AS WE SEE IT

Problems and pitfalls in relating climate variability to population dynamics

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ABSTRACT: We discuss 3 methodological issues involved in climate-population dynamics research. Precise alternative hypotheses are the first requirement, and correlational studies are the weakest way to test the multiple working hypotheses required. Large-scale effects are difficult to investigate because of heterogeneity in environmental variables, and long-term predictions require more patience to test adequately. Multifactorial hypotheses are required for the investigation of climatic effects but these are too often vague and qualitative. Complex computer models can almost never be empirically validated and their predictions should be carefully examined. We illustrate these problems with 3 case studies: snowshoe hares in Canada, desert rodents in Arizona, and red kangaroos in Australia. Correlations abound but mechanistic understanding is limited because of long causal chains and indirect effects.

KEY WORDS: Population dynamics · Hypothesis testing · Manipulative experiments · Mammals · Desert ecosystems

1. INTRODUCTION

Climate affects the distribution and abundance of mammals; the impact of climate change on ecosystems is the most critical problem of this century.

In order to begin understanding the effects of climate change on mammals we need to determine specifically the mechanisms, magnitude and frequency of climate changes that affect their populations. We need specific mechanistic hypotheses in order to translate climatic effects into population dynamics. For example, what are the effects on birth rates or death rates? Do they affect all age and sex groups in the population? Are negative effects an annual event, or sporadic? And in the long-term we need to address the issue of genetic adaptation in populations to climatic variables.

In this paper we firstly discuss the methodological issues involved in climate–population dynamics research, after which we present and discuss 3 case studies in which climatic variables affect populations of mammals, in order to illustrate some of the problems and pitfalls facing these studies.

2. METHODOLOGICAL ISSUES

2.1. Selecting an appropriate scientific approach

Correlational studies are a key part of ecological research but they suffer from a massive confounding of variables even in relatively simple ecosystems. Climate can be described using a very large number of variables. If one tests 10's to 100's of correlation hypotheses comparing climate and population parameters, 1 or more sets are certain to be highly correlated at a statistically significant level. Exploratory data analysis can be quite useful in discovering an unsuspected relationship, and we do not wish to dis-

pense with correlational studies in climate research, because they can generate hypotheses that can be tested with further data. Nevertheless, the track record for hypotheses derived from correlations is not particularly good. The last 50 yr of ecological research has demonstrated that highly significant correlations of demographic and climatic data are often invalidated by subsequent testing (e.g. Myers 1998).

The resulting uncertainty has led to an emphasis on experimentation as a preferred approach to developing understanding. Since we cannot manipulate climate, all our experiments must be observational. The key successful experiment design is to consider 2 or more detailed mechanistic models simultaneously. In retrospect it may turn out that the best model was not among the alternatives being used, but that is a standard problem in all scientific work in which we try to rank competing hypotheses as more or less consistent with the observed data (Hilborn & Mangel 1997).

There are 2 problems inherent in the multiple working hypotheses approach championed long ago by Chamberlin (1897), and discussed at length by Hilborn & Mangel (1997).

(1) You must have good quantitative data. Ecological methods are often imprecise, particularly if variables are considered at landscape scale. Standardization of methodology is difficult in field studies in which the human skill element is present but unmeasured. If 2 members of a research team set out to trap small rodents, one may catch many and the other few, only because of differing skill in setting the traps, even if they have both been given the same training. Additionally, live traps can have highly variable success because of differences in trap design and bait, or between target species.

(2) Precise alternative hypotheses are usually present only in advanced stages of a study and often apply only to secondary questions. For example, we have elegant methods to decide if survival varies with age, sex, or any climatic covariate in mammals, but the important issue would be to decide whether the climatic covariate for winter survival is total winter snowfall, maximum winter snow depth, average winter temperature, or extreme winter temperature (among other possibilities). It is important to specify precise climatic hypotheses rather than vague ones.

Aggregated climatic indices such as ENSO or the NAO can be used as surrogates of combined climatic effects (Stenseth et al. 2003), but there are advantages and disadvantages of this approach. The use of aggregated climatic indices can make it even more difficult to determine the mechanistic processes by which climate affects mammal populations. In a few simple systems, such as the Soay sheep (Coulson et al. 2001), the causal trace may be well understood. We do not yet know if such simplicity will apply to most other mammals. The key issue with all climate models is not how well they fit past data, but rather how predictive they are of future observations.

Hypotheses can arise in a variety of ways: (1) from description patterns and guessing what might cause them, (2) from analyzing past climates and their effects through paleoecological methods, or (3) from guessing about effects from knowledge of well-studied physiological processes. Any survey of current literature reveals a plethora of hypotheses available for testing.

2.2. Climate effects and the issue of scale

Geographic and temporal scale is a major issue with climate effects. One may be interested only in events at the local scale, in which standard experimental methods can be employed. The most interesting questions that face ecologists, however, are those dealing with climatic variation at larger scales (Callaghan et al. 2004), and thus in the present discussion we concentrate on how to test large-scale, long-term ecological hypotheses.

The study of large-scale effects such as changes in geographic distribution and abundance on a regional or continental scale, or extinctions that might result from shrinking populations, faces serious logistic difficulties. When dealing with issues of scale it is important to define a set of predictions with specific mechanisms and alternative hypotheses. Predictions are essential both for observational and manipulative experiments, and represent the key distinction between productive observational experiments and less useful correlational studies. Predictions must always precede data analyses, since making predictions after the fact, although it be independent of data collection, is always suspect, as there is no guarantee that trends in data set have not influenced their formulation.

Large-scale studies raise difficult heterogeneity issues, since large sections of habitat are always different in community composition, soil type, and other variables. There are 2 ways to resolve the heterogeneity problem in large-scale studies. (1) Ignoring it, with the assumption that if climate effects are large enough, they will be visible even in heterogeneous landscapes, and accept that small scale, subtle effects will certainly not be discovered at large spatial scales with aggregated data. (2) Using the heterogeneity to address mechanisms of climate effects. For example, in cold climates snow depth may affect ground level insulation and the potential survival rate of overwintering rodents. If there is regional variation in snow depth, one can use regional data to test for this effect by waiting for high-snow and low-snow years. But it may be

more precise to select within the larger region habitats or slopes that have microclimates with differing snow depths, and to measure survival within these patches. By converting regional hypotheses into smaller scale, local questions we might be able to streamline the modelling process.

Long-term questions are the most difficult of all issues to deal with in ecological systems. There are 4 potential ways to deal with these.

(1) To 'go back in time' (i.e. utilize historical records and paleontological data) and search for 'natural experiments' that have effectively already tested our hypotheses. Time has erased detailed evidence of past population dynamics, but fossil deposits can shed light on general hypotheses at large temporal and spatial scales (Barnosky et al. 2003). This is an important approach that can be used where good fossil beds are present, and will provide an opportunity to test some of the more general hypotheses about climate change.

(2) To make predictions and accept that we may have to wait a few decades before testing them. This approach is useful and important but will be viewed by most ecologists as an unsatisfactory time lag if management actions are required. The key question is how many years it will take to identify a clear climate signal in mammalian communities. Given the 30 yr it has taken to confirm the Earth's climate change, this cannot be a preferred methodology. However many population monitoring programs are maintained for management or conservation purposes, and they should certainly include detailed monitoring of local climatic variables.

(3) To dissect long-term hypotheses into shorter-term ones and test sub-hypotheses independently. This reductionist approach has its own pitfalls, however. Unless we can re-build the whole system from the sum of the reductionist parts, we may lose the ability to answer the key questions that initiated our search. However, this could be a most important approach if it was properly organized as a tightly-coordinated team effort that worked towards a long-term climate hypothesis.

(4) To substitute space for time. It is tempting to assume that populations in cooler areas will become similar to those in warmer areas as climatic warming occurs, so that spatial studies can be used to predict how temporal changes will occur in the ecosystems of cooler areas. However, this can work only in ecosystems where we can simply project the past onto the future in a manner that assumes a smooth series of changes with no thresholds or break points. Such ecosystems may be rare. If, however, we understand the mechanisms behind spatial variation, we might be able to carry out this substitution.

2.3. The multifactorial nature of climate effects

A further complication with hypotheses of climate effects on population dynamics is that these hypotheses will almost always be multifactorial. Multifactor hypotheses in ecology have a history of being vague and qualitative, so that it may be impossible to decide whether or not they are useful. We expect there to be an interaction between climatic changes and predation levels on a herbivore, or between climatic changes and food plant quality and quantity, complete with indirect effects, so that the result is a multifactorial hypothesis that is easy to visualize but difficult to test. Nevertheless, it is critical to devise such tests if we are to progress.

One way to test complex hypotheses, which is being used extensively, is with computer models that match climate predictions with distribution and abundance (Huntley et al. 2004, Seoane et al. 2004). It seems necessary to remind ecologists that most of these complex models have never been empirically tested, and we should view their output as possible scenarios or forecasts, rather than as firm predictions of future changes (Thuiller et al. 2004).

We prefer simple hypotheses and simple models that provide insight into an ecological system, but this does not mean that complexity should be avoided. The key is to devise hypotheses that are as simple as possible, given the knowledge of the ecological system under study and the questions being addressed. Natural systems are complex but we should not begin with complex hypotheses until we have tested simpler ones.

3. CASE STUDIES

We illustrate the problems described above with 3 case studies of climate effects on mammal populations. Each of these studies began with a simple hypothesis of how climate affects demography, and they illustrate how simple initial hypotheses have to be translated into more complex, specific multifactor hypotheses to further ecological understanding and to be consistent with the observed data. All of these case studies are at a local scale and of medium-term timescales.

3.1. Snowshoe hares in Canada

The snowshoe hare *Lepus americanus* is a keystone species in the boreal forests of North America (Krebs et al. 2001). Their populations fluctuate in 9–10 yr cycles, and one of the drivers of these cyclic changes is reproductive output. Females breed only after they reach 1 yr of age, and have 2–4 litters over a single summer breeding period. Total summer reproductive output
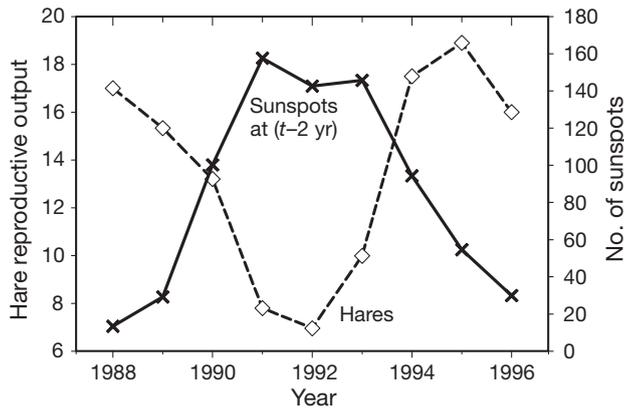
Fig. 1. *Lepus americanus*. Reproductive output (no. of young) of adult female snowshoe hares during a 10 yr population cycle in the southern Yukon. Data on hares from Stefan & Krebs (2001); sunspot numbers from www.ngdc.noaa.gov/ stp/SOLAR/ftpsunspotnumber.html

varies 2-fold over the population cycle (Fig. 1). The cause of this variation is not clear (Stefan & Krebs 2001), but it is highly correlated with sunspot numbers with a 2 yr time lag. This could be spurious, but there are data for snowshoe hares from northern Alberta from 1962 to 1976 (Cary & Keith 1979) with exactly the same pattern. In addition, the population dynamics of at least one other rodent population (North American porcupines in Quebec) is correlated with sunspots (Klvana et al. 2004). Nevertheless with only 3 studies performed on 2 species, one hypothesis might be that these are spurious correlations.

If the relationship between sunspots and hare reproductive output is real, there may be 2 possible mechanisms. Sunspots affect the weather, and in northwestern Canada snow depth is correlated with sunspot numbers. Snow depth might affect two biological processes: food supplies and lynx hunting behaviour. Food in turn will affect hare nutrition, which could affect reproductive output. Alternatively, predation could affect hare stress levels, which in turn could affect hare nutrition or hare reproduction directly (Boonstra et al. 1998). Which mechanisms are actually operating remains to be clarified, but it is noteworthy that the correlation between sunspot numbers and porcupine population dynamics is also mediated by snowfall.

The key point from this example is that climate effects on snowshoe hare demography are indirect and the causal chain must be specified before we can test the mechanisms of response.

3.2. Desert rodents in Arizona

Populations of desert rodents should be a simple model for deciphering climate effects on populations,

but in fact they have turned out to be more difficult than anyone would have predicted 20 years ago. The ecological model for these populations is simple: abundant rainfall increases plant growth and seed production, producing more food for rodents, and their populations grow. The prediction is that, with suitable time lags of a few months, rodent population densities and rates of increase should be closely associated with rainfall amounts.

This has turned out not to be correct. Jim Brown and his students have been following the desert rodent community in central Arizona for >23 yr (Brown & Earnest 2002); 4 main rodent species occur in the study area, and all of them fluctuated dramatically over the long-term study. Contrary to expectation, the correlation of rodent abundance with rainfall did not remain high, as more data accumulated, but completely failed after 22 yr (Fig. 2).

Why should this be? Brown & Earnest (2002) suggest several reasons. (1) The timing of rainfall is critical in desert systems, and aggregate measures of total rainfall are not precise enough to predict plant responses to rainfall. (2) Too much rainfall may be detrimental if it leads to flooding of burrows. (3) The rodent community is a multispecies system and the competitive interactions between the different species, as well as those with other seed eaters such as ants, are not understood. (4) The effects of predators on rodent abundance have not been taken into account. The bottom line is that no one doubts the truth of the basic general model that rainfall drives plant production and plant production drives rodent numbers, but the details of exactly how this works are still unclear. The basic linear model can be rejected (Fig. 2), and this has implications for simple models that attempt to predict rodent abundance as a result of rainfall events in these desert ecosystems,
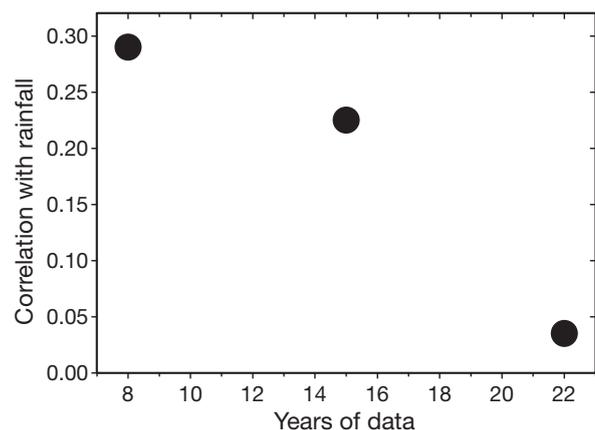

Fig. 2. Average correlation coefficients (r) for the association between rodent abundance in southeastern Arizona and rainfall over 6 mo periods for 3 windows of time spanning 8, 15 and 22 yr. After Brown & Earnest (2002)

and the subsequent transmission of hantavirus from rodents to humans in the southwestern USA (Mills et al. 1999).

Similar studies on South American desert ecosystems face the same difficulties reported by Brown & Earnest (2002). Populations of the leaf-eared mouse *Phyllotis darwini* in Chile are also expected to rise and fall with rainfall events in their desert habitat (Lima et al. 1999), but a simple rainfall model provides poor predictions of changes in abundance, in spite of the established belief that rainfall is the key variable in desert ecosystems.

3.3 Red kangaroos in South Australia

Red kangaroos *Macropus rufus* occupy arid and semiarid areas, and they are a large mammal analogous to the desert rodents of Arizona. Red kangaroos are grazers and effectively have no predators because of extensive dingo control. Changes in their population are thought to be driven by the same model discussed above: rainfall—forage supplies—abundance. Studies of red kangaroo populations in South Australia illustrate the problems of validating climatic models even for simple systems (Caughley et al. 1987).

Cairns & Grigg (1993) assumed that rainfall determined pasture biomass and fitted a numerical response to data from South Australia. Fig. 3 shows the relationship between the rate of population increase and the rainfall for 1974–1984. Rainfall is highly variable in South Australia, and a severe drought occurred in 1981 and 1982. Rains returned in 1983 and populations

began to increase. While no one seems to doubt the simple climate model for red kangaroo populations, it is clear from Fig. 3 that as a predictive model it is far from useful. The data gathered from 1985 to 1988 do not fit the line derived for earlier data (1978–1984) with 6 of the 12 points outside of the 95% confidence belt for the regression.

Why should this be? If the overall rainfall model is assumed to be correct, 2 possibilities exist. (1) Age and sex composition of the red kangaroo population differs dramatically in the years before and after a drought. Mortality during drought mostly affects juveniles and adult males, so that after a drought the age structure could be weighted in favor of fecund females, which would increase the population's growth rate. (2) Composition of the plant community may differ greatly before and after a drought, and consequently food resources may be qualitatively different for the same levels of summer–autumn rainfall (Cairns & Grigg 1993). Jonzen et al. (2005) reanalyzed the red kangaroo dynamics with a more complex model that included rainfall, harvesting, intraspecific competition, and interspecific competition with sheep, and found the best model could explain from 7 to 60% of the variation in kangaroo numbers. They concluded that estimating resources by surrogate measures like rainfall is more difficult than previously assumed.

The key point from this example is that climate effects on red kangaroos are indirect and mediated by intrinsic processes of birth, death, and age structure, as well as by primary production. The mechanistic causal chain must be specified in more detail before we can predict responses to climatic variation (Jonzen et al. 2005).
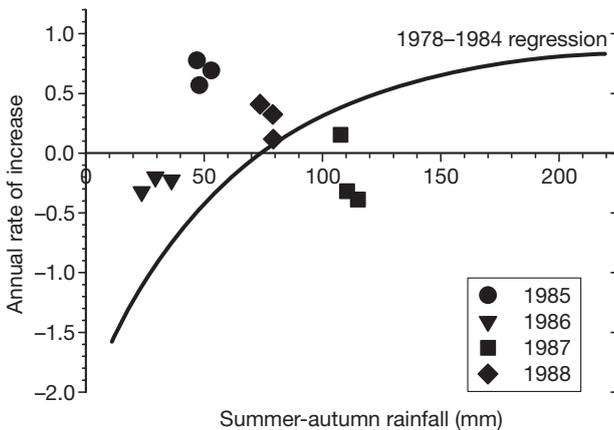
4. DISCUSSION

While no one doubts the general hypothesis that climate affects mammal population dynamics, the surprising fact is that the causal chains have proven difficult to unravel even in relatively simple arid and semi-arid ecosystems. This difficulty parallels experience with other taxa. For example, Myers (1998) analyzed recruitment in fish populations, which is typically postulated to be set by climatic conditions. In 74 published examples of environment–recruitment correlations, only 38% were subsequently validated with retest data, and, of the 42 previously published correlations, he could find only 1 that was actually used in fisheries management. This is the first pitfall in correlating climatic conditions with population dynamics—all climatic correlations must be replicated. The standard method of using only part of a dataset to establish a climatic hypothesis and the remaining part of the

Fig. 3. *Macropus robustus.* Annual rate of population change for the red kangaroo in the western part of the South Australia pastoral zone (89 900 km^2) for 1978–1984 (solid line) and subsequent data obtained for 1985–1988 (symbols). The data points for each year represent 3 kangaroo management zones, varying in size from 24 000 to 39 000 km^2. Data from Cairns & Grigg (1993)

data to test it, while good in principle, should be suspect in practice, because it is a weak form of inference, and in good, evidence-based science we should require validation by independent research data. The essence of good climate science is prediction, not postdiction.

Climate can affect mammal populations directly, e.g. by excessive temperatures or rainfall, but this is rare and the effects are usually indirect. These could be either bottom-up effects on food plant productivity or top-down effects on predator efficiency. All of these effects can be understood only if we have unraveled the causal linkages from climate variables to changes in birth and death rates. This is an important task, and will take time, because it requires an understanding of food web dynamics. Meanwhile we will have to make do with a host of correlational studies. One shortcut to developing models for predicting population changes in response to climate is to use density dependence as a surrogate for mechanisms (Sæther et al. 2004). This strategy will not work for predictive models, because every population of the same species shows a different density dependent relationship (Krebs 2002), so there is no predictive generality in the exact shape of this relationship. Climate change may have an effect on distribution and abundance of mammal species. Distributional changes that inject a new species into an established community can change predator–prey interactions as well as competitive relationships. A simple example is the northern expansion of the moose *Alces alces* into northwestern Canada, which has resulted in increased numbers of wolves *Canis lupus* and reduced survival of woodland caribou *Rangifer tarandus caribou* (James et al. 2004). Distributional changes thus translate into abundance changes affecting ecosystem function. The effects of climate change may be more easily seen at the level of distributions affecting community composition, and it is important not to stop at the descriptive stage of producing a geographical map of distributions changing over time, but to follow these changes as they lead into changes in abundance.

Changes in climate that affect geographic distributions are a major focus of modeling at present (Huntley et al. 2004). These models are predictive only on the assumption that geographic ranges are currently limited by climatic variables and are in equilibrium with the current climate. Empirical studies that show range extensions towards the north in the Northern Hemisphere (Parmesan & Yohe 2003) confirm this model for some species, but leave many other species unaccounted for. Changes in geographic distributions may or may not signal changes in abundance, and it is the changes in abundance that are critical to community and ecosystem dynamics at a local level.

Understanding the effects of climate change on bird and mammal populations requires ecologists to analyze how climate change will affect distribution as well as abundance. It may appear easier to make predictions about distributional changes if they are limited by climate, but this is an illusion. For many mammal and bird species the key questions concern habitat changes in plant community composition and structure, and the changes this will entail for herbivore populations, and ultimately for carnivore populations. How communities shifted at the end of the Wisconsin Ice Age may give some guidance, but the rates of change may be too rapid to make this analogy very useful as a guide (Lyons 2005). More importantly, habitat fragmentation has increased dramatically during the last centuries, which further complicates the usefulness of analogies in the past.

It is possible that we will gather the information needed to understand climate effects on distribution and abundance without ever being able to make predictions about future changes. In light of our poor ability to predict the consequences of climate change, our best short-term strategy is to measure and try to understand the observed small-scale changes in population parameters without pretending to be able to predict long-term consequences. We can model future scenarios, but we should be careful to recognize their hypothetical nature. Similar problems exist in natural resource management planning, and the limited success of weather forecasting in the presence of strong physical laws should humble ecologists who wish to make predictions of the effects of climate change on ecosystems (Sarewitz et al. 2000).

5. CONCLUSIONS

Climate influences the population dynamics of mammals — this is a tested hypothesis. The issue is rather a quantitative one: what specific effects do short- and long-term changes in climate have on the demography of a particular species? The first rule of climate change ecology must be: state a specific, detailed, mechanistic hypothesis. Much of our understanding at present comes from the analysis of ecological time series after the fact. These analyses all rest on the fundamental assumption that statistical correlations detect ecological cause-and-effect relationships, and this critical assumption cannot be tested by the popular evaluation of alternative models with AIC (Akaike's Information Criteria).

The central issue is that climate can be disassociated into a very large number of parameters, and if enough correlation hypotheses are tested, one or more will certainly be highly significant *a posteriori*. At best we can use these methods to develop hypotheses in an

inductive framework. The difficulty comes when we believe these hypotheses without critical testing by means of appropriate experiments. For the most part, manipulative experiments are logistically impossible. Observational experiments must be based on simple hypotheses, so that they may provide an adequate scientific test. We must avoid complex hypotheses, unless we can specify distinct predictions from alternative complex hypotheses.

Complex hypotheses with predictions tens of years ahead are fairy tales. There is no limit to ecologists' ability to explain events after the fact, and without rigorous scientific constraints, we will be little more than storytellers.

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