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FORUM

Weather packages: finding the right scale and composition of climate in ecology

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Summary

1. Animals are affected by local weather variables such as temperature, rainfall and snow. However, large-scale climate indices such as the North Atlantic Oscillation (NAO) often outperform local weather variables when it comes to explain climate-related variation in life history traits or animal numbers.
2. In a recent paper, Hallet *et al*. (2004, *Nature*, **430**, 71–75) document convincingly why this may happen. In this perspective, we identify from the literature three mechanisms why this is so: (1) the time window; (2) the spatial window; and (3) the weather composition component of climate.
3. Such an understanding may be used to derive even better 'weather packages' than the NAO.

Key-words: life history, mammals, migration, North Atlantic Oscillation, population ecology

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Introduction

Any sensible biologist, especially those getting their feet wet and cold while working in the field, would intuitively use covariates such as temperature, precipitation and snow depth whenever the aim is to deduce the climate-related variation in life history traits or animal numbers. No doubt, these are the climatic factors giving animals a good or hard time. Nevertheless, in a recent *Nature* paper, Hallett *et al*. 2004) demonstrate convincingly why global scale climate indices such as the North Atlantic Oscillation (NAO) index may better explain animal performances than the local weather variables biologists often select.

In 1997 (Post *et al*. 1997), the winter index for the NAO (Hurrell *et al*. 2003) – the sea surface pressure difference between the Azores and Iceland for months December through March – was, for the first time, used to explain variation in performance of red deer along the west coast of Norway. At first, the position that a large-scale climate proxy such as the NAO should be a better predictor of ecological phenomena in terrestrial ecosystems than local weather variables, such as precipitation and temperature was met by much scepticism. A follow-up study including some 16 populations of seven species of large herbivores showed that the NAO predicted variation in life history traits and population dynamics better than local climate in about half of the cases (Post & Stenseth 1999). It became difficult to question the predictive power of the NAO. The NAO subsequently became quite popular in ecological studies focusing on how ecology might be affected by climate variation and possibly climate change (Ottersen *et al*. 2001; Stenseth *et al*. 2002; Mysterud *et al*. 2003).

The time window component

What Hallett *et al*. (2004) have done is to convincingly demonstrate *why* the NAO index sometimes better explain animal performance than local weather variables – using the Soay sheep *Ovis aries* from Hirta in the St Kilda archipelago as an example. At high population density, the Soay sheep die in large numbers during periods of severe rainfall in winter due to starvation, caused, in part, by energetic constraints imposed by harsh weather (Coulson *et al*. 2001). Hallett and coworkers demonstrate that as previous studies used monthly values of rainfall (Catchpole *et al*. 2000), which is the most common temporal scale used (Weladji *et al*. 2002), they fail to capture that such incidences of severe rainfall may happen during the entire winter. In contrast, as the NAO is indexed for the entire winter

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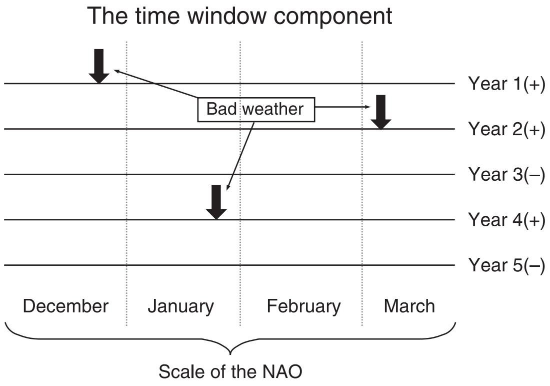

Fig. 1. The time window component of climate (Hallett *et al.* 2004) provides a mechanism for explaining why the NAO may better explain the dynamics of animal populations than monthly averages of local climate. Severe episodes of bad weather can happen during the entire winter and are not restricted to specific months. The sign in parenthesis indicate whether the NAO that year is in a positive (+) or negative (–) phase.

(December–March), the NAO index is a fairly good predictor of whether such a severe spell is coming this winter or not (Shabbar & Bonsal 2003). This is the time window component of climate (Hallett *et al.* 2004; Fig. 1). Indeed, the temporal scale provides an important feature of the link of climate and ecology, and as such explains why indices like the NAO may work better than local variables.

The spatial window component

Earlier we have reported another feature explaining why the NAO give a better predictive power than single site climate variables (Fig. 2). As the NAO is correlated with both increased precipitation and temperature along the west coast of Norway, the effect of the NAO on snow depth will vary according to altitude in heterogeneous landscapes, as altitude is a main determinant of whether precipitation comes as rain or snow (Mysterud *et al.* 2000). High phases of the NAO are thus correlated with less snow at low altitude, and more snow at high altitude. The same principle also applies to increasing latitude. This large-scale geographical feature of the NAO and similar indices explain why performance of migratory deer increase during high NAO values due to less snow in winter areas at low elevation, while more snow in high altitude summer ranges deer are offering deer better quality summer ranges due to an extended period of snow melt (Mysterud *et al.* 2001). We suggest to call this the spatial window component of climate (Mysterud *et al.* 2000, 2001).

The weather composition component

Another feature of the NAO and similar indices is that they incorporate the variation in several climate variables – temperature, precipitation, snow depth, wind speed, etc. It may not be that an animal is responding only to (for example) snow depth or cold temperature. Already in 1924, Elton (1924) noted that 'A good climate, like a good dinner, is more than the mere sum of its separate parts'. This weather-feature integrating aspect relates to what we suggest to call the weather composition component of climate (Elton 1924; Stenseth *et al.* 2003; Mysterud *et al.* 2003; Hallett *et al.* 2004). This highlights that it typically is not only one component

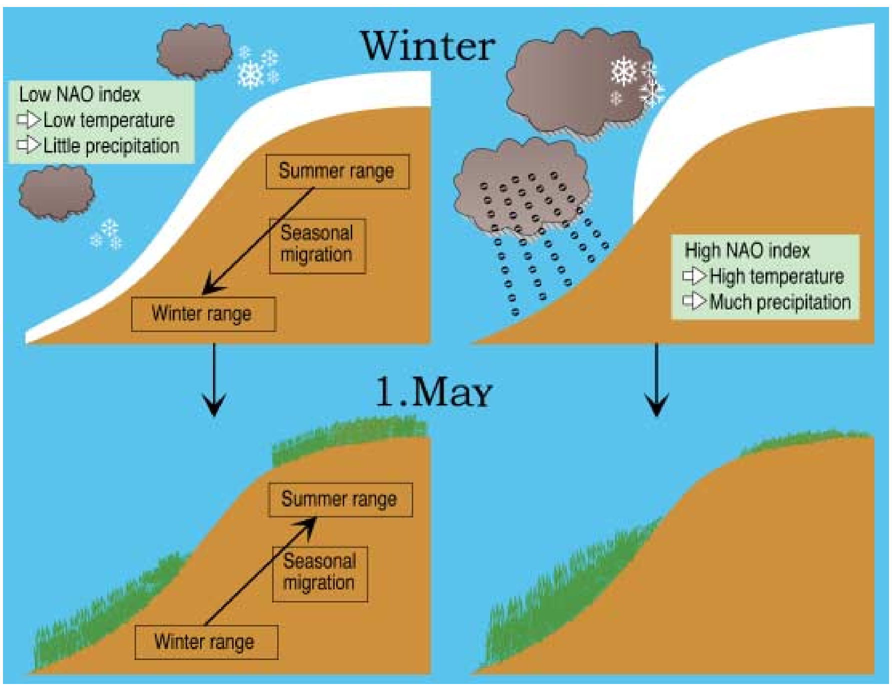

Fig. 2. The spatial window component of climate (Mysterud *et al.* 2000; Pettorelli *et al.* 2005) provides an alternative mechanism for explaining why the NAO may better explain the dynamics of animal populations than local climate at a single weather station (e.g. in weather station 1 or 2 on the figure).

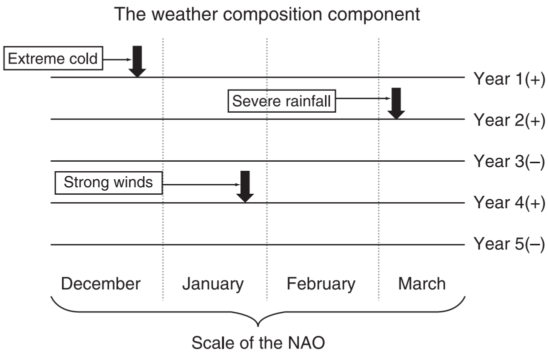

Fig. 3. The weather composition component of climate provides a mechanism for explaining why the NAO may better explain the dynamics of animal populations than averages of single local climate variables. For the Soay sheep (Hallett *et al*. 2004), increased mortality could either be due to severe rainfall, high winds or low temperatures, as they have a similar effect on the energy budget of the animal. The sign in parenthesis indicate whether the NAO that year is in a positive (+) or negative (–) phase.

of the weather that is an important determinant of the ecological processes of interest, but rather an entire package (including their intrinsic interactions) that is relevant to animal performance. In the case of the Soay sheep, increased mortality might be due to high rainfall, high winds or low temperatures or a combination of these (which all correlate with the NAO on St Kilda), as they all put a severe cost on the energy budget of the sheep (Fig. 3; Hallett *et al*. 2004). Hallett *et al*. (2004) is also the first convincing empirical demonstration of this principle. Typically, extreme cold or severe rainfall combined with wind is the more difficult for the animals to cope with (Moen 1973).

Discussion and conclusions

It is an empirical fact that indices such as the NAO often explains more ecological variation than single weather components. We suggest this is due to the fact that the NAO combines – what turns out to be – appropriate temporal and spatial features of several weather components (all of which being appropriately integrated). We are convinced that these are the features making the NAO (and similar large-scale climate indices) an appropriate 'weather package' applicable for several ecological studies (Mysterud *et al*. 2003; Stenseth *et al*. 2003). The study by Hallett *et al*. (2004) provide one important step towards an understanding of why this is so.

In our further efforts to understand how climate affect ecological processes, it is important that we take account of the fact that such climate-driven ecological effects typically are quite complex: organisms move over space (making the spatial window component of climate important); organisms are generally affected over a period of time (making the time window component of climate important); and organisms are typically affected by more than one feature of climate (making the weather composition component of climate important). This is why no single or a simple combination of a few meteorological features often convey less information than a package of weather such as the NAO, an index that empirical observations now demonstrate that integrate these three components (or dimensions) such as to convey ecological interpretable signals. Other packages of weather might certainly outperform the NAO and similar indices. However, to derive such new and better weather packages, much detailed understanding of the system in question is needed. For this reason more mechanistic approaches to understanding variation in demographic rates and how these are influenced by climate is highly recommended.

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