



INTRODUCTION

Measuring, understanding and projecting the effects of large-scale climatic variability on mammals

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An outburst of climate-related research has occurred in the field of ecology during the last decade; its goal is to better measure, understand and project ecosystem responses to our planet's changing climate. The practical outcomes of this science fall into 2 categories. (1) The ecological effects of climate change grab the attention of the public and thus influence climate management decisions (Walther et al. 2005, Schlesinger 2006). (2) Scientific work on climate and ecology may feed into the further development of strategies for the sustainable management of biodiversity, protected areas, or ecosystem services (IPCC 2001, Lovejoy & Hannah 2005, MEA 2005, Lovejoy 2006).

The more than 5400 species of mammals (Wilson & Reeder 2005) are a highly visible fraction of today's biodiversity and many mammals are important components of ecosystems. Not surprisingly, many mammalogists have recently directed their attention to the relations between climate and mammal populations. Mammals are prime study organisms for addressing several questions on the ecological effects of climatic variability because they occupy most ecosystems, and their economic value is such that long-term datasets describing fluctuations in numbers now exist for many populations.

Symposium on climate and mammals

A symposium entitled 'The effects of large-scale climatic variability on mammals' was held at the 9th International Mammalogical Congress in August 2005 in Sapporo, Japan. The symposium brought together empirical ecologists who evaluated the state-of-the-art

regarding this field of research. There are 3 main patterns of large-scale climatic variability: directional climate change (e.g. global warming), periodic fluctuations in climate (e.g. the El Niño Southern Oscillation, ENSO) and non-periodic, non-directional fluctuations in climate. All of these forms of climatic variability have been shown to affect the population ecology of some mammals. Effects of past and current climatic variability on mammals are our main source of information to understand the impacts of climate change on this group. We urged Symposium participants to think about the successes and failures they have encountered when trying to anticipate the future effects of climate change.

Mammal studies represent a substantial fraction of research investigating the ecological effects of large-scale climatic oscillations such as the North Atlantic Oscillation (NAO) and ENSO (Fig. 1). As shown in the following papers, highly sophisticated statistical techniques are now developed to link climatic fluctuations to population dynamics. This generates detailed descriptions of patterns and a plethora of exciting mechanistic hypotheses. Switching from descriptions and hypotheses to projections of climate-change effects is, however, a major challenge, and a sense of frustration emerges when this is attempted. The reason is that mammals have evolved powerful mechanisms to regulate their body temperature and have thus evaded some of the direct influences of climate. Instead they interact with climate mostly through indirect and complex pathways involving their food, predators, and habitats (Schneider & Root 2002). Mammals, in contrast to e.g. plants, are poorly represented in climate change studies (Fig. 1).

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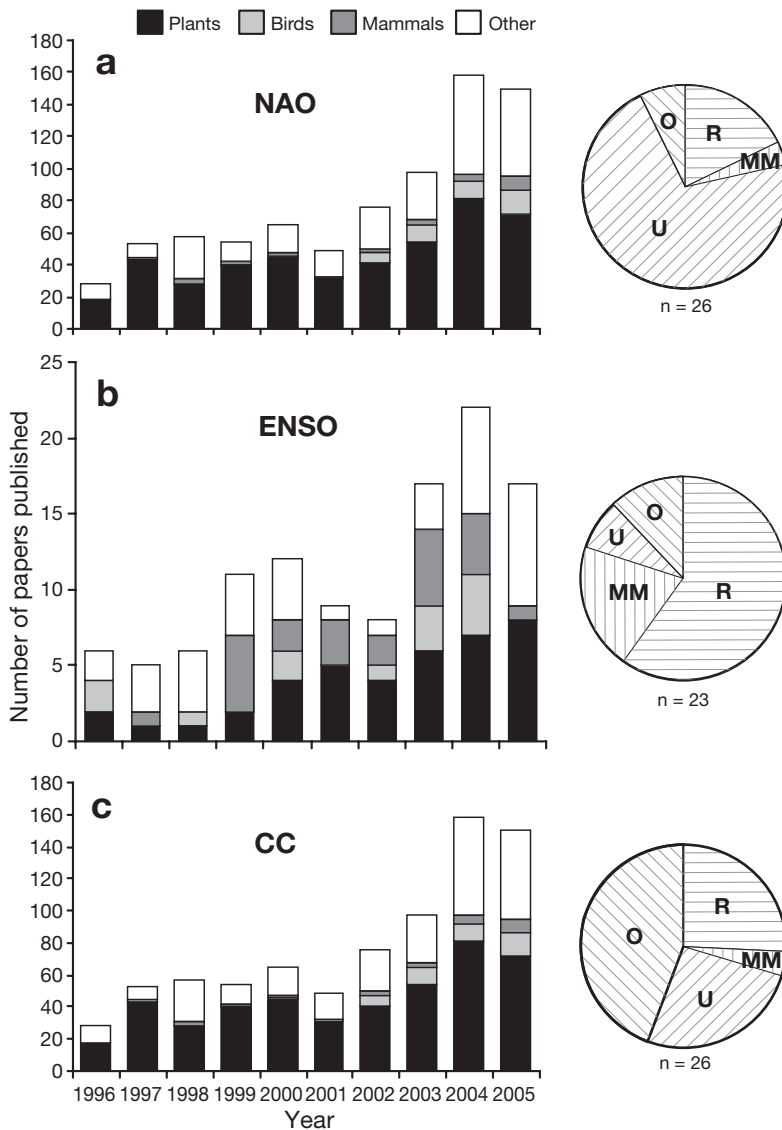


Fig. 1. Frequency distribution of published papers involving plants, birds, mammals and other taxonomic groups that relate to (a) the North Atlantic Oscillation, (b) the El Niño Southern Oscillation and (c) 'climate change', 1996–2005. We searched 16 major ecological journals (The American Naturalist, Annales Zoologici Fennici, Ecography, Ecological Monographs, Ecology, Ecology Letters, EcoScience, Functional Ecology, Global Change Biology, Global Ecology and Biogeography, Journal of Zoology, Oecologia, Oikos, Population Ecology, Proceedings of the Royal Society of London B, Trends in Ecology and Evolution) for papers dealing with large-scale climatic variability, using Web of Science® and the following key words: 'NAO or North Atlantic Oscillation', 'ENSO or El Niño or El Niño' (for El Niño Southern Oscillation), and 'Climate change' (CC). Pie charts indicate proportions of different mammal groups within the mammalian subset of the literature we found. R: rodents, MM: marine mammals, U: ungulates, O: other taxonomic groups

Overview of studies

Papers published in this issue reflect well the state of the art regarding research into the effects of large-scale climatic variability on mammals. Great efforts are devoted to describing patterns linking climate variability to mammals, some fieldwork is done to disentangle cause-effect relationships and there are few success stories regarding our capacity to anticipate. All papers in the series deal with rodents and ungulates, which reflects well the predominant role played by these 2 groups in the science linking climatic variability to mammals (Fig. 1).

The contributions by Tkadlec et al. (p 99–108, this issue) and Saitoh et al. (p 109–118, this issue) both use time series of climatic indices and various parameters of mammalian populations to describe some of the

complex relations between mammals and climate. They highlight both the usefulness of climatic indices such as the North Atlantic Oscillation (NAO) and the Aleutian Low Pressure Index (ALPI), and the ecological importance of interactions between climate, mammals and their resources and predators. Both papers are important in that they generate hypotheses linking climate and small herbivores, which in many parts of the world (in these examples, the Czech Republic and Japan) become pests when populations are abundant. They are also important in that they remind us of the usually indirect pathways through which mammals interact with climate.

Weladji & Holand (p 119–127, this issue) offer a dramatic example of the links between climate research, ecology, policy and (lack of) predictability. In a study of reindeer in Norway, they show that, although local and

global climate clearly affect reindeer through a variety of direct and indirect pathways, it proves difficult to predict even a general pattern of how future climate change will influence this species. Reindeer husbandry is a critical economic and cultural activity for the Saami People, but it is currently impossible to anticipate the practical and socio-economic implications of climate change for the reindeer husbandry industry.

Because of the complex sets of variables needed to describe both climate and population dynamics, it is no surprise that attempts to link climate to population dynamics generate heated debates about model building and interpretation. For example, Jacobson et al. (2004) examined a 45 yr time series of annual counts of alpine ibex *Capra ibex* in the Gran Paradiso National Park, Italy. Yearly changes in population size were correlated with seasonal average snow depth and population density over 39 yr. Ibex population size seemed to be limited by both density dependence and deep snow. A threshold model based on these factors and fit to the first 19 yr of data predicted an increase and subsequent decline in total population size over the final 20 yr of the study, but failed to reproduce population levels after the phase of population increase.

In this CR Special, Lima & Berryman (p 129–135, this issue) reanalyze the Alpine ibex dataset and uncover a non-additive and nonlinear interaction between climate and density. Their resulting models predict ibex numbers as well or better than previous threshold models, but with fewer parameters. The signal of the interaction between density dependence and snow cover in the ibex counts is thus strong enough that models with very different structures can represent it. However, Jacobson et al. (p 137, this issue) and Yoccoz & Gaillard (p 139–141, this issue) offer a caution regarding interpretation of the results provided by Lima & Berryman, and highlight the importance of considering the effects of age structure on population dynamics.

The focus of the symposium on predictability generated both excitement and frustration. Krebs & Berteaux (p 143–149, this issue) highlight the problems and pitfalls in relating climate variability to population dynamics. They argue that, although analyses of ecological time series after the fact (such as most examples discussed above) allow development of hypotheses, critical tests of climate-based population models can

occur only with proper experiments. Ecological relationships involving climate are typically scale dependent and multi-factor, and experiments are thus notoriously difficult to implement. This no doubt explains why current progress is made mostly through the analysis of time series. In a collective work originating from the Symposium and concluding this series, Berteaux et al. (p 151–158, this issue) start from the premise that while most papers and grant proposals related to climate claim relevance to projecting future effects of climate change, the steps leading from ecological description and understanding to reliable projection are rarely explicit. Building on numerous examples from the mammalogy literature, they remind us that all projections originate from correlative or causal models (or a mix of both), and show how this generates the various constraints to our ability to anticipate.

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