Time for predictive movement ecology: moving from patterns and processes to predictions

Vision: to develop a framework for forecasting changes in animal movement from future climate data using Scandinavian moose (*Alces alces*) as a model system, and to understand how changing climate drivers of animal movement are linked to emerging challenges in wildlife management.

1 Purpose and aims

The Earth's climate will experience widespread changes during the 21st century that will cause present-day arctic and sub-arctic climates to warm significantly, shrink in area, and experience altered rainfall patterns (Garcia et al., 2014) (fig. 1). Wildlife in these regions will be affected in diverse ways as their environments change, with some species likely to decline while others flourish (Araújo et al., 2013). Although it will be essential to adapt resource management policies in response to these changes, there are many sources of uncertainty to consider, both in the climate models and in their likely effects on different organisms (Stein et al., 2013). Climate change therefore poses new and difficult challenges for policy makers who must balance the concerns of multiple stakeholders in designing sustainable management plans for wildlife with high economic or societal importance. In what follows, we propose to develop predictive models of the effects of future climate changes on animal movements, with a focus on the migratory behavior of remotely-monitored moose throughout Scandinavia. We aim to determine how these critically important seasonal movements will be affected by changing climate conditions, and to evaluate the limitations and sources of error involved in making predictions about animal movement from future climate models.

2 Survey of the field

Movement is one of the most fundamental aspects of an organism's biology, and it has a central role in determining how the organism will be affected by a changing environment (Nathan, 2008). Many key life events and activities that affect individual survival and reproduction—including natal dispersal, migration, habitat selection, and home range formation—are ultimately defined by patterns of individual movement. Animal movement therefore provides key links between individual-level processes and population-level outcomes, including some pressing concerns for wildlife management under climate change such as species abundance, distribution, and demographic performance (Morales et al., 2010). Because animal movements are often triggered or shaped by environmental conditions (Nathan et al., 2008), the warming climate will undoubtedly bring with it changes in the ecology of wildlife (Post et al., 2009). These processes are likely to reshape the current landscape of pressures, synergies, and conflicts

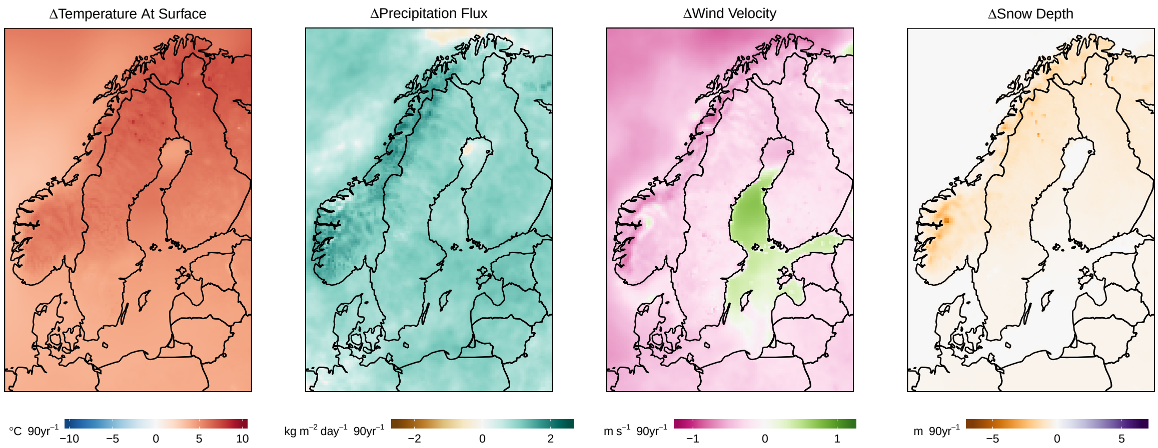

Figure 1: Examples of projected changes in decadal climate means from 2000s to 2090s. Scandinavia is predicted to get warmer and wetter with lower wind velocity and reduced snow depth. The data shown were produced for the EURO-CORDEX project by the Swedish Meteorological and Hydrological Institute's Rossby Centre using the HadGEM2-ES global climate model under the RCP8.5 climate warming scenario.

with human activities and socioeconomic concerns in the circumpolar North, from forest industries to agriculture to tourism.

Although the importance of movement has long been recognized, recent years have seen rapid progress in the field of movement ecology following technological advances that have enabled researchers to obtain highly-resolved, individual-level movement trajectories, physiological states, and environmental covariates (Dodge et al., 2013; Holyoak et al., 2008; Jachowski and Singh, 2015; Kays et al., 2015; Kuenzer et al., 2014; Neumann et al., 2015; Rutz and Hays, 2009). In addition, sophisticated analytical methods have been developed to model the mechanistic links between behavior and observed movement data while accounting for different sources of error (Jonsen et al., 2005; Patterson et al., 2008). Much of the burgeoning research in movement ecology centers around describing movement patterns and inferring the behavioral processes and external drivers that produce those patterns. Despite this progress, relatively little work has been done on predicting the effects of future climate states on individual movements (Seebacher and Post, 2015), although all of the necessary components heralding a new era of predictive movement ecology are now in place.

3 Project description

To meet the wildlife management challenges of the future, policy makers need empirically derived predictions on how species will be affected by future environmental conditions. Our approach to addressing this need centers on individual movement and will make use of recent year-to-year and geographical variation in climate conditions to create movement models that can be parameterized with future climate data. The proposed analyses will focus on Scandinavian species, and will specifically employ data from the Wireless Remote Animal Monitoring (WRAM) database (Dettki et al., 2014). This extraordinary database is one of the world's largest repositories of GPS telemetry and physiological sensor data from wildlife; it includes movement data from thousands of individual animals of 16 species spanning 8 countries. We will begin by focusing on moose (*Alces alces*), for which movement data exist for 681 individuals collared in different regions of Sweden between 2003 and 2015 (fig. 2). This kind of large-scale comparative data across a broad climate gradient can effectively be used as a surrogate for experimental manipulations, which are impractical in many wildlife studies, to identify causal mechanisms that link environmental conditions with movement behavior (McIntire and Fajardo, 2009). The movement and sensor data in the WRAM database are uniquely positioned to resolve questions about the effects of specific climate variables on movement patterns and to provide a solid basis for predictions based on future climate conditions. Once the analytical workflow has been established and validated for moose, the same approach can be extended to other species. The analysis will involve three general stages.

3.1 *Modeling climate effects on migration*

We will estimate movement paths from previously collected animal telemetry data using the state-space modeling approach developed by Johnson et al. (2008). A state-space modeling framework involves coupling a stochastic "process model" that describes the animal's state (e.g., its location) to an "observation model" that describes how the observed data are related to the animal's true state (Patterson et al., 2008). This is an appropriate framework for the research proposed here because it explicitly accounts for uncertainty in the input data, enables statistical inference about the effects of environmental covariates on the movement process, and provides a means to forecast spatially explicit future movement from fitted models. The approach developed by Johnson et al. (2008) is convenient for our research questions because it relies on a stochastic velocity process that can vary as a function of environmental covariates (e.g., climate conditions).

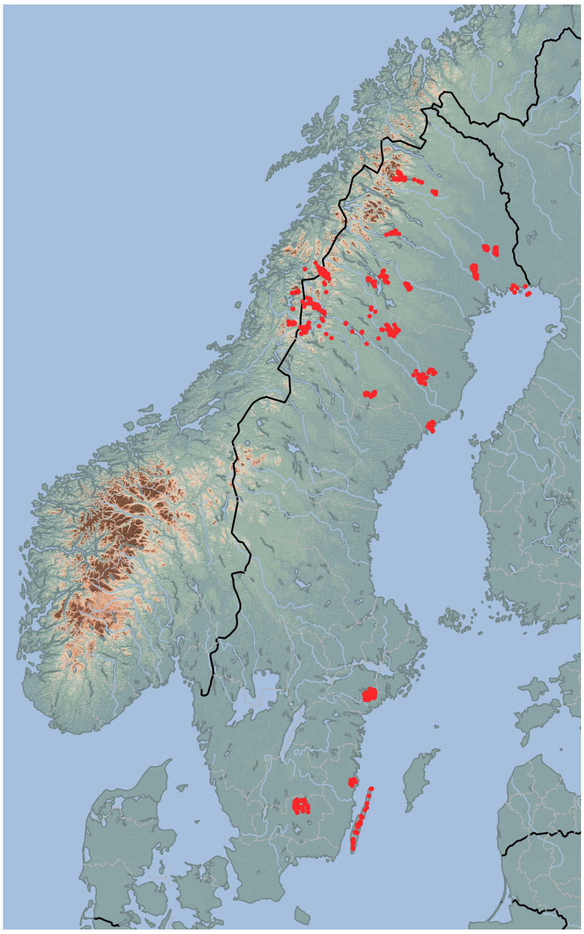

Figure 2: Starting locations (red dots) for 681 individual moose collared between 2003 and 2015 with tracking data in the WRAM database (Dettki et al., 2014).

Using these models, we will quantify the effects of specific climate variables on movement metrics. For the moose represented in the WRAM database (and for several other species as well), there is an existing body of knowledge about climate effects on movement patterns. We will build on this knowledge base by calculating a set of movement metrics. The state-space models described above will use observed telemetry data to estimate velocity parameters, which we can then relate to the climate conditions encountered along the estimated movement path. We will use the Env-DATA annotation system (Dodge et al., 2013) to match each movement step to a multitude of climate conditions experienced by the animal during the step, including ambient temperature, precipitation, snow depth, and wind speed and direction. The climate variables will be selected based on the environmental conditions known or suspected from previous research to be important influences on movement behavior. We will also use estimated movement paths to calculate higher-order movement metrics that may be more meaningful to policy makers, including net squared displacement (Bunnefeld et al., 2011), residence time (Barraquand and Benhamou, 2008), and time-to-return for biologically relevant spatial scales. For migratory movement phases, we also will examine the timing, distance, and duration of migratory movements, as well as the propensity to undertake migration (Jachowski and Singh, 2015; Singh, Börger, et al., 2012).

3.2 Movement forecasting

We will simulate movement paths from these fitted models using future climate projections from the the CMIP5, the foremost international climate-change research initiative, which combines the expertise of 28 world-leading climate modeling research groups (Taylor et al., 2011). A high-resolution ensemble of regionally downscaled CMIP5 projections for Europe, representing a range of different possible climate futures, has been produced for the EURO-CORDEX program (Jacob et al., 2013). EURO-CORDEX includes about 30 combinations of different driving models and warming scenarios for each of approximately 50 climate variables (such as the four shown in fig. 1), for a total of over 1500 high-resolution climate forecasts for the European region. We will use this data to assess the range of probable effects of changes in climate means (e.g., warmer or wetter average conditions), changes in the amount of variability around those means (e.g., a wider or narrower annual temperature range), and changes in climate seasonality (e.g., timing of snow melt and early spring temperature) on animal movement.

For each observed migration event in our data set, we will generate a "movement forecast" that essentially poses the question: given the movement that we have observed for a particular animal, how would we expect its movement to change if it were starting from the same location but facing the climate conditions that are projected to occur in the future? Each forecast will consist of a large number of simulated paths generated from an individual movement model that has been parameterized with data from multiple climate models at regular future points in time. The resulting set of spatially-explicit movement predictions will provide a basis for inferring how important ecological processes such as migration will change over both space and time from local to regional scales.

3.3 Assessing uncertainty

Generating the predictions described above will be a computational exercise made possible by our unique animal movement data. But in order for the predictions to be useful, it is essential that they be evaluated critically to determine whether they are sufficiently reliable to serve as a basis for adapting wildlife policies to meet emerging challenges. There are various sources of error and uncertainty inherent in the different data. We will undertake a thorough evaluation of major sources of uncertainty to determine how they affect the reliability of our predictive models.

The first major source of error is associated with the movement data, which cannot be recorded with complete accuracy due to practical and technological limitations. The state-space modeling framework explicitly allows for observational uncertainty in the parameter estimation process. However, it is important to consider whether such error may multiply when projections are made. We will examine the sensitivity of the parameter estimates and simulated movement paths to observation error in the telemetry data.

An additional major source of potential error is associated with the climate models: there is a large amount of uncertainty involved in making spatially explicit forecasts about regional climate conditions a century into the future. This issue is central to the multimodel design of the CMIP5 (Taylor et al., 2011), as it draws together the expertise of many independent climate research groups to make unbiased projections for wide range of possible greenhouse gas emission scenarios. Moreover, each modeling group in the CMIP5 was asked to evaluate how well their models could replicate known climate history. The results of the multimodel ensemble and the historical simulations therefore provide valuable information about the spread and degree of consensus among the different future climate projections, and consequently, about the confidence that can be placed on the results.

4 Significance

This research aims to spark a broader shift from describing movement patterns and inferring movement processes to making predictions under specific future-change scenarios. We believe that our discipline is now poised to take advantage of recent advances—better-quality location data, improved biosensor technology, advanced climate models, and sophisticated movement models that explicitly account for different sources of uncertainty—to build a science of predictive movement ecology. We anticipate that the proposed research will provide valuable information for guiding effective wildlife management policies during the next century. For wildlife threatened with extinction and/or with limited dispersal capacity, this information will help to evaluate whether existing management policies and protected areas will support their long-term persistence. For wildlife with high economic or societal importance, such as moose, our predictions will help to identify and address novel challenges and stakeholder conflicts that will emerge as the climate changes. This research will also shed light on the importance of different sources of uncertainty and their possible ramifications for whether it is possible to make confident predictions about how animals will adapt their movements to changing environmental conditions.

5 Preliminary results

Previous research on these moose populations has revealed a variety of intrinsic and extrinsic influences on their movement patterns (Jachowski and Singh, 2015; Månsson et al., 2012; Singh, Börger, et al., 2012; Singh and Ericsson, 2014; Singh and Leonardsson, 2014). We will expand on this knowledge for specifying, fine-tuning, and fitting the state-space models to individual movement data. Several important methodological steps in the proposed research are currently underway. The moose movement data have already been collected and processed in collaboration with Dr. Göran Ericsson at Sveriges lantbruksuniversitet in Umeå. We are currently exploring partnerships that will enable us to extend the approach to other animal species. Using small subsets of data, Campos has authored and validated key analysis pipelines in the R programming environment for (1) distinguishing migratory from nonmigratory movement phases in the movement data, (2) requesting environmental annotation for the movement data using the Env-DATA system, and (3) automating the download and batch-processing of EURO-CORDEX data on future climate conditions to be matched with simulated movement paths.

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