Beyond Habitat Selection: Physiological Responses of Species to Climate

Betsy Reardon
GEO 387H: Physical Climatology
Literature Review
Professor: Dr. Zong-Liang Yang
November 20, 2007

Abstract

The vast majority of current predictions about climate change effects on species geographic ranges are based on the climate envelope approach. Current species distributions are used to define a species niche, and this niche space is then projected into the future by tracking the climatic forecast. In opposition to climate envelope methods to describe shifts in species' geographic ranges, predictions based on mechanistic approaches tend to be more robust. These models rely on examining key physiological events in a species life and their relationship to climate. This review explores how tightly key life history events are connected to climatic conditions. Specifically, the following addresses migration triggers, reproduction, phenology, and sex determination. Clearly the importance of these events and their demonstrated relationship to climate reinforce the need to approach climate change predictions from a mechanistic approach.

Introduction

Each species has a discrete portion of the globe which it inhabits. The area of occupation of a particular species is defined as its geographic range. More generalist type species might have a relatively large range size. While other species might be limited to a very restrictive range (often referred to as endemic species). Species may have fairly consistent population sizes throughout their distribution until they abruptly reach the edge of their range.

This abrupt transition from habitat to non-habitat might be due to a hard geographic barrier, like water or mountains, or hard physiological barrier, like an unacceptable temperature for the gestation of young. In opposition and more common than abrupt transition, are populations that occur along a gradient with decreasing abundance. These species typically have a zone of high population size in the core of the range and a smaller diminishing population on the edges.

Defining this geographic boundary is a key goal of ecology. Essentially, ecologists are interested in examining where species occur and why they are there as opposed to else where ((Hutchinson 1957, Austin *et al.* 1990, Leibold, 1995). Despite the initial simplistic appearance of these questions, they are often complex and difficult to definitively answer. Often each species, even those existing within a single community composed of relatively similar species, have different factors restricting the individuals' range. Also, a single species might be influenced by several different factors. Factors controlling range size may include climatic tolerances, resource availability, mate availability, or environmental needs.

Species range limits may also be dynamic through time, and not static barriers to species range expansion or contraction. Ranges adjust to accommodate resource needs or fluctuating environments and climates. Species are also able to expand their range limits by adapting at the boundary, and using evolution to further their geographic holdings. Species also experience contractions to range by advancing human developments. In addition to understanding where species presently reside, ecologists have recognized the importance of predicting these shifts in geographic range. Recent understandings and increasing concerns about global climate change has escalated the need for accurate predictions of shifts in geographic ranges and emphasizes its indispensability to conservation of species.

Predictive models of species range limits are most commonly constructed using principles of climate envelope models (Pearson and Dawson 2003, Guisan and Thuiller 2005).

These models assume that each species has a defined niche space based on environmental tolerance- its climate envelope. To determine a species' climate envelope, the current distribution of the species is mapped. Then the correlative values for environmental variables are measured. These models assume that that species will track these values in the future (Guisan and Zimmermann 2000, Araujo *et al.* 2005). Researchers also assume that they have accounted for all essential environmental variables.

Parmesan and Yohe (2003) conducted an extensive meta-analysis of such studies to determine if a species, which has experienced a shift, was in line with what would be expected with changes in climate. Of the 1598 species that experienceda shift in range during the course of the individual studies, 59% presently display shifts that were in line with shifts of climate. Essentially, these species movedeither poleward or upward in elevation to track the climatic changes (principally temperature). Jetz *et al.* (2007) conducted a similar type of analysis by attempting to predict bird abundances basedon availability of habitat under climate change. They predicted 400 species of2750 would have a decrease in habitat area greater than 50% by 2050, and 900 species of birds by 2100.

Clearly, climate envelope models are intended to give us a general understanding of future geographic range limits. However, with the increasing threat of climate change to wildlife, it is imperative to improve our ability to predict shifts in geographic ranges (Ibanez*et al.* 2006). As was displayed by Parmesan and Yohe (2003), species are presently feeling the impacts of climate change. More thorough investigations of species mechanistic relationships to climate are essential to improving this understanding.

The goal of this paper is to provide a review of research that illustrates how critical events in species life history are tied to climate. Specifically, the review will explore climate links to migration, sex determination, breeding, and phenological relationship in communities.

Even though all species of plants and animals are bound by these relationships to climate, this review will focus on terrestrial species. It will become clear that species are not only constrained by climatic tolerances throughout their lives, but their success is ultimately dependent on climatic conditions during critical life events.

Migration

Studies investigating migration timing events have historically examined either variation in temperature (such as Liechti *et al.* 2000 and Sparks *et al.* 2007) or diurnal lightening variation (such as Tsvey *et al.* 2007 and Vrugt *et al.* 2007). But some recent studies suggest that migration events might more closely in sync with larger global climatic phenomena. For example, O. Huppop and K. Huppop (2003) have correlated long-term migratory data from 24 bird species in the southeastern North Sea to an index describing the North Atlantic Oscillation (NAO).

The NAO is used to describe the dominant pattern of atmospheric circulation in the regions surrounding the Atlantic basin. In periods when the winds of the NAO are stronger from the west, the temperatures in northern Europe are typically warmer and there are higher levels of precipitation. The strength of the NAO is measured by an NAO index, with a positive NAO index corresponding to a period of strong westerly winds. Over the past 40 years, the numbers of winter with a positive NAO index has increased significantly.

The Huppop and Huppop (2003) study discovered that 23 out of 24 birds show a trend towards earlier mean spring passage. Also, during the course of the study the average spring temperature increased and was correlated to the increase in migration timing. But these daily temperatures at migration are not significantly correlated to migration activity. Therefore, the authors speculate that there may be other environmental variables associated with the strongly positive NAO index. For example, warmer springs with relatively high precipitation have larger populations of insects. Perhaps the migration is not strictly driven by temperatures but local parameters determined by larger global patterns of climate.

This connection between climate and migration is not limited to species affected by the NAO. The El Nino Southern Oscillation (ENSO), a large scale ocean-atmosphere circulation phenomenon, brings warm nutrient poor waters in place of the otherwise nutrient rich Humboldt Current. ENSO also modifies large scale precipitation patterns due to these shifts in oceanic currents. ENSO have drastic effects on species population numbers, even on migratory species that move between ENSO impacted areas to non-impacted areas. The black-throated blue warbler (*Dendroica caerulescens*) has significantly reduced population numbers during El Nino years (Sillett *et al.* 2000). Their winter ground in Jamaica receives less precipitation and as a result there is less available food for the warbler. Not only do the population numbers decrease during the ENSO, but relative reproductive rates also decrease. Since there are fewer individuals breeding less, the warbler populations require a substantial time to rebound.

This relationship between climate and migration is not exclusively a relationship with migratory birds. Both butterflies and moths of Great Britain have displayed the same correlations between temperature and NAO to migration (Sparks *et al.* 2005) as the above example of North Sea birds. Even though it is unclear whether bat (Rojas-Martinez 1999) and ungulate (Berger *et al.* 2006) migration is driven more by resource needs or climatic tolerance, climate is clearly a factor either primarily or secondarily through resources.

In addition to presence of optimal climatic conditions, migration success is often dependent on the availability of adequate stop-over land (Tankersley 2004). Stop-over land is predominantly lost due to human development of wildlife habitat (Gibbs 2007). However, there is considerable concern about loss of stop-over land because of the impacts of climate change.

Wetlands are prime stop-over areas for migratory species, since they provide all key resources such are shelter, food, and water. Wetlands are also fragile ecosystems, which are dependent on proper hydrology, temperatures, and precipitation.

The North American prairie pothole region is a critical wetland habitat for migratory bird species (Austin 2002). Recent climate change simulations predict a shift to drier and less productive wetlands in the western portions of this region, where the highest population numbers of waterfowl currently utilize. This shift is based on prediction about daily temperature and mean daily temperature to estimate wetland water balance. The eastern regions are predicted to retain adequate waterlevels, but these areas are within close proximity to human development. This particular predicted shift in wetland availability could impact 50-80% of US ducks (Johnson *et al.* 2005).

Sex Ratio

Human sex determination is based on sex chromosomes located in both the male and female gametes. This type of sex determination ensures long-term statistical equal distribution of females and males. This system is not universal for the entire animal kingdom. There are several organisms, mostly reptiles, which base sex determination on temperature (Bull 1980). The developmental pathway between maleand female is based on a threshold temperature. Typically above one temperature, the individual will develop the hormones that lead to female development. Even though sex-determination is based on environment, fertilization requires male and female gametes.

This type of sex determination mechanism clearly presents several warning flags when considering the impacts of climate change on these species. In 1994, Janzen conducted an extensive study of painted turtles (*Chrysemys picta*) to determine the impacts of increased temperature during nesting. He illustrated with a mean temperature increase of less than 2ºC the sex ratio was drastically skewed towards females. He also suggests that with a rapid temperature increase of greater than 4ºC the species would be unable to adapt and rebound.

Although environmental sex determination is predominately a reptile phenomenon, other animals have displayed skewed sex ratio which correlates to temperature variation. For example, colonies of Formosan leaf-nosed bats (*Hipposideros terasensis*) in Taiwan are skewed toward females in higher temperatures (Cheng and Lee 2004). This observation has not been linked to actually sex determination of offspring. It is more likely related to the relative fitness of female versus males in higher temperature (Cryan and Wolf 2003). This skewed fitness of the sexes is not less concerning than the above example of painted turtles when considering climate change. If the males of the species are incapable of surviving the higher temperature predicted by climate change, the success of the species is unlikely.

Phenology

Phenology is the study of timed annual events. Historically, this has been of great interest for humans especially after the transition to a predominantly agricultural dependent species. People have long-term data related to key natural events associated to agriculture, like first and last frost. Also, people have collected data related to timing of aesthetically interesting natural events, like the date of first flower or the arrival of migratory songbirds. These long-term data are helpful in studying the impacts of climate change. It is possible to determine if events are occurring earlier due to warming temperatures throughout the year. Additionally, we are able to investigate if coupled natural events are moving out of sync.

Bradley *et al.* investigate 55 phenological data sets from Wisconsin that have recorded data over 61 years. They found that 19 have advanced in date consistent with what would be predicted by global climate change. The remaining were either inconclusive or experienced no shift in data. Unfortunately, the data sets did not include information on local temperature. However, it is estimated that global temperatures have increased 1°C over the last 50 years. This also assumes that these shifts are due to temperature and not other environmental variables such as water or other resource availability.

Phenological studies of shifts in natural events provide insights into the potential effects of climate change. Shifts in the timing of natural events have the potential to have major ramifications for ecological relationships (Cleland *et al.* 2007). Feeding relationships between species have evolved through considerable periods of coevolution, and disproportionate effects of climate change on one will alter the entire food web. For example, van Asch and Visser (2007) explore the feeding relationship between trees and leaf-eating insects. If plants begin to bud earlier in the spring due to warmer spring temperatures or increased rains, the feeding insects will need to rapidly adapt. Often plants are able to fluctuate annually depending on environmental conditions, while insects are more rigid and require more time to adjust genetically. Van Asch and Visser do speculate that some insects will be able to rapidly adjust and will also benefit from these longer growing seasons. Unfortunately, these are most-likely to be pest species like gypsy moths (*Lymantria dispar*).

Reproduction

Despite being presented as two discrete topics in this review, often reproduction and migration are coupled (Thorup *et al.* 2007). Migratory species relocate periodically to exist in optimal environmental conditions. Often the end of the migration is the catalysis of the breeding season. The relationship between the migration triggers and peak breeding conditions has been optimized through evolution. However, relatively rapid climate change may cause a disassociation between migration and peak breeding conditions that evolution will not be promptly adjusted.

Both and Visser (2001) have already demonstrated the earlybreakdown of this relationship between migration and reproduction in the pied flycatcher (*Fidedula hypoleaca*). The spring migration of the pied flycatcher is triggered by the variations in the day-night cycle, which is invariant under climate change. Once they reach their summer homes, breeding season begins. Temperatures over the last twenty years have increased significantly in their west Africa breeding region, and has caused a 10 day shift to earlier laying dates. This means that earlier breeding pairs are being preferentially favored, but the decreasing window for breeding is drastically reducing the reproductive success.. If warming trends continue, the breeding pairs will be arriving past peak breeding and rearing conditions. The already high temperature will decrease hatching and chick rearing success.

Although studies on mammals are rare because the large amount of data required to make concrete conclusions, there are preliminary results suggesting impacts of climate change on ungulate reproduction. Red deer (*Cervus elaphus*) born after warmer than average winters in Norway are smaller in size compared to other years' cohorts of deer (Post *et al.* 1997). This discrepancy is retained throughout their life, and is also correlated to decreased fitness and reproductive success. As the frequency of warm winters increase, we would expect to see a decline in red deer size and number of young born per year.

Discussion

Over the course of approximately 157 years, weather instruments have recorded an average increase in global temperature (IPCC 2007). This increase has occurred in two major time periods. The first occurred from 1910-1940 with an increase of 0.35°C, and secondly from the 1970s to present with an increase of 0.55°C. As temperatures are predicted to continue to increase, other climatic variables (such as precipitation, ocean and atmospheric circulations) are expected to move away from the current and historic norms. The rate and amplitude of these changes are contingent on multiple factors, including human contributions of aerosols and greenhouse gases.

If ecosystems have already felt the effects of current changes in the climate and the climate is predicted to continue its deviation from the norm, then reliable methods need to be developed to understand the consequences on the environment. This improved understanding will assist with species conservation, resources management, and ultimately human population endurance.

Past research efforts to predict the effect on climate change have focused on using methods related to niche description and future locations of that niche. Mechanistic approaches to modeling species reaction to climate change might prove to be a more robust method. This approach will include research of key physiological constraints for a species, like the examples discussed above concerning reproduction, migration, sex ratio, and phenological synchrony, and exploring their relationships to the climate. For example, a species might be able to spend its mature life in a wide range of temperature variation, but a very narrow temperature window is necessary for reproduction.

Despite being a more robust method, mechanistic approaches have their clear drawbacks when compared to climate envelope models. Mechanistic models require high levels of data, and each species might need to be examined individually. The climate envelopes models can be computed relatively easily for several species with limited distribution data. Ease of calculation and minimal data allow climate envelopment models to be an inexpensive method of analysis. Despite requiring more data and being time intensive, the insights provided by mechanistic models prove to be worth the input.

It is often suggested that biological species will simply adapt to the changing environment, after all, they have evolved to correspond to the current climatic changes. The evolution of a species takes place over a very long time scale. As stated above, the IPCC estimates current warming trends over the past 157 years. Climate change is occurring at a much faster rate than the evolutionary rate. Most species, especially those with longer generation times, will be unable to adapt to this accelerated rate of climate change.

References

Austin, M.P., Nicholls, A.O. & Margules, C.R. (1990) Measurement of the Realized Qualitative Niche: Environmental Niches of Five *Eucalyptus* Species. Ecological Monographs 60: 161–177.

Austin, J.E. 2002. Response of Dabbling Ducks to Wetland Conditions in the Prairie Pothole Region. Waterbirds 25: 465-473.

Araujo, M.B., R.G. Pearson, W. Thuillers, and M. Erhard. 2005. Validation of Species-Climate impact Models under Climate Change. Global Change Biology 11: 1504-1513.

Both, C., and M.E. Visser. 2001. Adjustment to Climate Change is Constrained by Arrival Date in a Long-Distance Migrant Bird. Nature 411:296-298.

Berger, J., S.L. Cain, and K.M. Berger. 2006. Connecting the Dots: An Invariant Migration Corridor links the Holocene to the Present. Biology Letters 2: 528-531.

Bradley, N.L., A.C. Leopold, J. Ross, and W. Huffaker. 1999. Phenological Changes Reflect Climate Change in Wisconsin. Proceedings of the National Academy of Science of the United States 96: 9701-9704.

Bull, J.J. 1980. Sex Determination in Reptiles. The Quarterly Review of Biology 55: 3.21.

Cheng, H.C. and L.L. Lee. 2004. Temporal Variations in the Size and Composition of Formosan Leaf-Nosed Bay (*Hipposideros terasensis*) Colonies in Central Taiwan. Zoological Studies 43: 787-794.

Cleland, E.E., I. Chuine, A. Menzel, H.A. Mooney, and M.D. Schwartz. 2007. Shifting Plant Phenology in Response to Global Change. Trends in Ecology and Evolution 22: 357-365.

Cryan, P.M., and B.O. Wolf. 2003. Sex Differences in the Thermoregulation and Evaporative Water Loss of a Heterothermic Bat, *Lasiurus conereus,* during its Spring Migration. The Journal of Experimental Biology 206: 3381-3390.

Guisan, A. and N.E. Zimmerman. 2000. Predictive Habitat Distribution Models in Ecology. Ecological Modelling 135: 147-186.

Guisan, A., and W. Thuiller. 2005. Predicting Species Distribution: Offering more than Simple Habitat Models. Ecology Letters 8: 993-1009.

Gibbs, J.P. 2007. Wetland Loss and biodiversity Conservation. Conservation Biology 14: 314-317.

Huppop, O. and K. Huppop. 2003. North Atlantic Oscillation and Timing of Spring Migration in Birds. Proceedings of the Royal Society 270:233-240.

Hutchinson, G.E. 1957. Concluding remarks: Cold Spring Harbor Symposium on Quantitative Biology: 22, 415–457.

Ibanez, I., J.S. Clark, M.C. Dietze, K.Feeley, M. Hersh, S. LaDeau, A. McBride, N.E. Welch, and M.S. Wolosin. 2006. Predicting Biodiversity Change: Outside the Climate Envelope, Beyond the Species-Area Curve. Ecology 87: 1896-1906.

Janzen, J.J. 1994. Climate-Change and Temperature-Dependent Sex Determination in Reptiles. Proceedings of the National Academy of Science of the United States 91: 7487-7490.

Jetz, W., D.S. Wilcove, and A.P. Dobson. 2007. Projected Impacts of Climate and Land-Use Change on the Global Diversity of Birds. PLOS Biology 5: 1211- 1219.

Intergovernmental Panel on Climate Change (IPCC). 2007. Climate Change 2007: the Physical Science Basis. Contribution of Working Group I to the Fourth Assessment report of the IPCC. Cambridge University Press, New York.

Johnson, W.C., B.V. Millett, T. Gilmanov, R.A. Voldseth, G.R. Guntenspergen, and D.E. Naugle. 2005. Vulnerability of Northern Prairie Wetlands to Climate Change. BioScience 55: 863-872.

Lehikoinen, E., T.H. Sparks, and M. Zalekevicius. 2004. Arrival and Departure Dates. Birds and Climate Change Advances in Ecological Research 35: 1-31.

Leibold, M.A. (1995) The Niche Concept Revisited: Mechanistic Models and Community Context. Ecology 76: 1371–1382.

Parmesan, C., and G. Yohe. 2003. A Globally Coherent Fingerprint of Climate Change Impacts across Natural Systems. Nature 421: 37-42.

Pearson, R.G., and T.P. Dawson. 2003. Predicting the Impacts of Climate Change on the Distribution of Species: Are Bioclimate Envelope Models Useful? Global Ecology and Biogeography 12: 361-371

Post, E., N.C. Stenseth, R. Langvantn, and J.M. Fromentin. 1997. Red Deer Cohorts. Proceedings of the Royal Society of London 264: 1317-1324.

Rojas-Martinez, A., A. Valiente-Bauet, M.D. Arizmendi, A. Alcantara-Eguren, and H.T. Arita. 1999. Seasonal Distribution of the Long-Nosed Bat (Leptonycteris curasoae) in North America: Does a Generalized Pattern Really Exist? Journal of Biogeography 26: 1065-1077.

Sillett, T.S., R.T. Holmes, and T.W. Sherry. 2000. Impacts of a Global Climate Cycle on Population Dynamics of a Migratory Songbird. Science 288: 2040-2042.

Sparks, T.H., D.B. Roy, and R.L.H. Dennis. 2005. The Influence of Temperature on Migration of Lepidoptera into Britain. Global Change Biology 11: 507-514.

Sparks, T.H., K. Huber, R.L. Bland, H.Q.P. Crick, P.J. Croxton, J. Flood, R.G. Loxton, C.F. Mason, J.A. Newnham, and P. Tryjanowski. 2007. How Consistent are Trends in Arrival (and Departure) Dates of Migrant Birds in the UK? Journal of Ornithology 148: 503-511.

Tankersley, R.D. 2004. Migration of Birds as an Indicator of Broad-Scale Environmental Condition. Environmental Monitoring and Assessment 94: 55-67.

Thorup, K., A.P. Tottrup, and C. Rahbek. 2007. Patterns of Phenological Changes in Migratory Birds. Oecologia 151: 697-703.

Tsvey, A., V.N. Bulyuk, and V. Kosaev. 2007. Influence of Body Condition and Weather on Departures of First-Year European Robins (*Erithacus rubecula*) from an Autumn Migratory Stopover Site. Behavioral Ecology and Sociobiology 61: 1665-1674.

van Asch, M., and M.E. Visser. 2007. Phenology of Forest Caterpillars and Their Host Trees: The Importance of Synchrony. Annual Review of Entomology 52: 37-55.

Vrugt, J.A., J. van Belle, and W. Bouten. 2007. Pareto Front Analysis of Flight Time and Energy use in Long-Distance Bird Migration. Journal of Avian Biology 38: 432-442.