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AS WE SEE IT

Constraints to projecting the effects of climate change on mammals

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ABSTRACT: Ecologists are under pressure to anticipate the ecological effects of climate change. Therefore many ecological publications (and most grant proposals) related to climate claim relevance to the projection of future climate change effects. Yet the steps leading from ecological description and understanding to reliable projection are rarely explicit. A good understanding of the factors which allow the ecological effects of climate change to be effectively anticipated is critical to both the quality of basic science and its application to public policy. We used research performed on mammals to explore scientific approaches to anticipation of climate change effects. We distinguished forecasting models based on correlations from predictive models based on cause-effect relationships. These categories represent extremes along a continuous gradient between pattern description and causal understanding. We suggest that the constraints to our capacity to anticipate fall into 6 broad categories rooted in the development and application of forecasting and predictive models. These categories help to identify the conditions that allow or prevent projection of the effects of climate change on ecosystems. This approach should also help to identify which research avenues will likely be most fruitful.

KEY WORDS: Cause-effect relationships · Climate change · Ecology · Forecasting · Mammals · Models · Prediction · Scientific projection · Time series

1. INTRODUCTION

There is no question of the reality of global climate change (IPCC 2001). Changes in recent decades are apparent at all levels of ecological organization: population and life-history, phenology and geographical range, species composition of communities, and structure and functioning of ecosystems (McCarthy 2001). Parmesan & Yohe (2003) recently defined a diagnostic fingerprint of ecological responses uniquely predicted by twentieth

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century climate trends. Additional threats will emerge as climate continues to change, especially as climate interacts with other stressors such as habitat fragmentation (Root & Schneider 2002, Lovejoy & Hannah 2005).

Whereas ecological monitoring allows us to detect changes and potentially react soon after some major perturbations have occurred, projections into the future improve our capacity to mitigate or adapt to changes. The capacity to predict is also a clear measure of scientific success (Lipton 2005), and an important component of our science if knowledge provided by ecologists is to have any policy effect (Walther et al. 2005, Sutherland 2006). Projecting the future ecological consequences of climatic change is, however, a formidable challenge (Stenseth & Hurrell 2005), largely because climate change will bring entirely novel conditions (Sutherland 2006).

Mammals are studied worldwide at all levels of biological organization, in all habitats, and for theoretical as well as practical reasons (Berteaux & Stenseth 2006, this issue). Anticipating the future effects of climate change on mammals is needed because of the conservation, societal, and economic consequences of change in mammal populations (e.g. ACIA 2004). As part of a series of symposium papers analyzing the effects of large-scale climatic variability on mammals, here we explore our ability to project the consequences of climate change on this group of organisms. Since most symposium papers address predictability through empirical case studies, this work presents a collective effort to highlight and organize the constraints faced by mammalogists trying to anticipate the ecological effects of climate change. This effort was needed given that most publications (and most grant proposals) that relate to mammals and climate claim relevance to projecting future effects of climate change, although the steps leading from description and understanding to projection are rarely explicit.

We first summarize the main principles of scientific projection and how they apply to climate change ecology. Next we present the characteristics and outcomes of pattern versus process-oriented ecological research. We then discuss the main constraints to projecting the ecological effects of climate change, and apply this framework to a sample of well-known questions asked by mammalian ecologists. We finally derive indications as to what approaches may now be most fruitful.

2. PROJECTING THE EFFECTS OF LARGE-SCALE CLIMATIC VARIABILITY ON MAMMALS

Rather than entering into the philosophical debate about the predictive power of ecology (Peters 1991), we simply seek to present a pragmatic framework to analyze the approaches used to project the future effects of climate change on mammals.

We often pool under the term prediction all attempts to describe an unknown situation from some current information. Legendre & Legendre (1998) remind us, however, of the useful distinction between forecasting and prediction in ecology. Forecasting models take structural relationships among descriptors that have been quantified for a given data set and extend these to different situations. These models work from correlations and do not assume any causal relationship between variables. In contrast, predictive models describe known or assumed causal relationships. They project, from a known situation, the consequences of a set of cause-effect relationships.

The distinction between forecasting and predictive models has been expressed in numerous ways (e.g. statistical vs. mechanistic models or correlative vs. causal models). Similarly, O'Hara (2005) recently described correlative laws of nature (observed regularities derived as generalizations from a large number of observations) vs. causal laws of nature (statements about the mechanisms that give rise to observed regularities). Below we use this dichotomy to structure our thinking about anticipation of climate change impacts on mammals, and to benefit from the useful distinction between the terms 'forecast' and 'prediction'. We always use the word 'prediction' in the restricted sense explained above (see Table 1 for definitions of terms used in this paper). It is noteworthy that for climate change scientists, who only work from cause-effect relationships when modeling future climate, prediction, forecast, and projection all refer to mechanistic models (MacCracken, 2001). The Intergovernmental Panel on Climate Change (IPCC) and the US National Assessment have used the distinctions outlined by MacCracken (2001). In an ideal world all scientists would use terms similarly, but the reality is that terminology varies between (and sometimes within) disciplines for historical or practical reasons.

Table 1. Glossary of important terms used in this paper

Term	Definition
Projection	Description of an unknown situation from some current information (general term)
Anticipation	Description of an unknown, future situation from some current information
Forecasting	Description of an unknown situation based on correlational relationships among descriptors
Prediction	Description of an unknown situation based on causal relationships among descriptors

Ecological projections are often based on mixed approaches, relying for example on correlations between climatic and ecological trends that are partially explained by tested mechanistic hypotheses. The dichotomy between forecasting and prediction thus represents extremes along a gradient of scientific approaches leading to scientific projection.

There are 2 main necessities for sound forecasting and 3 main necessities for sound prediction (numbering below corresponds to Constraint numbering in Table 3). Forecasting is successful if (Legendre & Legendre 1998):

(1) Values of and interactions between all important variables that have not yet been observed are similar in the new situation as they were when the forecasting model was built;

(2) There is no extrapolation beyond the observed range of the explanatory variables.

When the above conditions are met, then quality of forecasts depends on the degree of statistical association between predictors and dependent variables.

Prediction is successful if (Loehle 1983):

(3) Initial conditions of the system are well described (inherent noise is small);

(4) No important variable is excluded from the model (boundary conditions are defined adequately);

(5) Variables used to build the model are related to each other in the proper way (aggregation/representation is adequate).

Whether the above constraints are met or not cannot be known *a priori*. Only in testing predictions against the real world can one decide if a model is successful. Similarly, the degree of precision required for the predictions has to be decided by the user, and there is no objective way to define when initial conditions are described well enough (Constraint 3, above; see also Table 3), or when a variable is important enough to be included (Constraint 4).

Forecasting and prediction are both used to anticipate the effects of climate change on mammals (see examples in Table 2), although most models fall in some intermediate categories. As part of this series of symposium pa-

Table 2. Examples of projections derived from climate-change studies within ecology, as applied to mammals. The first column indicates the type of model used to derive the projection and the level of organization to which the projection applies. All projections were given explicitly by the authors, rather than derived by us

Models and levels of organization	Climate change	Biological event anticipated due to climate change	Qualitative vs. quantitative	Source
Forecasting				
Organism	Warmer winters	Warmer winters will result in reduced body weight of reindeer calves in areas where winters with a high NAO index are severe	Qualitative	Weladji & Holand (2003)
Population	Drier	Should the climatic conditions that prevailed from 1982 to 1995 be replicated from late 2002 onwards, by 2016 sable antelope and tsessebe from Kruger National Park would be reduced to fragmented remnants of 285 and 70 animals, respectively	Quantitative	Ogutu & Owen-Smith (2003)
Community	Colder	Shift back to lasting negative NAO-index values, causing a return to colder winters, would reinitiate pronounced 3–4 yr cyclic dynamics of voles and their predators	Qualitative	Hörnfeldt et al. (2005)
Ecosystem	Warmer winters	The responses of plants to winter warming may be more subtle than the responses of large herbivores	Qualitative	Post & Stenseth (1999)
Predictive				
Organism	Warming and sea ice melting	By the 2050s, the minimum sea ice extent in the polar basin should prevent pregnant polar bear females from reaching their denning areas on Wrangel Island and the Svalbard Archipelago	Qualitative	Derocher et al. (2004)
Population	Warmer	Pronounced northward range expansion of hibernating little brown bats within the next 80 yr in North America	Quantitative	Humphries et al. (2002)
Community	Warmer winters	Increased frequency of mild weather leading to the formation of ice on the ground should disrupt normal cyclic dynamics of northern small rodents	Qualitative	Aars & Ims (2002)
Ecosystem	Changes in several climatic variables	Climate change effects in the Greater Yellowstone Ecosystem will cascade into spread of the blister rust fungus, decrease in whitebark pine seed production, and decrease in grizzly bear abundance	Qualitative	Koteen (2002)

pers, Lima & Berryman (2006) and Jacobson et al. (2006) provide specific examples of attempts to refine models projecting responses of mammals to climatic variation.

The constraints faced when anticipating effects of climate change fall into 6 broad classes. Constraints 1 to 5 are rooted in the development and application of models, as outlined in the 5 numbered points above. For example, although long and detailed time series may exist between spring temperature and reproductive phenology of a given species, climate warming may result in future spring temperatures being out of the range of temperatures observed in the past, so that forecasting without extrapolation may be impossible (Constraint 2). The 6th constraint rests in the uncertainties of the climatic scenarios given to us by climatologists. This constraint is usually made explicit in scientific papers (e.g. Jacobson et al. 2004). The only possible answer to this constraint is to work from a range of scenarios and provide a range of projections. Table 3 shows concrete examples of constraints belonging to the above 6 categories.

Authors rarely identify explicitly the limitations they face when attempting to project the ecological effects of climate change. We know of no synthesis attempting to organize these limitations. However, in reviewing the literature we have found no constraint that did not fit into 1 of the 6 categories just presented.

3. ANTICIPATING THE EFFECTS OF CLIMATE CHANGE ON MAMMALS: ACHIEVEMENTS AND DIFFICULTIES

Building on the framework presented above, we now use progress made on 3 well-known questions asked by mammalogists to illustrate the factors allowing or preventing anticipation.

3.1. Anticipating the effects of climate change on geographical distribution

Range limits of many species correspond closely with isotherms, and there are numerous correlations between changes in climate and shifts in species distribution (Walther et al. 2002, Root et al. 2003). It is therefore tempting to relate — through models — present day distributions to current climate, and then use climate change scenarios to project future spatial shifts in species′ climatic envelopes (Thuiller 2003). Some of the earlier projections of climate change on mammal distributions have used this approach in rather simplistic ways (Kerr & Packer 1998), but more sophisticated approaches have now gained popularity (Peterson et al. 2002). However little has been done to assess the reliability of such projections (Thuiller 2004), and the

Table 3. Examples of constraints encountered by authors attempting to project the effects of climate change on mammals. The first column indicates the type of model used and the type of constraint encountered. Asterisks indicate when constraint was not explicitly given in the paper and was thus inferred by us

Constraint	Example	Source
Forecasts		
1. Values of unobserved variables potentially changing	Our model assumes that vegetation is the only driving variable in the current distribution of each species and therefore ignores potentially important anthropogenic affects that are independent of climate effects	Johnston & Schmitz (1997)
2. Need to extrapolate beyond the range of observations	Forecasting models can project future population dynamics of 3 African ungulate species, provided that observed climatic conditions recur, but cannot make safe projections beyond the range of observed climatic conditions*	Ogutu & Owen-Smith (2003)
Predictions		
3. Inherent noise is large	Predictions as to which arctic species will evolve fast enough to adapt to new climatic and ecological conditions are currently difficult because there is a lack of data on the quantitative genetics of many species	Berteaux et al. (2004)
4. Need for better definition of boundary conditions	The model assumes that the length and severity of seasonal energetic bottlenecks, and not the distribution of prey, predators, or caves, determines the winter range limits of little brown bats*	Humphries et al. (2002))
5. Need for additional fine tuning regarding aggregation/ representation	Despite it being one of the best-understood mammalian species distributional limits, mechanisms underlying the northern limit of Virginia opossums remain enigmatic. There are 3 major areas of inadequate understanding: the microclimates actually experienced by opossums, the exact relationship of opossum foraging behavior to ambient temperature, and the role of human-related resources operating to mitigate restrictive climatic effects	Kanda (2005)
Both		
6. Uncertainties of climatic scenarios	A different climatic scenario with a faster rate of temperature change would result in an increased mismatch between the rate of habitat change and the rate at which species can relocate to occupy new habitats in appropriate climate envelopes	Callaghan et al. (2004)

non-climatic influences on the distribution of species cast doubts on the relevance of this 'color mapping' approach (Schmitz et al. 2003). What we see here are the clear limitations of forecasting when one or more important variables that have not been observed are not constant (Constraint 1).

As an alternative to forecasting, attempts have been made to scale up physiological predictions into predictions at higher levels of organization. McNab (2002) provides multiple examples of potential physiological limits to species distributions. The breeding distribution of gray seals *Halichoerus grypus* may be limited by the effects of cold air temperatures on the fasting endurance of recently weaned pups (Hansen & Lavigne 1997). The winter distribution of little brown bats *Myotis lucifugus* is limited to latitudes where hibernacula are warm enough to maintain winter energy needs at levels lower than energy available from autumn fat reserves (Humphries et al. 2002).

However, range limits of many mammals will not be imposed by simple physiological constraints operating independent of key ecological factors such as predator abundance or inter-specific competition. Some of the most conspicuous features observable at the sub-organism scale do not reveal the dominant processes that generate larger-scale patterns (Root & Schneider 1995). Projections become increasingly sensitive to boundary conditions (Constraint 4) as we move upscale. Whereas forecasting models face Constraint 1, predictive models face mainly Constraint 4 (important variables are excluded from the model) when it comes to projecting species' ranges. Making explicit these limitations in projecting climate change impacts on species distribution should help concentrate research efforts. For example, Root & Schneider (1995, 2003, 2006) have advocated the use of the 'strategic cyclical scaling' paradigm, where top-down and bottom-up techniques are combined strategically across many scales and through several cycles of enquiry.

3.2. Anticipating the effects of climate change on phenology

Most research on mammal phenology concentrates on reproduction. Reproductive phenology is responsive to climate change (Root et al. 2003), and energetic approaches provide considerable promise in quantifying the causes and consequences of reproductive timing in mammals, and thus to develop predictive models about phenology. Most mammals alter the timing of breeding according to climate, body condition, and food availability. Energetic studies may help us understand why, by identifying the effects of climate on reproductive effort and success. Some of the most detailed work on the reproductive energetics of free-ranging mammals involves seals (e.g. Donohue et al. 2002, Arnould et al. 2003) and squirrels (Kenagy 1990, Humphries & Boutin 2000), but we are unaware of any detailed mammalian studies of the energetic consequences of the seasonal timing of reproduction relative to resources and climate, as has been achieved in birds (Thomas et al. 2001). Therefore predictive models linking climate change to phenological responses in mammals are still in their infancy.

Forecasting models may offer the quickest routes to anticipation, at least in the short term. The phenology of plants used by herbivores is directly linked to climate, and the reproductive timing of herbivores matches vegetation dynamics (Robbins 1993). Therefore, a multi-trophic perspective is needed to disentangle direct and indirect effects of climate variation on population dynamics (see the match/mismatch theory; Cushing 1990). Until recently, these multi-trophic approaches have been partially hampered by the difficulty of gathering information on all trophic levels and at multiple temporal and spatial scales (Constraint 3). For example, field data on plants are difficult to use for predicting global changes because they are generally not collected in a standard way across large spatial scales (Kerr & Ostrovsky 2003). New tools, such as the Normalized Difference Vegetation Index (NDVI), may change this situation (Pettorelli et al. 2005). Clearly, such indices are meant to build forecasting models at large temporal and spatial scales, whereas finer-scale studies are needed to understand the processes leading to a correlation between NDVI and herbivore performance.

3.3. Anticipating the evolutionary effects of climate change

If contemporary evolution induces fast responses to climate change, then ecologists also need to anticipate the evolutionary effects of climate change (Berteaux et al. 2004, Bradshaw & Holzapfel 2006). Changes in climate have been associated with previous evolutionary changes in mammals across temporal scales ranging from generations (Réale et al. 2003) to hundreds of millennia (Barnosky & Bell 2003) and beyond (van Tuinen et al. 2004). The analysis of ancient DNA allows examination of genetic responses of extant species to previous climatic events (Hadly et al. 2004). This provides potential opportunities to project future responses through forecasting (Barnosky et al. 2003). However, the level of details available from past evolutionary events is far lower than that needed to project consequences of contemporary evolution induced by climate change. Formulating evolutionary projections thus requires a mechanistic understanding of linkages between climate and components of micro-evolution, such as levels of genetic variation and the strength, direction and mode of climate mediated selection.

For decades, animal scientists have used the breeder's equation (Falconer & MacKay 1996) to predict the evolutionary response of a quantitative trait to artificial selection. A derivation of this model allows evolutionary biologists to predict the evolutionary response of phenotypic traits to natural selection (Lande 1979). Contemporary levels of genetic variation in ecologically relevant traits can be quantified (Réale & Festa-Bianchet 2000, McAdam et al. 2002) but the absence of studies examining the effects of climate on the expression of genetic variation in these traits limits our ability to anticipate the potential for evolution under future climate scenarios.

Identifying clear linkages between climate and phenotypic selection also poses a substantial challenge. For example, while selection for earlier spring breeding in red squirrels *Tamiasciurus hudsonicus* was associated with a decadal increase in spring temperatures (Réale et al. 2003), concomitant increases in food abundance confounded a clear linkage between increases in spring temperature and selection on breeding date. Unambiguously identifying environmental mechanisms of adaptation requires experimentation (Endler 1986, Wade & Kalisz 1990), which poses serious logistical hurdles for populations of free ranging mammals and a putative selective agent such as climate. Even in some of the most actively studied vertebrate populations, future evolutionary changes have been notoriously difficult to predict (Grant & Grant 2002).

To summarize, using past evolutionary responses of mammals to climate change as a means of forecasting future evolution is not realistic because of the many new variables that can play a role (Constraint 1). In contrast, predictive models based on general evolutionary principles do offer opportunities for rough predictions (Berteaux et al. 2004). The main limitations to increasing the precision of these predictions will always include the difficulty of adequately defining boundary conditions of models (Constraint 4).

4. CONCLUSIONS

Constraints to the anticipation of climate change effects on mammals are varied, and we believe that making them more explicit would benefit future research. Predictive models are preferable because climate change will quickly bring average and extreme annual values out of the observed range, so that forecasting without extrapolation will be unfeasible.

Yet correlations between large-scale climatic variability and mammal populations can be used efficiently in several ways. First, observed patterns generate testable hypotheses and thus seed predictive models (see this issue, Saitoh et al. 2006, Tkadlec et al. 2006). Second, observed patterns can be used to test ecological hypotheses through natural experiments. However, this testing approach must be set apart strictly from the *a posteriori* correlational approach. Third, forecasting offers the safest route to anticipation of events occurring over the short-term and across large spatial scales when one deals with complex, multi-species and poorly known systems. For example, a regression model between annual changes in population abundance and dry season rainfall has projected near extirpation of 3 ungulate species from South Africa's Kruger National Park, should the 1977–1996 climatic conditions recur (Ogutu & Owen-Smith 2003). No concurrent predictive model exists to build sound predictions.

When faced with the difficult task of understanding and anticipating the ecological effects of climate change, we are too often forced to rely on conceptual and poorly validated models which are only able to generate vague projections (e.g. Derocher et al. 2004). Hopefully the increased demand for practical applications of ecological projections will weed out unfit models more quickly (Ginzburg & Jensen 2004). But humility is no doubt required for ecologists trying to anticipate climate change impacts on ecosystems (Krebs & Berteaux 2006, this issue), as shown in a detailed example in this issue of Climate Research (Weladji & Holand 2006, this issue). A better understanding of the routes that lead to scientific projection in this field is one key to future progress.

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