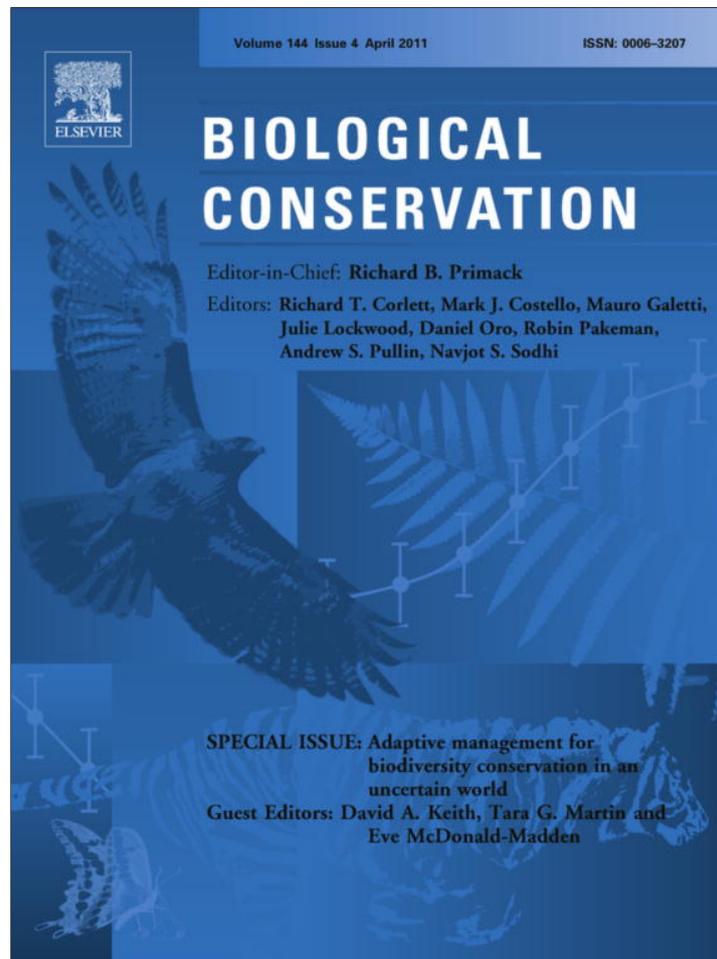


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Special Issue Article: Adaptive management for biodiversity conservation in an uncertain world

Conservation in the face of climate change: The roles of alternative models, monitoring, and adaptation in confronting and reducing uncertainty

Michael J. Conroy^{a,*}, Michael C. Runge^{b,c}, James D. Nichols^b, Kirk W. Stodola^a, Robert J. Cooper^a^a Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, USA^b USGS, Patuxent Wildlife Research Center, Laurel, MD 20708, USA^c Australian Centre of Excellence for Risk Analysis and the Applied Environmental Decision Analysis Hub, University of Melbourne, Victoria 3010, Australia

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ABSTRACT

The broad physical and biological principles behind climate change and its potential large scale ecological impacts on biota are fairly well understood, although likely responses of biotic communities at fine spatio-temporal scales are not, limiting the ability of conservation programs to respond effectively to climate change outside the range of human experience. Much of the climate debate has focused on attempts to resolve key uncertainties in a hypothesis-testing framework. However, conservation decisions cannot await resolution of these scientific issues and instead must proceed in the face of uncertainty. We suggest that conservation should precede in an adaptive management framework, in which decisions are guided by predictions under multiple, plausible hypotheses about climate impacts. Under this plan, monitoring is used to evaluate the response of the system to climate drivers, and management actions (perhaps experimental) are used to confront testable predictions with data, in turn providing feedback for future decision making. We illustrate these principles with the problem of mitigating the effects of climate change on terrestrial bird communities in the southern Appalachian Mountains, USA.

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1. Introduction

A broad scientific consensus has emerged that a global transition in climate conditions is underway and may be accelerating (McNeil and Matur, 2008; Zhang et al., 2008; Rockström et al., 2009). In spite of this consensus, scientific opinion differs pertaining to the relative roles of anthropogenic agents and background climate cycles, the spatial and temporal distribution of climatic changes, and the feasibility of interventions to arrest or reverse this transition. Because of its potential magnitude, the climate issue has caught the attention of policy makers, economic and political planners, and decision-makers in private enterprise. However, a collective response to incipient climate change is currently lacking, partly because the climate debate has mainly been cast as an issue of scientific discovery, rather than one of decision making (Maxwell, 2008).

We believe that the first step in properly framing the climate debate in a decision making context relevant to biological and ecological conservation, is to acknowledge that (1) continued climate transition seems inevitable in the near term (next 50–150 years) and (2) our knowledge of how climate transitions behave is being challenged and found wanting (Allen et al., 2000; Watson, 2008). The first point means that natural systems exhibit non-stationary

dynamics, which has profound implications for decision making by natural resource managers. The second point means that the ability of natural resource managers to predict and respond to climate change is subject to an extreme form of structural uncertainty that may be irreducible. The first point is the backdrop for a specific issue of conservation that follows, while we return to the second point when considering how or whether climate impacts can be dealt with proactively, and the degree to which adaptive learning is possible.

We illustrate the construction of a decision making framework around the climate issue by considering the effect of climate change on avian communities in North America. We specifically outline (1) the current predicted impacts of climate change, given what is known, (2) feasible management actions to mitigate the predicted negative consequences associated with climate change, (3) a decision context to formalize the relationship between predicted impacts of climate change and the effectiveness of management actions, and (4) a monitoring scheme to provide feedback about system change following management and to reduce uncertainty via adaptive learning.

2. Predicted impacts of climate change on avian communities

We have chosen to focus on avian communities for several reasons: birds are globally distributed, relatively easily observed, and

* Corresponding author. Tel.: +1 706 542 1167; fax: +1 706 542 8356.

E-mail address: mconroy@uga.edu (M.J. Conroy).

a broad body of knowledge exists about their life history, behavior, physiology, distribution, and habitat affinities. This knowledge forms the basis for a robust theory of how bird populations and communities evolved and are maintained; i.e., evolution of behaviors determining migration pathways, breeding chronology, hierarchical use of resources, and development of community structure within physiological and resource constraints. Theory also provides a basis for prediction of how birds are likely to respond to climate transitions. Current climate models project increasing average global temperatures, but there exists much uncertainty about how changes in temperature and other environmental factors will be distributed spatially (Allen et al., 2000; Berliner, 2003; Knutti et al., 2008; Räisänen, 2007; Watson, 2008). Thus, at broad spatial scales (e.g., range wide) many bird populations are predicted to adapt to warming by shifting ranges toward the poles, selecting local environments at higher elevations, or both (Parmesan and Yohe, 2003; Root et al., 2003). However, the underlying population-level mechanisms for range shifts are largely unknown.

One possible mechanism leading to population-level consequences is centered on asynchronous phenological shifts across varying trophic levels. For instance, advancement of seasonal events that affect birds, such as leaf and insect emergence, are predicted under a warming scenario (Walther et al., 2002; Parmesan, 2006). Given this prediction, we would expect birds to advance their breeding to match these shifts in vegetation and food abundance. However, migratory strategy may impede the ability to do so. Specifically, resident and short-distance migratory species may be better able to respond to advanced phenological events occurring on the breeding grounds than long-distance migratory species, because they could react to either the ultimate factor driving the timing of breeding (food), or the proximate factor driving leaf phenology and insect emergence (temperature). While long-distance migratory birds may also adapt through shifts in migratory behavior (Crick and Sparks, 1999), these species must rely on circannual rhythms (Gwinner, 1996) or other cues not associated with the breeding grounds to initiate migration and time the start of their breeding season. Thus, it is unknown whether long-distance migratory species would be as capable of matching phenological shifts at lower trophic levels in comparison to resident and short-distance migratory species, if these shifts occur in a novel, rapid fashion (Visser and Both, 2005). Failure to make this match could have deleterious consequences (Thomas et al., 2001; Sanz et al., 2003; Both et al., 2006).

Given the above theory, several general predictions (Table 1) are possible in terms of distribution and local demography. For

instance, we predict that Northern Hemisphere long-distance migratory birds would (P1) have higher probabilities of local extinction and (P2) exhibit lowered reproduction and survival rates near the southern terminus of their breeding ranges and at lower elevations. Likewise, we would predict increases in occupancy and range extension at the northern range limits, with the central portions of the range remaining relatively stable (although latitude effects may be mediated by elevation; see below). Finally, although bird community structure has evolved within temporally dynamic resource constraints, climate transition may rapidly move environments to new states that have not been experienced for millennia. As seen by our example (below), finer scale predictions are required to support regional and local efforts to mitigate the impacts of climate on birds.

In the remainder of the paper, we narrow the focus somewhat, couching the discussion of climate impacts in the context of the southern Appalachian bird conservation problem. This region is important to North American bird communities for several reasons. First, a high diversity of species occurs in this region due in part to diverse topography and habitats; the region is important during the breeding period for species nesting locally, during the winter period for resident and short-distance migrants from more northerly reaches, as well as during spring and autumn migration periods. In addition, several species of Nearctic–Neotropical migrant birds, a number of which are of conservation concern due to apparent recent population declines, are at or near the current southern terminus of their ranges in the region.

Finally, although we are interested in ‘discovery’ about underlying climate change processes and their impacts, our primary focus is the need to apply existing knowledge and prospective learning to conservation actions.

3. Mitigating the effects of climate change on southern Appalachian birds

Our region of focus is the southern Appalachian Mountains of eastern North America (N 35°W83°). Given the general considerations discussed above (Table 1) we would predict the species residing in this region to be particularly sensitive to climate change, and therefore that broad-scale changes in distribution, site occupancy, abundance, and species turnover would be most likely to occur here. This region is also characterized by dramatic terrain changes over relatively short distances, with associated dramatic changes in local temperature, precipitation, and vegetative and animal communities. Thus, at a given latitude, elevation gradients

Table 1
General predictions about the response of bird populations to directional climate change (warming).

Scale	State variable/response/mechanism	Prediction	References/data
Global, multiple species	Occupancy/Abundance	Poleward shift in range	Parmesan and Yohe (2003) Root et al. (2003) BBS
N. Hemisphere migratory birds rangewide		Increasing in N	
		Decreasing in S Short-distance migrant and resident species increase	Lemoine and Bohning-Gaese (2003)
Breeding population	Reproduction	Long-distance migrant species decrease Reduced annual reproductive output in southern portions of range	Ahola et al. (2007) Both et al. (2006) Crick and Sparks (1999)
	Survival	Decreased survival in southern portions of range	Thomas et al. 2001
	Movement	In southern range, greater emigration from unsuitable sites and lack of juvenile colonization	Studds et al. 2008
Local (breeding territory)	Local colonization/ extinction rates	Increased colonization at northern range periphery, increased extinction at southern	
	Habitat selection	Select higher elevation sites in southern range	Studds et al. 2008
	Behavior	Shift to earlier breeding	Crick and Sparks 1999

might mediate the influence of climate, with lower elevations generally associated with warmer temperatures and earlier spring phenology. In particular, we predict that birds at lower elevations near their southern range terminus would be especially sensitive to climate drivers.

3.1. A structured approach to decision making for the climate problem

Faced with a bewildering array of potential system changes and concomitant impacts to natural resources, natural resource managers are understandably torn between inaction (“wait and see”) and actions that while well intended, may or may not be effective. We instead advocate a structured approach (Hammond et al., 1999; Goodwin, 2004) to decision making in response to climate. Under this approach, any decision problem, conservation or otherwise, is decomposed into key elements. First, there must be a well-defined (and typically quantifiable) *objective* that captures what it is we are trying to achieve (or avoid) with our decision. Second, we (the decision makers) must have a range of *decisions* or actions that have the potential to lead us toward our defined objective. Third, we need a basis for predicting how our system will respond to our decisions; in other words, a *model* of each candidate decision’s influence on the system, and in turn, on the objective. Finally, we need a means of *optimizing* or selecting among our alternative decisions so as to choose the one that best fulfills our objectives. The first and second of these elements set up the *decision context* for our problem; together the four elements provide us with a basis for choosing among the actions at our disposal.

3.2. Decision context for the impact of climate drivers on bird populations

An important step in defining any decision problem is properly characterizing the scope and context of the decision. For managers (agencies, NGOs) of migratory bird populations faced with climate change, one of the questions we need to ask is what is under our control? A natural resource manager at this level is not likely through the tools of natural resource management, to control the levels of carbon dioxide in the atmosphere or the global mean temperature; those questions, while important, are outside the sphere of this decision context. To be certain, the concentration of CO₂ and the global mean temperature are relevant to conservation decision making, but are for the most part outside the scope of natural resource decision makers, and in that context are best viewed as external drivers. Efforts such as payments to reduce deforestation via carbon payments can be effective in mitigating climate change (Venter et al., 2009), but are mostly directed at tropical deforestation. Although conservationists in North America are involved in these efforts, they must still deal with the reality that climate drivers are largely beyond the scope of their agencies or organizations, and that mitigation inevitably occurs at vastly more expansive spatial scales than under the usual purview of conservation. Thus, for the purposes of this discussion, we consider migratory bird conservation in the context of climate drivers that decision makers cannot control but must nevertheless respond to.

Broadly speaking, the decision context for this problem involves an objective of maintaining avian diversity at a regional scale (possibly weighted toward key species of interest), over an indefinitely long time horizon, subject to constraints imposed by costs, competing use of resources, and interactions with other societal needs. We note that local species loss might be acceptable under this strategy, e.g., due to range shifts, if regional or range-wide persistence was maintained. Actions at our disposal include, but may not be limited to, land acquisition and management, silviculture and reforestation, and provision of landowner incentives to conserve habitats. Climate change introduces a large, uncontrolled factor

into our predictive understanding of how birds interact with their environments, and thus, presumably has implications for just what conservation strategies will and will not be effective.

3.2.1. Objectives

Clearly, we would like to identify those management actions most likely to be effective given the resources expended, and to avoid those likely to be ineffective. This interplay between the costs and benefits of the alternative actions form the basis of our objective function. At its heart, this is a multiple-objective problem, with multiple species of interest, and a desire to minimize costs as well. There may be complex trade-offs, such that certain actions may favor one guild of species over another, and one of our challenges is to balance those tradeoffs. But perhaps we can find a way to remove the dimensionality of our objectives. First, we might be able to express the environmental benefits as a weighted sum across species; while this masks complex tradeoffs among species, it does allow us to value species differently, if so desired. Then, we might also be able to fold environmental benefit and cost into a single objective, by decreasing the value of the weighted species abundance when costs are high. Thus, more explicitly, an objective function that reflects range-wide conservation of species diversity might aggregate costs and benefits as

$$J(\underline{a}) = \sum_i v_i x_{i:T} \left(1 - \frac{\sum_k \sum_t c_{k,t} I(a_{k,t})}{c_{\max}} \right) \quad (1)$$

where v_i is a value index representing relative species conservation priority, $x_{i:T} = I(N_{i,T})$ is an indicator of persistence with $I(N_{i,T}) = 1$ if $N_{i,T} > 0$ and 0 otherwise; $N_{i,T}$ is the range-wide abundance of species i at time T (the endpoint of the time horizon of interest), $c_{k,t}$ is an index representing the cost of action k (time-specific to allow inclusion of discounting, etc.), $I(a_{k,t})$ is an indicator that action k is taken at time t , c_{\max} represents the maximum permissible cost, summed over time, of actions that could occur, and \underline{a} is a vector of actions over the time frame. This (or a similar) objective function could be separated into components, e.g., to reflect regional priorities for conservation and economic or political considerations. One of the challenges of writing objectives for conservation applications is understanding how our values are affected by temporal considerations. In the formulation given in Eq. (1), we evaluate the presence of each species at some point long into the future (T), reflecting our desire to conserve these species for generations to come. The choice of T is not trivial and will possibly interact with the timing of expected system change to affect the optimal strategy; more generally, how we value resources into the future, for example whether and how we discount them, is an important aspect of the objective. We leave aside details as to how such an objective function is evaluated, for example requiring averaging over uncertain future outcomes.

The preceding development is based on the notion of a static objective that we are trying to achieve in the face of climate transition. However, one of the consequences of climate change might be that some past objectives are no longer achievable. For instance, moose (*Alces alces*) hunting in northern Minnesota is a long-standing tradition, but recent trends and forecasts from climate models suggest a substantial increase in temperature and corresponding decrease in suitable moose habitat (Murray et al., 2006). The challenge is to identify appropriate fundamental objectives, perhaps at broader scales than we have been accustomed to in the past. For Minnesota hunters, this may suggest a fundamental objective to provide ungulate but not necessarily moose hunting. Likewise, maintenance of breeding populations of several Neotropical migrants at the southern range termini (e.g., South Carolina) may no longer be feasible. For bird conservation the appropriate objective may be persistence in eastern North America, but not necessarily South Carolina.

3.2.2. Feasible actions

Specific actions that might be anticipated to mitigate climate impacts include the establishment of corridors to allow movement under altered migratory patterns, preservation of both currently preferred habitats and habitats in locations to which expansion and colonization are predicted, management of habitats to promote a diverse array of phenological conditions, control of invasive species and diseases released by climate change, translocation of individuals to suitable habitats, and silviculture to favor tree species that leaf out later (Millar et al., 2007). Our ability to effectively use these or other actions obviously depends on our ability to understand and predict the specific response of bird communities to novel environments. Each of these actions connects in a presumed manner to an anticipated response that will hopefully mitigate the impacts of climate transition, but which has costs and other tradeoffs. We first consider, in more detail, the objectives, and then return to the issue of predicted impacts of our candidate actions.

3.3. Predictive basis for decision making

Our body of theory about avian populations and resource selection, as modified by predictions under climate change and augmented by historical data, allows predictions about the relative efficacy of alternative conservation strategies to mitigate climate impacts and maintain bird communities (e.g., Table 3). In the past, we built such predictions either out of accumulated experience, intuition, or sometimes even quantitative models based on empirical data. The challenge posed by climate change is that predictions based on historical observations and experiences may no longer be appropriate; we must now make predictions about the effects of management actions on natural resources in a changed and changing system. The objectives and feasible actions (what is it we want to achieve and what options do we have for achieving it?), along with a temporal and spatial frame of reference (over what time frame and spatial extent are we considering decisions?), provide the decision context. The predictions (or models that produce them) are the way we identify decisions most capable of fulfilling our objectives. Thus, from a practical standpoint, a focus on the science of climate change divorced of the decision context is only an exercise in academic curiosity; what is needed is an understanding of how climate change will affect our decisions.

3.3.1. Dynamic model of decision impacts

To evaluate alternative decisions with respect to their expected objective value, we need a dynamic model that is capable of predicting where the system is likely to go in response to management and other factors. Such a model needs to include relevant transition parameters and functional relationships, including feedback mechanisms and threshold responses. For example, a general model for state transition of site-specific abundance is

$$N_{i,k(j),t+1} = N_{i,k(j),t} + \Gamma(N_{i,k,t}, a_{k,t}, \delta_{k(j),t}, Z_{k(j),t}) \quad (2)$$

where $N_{i,k(j),t}$ is abundance of species i on site j within region k at time t , $\delta_{k(j),t}$ are local climate drivers at time t , $a_{k(j),t}$ are management actions, and $Z_{k(j),t}$ are stochastic factors; $N_{i,k(j),t}$ represents abundance at site $k(j)$. The function Γ involves survival, reproduction, and movement (including colonization) parameters; these parameters are, in turn, hierarchically specified as functions of $\delta_{k,t}$, $a_{k,t}$ and $Z_{k,t}$, depending on the hypothesis being entertained, as discussed further below (Uncertainty in decision making). For example, given a combination of predictions P2a and P2b (H2; Table 2), per-capita reproduction rates at a specific site are predicted to be a function of local climate drivers (influenced in part by elevation), phenological asynchrony, and random factors, e.g.,

$$b_{i,k(j),t} = \exp(\beta_0 + \beta_1 \delta_{k(j),t} + \beta_2 a_{k(j),t} + Z_{k(j),t}) \quad (3)$$

where $\beta_1 < 0$, $\beta_2 > 0$ represent, respectively, the influence of climate drivers and management (e.g., silviculture) on reproduction rates. The above relationship could be easily modified under alternative hypotheses: e.g., given an interaction between phenology and latitude, influence of climate drivers would be principally at the regional scale. Likewise, we can form a similar dynamic model, but for the reduced state space of local species occupancy as

$$x_{i,k(j),t+1} = x_{i,k(j),t} + \Omega(x_{t,k}, a_{k(t),t}, \delta_{k(j),t}, Z_{k(j),t}) \quad (4)$$

where $x_{i,k(j),t} = I(N_{i,k(j),t})$ and Ω would involve hierarchical modeling of local extinction and colonization probabilities given the hypotheses under consideration.

To implement models such as those above in a predictive, decision making context, we must first select specific functional forms (e.g., Γ or Ω) and values for the parameters representing state transitions (birth, survival coefficients relating these transition parameters to predictors, e.g., β above). Some parameters may be estimable using data from existing monitoring programs. For example, occupancy, local extinction and colonization, and the influence of management and climate factors may be inferred at moderately broad scales (e.g., 100–1000 km²) using data from programs such as the Breeding Bird Survey (Robbins et al., 1986). Other parameters (e.g., site-specific reproduction and survival rates, coefficients representing the influence of site-specific environmental conditions and management) will require more intensive, directed studies or experiments to collect the appropriate data, such as capture-mark-recapture and nest success (Williams et al., 2002).

3.3.2. Incorporating hierarchical relationships

As suggested above, bird responses to climate change likely are manifest at multiple spatial scales, from range wide to individual breeding territory. Hierarchy theory suggests that systems interact across hierarchical scales with broad-scale mechanisms acting as constraints on dynamics at finer scales (Allen and Hoekstra, 1992). For example, a model where local climate drivers, management, and random factors influence reproduction rates (Eq. (3)), but with these effects now constrained by factors at regional scales, is

$$b_{i,k(j),t} = \exp(\beta_0(k) + \beta_1 \delta_{k(j),t} + \beta_2 a_{k(j),t} + Z_{k(j),t}) \quad (5)$$

where

$$\beta_0(k) = \exp(\gamma_0 + \gamma_1 \delta_{k,t} + \gamma_2 a_{kt} + Z_{k,t})$$

Here prediction at the local scale ($b_{i,k(j),t}$) is constrained by average processes at the regional (k) scale ($\beta_0(k)$), in turn parameterized by the coefficients (γ), climate drivers ($\delta_{k,t}$), management actions (a_{kt}), and random effects ($Z_{k,t}$) operating at that scale. The models of state transitions for abundance (Eq. (3)) and occupancy (Eq. (4)) extend naturally to community structure, with the inclusion of parameters that express the potential influence of other species (resource competition) on local abundance, or on local species occupancy.

Hypotheses about the impact of climate change can be included at the appropriate scale(s) of state-space resolution. For instance, under P1 (Table 1) local site colonization and extinction probabilities are predicted to be functions of local (e.g., elevation) climate gradients, possibly mitigated by management

$$\begin{aligned} \gamma_{ik(j),t} &= \text{expit}(\beta'_0 + \beta'_1 \delta_{k(j),t} + \beta'_2 a_{k(j),t} + Z_{k(j),t}) \\ \varepsilon_{ik(j),t} &= \text{expit}(\beta''_0 + \beta''_1 \delta_{k(j),t} + \beta''_2 a_{k(j),t} + Z_{k(j),t}) \end{aligned} \quad (6)$$

with cross-scale, hierarchical relationships formed as earlier for the reproduction model.

Hierarchical views of dynamics and management of bird populations and communities are relevant in times of system

Table 2
Predictions under alternative hypotheses for effect of climate change on southern Appalachian migratory birds.

Scale	Hypothesis	Prediction	Tests/data
S. Appalachian avian community	H1: Climate change will affect avian community structure along elevational and latitudinal gradients	P1a. At southerly latitudes, long-distance migratory species (LDM) will shift to higher elevations in years with warm springs and advanced phenology	Occupancy sampling along replicated elevational gradients in southern Appalachians (Fig. 2a) and BBS data with occupancy models at different latitudes within region
		P1b. LDM species will decrease in abundance and site occupancy at southerly latitudes, and at lowest elevations at more northern latitudes; short-distance migrants/residents (SDMR) will remain constant or increase in abundance	At subsample of occupancy sites, estimation of abundance for selected LDM/SDMR using point sampling and distance estimation; proportion of sites occupied as surrogate for abundance (Fig. 2a and b)
Rangewide		P1c: LDM species will exhibit greater variability in abundance and greater turnover in occupancy at southernmost locations than will SDMR species.	Occupancy sampling and abundance sub-sampling at replicated study sites at northern and southern extremes and mid-range for selected LDM/SDMR (Fig. 2b); proportion of sites occupied as surrogate for abundance (Fig. 2b)
Breeding populations throughout range/elevation gradients	H2: Climate change will influence the synchrony between breeding and insect phenology, with consequences for demography	P2a: Annual reproductive output (ARO) and survival will be greater for birds breeding at elevations where breeding and insect phenology are closely matched	Subsample to monitor reproductive output, survival, and insect abundance along elevation gradients
		P2b: ARO and survival will be greater for birds breeding at latitudes where breeding and insect phenologies are closely matched	Subsample to monitor reproductive output, survival, and insect abundance at northern, southern, and mid-range latitudes
		P2c: Enhanced food and delayed breeding will have a larger influence on ARO and survival for birds breeding at lower elevations	Supplemental feeding and delayed breeding experiments along elevation gradients
		P2d: Enhanced food and delayed breeding will have a larger influence on ARO and survival for birds breeding at southerly latitudes	Supplemental feeding and delayed breeding experiments replicated in southern, northern, and mid-latitude of range
	H3: Climate change will influence parental behavior	P2e. Effects of enhanced food and delayed breeding on ARO and survival will be influenced by elevation and latitude in a non-additive manner, so that southernmost birds at low latitudes will show the greatest effects	Same design as P2d
		P3a: Parental provisioning and nestling quality will be greater for birds breeding at higher elevations	Supplemental feeding and delayed breeding experiments along elevation gradients
		P3b: Parental provisioning and nestling quality will be greater for birds breeding at northerly latitudes, with	Same design as H2, behavioral metrics recorded on subsample
		P3c: Enhanced food and delayed breeding will have a larger influence on parental provisioning and nestling quality for birds breeding at lower elevations	Same design as H2, behavioral metrics recorded on subsample
H4: Climate change will affect settling patterns of breeding adults due to its influence on spring-season climate and leaf emergence phenology	P3d: Enhanced food and delayed breeding will have a larger influence on parental provisioning and nestling quality birds breeding at southerly latitudes	Same design as H2, behavioral metrics recorded on subsample	
	P3e. Parental provisioning and nestling quality will be influenced by latitude and elevation in a non-additive manner (see P2e)	Same design as H2, behavioral metrics recorded on subsample	
	P4a: In years with warm springs and early onset of leaf emergence, first-year breeding adults will be less likely to settle at lower elevations than in years with cooler temperatures and delayed spring phenology	Sub-sampling along elevation gradients to estimate age structure based on plumage and other morphological characteristics	
	P4b: First-year breeding adults will be more likely to settle in the south in years with cool April temperatures and delayed spring phenology	Sub-sampling at replicate sites in northern, mid, and southern portions of range to estimate age structure based on plumage and other morphological characteristics	

stationarity as well as in times of system change. However, we believe that consideration of multiple scales will be especially important in the face of climate change. In particular, we suspect that time–space dynamics of habitat suitability will force us to abandon management of specific populations or communities that focus on single spatial units. Instead, predicted climate change is expected to produce a moving target of suitable habitat that changes along a north–south gradient. Thus, we suspect that wise management approaches will consider both present locations of populations and expected future locations elsewhere in the same region. Such anticipatory management of both habitats and birds

(e.g., via translocations) necessitates a dynamic, hierarchical perspective.

4. Uncertainty in decision making

Most important decisions are made in the face of uncertainty, so this general problem is neither new nor specific to climate change. Indeed, adaptive resource management (e.g., Walters, 1986; Williams et al., 2002, 2007) is an approach to informed decision making that was developed explicitly to deal with various types of uncertainty. Here we first consider the broad classes of

Table 3
Predicted response of avian communities to management actions directed at mitigating the effects of climate change.

Management action	Prediction under H1 (Table 2)			
	P0 ^a	P1a	P1b,c	P1a + P1b,c
No action	0 ^b	–	–	–
Local connectivity	0	+	0	+
Broad-scale connectivity	0	0	+	+
Local + Broad scale	0	+	+	++

^a Null prediction of no effect of climate change on avian community state (alone or in combination with elevation or latitude).

^b Predicted efficacy of management action under hypothesis. 0, no effect; –, deleterious; +, positive.

uncertainty and how they are can be dealt with in decision making in general. We then turn to some specific challenges presented by the climate issues.

4.1. Types of uncertainty

In natural resource management, we have found it useful to classify uncertainty into four categories (e.g., Williams et al., 2002, 2007), and each of these uncertainties is exacerbated by climate change. The first category is environmental variation. Such uncertainty characterizes all natural systems and is well-known to most biologists, requiring little explanation. Some of the predictions about climate change involve changes in the spatial and temporal variation in natural systems; in many cases, an increase in variation is expected, but this expectation varies spatially. In many models used in natural resource management, environmental variation is characterized by distributions of relevant climatic variables that are stationary over time (e.g., precipitation as an important climatic variable for North American mallard ducks, see Nichols et al., 1995; Williams et al., 2002). Climate change is expected to induce non-stationarity of such variables, forcing a different way of dealing with them in models and associated predictions.

The second type of uncertainty is partial observability, which refers to our inability to directly observe nature. Instead we are forced to estimate relevant quantities that characterize natural systems. One price of this estimation is sampling variances and covariances that are associated with parameter estimates and climate change has the potential to increase difficulties in estimating these quantities of interest. For example, range changes are predicted as a response to climate change for many species. At a minimum, such changes will require periodic establishment of new geographic sampling frames.

The third type of uncertainty is partial controllability, which refers to the frequent inability to apply management actions directly and with great precision. An example is the regulation of sport harvest for waterfowl in North America. Management occurs via the establishment of hunting regulations that specify the length of the hunting season and the allowable number of birds that one hunter can shoot in a day. Partial controllability here refers to the imprecision associated with the translation of such hunting regulations into mortality rates associated with hunting. Specifically, a given set of hunting regulations can produce very different harvest rates in different years, depending on such factors as the rate of north–south migration and weather conditions at stopover areas along migration routes.

The fourth type of uncertainty can be termed structural uncertainty and refers to uncertainty in the models that predict system responses to specific management actions. Structural uncertainty is often represented by alternative models of system dynamics, each with associated measures of relative credibility. Such uncertainty is common in natural resource management, and its reduction is a key objective of adaptive management (Walters, 1986;

Williams et al., 2002). Climate change is expected to exacerbate structural uncertainty, possibly moving systems into regions that differ from historical state spaces and dynamics. This possibility of sudden and dramatic change, accompanied by likely non-stationarity, has the potential to add substantial uncertainty to the development of predictive models of system behavior. Thus, while we ordinarily would think of structural uncertainty as reducible (e.g., under adaptive management), climate change may involve an extreme form of structural uncertainty that possibly is irreducible. We return to this issue below when we consider the issue of “learning” under adaptive management.

4.2. Making decisions under uncertainty

Uncertainty is dealt with in decision making firstly by recognizing its existence, secondly by establishing rules whereby an optimal decision can be made in the face of uncertainty, and thirdly, by reducing uncertainty where possible. The first three types of uncertainty listed above often can be described by statistical distributions (e.g., environmental variability summarized by the mean and variance of a normal distribution). These distributions can then be combined with the specified objective function (e.g., Eq. (1)) and predictive model (Eq. (2) and following) to provide a series of distributions for the objective, conditioned on proposed decisions. Thus, if $a = \{a_1, a_2, a_3\}$ is a set of possible alternative actions, $J(x|a)$ now represents the value of the objective given a random outcome for x . To take a simple example, suppose that x follows the discrete distributions below for each candidate action in a , and that $J(x) = I(x \geq 100)x$ so that there is no value accrued in the objective if x falls below 100.

Action	Prob($x < 100$)	Prob($100 \leq x \leq 250$)	Prob($x > 250$)
a_1	0.5	0.25	0.25
a_2	0.25	0.5	0.25
a_3	0.25	0.25	0.5

One (but not the only) approach for dealing with uncertainty is to select the decision that maximizes the expected objective value under our model. In this example these values are easily computed as the weighted average of the objective values over the probability distribution, e.g. $E[J(x|a = a_2)] = 0.25(0) + 0.5(150) + 0.25(250) = 137.5$, and it is easily seen that this leads to $a = a_3$ as the decision that maximizes expected objective value. This approach readily extends to more complex objective functions (e.g., Eq. (1)) and models (Eq. (2) and following). When decisions are dynamic (recurring through time) the mechanics of optimization become more complicated, and approaches such as dynamic programming (Bellman, 1957) are required, but the principle is the same.

4.2.1. Structural uncertainty and adaptive management

The above development effectively assumes that we have a single model of system dynamics (e.g., Eq. (2) or Eq. (5)), thus ignoring the issue of model or structural uncertainty. Obviously that is practically never the case; as previously suggested, the issue of structural uncertainty and alternative hypotheses is central to our casting of the climate issue. Thus for instance, instead of a single model of local abundance as in (2)

$$N_{i,k(j),t+1} = N_{i,k(j),t} + \Gamma(N_{i,k,t}, a_{k,t}, \delta_{k(j),t}, Z_{k(j),t})$$

we essentially have M models

$$N_{i,k(j),t+1} = N_{i,k(j),t} + \Gamma_m(N_{i,k,t}, a_{k,t}, \delta_{k(j),t}, Z_{k(j),t}), \quad m = 1, \dots, M, \quad (10)$$

one for each of our plausible, alternative hypotheses.

One of the critical questions to ask is which uncertainty is important to include in the set of alternative models (Runge et al., 2011). There are many uncertainties that we could

articulate, but not all of them are relevant to the decision at hand. The uncertainty that matters, particularly in an adaptive management context, has two properties: first, there is high expected value of information associated with its resolution; and second, we expect to have high power to resolve it. The first condition is an important one; we need to ask which uncertainty will affect what action we would take. There are many uncertainties that could change our expected performance, but if they do not affect what action we would take, their resolution does not matter to our decision. In the context of climate change, we need to ask what aspects of the alternative futures would lead us to take different management strategies. In our example, the alternative hypotheses likely provide predictions about the responses of key state variables and transitions in relation to latitude, elevation, species migratory behavior, climate drivers, and management.

Because the objective function that we are evaluating depends on the predicted response of our state variable $N_{i,k(j),t+1}$ to our management actions, our predicted performance is also model-specific. Thus, given the objective function from Eq. (1), we can write

$$J_m(\underline{a}) = \sum_i v_i x_{i,T,m} \left(1 - \frac{\sum_k \sum_t c_{k,t} I(a_{k,t})}{c_{\max}} \right) \quad (11)$$

to show that the expected performance depends on the model. Evaluation of any management alternative requires averaging over uncertain future outcomes, so that the expected performance is

$$\bar{J}(\underline{a}) = \sum_{m=1}^M \pi_m J_m(\underline{a})$$

where π_m are the evidentiary weights for each model (m).

An adaptive decision making process can be summarized as follows (Williams et al., 2002):

Establish (or update) the evidentiary weights ($\underline{\pi}$) based on current evidence.

Based on the current observed state (x_t) and the current weights, select the policy (\underline{a}) that maximizes the weighted average objective function.

Predict $\hat{x}_{i,t+1}$ under each alternative model m

Given observations of x_{t+1} calculate likelihoods under each model and update $\underline{\pi}$ via Bayes' Theorem.

The AM process provides a natural way to imbed feedback into decision making, and allows objective driven decision making to proceed under even profound uncertainty about underlying processes.

4.3. How do we monitor and update effectively?

Under the above scheme of adaptive decision processes, monitoring serves four primary roles. First, estimates of state variables (e.g., species-level population size or occupancy) are important for making state-dependent decisions. Second, estimates of state and other goal-related variables are needed to assess the degree to which objectives are being met. Third, estimates of state variables and possibly selected model parameters are used to update evidentiary weights. Fourth, estimates of rate and other model parameters are used in initial model construction and in possible model modification in the double-loop stage of adaptive decision making.

Several aspects of the above development on structural uncertainty are relevant to the issue of monitoring and updating in the context of climate change. First, as previously noted, hierarchical relationships exist among potential state variables, both with respect to spatial resolution and to the resolution at which the sys-

tem state is quantified, and also functionally, in that factors that determine state transition at one scale can influence, or are constrained by, factors that influence other scales. For example, local extinction and colonization are obviously related to (and in a sense the aggregation of) the population-level processes of survival, reproduction, and movement. This is relevant because whereas we might be interested in all of these processes, they cannot all be monitored everywhere. Instead, models can be built in which explicit linkages are made between parameters across spatial or state resolution scales, so that predictive inferences based on local occupancy share functional relationships with those based on abundance modeling. Then, data that are acquired according to hierarchical sampling designs can be effectively integrated into models to allow parameter updating. Again, some monitoring schemes (e.g., BBS) exist that, while not designed with these specific questions in mind, nevertheless may provide useful data for parameterizing and updating predictive models under adaptive management. Clearly, data specifically directed at evaluating hypotheses important to management are best acquired by following sampling and experimental designs with these hypotheses in mind. However, resources are finite, and it is impossible to quantify system states and transitions everywhere to arbitrary resolutions. Therefore, strategic decisions must be made about how to allocate resources in space and time to best accomplish the objective of informed decision making, exploiting hierarchical relationships among the data. Also, appropriate designs and statistical models need to allow valid inference from monitoring data to inform conclusions about the system and its transitions. In particular, appropriate data must be gathered and statistical models used to avoid unnecessary and unsupportable assumptions about perfect or homogenous detection. Finally, although not necessary for adaptive learning, spatial and temporal controls in a quasi-experimental design may increase the rate at which learning occurs, if the design is directed at the testing of predictions under alternative hypotheses versus simply assessing differences relative to arbitrary baselines.

These principles guided our thinking for a proposed scheme for adaptive monitoring of migratory birds in the southern Appalachians that addresses the issue of climate impacts (Fig. 1). We propose a system of broad scale monitoring that occurs along latitudinal gradients. Imbedded in this design we propose replicate study sites that are situated in northern, mid, and southern portions of the southern Appalachian mountain range, with sampling along elevation gradients within the study sites. In addition, study designs could incorporate management factors via spatial controls, in which study sites are selected at locations where management actions are, and are not, being taken. At the study sites, we suggest focused demographic, behavioral, and experimental work to estimate key demographic parameters and functional relationships, and to test alternative hypotheses. We also see a role for manipulative experiments in this monitoring scheme, as long as these are directed at testing predictions of specific, management-driven hypotheses (Table 2). Thus, for instance, prediction P2a can be tested via a controlled, supplemental feeding experiment, and interactions with elevation and latitude by supplemental feeding combined with spatial controls for these factors.

4.4. Unique challenges from climate transition

There are several features of climate change, however, that provide substantial challenges to our decision making. First, we are uncertain about the specific changes that will occur to the climate, particularly at local scales, and we are uncertain about how these changes will affect wildlife populations, and the optimal actions we should take to manage them. But when we recognize that this uncertainty is about the predictions from the models we use in a

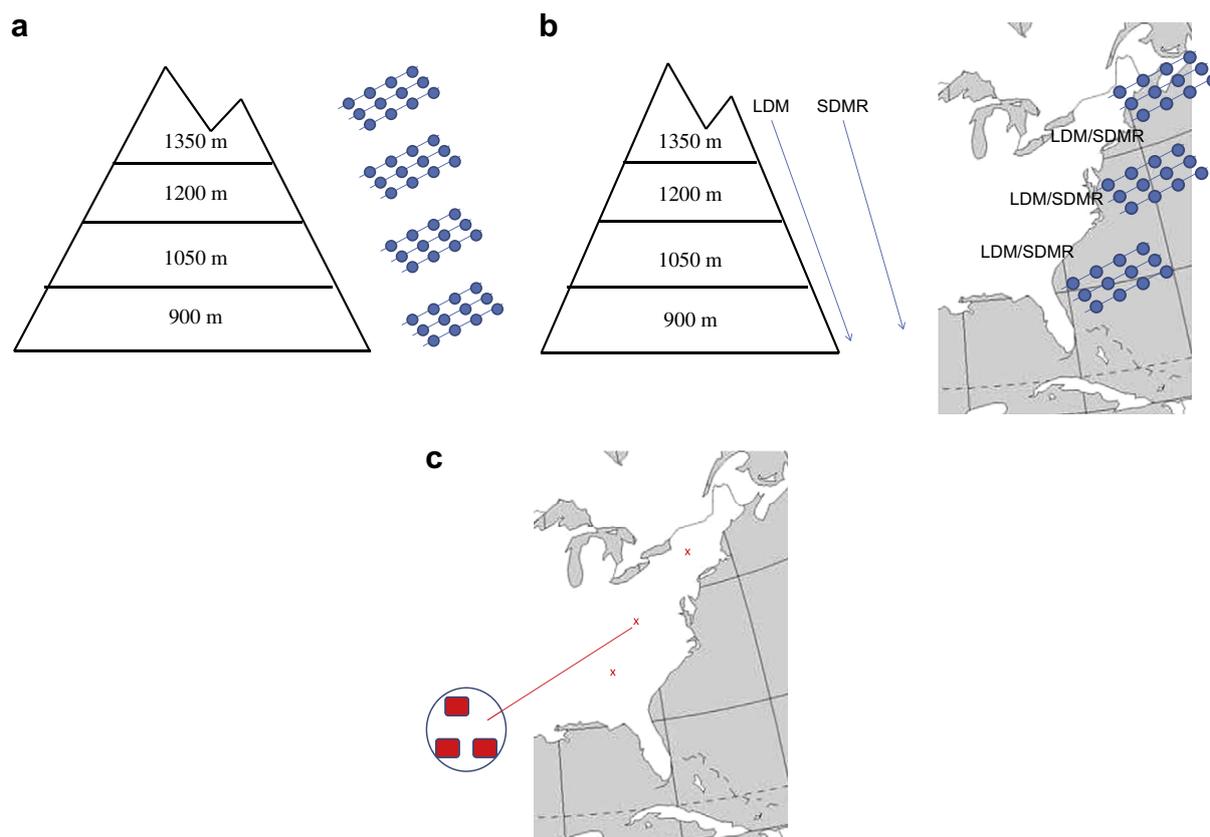


Fig. 1. Sampling designs for investigation of specific hypotheses about impacts of climate change on migratory birds. (4a) Occupancy sampling along elevation gradients in southern Appalachians with temporal controls. (4b) Sub-sampling to estimate abundance for selected pairs of long-distance migrants – short-distance migrants/residents. (4c) Replicated study sites at northern and southern terminus and mid-range.

decision context, we realize we have the tools to grapple with it: articulating alternative hypotheses and making decisions in the face of uncertainty (see above). Second, although some aspects of climate change are currently observable (e.g., decadal trends in average temperature), many predicted impacts of climate change involve future system change, for which we have limited empirical basis for alternative models. Thus, in addition to more familiar approaches to model development, decisions makers may need to incorporate expert judgment, scenario planning, futures thinking, horizon planning and other new tools (Inayatullah, 2008).

4.4.1. Novel conditions

As noted above, one of the particular challenges of climate change is that we need to make predictions for system conditions we have never observed, so we may not be able to rely on empirical estimates for parameters in our models. In some cases, we can make inference based on empirical data, but in other (perhaps many) cases, in lieu of empirical support for specific parameter values, decision makers may need to rely on deductive reasoning and expert judgment to develop reasonable models of change (Martin et al., 2005). We do, of course, anticipate that we will be able to monitor these systems as they change, so we expect to adaptively update our models through time if we implement appropriate monitoring. Thus, the model structures and parameter estimates that come from deduction and expert judgment should be viewed (as to a Bayesian) as “savvy priors” that, while not necessarily providing accurate predictions, at least capture basic belief in the likely magnitude and direction of functional responses. Indeed, we favor dynamic models whose parameter structure and functional forms are strongly motivated by theory, rather than purely

empirically derived, as most likely to be robust when data are weak or underlying system dynamics are evolving. This preference is closely related to the preference for mechanistic models over phenomenological models in cases where systems are expected to move outside the range of historical values (Williams et al., 2002).

4.4.2. Non-stationarity and extreme structural uncertainty

Although the adaptive optimization and monitoring procedures described above are straightforward in principle, they are greatly complicated by two unavoidable aspects of the climate problem. First, under scenarios in which climate transition continues or accelerates, several plausible models (above) would predict non-stationary dynamics in our bird systems. For instance, if regional climate drivers are forcing reproductive output downward (or upward for some other species), or if climate change influences the functions (e.g., Γ and Ω) that define state transitions, then stationary policies to optimize long-term objectives (such as species persistence) are not expected to exist. We need to be fairly specific here: a fundamental change in state dynamics (such as a phase shift) is indeed a system change, but it might result in a new stationary condition. In such a case, if we can predict the phase shift, the decision problem is how to manage through it. On the other hand, climate change might result in a long period of non-stationarity, in which the environment continues to change, whether monotonic or not, creating difficulties in determining management strategies that fulfill long-term objectives. The other issue, alluded to earlier, is that of extreme and potentially irreducible structural uncertainty, where it is unknown which of several divergent functional responses will occur. For instance, suppose that under one

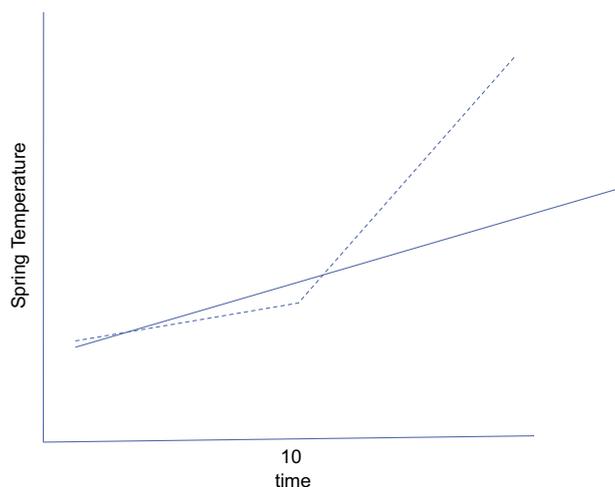


Fig. 2. Extreme structural uncertainty under possible threshold relationships for the impacts of climate change.

plausible model, an important climate driver (e.g., mean spring-time temperatures) increases in a linear fashion for the next 50 yr, whereas under an alternative model the driver passes a “tipping point” in 10 yr (Fig. 2), after which change is much more rapid (steeper slope). Suppose further that the driver is related to bird demography according to the loglinear model specified in (3). Finally, suppose that there is essentially equal *a priori* support for these alternative models. Under some circumstances, we could expect predictions under alternative models to perhaps agree closely in the short term, but diverge markedly after 10 yr. In this case adaptive learning would not occur rapidly until after the tipping point. In some cases, this learning may essentially be too late to do anything in terms of decision making feedback: by the time adaptive feedback occurs, the system will have moved to a state that may not be reversible. The other possibility is that the learning does permit management actions that lead to desired results. At a minimum, the recognition of structural uncertainty lends non-negligible evidentiary weight to the tipping point model, and thus leads to more robust decisions than would sole reliance on the model reflecting linear change.

We have no good answers for either of these issues, but offer some thoughts about how to proceed. Specifically, the issues of non-stationarity and extreme structural uncertainty suggest at least three possible approaches. The first approach seems reasonable in the case where the nature of change in the important climate variables can be anticipated and modeled. This approach involves incorporation of important climatic variables as state variables in system models. System models would now deal not only with biological state variables of specific management interest, but also with climate variables that influence the state variables of primary interest and that are expected to exhibit change. Policies resulting from dynamic optimization approaches would be expected to yield time-specific, rather than stationary, solutions, but such time-specificity will be appropriate for systems exhibiting non-stationary dynamics.

An alternative is to recognize that, while we still seek long-term objectives, long-term outcomes may be difficult or impossible to predict in the face of extreme uncertainty. Instead a reasonable, pragmatic approach may be to implement policies that are optimal over short-term time horizons, perhaps 5- to 10-years, but that also place appropriate value on the terminal value of the system state variable, as the terminal value that is actually attained will become the starting point for future management. This approach

will essentially assume system stationarity as an approximation to reality over each of a series of short time horizons, with the expectation of changing system models based on monitoring data, at the end of each series. The approach exploits double-loop learning, with frequent revisiting of system models, as a pragmatic approach to dealing with unanticipated climate change. This places a premium on learning about system change at the end of each series of short-term time horizons, and emphasize short-term, “probing” actions throughout each short-term time series, as a means of rapidly discovering the current nature of state dynamics. For example, within an optimization framework, probing could be emphasized by including in the objective function a focus on certain characteristics of the terminal value of the information state (e.g., focusing on high diversity of the evidentiary weights). Slower adaptive management approaches, whether passive or active (Williams et al., 2002) may indeed be too slow, and too inflexible.

5. Summary and conclusions

There is no question that climate change poses substantial challenges to those charged with the management of natural resources. However, management decisions must be made in spite of these challenges and difficulties, and cannot await resolution of uncertainties, no matter how great they may be. A focus on decision making in the face of uncertainty, rather than on discovery, appears to us to hold the best promise for simultaneously responding to and learning about the looming impacts of climate change on natural systems. Key elements of this approach include (1) prediction under multiple, plausible hypotheses about climate impacts, (2) decision making to achieve long-term objectives, (3) monitoring and experimentation (possibly via a series of short-term probing actions) to evaluate the response of the system to climate drivers and management actions and to confront testable predictions with data, and (4) repeated feedback of information (e.g., through use of updated evidentiary weights) to inform decision making. Although we focused on terrestrial birds in North America, we believe this approach is generic and should be applicable to other systems worldwide.

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