data provide novel opportunities to link changes in migration phenology and population dynamics of migratory birds to changes in resource phenology.

(4) Low priority

- (a) Hypothesis 3b: migration distances will lengthen for long-distance migrants
- (i) Uncertainty score 3. A growing body of research suggests that the distance and duration of annual migrations can change rapidly through both natural selection (Berthold et al., 1992) and individual plasticity (Berthold et al., 2001). As breeding distributions shift northward (hypothesis 1a), long-distance migrants may be forced to migrate longer distances to reach their historic wintering grounds (Doswald et al., 2009; Howard et al., 2018). Longer migrations could lead to reduced survival and delayed reproduction, which could have negative consequences for population abundance and viability of priority species. Few studies, however, have documented changes in the migration distance of long-distance migrants.

By combining breeding and winter SDMs, Doswald et al. (2009) found that the average migration distance of trans-Saharan European migrants would increase by 413 km by the end of the 21st century. Theoretical work by Howard et al. (2018) also found that the breeding and winter distributions of long-distance European migrants are likely to shift in different directions, resulting in longer migration distances for up to 86% of species. By contrast, Visser et al. (2009) found that 12 of 24 long-distance European migrants had actually shortened their average migration distances based on long-term band recovery data. Contrary to the predictions of Doswald et al. (2009) and Howard et al. (2018), the authors conclude that these changes are mainly the result of improved conditions allowing species to winter further north, thus shortening the distance between breeding and wintering grounds. The largest decreases occurred in species that inhabited dry, open habitats while species that inhabit wet, open habitats showed the smallest changes. The general lack of theoretical investigations on this hypothesis, combined with the very small number of empirical studies, result in a large degree of uncertainty regarding this hypothesis.

(ii) Relevance score 1. Because most long-distance migrants winter outside the focal areas of federal LA programs, changes in migration distance are not likely to influence decisions through their effects on distributions. However, longer migrations could lead to lower survival during this period, potentially increasing the importance of stopover or staging habitats that would become increasingly necessary for successful migration. If this is the case, protecting these stopover habitats may become more important relative to protection of breeding habitat under future conditions, particularly for species that may experience bottlenecks at critical stopover locations [e.g. many shorebirds (Iwamura et al., 2013; Studds et al., 2017)].

(iii) Reducibility score 1. Unlike measuring range shifts, which requires only information about occupancy or abundance, documenting changes in migration distance requires information about the migration routes used by specific populations. These data may exist for a few species in the form of band recoveries but in general there are few sources of historic data that can be used to answer this question retrospectively. Recent advances in tracking technologies are providing powerful new methods to measure migration distances of many species but documenting changes in migration distances will require large samples collected over long periods of time. Predictive models can provide insights into whether and how some species may change migration strategies under future climate and land-use scenarios but the value of these models for LA decisions will be limited without empirical data on migratory connectivity and individual movements to test their predictions.

- (b) Hypothesis 4a: climate change will result in a lower proportion of migratory species in temperate avian communities due to increased competition with resident species
- (i) Uncertainty score 2. The abundance of many resident and short-distance migrant species is limited by overwinter

survival (Nilsson, 1987; Forsman & Mönkkönen, 2003; Link & Sauer, 2007), which in turn is determined primarily by winter temperature (Robinson, Baillie, & Crick, 2007). If climate change results in milder winters, resident species may increase in abundance (see hypothesis 2a). Higher abundance of residents and short-distance migrants may in turn increase competitive pressures on long-distance migrants, which may lead to decreased relative abundance of these species within avian communities (Herrera, 1978; Lemoine & Böhning-Gaese, 2003). Few empirical studies, however, have documented increased interspecific competition between long-distance migrants and resident species as a result of climate change. Some evidence from cavity-nesting species suggests that competition for nest sites is severe between migratory and resident species (Newton, 1994), with residents potentially benefitting at the expense of migratory species due to their earlier nesting phenology (Slagsvold, 1976; Newton, 1994; Ahola et al., 2007). Outside of a few wellstudied cavity-nesting species, there is little direct evidence of interspecific competition between migratory and resident species, making it difficult to draw firm conclusions about how climate change may affect competitive relationships. However, several studies have found indirect evidence that increased competition with residents may be contributing to the declines of long-distance migrants. For example, Lemoine, Schaefer, & Böhning-Gaese (2007b) and Lemoine et al. (2007a) documented a decline in the proportion of longdistance migrants between 1980 and 2000 after controlling for the effects of spatial auto-correlation, habitat type, and latitude.

Although observed changes in the relative proportion of resident and migrant species are consistent with the prediction that migrants suffer from increased competition with residents, long-term declines of migrant birds have been linked to factors other than competition, including breeding habitat fragmentation (Donovan *et al.*, 1995), winter habitat loss (Rushing *et al.*, 2016), and declining winter precipitation (Peach, Baillie, & Underhill, 1991; Morrison *et al.*, 2013; Pearce-Higgins *et al.*, 2015; Pearce-Higgins & Crick, 2019). Thus, despite the existence of mechanistic theory and a moderate number of consistent empirical studies, the degree to which increased competition with residents effects the abundance of migratory species remains uncertain.

(ii) Relevance score 1. If these dynamics are widespread, climate-induced changes in interspecific competition could be an important driver of future abundance and occurrence of priority species for LA programs. If this is the case, prioritizing sites where priority species will have limited contact with resident competitors or prioritizing habitats where migrants will remain competitively dominant to residents could be important considerations for LA decisions. However, given the general lack of evidence that interspecific competition plays a substantial role in limiting populations of migratory birds compared to intraspecific processes (Newton, 2004), focusing on better understanding intraspecific demographic processes is expected to be more important for improving future LA decisions.

(iii) Reducibility score 1. Although documenting relative changes in the proportions of migratory and resident species can provide some evidence for the role of competition, these types of studies will always be limited by their ability to distinguish different mechanisms that might produce similar patterns in abundance. Therefore, reducing uncertainty about the role of climate change in altering competition requires detailed studies, including experiments, demonstrating changes in competitive relationships that cannot be explained by changes in, for example, land use. Recent development of multi-species modelling approaches that account for interspecific interactions may offer some insights into the role that competition plays in structuring avian communities (Pollock et al., 2014; Harris, 2016; Guillera-Arroita, 2017), however the ability to predict interspecific interactions under future conditions remains challenging (Alexander et al., 2016).

(c) Hypothesis 2c: reduced precipitation on the non-breeding grounds will decrease abundance of species that overwinter in tropical areas

(i) Uncertainty slope 3. For species that overwinter in tropical areas, rainfall, rather than temperature, has been shown to be a primary driver of survival (Sillett, Holmes, & Sherry, 2000; Rockwell et al., 2017) and reproductive success (McKellar et al., 2013) of many species, including migratory songbirds (Peach et al., 1991; Sillett et al., 2000; Boano, Bonardi, & Silvano, 2004; Robinson et al., 2007), seabirds (Brichetti, Foschi, & Boano, 2000), waders (Nevoux, Barbraud, & Barbraud, 2008), and shorebirds (Yalden & Pearce-Higgins, 1997). In many tropical regions that support large numbers of wintering migratory birds, including Central America, the Caribbean, and sub-Saharan Africa, climate models predict less rainfall and increased drought (Neelin et al., 2006). If these changes reduce survival and reproductive success of species that winter in these regions, climate change on the wintering grounds could lead to widespread declines in abundance.

For songbirds in particular, a number of independent studies linking breeding abundance to rainfall in the Sahel region of Africa has led some authors to conclude that winter rainfall is the primary limiting factor of long-distance European migrants (Morrison et al., 2013). In several cases, the rate of declines of long-distance migrants have also been linked to winter conditions (Brooks & Temple, 1990). Foppen et al. (1999) found that abundance of sedge warblers (Acrocephalus schoenobaenus) breeding in fragmented marsh habitats was strongly correlated with rainfall in the western Sahel zone of Africa whereas abundance of warblers breeding in unfragmented habitats was less correlated with winter climate. These results suggest that vulnerability to winter climate may be mitigated for populations in high-quality breeding habitat, a conclusion that has been corroborated by more recent multi-species analyses (Morrison et al., 2013). In addition, a large number of studies have linked the demographic rates of species that winter in the tropics to non-breeding rainfall patterns and nearly all studies have

found that decreasing rainfall has negative effects on demographic processes. Fewer studies, however, have linked winter rainfall to population dynamics with those that have finding substantial intraspecific variation in the strength of the relationship (Wilson *et al.*, 2011; e.g. Rushing *et al.*, 2016). The observed variability in this small number of studies, combined with the lack of theoretical studies on this topic, leads to a relatively large degree of uncertainty about the extent to which changes in winter rainfall will affect migratory bird populations.

(ii) Relevance score 0. If this hypothesis is true, decreasing winter precipitation will increase the strength of winter limitation for many migratory birds, even species that may currently be more limited during the breeding season. However, LA programs with jurisdiction in North America will have little ability to protect winter habitat of longdistance migrants that spend the non-breeding season in Latin America and the Caribbean. High-quality breeding habitat may buffer populations against the negative effects of decreasing winter precipitation (Foppen et al., 1999), and therefore protecting these parcels may serve as a proactive means of increasing population viability in the face of climate change. However, patches that provide high-quality breeding habitat would likely be prioritized regardless of whether this hypothesis is true. Therefore, reducing uncertainty about the climate change effects of winter precipitation on abundance of migratory birds is unlikely to change LA decisions within the U.S.

(iii) Reducibility score 1. As for species wintering in temperate areas, determining whether species are currently breeding versus winter limited is challenging. These challenges are amplified for long-distance migrants that winter in the tropics due to a lack of monitoring data in these regions. For some species, uncertainty about the effects of winter climate on breeding dynamics of long-distance migratory birds may be reduced by combining breeding abundance data from monitoring programs with remote-sensing data from tropical regions (Wilson et al., 2011; Rushing et al., 2016) but these methods can only provide correlative evidence that winter precipitation influences breeding abundance. Integrated population models may provide additional power to infer limitation and the effects of winter climate on population dynamics (Rushing et al., 2017; Robinson et al., 2018) but the general lack of widespread demographic monitoring data during the winter and information about migratory connectivity will restrict the application of these methods in the foreseeable future.

(d) Hypothesis 3a: migration distances will shorten for short-distance migrants

(i) Uncertainty score 3. Many short-distance migrants winter in temperate regions that are expected to experience decreased winter severity due to climate change. Because short-distance migrants often migrate only as far as necessary to find suitable habitat and therefore tend to have lower fidelity during winter than during summer (Hestbeck, Nichols, & Hines,

1992), climate change may allow individuals to winter further north and thereby shorten their migrations. Shorter migrations may in turn result in higher annual survival, earlier arrival on the breeding grounds, and higher reproductive success (Ketterson & Nolan, 1983). Theoretical studies have derived predictions about how migration behaviour of short-distance migrants will respond to climate change from first principles and found that many populations will shorten their migrations and possibly cease migrating by the end of the 21st century (Aagaard, Thogmartin, & Lonsdorf, 2018). By contrast, Howard et al. (2018) used a combination of physiological flight models, climate simulations, and radar data to predict that migration distances are likely to remain relatively unchanged for short-distance European migrants because breeding and winter distributions will shift northward in tandem.

Direct evidence of changes in migration distances are rare. Winter ring recoveries of white storks (Ciconia ciconia) indicate that during the 1950s-1980s, migration distances of birds breeding in eastern Europe decreased as individuals started wintering in southern Europe rather than their historic African winter range (Berthold et al., 2001), likely the result of increasing suitable habitat. Starting in the 1950s, European blackcaps (Sylvia atricapilla) that historically wintered in southern Europe and north Africa began to winter in the British Isles, likely due to increasing winter food supplied by bird feeders, potentially reducing their annual migration distance by approximately one third (Plummer et al., 2015). Barnacle geese (Branta leucopsis) established novel breeding sites in Iceland and the Netherlands, shortening migration distance by 500-1300 km (Larsson et al., 1988; Forslund & Larsson, 1991). By contrast, banding data have shown that several species, including Egyptian populations of great white pelicans (*Pelecanus onocrotalus*; Crivelli *et al.*, 1991) and populations of pink-footed goose (Anser brachyrhynchus) in Britain (Gill, Watkinson, & Sutherland, 1997), have increased their migration distances due to loss of preferred habitat. Conflicting theoretical predictions, combined with a small number of empirical studies, provide evidence that climate change can influence migration distances of short-distance migrants but leave substantial uncertainty about the mechanisms, direction, magnitude, and taxonomic scope of these changes.

- (ii) Relevance score 0. As described above (hypothesis 3b), changes in migration distance are not likely to change the decisions made by LA programs unless these changes result in stopover habitat becoming less limiting in the future. However, unlike long-distance migrants, short-distance migrants are unlikely to be limited by stopover habitat to any substantial degree (Newton, 2004) and therefore we do not expect reducing uncertainty regarding this hypothesis to result in different LA decisions relative to the current level of uncertainty.
- (iii) Reducibility score 1. Reducing uncertainty about this hypothesis requires information about the migration routes used by specific populations (see *Reducibility* for hypothesis 3b). Given the low rate of band recoveries for many migratory species and the historic lack of tracking technologies,

adequate data do not likely exist for the majority of species. New tracking technologies have revolutionized our ability to follow migratory birds across their annual cycle, but documenting systematic changes in migration distance will require years or decades of new data collection.

IV. CONCLUSIONS

- (1) We identified research priorities for improving the outcomes of U.S. federal migratory bird LA decisions in the face of climate change (Table 4). The analysis was based on a comprehensive literature review, expert elicitation, and professional judgement, combined with using a QVoI analysis. Application of VoI principles provided a rigorous and transparent approach to prioritizing research priorities despite the inherent complexity of climate change effects on migratory birds. Results from this analysis provide government, academic, and non-governmental organizations with a list of priority topics for future research and a clear rationale for allocating research effort.
- (2) Unsurprisingly, hypotheses that focus on the spatial distribution of focal species or their habitat ranked more highly than hypotheses that focus on temporal changes in phenology or changes in species composition. Federal LA programs generally protect parcels of land in perpetuity, so climatedriven range shifts have potential to significantly alter which parcels will help meet fundamental objectives in the future. Poleward range shifts during both the breeding and nonbreeding seasons (hypotheses 1a and 1b) were found to have high QVoI ranks (≥4), driven primarily by high relevance scores (≥ 2). Both hypotheses also ranked highly with regards to reducing uncertainty (>2) in light of both the existence of large-scale monitoring data and the continued improvement of analytical frameworks for modelling past and future distributions (Bateman et al., 2013; Guillera-Arroita, 2017; Zhao, Boomer, & Royle, 2019). Continued refinement of these methods, particularly the continued development of mechanistic distribution modelling approaches (Evans et al., 2016; Zurell, 2017), and application to a wider variety of taxonomic groups has the potential to reduce uncertainty regarding which species will shift their distributions in response to climate change (and which will not), the magnitude and timing of these shifts, and which parcels of land will be important for future persistence of priority species.
- (3) Our analysis also indicated that research on the role that climate change will play in biotic homogenization should be a top research priority for improving LA decisions. Although this hypothesis does not deal with the spatial distribution of migratory species, many of the species that are prioritized by federal LA programs are, by definition, rangerestricted or habitat specialists (Table 1). Both theory and empirical results suggest that these species may be most at risk as climate and weather patterns are disrupted, although how climate change will interact with other habitat alterations (conversion, urbanization, etc.) and species' life-history

traits remains poorly understood. Reducing these sources of uncertainty is expected to be highly achievable given the large amounts of large-scale monitoring data and could help identify parcels that will continue to support priority species in the face of increasing habitat and climate disruptions.

- (4) Two hypotheses (2a and 2b) ranked highly with regard to QVoI (≥4) but received reducibility scores of 1. These hypotheses, which deal with changes in abundance due to warming winter temperature and changing precipitation patterns, present somewhat of a quandary for prioritizing research efforts. Resolving uncertainty about these hypotheses is predicted to have high value for LA decisions, comparable to or exceeding the value of the highest ranked hypotheses (1a, 1b, and 4b). However, reducing uncertainty about these hypotheses will not be easy – new data will need to be collected, new analytical frameworks will need to be developed, and useful insights may be years or even decades away. Thus, these topics have potentially high pay-off in terms of improving LA programs in the U.S. but these benefits should be carefully weighed against both the long-term costs and the benefits of the highest priority topics.
- (5) Several hypotheses that deal with changes to phenology received high scores for uncertainty and reducibility but low scores for relevance due to the static nature of LA decisions. Our results suggest these topics may need to be deemphasized relative to the higher-priority topics identified here and relative to sources of uncertainty unrelated to climate change (e.g. habitat loss; Tingley, Estes, & Wilcove, 2013). We emphasize that, as in all VoI analyses, our results do not imply that reducing uncertainty about these hypotheses should not be pursued, only that in the specific decision context of federal LA decisions, reducing these sources of uncertainty is not expected to improve management outcomes. For other management actions or for LA programs with different geographic jurisdiction, reducing uncertainties about phenological changes may be worthwhile. For example, changes to migration and breeding phenology may be highly relevant to dynamic conservation actions, whereby habitat is provided temporarily at locations where priority species undertake a critical phase of their annual cycle (e.g. managing water levels at stopover locations for shorebirds; Reynolds et al., 2017). Given the scale and complexity of migratory bird conservation, protecting priority species in the face of climate change will require a diversity of management approaches. Prioritizing research and monitoring to improve the outcomes of these approaches will require identifying the sources of uncertainty with the greatest value to each decision context. As we have demonstrated here, QVoI provides a practical method for identifying research priorities that can be applied to other decision contexts.
- (6) Although beyond the scope of our analysis, some of the most important sources of uncertainty for federal LA programs may be related to the relationship between climate and land-use change (Dale, 1997). Warming temperatures and changes in the location and frequency of precipitation events have major implications for agricultural conversion or farming methods, with important implications for the

availability and quality of migratory bird habitat (Voldseth et al., 2009; Rashford et al., 2016). Predicting how and where climate change will influence land-use patterns is likely to be highly relevant to LA programs but will require close collaboration between biologists, economists, and social scientists.

(7) Many issues in natural resource management are characterized by complex and highly uncertain ecological systems. In these situations, QVoI can be an important tool for improving management decisions in the face of uncertainty. We emphasize, however, that QVoI should be viewed as an alternative when quantitative VoI is not possible, not as an excuse to avoid the difficult but important process of formalizing hypotheses in a quantitative framework, which should always be preferred. However, by providing a rigorous and transparent approach to prioritizing research efforts in cases where traditional quantitative VoI analysis is not possible, QVoI is a valuable tool for prioritizing research and improving management decisions.

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AUTHOR CONTRIBUTIONS

M.R., J.E.L., and M.C.R. conceived the study and all authors participated in the expert elicitation. C.S.R. conducted the literature review. C.S.R. and M.R. drafted the manuscript and all authors contributed to subsequent revisions.

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