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PERSPECTIVES IN ORNITHOLOGY

CLIMATE MODELS AND ORNITHOLOGY

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During the past century (1906–2005), mean global temperature has risen ~0.74°C (Intergovernmental Panel on Climate Change [IPCC] 2007). Ecologists suspect that this temperature change has influenced the phenology and distribution of many organisms (Walther et al. 2002, Root et al. 2003, Parmesan 2007), yet the magnitude of these ecological changes may be relatively minor compared with those in future years. Climatologists predict that global temperatures will increase by as much as 1.1–6.4°C during the next century (Duffy et al. 2006, IPCC 2007). In addition, changes in the amount and timing of precipitation, the frequency of extreme weather events, and sea level are expected (Hayhoe et al. 2004, IPCC 2007). All of these changes are likely to affect ecological processes and the distribution, abundance, and persistence of many organisms (Hannah et al. 2002, McLaughlin et al. 2002, Root and Schneider 2006). As a result, ornithologists are increasingly concerned with understanding the response of bird populations to climate change (Sanz 2002, Winkler et al. 2002, Crick 2004, Both et al. 2006, Rodenhouse et al. 2008). To meet the challenges of understanding and communicating the effects that climate change will have on bird populations, it is imperative that ornithologists begin to develop and maintain a working knowledge of climate models, emissions scenarios, and the capabilities and limitations of climate projections.

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Various authors have reviewed the effects of climate change on birds (Crick 2004, Chambers et al. 2005, Wormworth and Mallon 2006) and discussed methods of incorporating climate change into demographic modeling (Sæther et al. 2004, Ådahl et al. 2006). Here, we provide an introduction to climate models and demonstrate how collaborations with climatologists can contribute to ornithology. To provide a context for the use of climate models in ornithology, we begin by briefly describing three general approaches used to understand how climate change has already influenced, or will

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influence, bird populations. We then review basic information on climate models, emissions scenarios, and issues associated with linking large-scale climate projections to the local scale at which many ornithological studies are conducted. To illustrate how climate models and weather-related avian research can be integrated, we have combined climate model projections for central coastal California with published data from that region on reproductive success of Song Sparrows (*Melospiza melodia*). We conclude by discussing approaches and recommendations for integrating climate models with avian ecology.

Approaches to Understanding Effects of Climate Change on Bird Populations

Ecologists have generally taken one of three approaches to understanding the ecological effects of climate change. The first is to document changes in phenology or distribution that are consistent with long-term changes in climatic conditions (Parmesan and Yohe 2003, Root et al. 2003, Parmesan 2007). The hypothesis that avian phenology and distribution are being influenced by climate change is supported by shifts in migration timing (Butler 2003, Murphy-Klassen et al. 2005, MacMynowski et al. 2007) and initiation of breeding (Crick and Sparks 1999, Dunn and Winkler 1999) and changes in elevational (Pounds et al. 1999, Peh 2007) and latitudinal distributions (Thomas and Lennon 1999, Hitch and Leberg 2007, La Sorte and Thompson 2007). However, the extent to which these changes can be attributed solely to climate change may be complicated by changes in land use or avian population size that have occurred over the same period (Tryjanowski and Sparks 2001).

A second approach uses distribution modeling to predict how future climatic conditions may affect distributions of animals and plants (Guisan and Zimmermann 2000, Beaumont et al. 2007). With this approach, ecologists have used historical distribution data to predict the occurrence of a species as a function of climatic, land-use, or habitat variables and then evaluated changes in distribution predicted under future climate scenarios (Peterson et al. 2002, Kueppers et al. 2005, Jetz et al. 2007). Application of these models to bird communities has suggested that climate change may have profound effects, such as the loss of ≤20% of manakin (Pipridae) species in South America (Anciães and Peterson 2006), a decrease in the species richness and geographic range of birds in Europe and Africa (Huntley et al. 2006), and large changes in bird community composition in northeastern North America (Rodenhouse et al. 2008). However, the accuracy of these models rests on a number of simplifying assumptions, most notably omitting the effects of species interactions on patterns of distribution while assuming that future climate–distribution relationships will be the same as those observed today (Davis et al. 1998, Guisan and Thuiller 2005, Heikkinen et al. 2006, Ibanez et al. 2006). In addition, because these models are generally used to describe species distributions at a relatively coarse spatial scale, they may be of limited use for understanding changes at the finer spatial scale at which many management decisions are made.

A third approach is based on understanding the underlying demographic mechanisms through which climate change influences population dynamics (Root and Schneider 1993, Sæther et al. 2004, Ibanez et al. 2006). Ornithology has an established history of describing weather-related effects on avian demography. Although "weather" and "climate" are sometimes used interchangeably, here we use "weather" to refer to the state of the Earth's atmosphere at a given point in time (e.g., day, month, or year) and "climate" to refer to long-term (>30 years) characteristics of weather. Ornithologists interested in weather-related research have typically described relationships between variation in local weather (e.g., annual rainfall, winter temperatures) or large-scale indices (e.g., El Niño–Southern Oscillation [ENSO]) and variation in demographic parameters such as fecundity (Sillett et al. 2000, Chase et al. 2005, Lehikoinen et al. 2006), survival (Peach et al. 1991, Robinson et al. 2007), and breeding phenology (Frederiksen et al. 2004). Evaluating how, when, or whether these relationships will be important for understanding climate change requires that the results of such studies be interpreted in the context of climate projections. This approach has already been applied to birds in investigating the demographic consequences of climate change for Pied Flycatchers (*Ficedula hypoleuca*; Sanz 2003, Both et al. 2006) and European Dippers (*Cinclus cinclus*; Sæther and Bakke 2000).

The latter two approaches rely on projections of future climatic conditions. In the following section, we provide an introduction to climate models that we hope will serve as a utilitarian introduction for ornithologists interested in learning more about climate models and applying them to their research.

Emissions Scenarios and Global Circulation Models

Climate forcings are natural and anthropogenic factors that influence the Earth's climate (IPCC 2007). Important anthropogenic forcings include "greenhouse" gases and patterns of land use (Stott et al. 2000). To project future climate, climate modelers use emissions scenarios that describe how forcings will change over time. The IPCC has generated 40 emissions scenarios that are grouped into families representing common themes. Nakićenović and Stewart (2000) presented four families of scenarios (identified as A1, A2, B1, and B2) used to describe future patterns of human population growth, energy-technology development, and land-use patterns. The A scenarios are based on a future in which energy technology and population size change, but with little effort to reduce greenhouse-gas emissions. The A1 scenario describes rapid economic growth, relatively low population growth, and economic convergence among the regions of the world. By contrast, the A2 scenario describes rapid population growth and unequally distributed resources. The B scenarios describe a future in which economic, social, and environmental sustainability are emphasized. The B1 scenario describes global efforts to achieve sustainability and reduce emissions, whereas the B2 scenario depicts local developments in technology and regulation that promote sustainability. The A1 and B1 scenarios have been used to bracket the most (A1) and least (B1) extreme increases in anthropogenic climate-forcing (Hayhoe et al. 2004). As a tool for decision making, emissions scenarios are important for understanding how particular emissions policies may influence the future climate. Mismatches between emissions scenarios and future conditions are a source of uncertainty for this forecasting tool—already, CO_2 concentrations are above the levels projected in the most extreme scenario (A1) developed in the late 1990s (Raupach et al. 2007).

Emissions scenarios are used as inputs for global circulation models (GCM), which are at the core of most climate projections (IPCC 2007). Atmospheric global circulation models (AGCM) describe the dynamics of air pressure, velocity, temperature, and water vapor. Oceanic global circulation models (OGCM) provide a complementary description of sea surface temperatures, ocean currents, and sea ice. Because atmospheric processes and ocean conditions are interdependent, many climate models (e.g., the HadCM3 model and GFDL CM2.X model) are coupled atmospheric and oceanic global circulation models (AOGCM).

Understanding the sources of uncertainty in climate-model projections remains an area of rapid development (Déqué et al. 2007). In addition to uncertainty about which emissions scenario will best describe future conditions, climate projections are uncertain because different GCMs generate different projections (model uncertainty) and because estimates of projected climate change are based on a finite sample of observations (sampling uncertainty) (Déqué et al. 2007). By summarizing the results of multiple models or multiple runs of the same model, forecasters can incorporate model and sampling uncertainty into model projections (Crossley et al. 2000, Giorgi and Francisco 2000). Thus, climate model projections may represent the results of a single model, scenario, or run, or the aggregated results from multiple models, runs, and scenarios that are referred to as "ensembles."

Statistical Downscaling and Regional Climate Models

Application of the results of AOGCMs to many ecological questions may be limited by their relatively coarse spatial resolution: AOGCM grid cells often span hundreds of kilometers. At this scale, a single grid cell for central California could extend from the coast to the foothills of the Sierra Nevada Mountains. Because this area is climatically diverse, it is unlikely that a climate projection at such a coarse spatial scale will be meaningful for understanding the local ecological effects of climate change. There are two tools available for expressing AOGCM results at a finer spatial scale: statistical downscaling and regional climate models.

Statistical downscaling involves the use of a statistical model to predict local climate on the basis of interactions between large-scale climate and local physiography (e.g., topography, water bodies, and land use; von Storch et al. 1993). A statistical model is developed by using AOGCM simulations of current climate and local physiography to predict climate measurements collected at a finer spatial resolution (e.g., those generated from local weather stations). These statistical relationships can then be used to downscale AOGCM projections of future climate to local predictions at finer spatial resolutions. Statistical downscaling is relatively simple, does not require extensive computing power, and performs quite well in many cases (Kidson and Thompson 1998, Hayhoe et al. 2007). However, the underlying assumption is that statistical relationships between large-scale and local climate today will persist in the future. This assumption may not be valid if changes in local climate-forcings occur (Root and Schneider 2006).

Regional climate modeling (RCM; also referred to as "dynamical downscaling") is an alternative to statistical downscaling. Like GCMs, RCMs are mathematical descriptions of the physical processes that drive climatic conditions (Giorgi and Mearns 1991). Regional climate models are nested within larger AOGCMs that provide the information for the boundary conditions of the former; the RCMs, in turn, produce climate information on a grid size that can be as small as 5 km (Giorgi 2006, Liang et al. 2006). An advantage of RCMs is that they may be better able to predict future climatic conditions than statistical downscaling when the historical relationship between large-scale and local-scale climate is disrupted by the dynamics of local-scale climate-forcing (Vrac et al. 2007). A disadvantage is that, because of their complexity, RCMs require a substantial investment of computing power and time. Regional climate models and statistical downscaling both continue to be widely used, and the relative performance of each remains an area of active research (Murphy 1999, Busuioc et al. 2006, Fowler et al. 2007).

An Example of the Process

To illustrate how climate model projections can be integrated with weather-related studies of avian demography, we will use results from a long-term avian demography study in central coastal California as an example. Since 1966, PRBO Conservation Science has collected avian demographic data at the Palomarin Field Station in Point Reyes National Seashore north of San Francisco, California (Fig. 1). At Palomarin, the seasonal fecundity (total number of fledglings produced per female per year) of Song Sparrows was positively correlated with total bioyear (July to June) precipitation (Chase et al. 2005). This relationship provides the basis for evaluating the potential effects of climate change on the reproductive success of Song Sparrows.

We obtained current and future climate data for Palomarin from the Worldclim database (see Acknowledgments). This database includes information on current global climate based on data collected from 1950 to 2000 and interpolated to a resolution grid of 2.5 arc min (~5-km^2 grid cells at the equator, and smaller cells elsewhere) using information on latitude, longitude, and elevation (Hijmans et al. 2005). Also available at this site are climate projections for the year 2100, generated using the National Center for Atmospheric Research's Community Climate Model (NCAR CCM3), a GCM model, and prescribed sea-surface temperatures simulated independently with a second model (Govindasamy et al. 2003). The projection is based on an emissions scenario that specified a doubling of CO_2 and concurrent increases in other greenhouse gases by 2100. This relatively simple scenario, sometimes referred to as a "business as usual" (BAU) scenario, was commonly used before the current IPCC scenarios were developed (Dai et al. 2001a). This BAU scenario is roughly equivalent to the average of the current IPCC scenario families (Dai et al. 2001b). The model was run on a resolution grid of 2.8 arc degrees (~75-km^2 grid cells at the equator, and smaller cells elsewhere), and the results were statistically downscaled to a 2.5-min resolution grid that matches the resolution for the historical climate. As noted by the authors (Govindasamy et al. 2003), this climate projection model is relatively simple, in that it is based on only a single GCM and uses prescribed, rather than dynamically coupled, sea surface temperatures.

One of the challenges of integrating climate models with local avian demography is meshing spatial and temporal metrics from

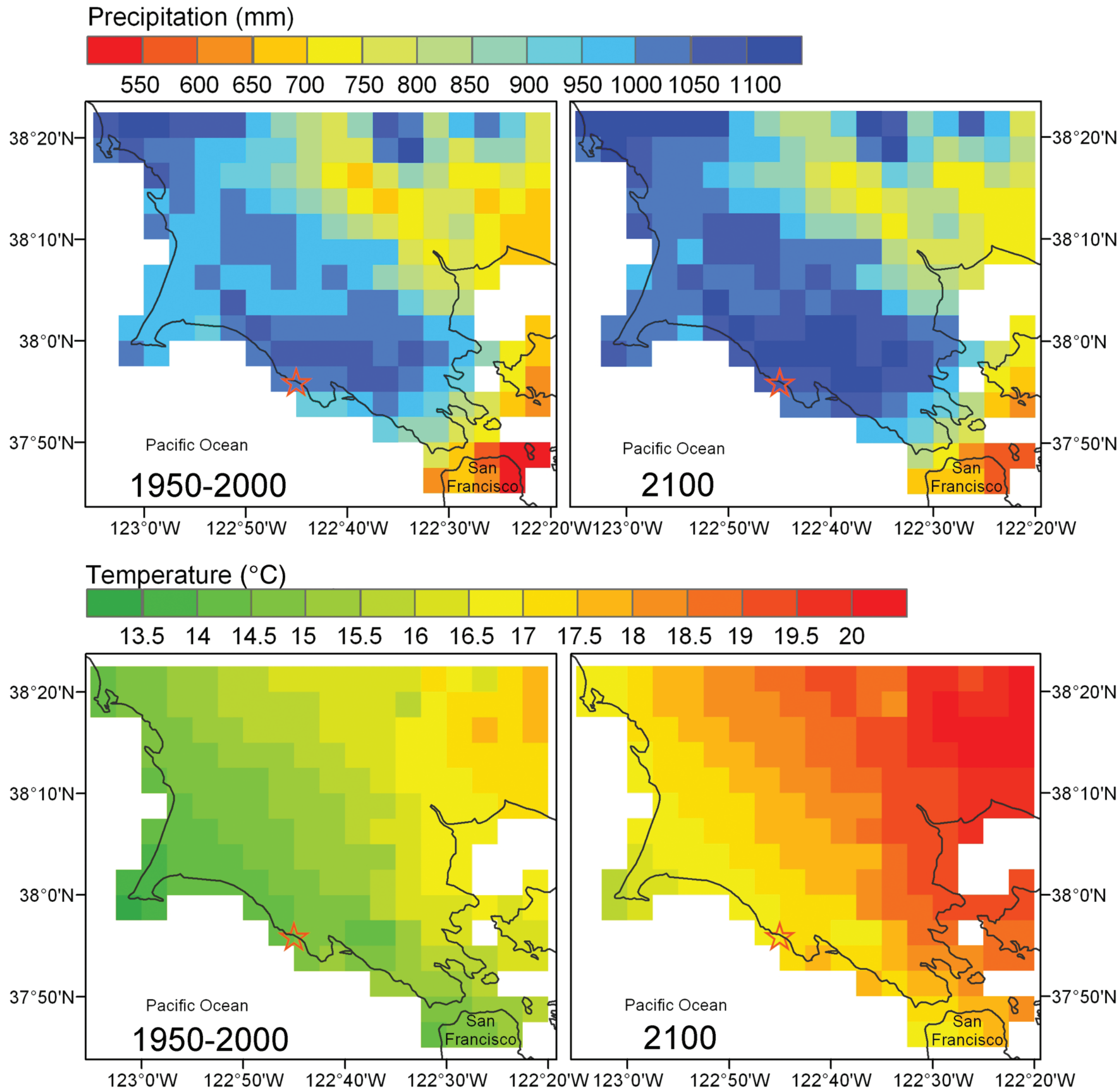

Fig. 1. Climate maps for Marin County, central coastal California, with historical (1950–2000) average annual precipitation and May–June temperatures and projected conditions (CCM3 model, 2× CO_2 concentrations) for the year 2100.

climate models with the metrics that describe local weather. We used the Worldclim data on historical and projected climate to calculate bioyear precipitation and mean May–June temperature. To calculate total bioyear precipitation, we summed the monthly precipitation values for the same 12-month period. To calculate mean May–June temperature, we averaged monthly temperature for May and June. To verify that climate metrics were comparable to corresponding weather metrics measured at Palomarin, we compared the 1950–2000 climate to the annual values recorded at Palomarin between 1980 and 2000. The long-term average of these metrics was generally located within the center of variation of the annual measurements collected at Palomarin (Fig. 2). On the basis of Worldclim data, annual precipitation for the Palomarin Field Station area is expected to increase from a current long-term average of 1,029 mm year^{-1} to 1,091 mm year^{-1} in 2100 (Fig. 1). Using these values in the regression equation presented by Chase et al. (2005; their fig. 3), the long-term average of seasonal fecundity for female Song Sparrows would increase from ~2.55 to ~2.63 young (4% increase; Fig. 2).

This example illustrates another use of climate models: to identify situations in which historical weather may provide limited information about novel combinations of future climatic conditions (Williams and Jackson 2007, Williams et al. 2007). Plotting annual variation in rainfall and average May–June temperatures at Palomarin, as calculated by Chase et al. (2005), suggests that these two variables are correlated: years are generally dry and warm or wet and cool (Fig. 2). On the basis of Worldclim data, the average May–June temperature in 2100 at Palomarin is expected to be substantially warmer (by 2.5°C), whereas annual precipitation is expected to be only slightly higher (62-mm increase), compared

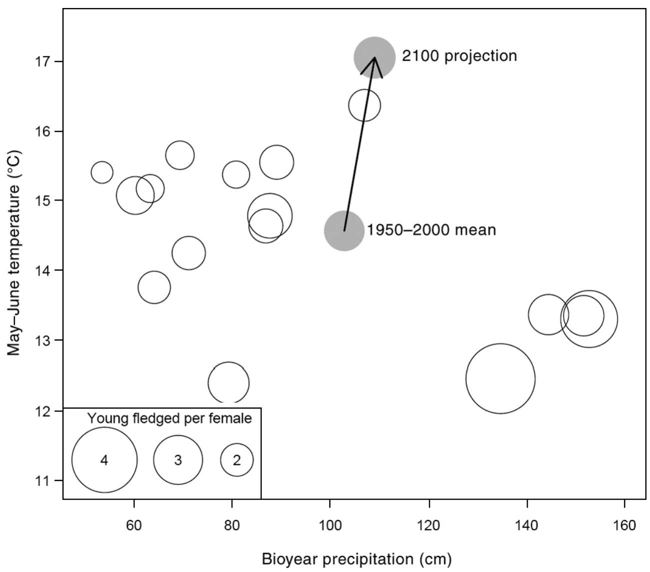

Fig. 2. Data from Chase et al. (2005) on summer temperature, bioyear precipitation, and seasonal fecundity (young fledged per female) of Song Sparrows at Palomarin Field Station in central coastal California between 1980 and 2000. The arrow originates at the mean summer temperature and bioyear precipitation values for the period from 1950 to 2000 and terminates at the values that correspond to the projected climate in 2100 based on data available in the Worldclim database (see text for details). The shaded circles represent the predicted seasonal fecundity for the current and future climate based on the regression line presented by Chase et al. (2005).

with current conditions (Fig. 1). Such a change would shift climatic conditions outside the range of historical variation (Fig. 2), such that future weather will present combinations of temperature and precipitation that were rarely or never observed during this field study (Fig. 2). As a result, the observed relationship between precipitation and seasonal fecundity may not hold under warmer conditions.

Other Approaches to Integrating Climate Models and Weather-related Research

In the preceding example, we focused on the effects of climate change on one aspect of Song Sparrow demography for which climate projections were readily available. However, there are several alternative approaches for integrating climate models and weather-related avian research. Here, we briefly discuss some other ways to integrate climate projections with avian ecology.

Other demographic processes and population modeling.—In addition to fecundity, climate change may affect other vital rates. For example, survival rates can be associated with weather variables, including temperature (Arcese et al. 1992) and precipitation (Dugger et al. 2000, Sillett et al. 2000). Because the effects of climate on survival and immigration may counteract or compound any effects of climate on productivity, the relative importance of these vital rates in affecting the population's growth rate should be considered (Ådahl et al. 2006). Ultimately, the demographic consequences of climate change will need to be synthesized in the context of population growth rates rather than the effects on a single vital rate (Sæther et al. 2004, Ådahl et al. 2006).

Indirect effects.—In many cases, the effects of climate change may be mediated indirectly through changes in vegetation, food availability, or effects on competitors and predators. For example, shifts in precipitation and temperature may have large effects on vegetation structure and composition (Lenihan et al. 2003). Because vegetation structure and composition are important determinants of bird distribution and abundance (James and Wamer 1982, Rotenberry 1985, Lee and Rotenberry 2005), climate change may have indirect effects on birds through climatically driven changes in vegetation. Similarly, there is increasing evidence that climate change may influence the phenology and abundance of many invertebrates that act as important food resources for many birds (Both et al. 2006). The time-scale at which these indirect effects may be important is likely highly variable; invertebrate populations may respond to changing climate in a matter of years, whereas vegetation structure and composition may change over decades or even centuries.

Seasonal timing.—Because some climate model projections can provide quarterly and monthly values for temperature and precipitation, they can be used to investigate the importance of the seasonal timing of these variables. In our example, we considered only changes in total annual precipitation, neglecting the possibility that changes in the monthly distribution of rainfall may also be important. Both Chase et al. (2005) and DeSante and Geupel (1987) presented evidence that in years with increased May rainfall, avian reproduction at Palomarin is depressed. These observations suggest that effects of climate change on the seasonal timing of precipitation may have important consequences for bird populations.

Other climate variables.—Climate models can provide a wide range of output variables that may be applicable to a wide range of ecological systems. For example, climate models that describe sea surface temperatures (Manabe et al. 1991) could be applied to relationships between sea surface temperatures and seabird reproduction and survival (Jenouvrier et al. 2003, Lee et al. 2007). Similarly, surface wind output from a regional climate model has been used to estimate changes in upwelling along the coast of western North America and to make projections of the effect of climate change on breeding success of Cassin's Auklets (*Ptychoramphus aleuticus*) along the coast of California (Snyder et al. 2003, Wolf 2007). Because wind patterns are also an important component of migration strategies (Butler et al. 1997, Liechti and Bruderer 1998, Sinelschikova et al. 2007), these models could also be applied to the consequences of climate change for bird migration. Climate models can also be used to make projections about hydrological consequences of climate change (Fowler et al. 2007), which may be important for many riparian-associated species (Moreno-Rueda and Rivas 2007).

Extreme weather events.—Changes in the frequency and intensity of extreme weather events are recognized as an important component of climate change (Parmesan et al. 2000, Jentsch et al. 2007). Events such as late-winter snow storms, floods, droughts, and heavy rains may have important demographic consequences for some birds (Martin and Wiebe 2004, Altwegg et al. 2006). For example, >90% of the Song Sparrow population on Mandarte

Island died following an unusually cold period in February 1989 (Arcese et al. 1992). Climate models that predict the magnitude and frequency of extreme events continue to be developed (Easterling et al. 2000, Bell et al. 2004), and integrating them with stochastic models of population growth will be an important component of understanding the response of bird populations to climate change (Lusk et al. 2001, Sæther et al. 2004).

Large-scale climate fluctuations.—Climate models can also be used to describe the frequency and intensity of large-scale climate fluctuations, such as ENSO and the North Atlantic Oscillation (Christoph et al. 2000, Lin 2007). For numerous bird species, demography (Sillett et al. 2000, Lehikoinen et al. 2006, Sedinger et al. 2006, Lee et al. 2007) and phenology (Forchhammer et al. 2002, MacMynowski et al. 2007) are associated with variation in these indices. Current models suggest that increased greenhouse-gas concentrations will increase the frequency and intensity of ENSO events (Timmermann et al. 1999). For Galapagos Penguins (*Spheniscus mendiculus*), population modeling revealed that relatively small increases in the frequency of ENSO events increased the probability of extinction to 80%, more than double the probability calculated for the current ENSO regime (Vargas et al. 2007).

The Importance of Collaborating with Climate Modelers

Understanding the effects of climate change on bird populations will require multiple lines of research. Root and Schneider (1995) emphasized the importance of combining large-scale, distribution-oriented research with small-scale, process-oriented research. They termed this research approach "strategic cyclical scaling" (SCS), because it emphasizes continuous cycling between large- and small-scale studies. Within the context of SCS, analyses of migratory and reproductive phenology, distribution modeling, and the influence of climate variability on demographic processes will all remain important components of understanding how climate change will affect bird populations. Collaborations with climate modelers will play an important role in the success of ornithologists in conducting these analyses.

Online sources of climate projections, such as Worldclim, may provide an initial guide to the magnitude of expected climate change. As we were preparing this manuscript, a much more extensive set of down-scaled climate projections from the World Climate Research Programme (WCRP) was made available online (see Acknowledgments). However, because the validity of down-scaled climate data remains uncertain and the techniques are rapidly evolving, these data should be interpreted with caution and with input from experts in the field (Daly 2006). Every year brings important developments in both the complexity of climate models and the computing power available for implementing them. Fifteen years ago, models with a global grid so large that the Sierra Nevada and Rocky Mountains were contained in a single cell took up to 10 h of computation time on a Cray supercomputer, and models on a 50×50 km grid would take up to a year of computation time (Root and Schneider 1993). Today, a regional climate model with a 50×50 km grid for the continental United States can now simulate 20 years of climate data within a week. As models and technology continue to improve, they will become an even more important resource for ornithologists.

The uncertainty regarding future conditions remains the fundamental challenge in forecasting the effects that climate change will have on bird populations. Not only is the magnitude of projected climate change uncertain (Snyder and Sloan 2005), but so is the extent to which ecological processes may respond unpredictably to novel climatic conditions (Schneider and Root 1996, Suttle et al. 2007, Williams and Jackson 2007). Given these uncertainties, it is unlikely that models will ever provide highly accurate forecasts of future conditions. However, despite their many limitations, models are one of the few tools available for understanding how and why climatic conditions and bird populations may change over the next century. As such, their utility may not be defined by how accurately they forecast the future, but by how useful they are in understanding the mechanisms by which climate influences bird populations (Box and Draper 1987).

Conclusion

Understanding, mitigating for, and adapting to the effects of climate change on bird populations presents a unique and important set of challenges for ornithologists and conservation biologists. Model uncertainties, climatic conditions that fall outside the historical range of variability, shifting vegetation communities, and novel bird communities all pose extreme challenges to predicting how bird populations, and ecological systems in general, will respond to climate change (Schneider and Root 1996, Berteaux et al. 2006, Krebs and Berteaux 2006). Climate models will play an important role in this process. Ornithologists can take several steps to put their work in the context of these models. Regional summaries of climate projections provide one resource for ornithologists interested in understanding the magnitude of effects projected for their study sites. Examples of such reviews include those for California (Hayhoe et al. 2004), the northeastern United States (Hayhoe et al. 2007), Europe (Räisänen et al. 2004), and Africa (Paeth and Thamm 2007). More specifically, ornithologists can use online resources to put weather-related research in the context of future climatic conditions. Finally, and most importantly, we encourage ornithologists to collaborate with climatologists to address the very real challenges of uncertainty and novel climatic conditions associated with understanding the effects of climate change on bird populations.

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