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## Synchronization of animal population dynamics by large-scale climate

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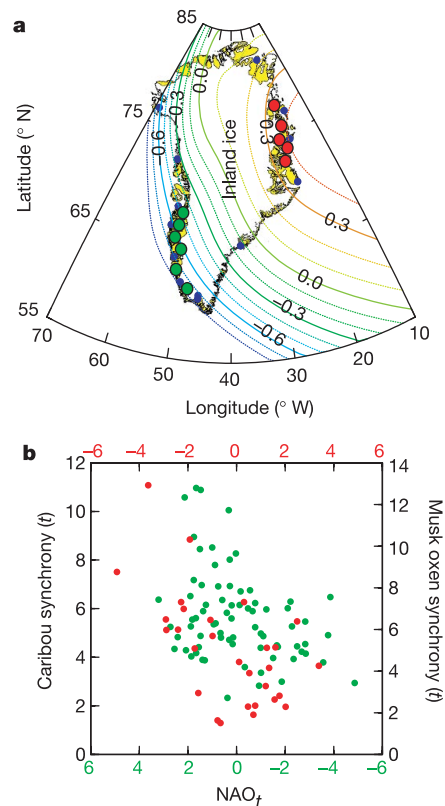
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The hypothesis that animal population dynamics may be synchronized by climate<sup>1</sup> is highly relevant in the context of climate change because it suggests that several populations might respond simultaneously to climatic trends if their dynamics are entrained by environmental correlation. The dynamics of many species throughout the Northern Hemisphere are influenced by a single large-scale climate system, the North Atlantic Oscillation (NAO)<sup>2,3</sup>, which exerts highly correlated regional effects on local weather<sup>4</sup>. But efforts to attribute synchronous fluctuations of contiguous populations to large-scale climate are confounded by the synchronizing influences of dispersal or trophic interactions<sup>5</sup>. Here we report that the dynamics of caribou and musk oxen on opposite coasts of Greenland show spatial synchrony among populations of both species that correlates with the NAO index. Our analysis shows that the NAO has an influence in the high degree of cross-species synchrony between pairs of caribou and musk oxen populations separated by a minimum of 1,000 km of inland ice. The vast distances, and complete physical and ecological separation of these species, rule out spatial coupling by dispersal or interaction. These results indicate that animal populations of different species may respond synchronously to global climate change over large regions.

Despite widespread evidence that several species' populations respond to large-scale climatic fluctuation<sup>2,3</sup>, attributing spatial synchrony in animal population dynamics to environmental forcing is problematic<sup>6</sup>. The correlated dynamics of populations of Soay sheep (*Ovis aries*) on separate islands<sup>7</sup> is strongly indicative of spatial coupling by climate, as is the segregation of the structural dynamics of Canada lynx (*Lynx canadensis*) populations into regions experiencing similar climatic regimes<sup>8</sup>. But the high degree of gene flow among the lynx populations indicates that there is also a high degree of dispersal among them<sup>9</sup>. The pervasive influence of the NAO<sup>10</sup> in the population dynamics of vertebrates throughout

the Northern Hemisphere<sup>2,8,11–13</sup>, including Soay sheep<sup>13–15</sup> and Canada lynx<sup>8</sup>, suggests that the NAO has the potential to contribute to spatial synchrony across broad geographic scales in these and other populations<sup>16</sup>. The challenge therefore lies in identifying systems in which the climatic signal in population synchrony is not obscured by dispersal or trophic interactions.

We have analysed continental-scale data on the long-term dynamics of caribou (*Rangifer tarandus*) and musk oxen (*Ovibos moschatus*) in Greenland, where a continent-wide ice sheet separates the two species physically and ecologically (ref. 17 and Fig. 1a). Caribou are indigenous to west Greenland but do not inhabit northeast Greenland, where musk oxen are indigenous (Fig. 1a). Although time series data on population dynamics exist for seven caribou and six musk oxen populations in Greenland, our analysis focuses primarily on six caribou and five musk oxen populations whose dynamics are influenced by the NAO (Methods). The physical isolation of these two species, coupled with their lack of interspecific competition for food or shared predators in Greenland, greatly simplifies the analysis of climate-induced synchrony. In addition, evidence indicates that the dynamics of populations of



**Figure 1** Correlations between the NAO and local weather and population synchrony in Greenland. **a**, Spatial gradient in the correlation between local winter temperature and the winter NAO index across Greenland. Contours (interval 0.1) denote correlations between the NAO winter index and average winter (December to March) temperature from 12 weather stations (blue dots) over the period 1967 to 1995. Correlative contours were constructed as described<sup>29</sup> using linear interpolation<sup>30</sup>. Red and green circles show the location of the respective musk oxen and caribou populations used in our analyses. **b**, Correlations between the winter NAO index and synchrony (Methods) across populations of musk oxen (red;  $R^2 = 0.45$ ,  $P < 0.001$ ) and caribou (green;  $R^2 = 0.43$ ,  $P < 0.001$ ) in northeast and west Greenland, respectively. Inclusion of the two populations that are not influenced by the NAO resulted in poorer correlations for both species (Methods). The top x-axis applies to the correlation with musk oxen synchrony, the bottom x-axis applies to the correlation with caribou synchrony; axes are reversed to show the same gradient from cold (left) to warm (right).

both species in Greenland are influenced by the effect of the NAO on local winter temperatures<sup>18</sup>; notably, these temperatures correlate with the NAO index along a spatial gradient across Greenland, from positive correlation on the east coast to negative correlation on the west coast (Fig. 1a). Consequently, any potentially synchronizing influence of the NAO on the dynamics of caribou and musk oxen populations in Greenland should be apparent in a similar spatial dichotomy from east to west.

Among those populations in each species whose dynamics are influenced by the NAO, interannual variation in the degree of spatial synchrony correlates significantly with interannual fluctuations in the winter NAO index (Fig. 1b). Inclusion of the two populations that are not influenced by the NAO weakened this relationship for both species (Methods). Thus, the climatic signal in population synchrony is clearest when examining only those populations that are influenced by climate<sup>1</sup>. The dichotomous influence of the NAO on population synchrony in each species (positive for caribou and negative for musk oxen; Fig. 1b) is in agreement with the dichotomous influence of the NAO on local winter temperatures on opposite coasts of Greenland (Fig. 1a) and suggests that population synchrony in both species is highest after cold winters and lowest

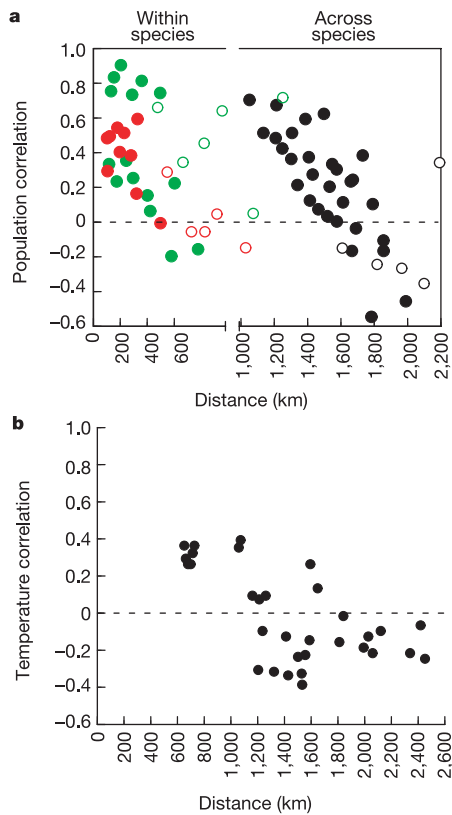
after warm winters. Cold winters might synchronize population fluctuations in each species through increased juvenile mortality resulting, for example, from ice-crust formation<sup>19,20</sup>. Alternatively, increased spatial synchrony of plant phenology after cold winters<sup>13,31</sup> might synchronize offspring production in both species, because timing and synchrony of parturition in arctic ungulates are highly correlated with plant phenology<sup>21,22</sup>.

Population synchrony is also evident in the correlated dynamics among populations of both species, and scatter plots reveal a decline in the degree of pairwise correlation between populations with increasing distance separating them (Fig. 2a). A high degree of spatial correlation is also apparent in local winter temperatures measured at stations along each coast (mean cross-correlation between weather stations, west coast  $r = 0.94$ ; east coast  $r = 0.69$ ). Although these correlations, and those in Fig. 1b, suggest that synchrony among populations in each species may relate to spatial auto-covariation in local winter weather driven by the NAO, we cannot rule out the potential synchronizing influence of dispersal. This seems particularly relevant to the dynamics of caribou, which undertake long-distance migrations; indeed, inclusion of the single caribou population that is not influenced by the NAO reveals fairly high synchrony with some of the other caribou populations (Fig. 2a).

Clearer support for the hypothesis of spatial coupling of these populations by climatic fluctuation is evident, however, in an analysis of cross-species synchrony. Calculation of all possible pairs of cross-species correlations shows that the dynamics of caribou and musk oxen are highly synchronized over a range of considerable distances, from a minimum of 1,000 km up to about 1,700 km (Fig. 2a). At distances beyond 1,700 km, cross-species pairs of populations are increasingly out of phase with each other (Fig. 2a). The largely similar spatial pattern of correlation in local winter temperatures measured at weather stations on opposite coasts of Greenland, including negative covariation at distances greater than 1,700 km, suggests that this population synchrony is attributable to spatio-temporal climatic variation (Fig. 2b).

The results shown in Fig. 2a present a conundrum: the cross-species population correlations of many pairs are higher than the within-species population correlations. We suggest that this may reflect the combined, and perhaps opposing, influences of dispersal and climate on population synchrony in each species. Both caribou and musk oxen migrate seasonally and may disperse under certain climatic conditions<sup>19,20</sup>. The direct climatic influence on population synchrony, operating perhaps through winter mortality, might be distinct from the climatic conditions that trigger long-range dispersal because such movements tend to occur when climatic conditions are favourable for population increases<sup>20</sup>. In addition, intra-species population synchrony might reflect the influence of spatially autocorrelated noise on a more local scale overlaid by that of dispersal and large-scale noise<sup>6</sup>, that is, the NAO. By contrast, cross-species correlation is not, in this example, muddled by local noise or dispersal among populations; nor is it obscured by shared predators or competition because all of the populations are completely separated geographically.

To investigate further the potential synchronizing influence of large-scale climate in cross-species correlations, we applied a technique analogous to the log-response ratio commonly used in meta-analysis<sup>23</sup>. This analysis revealed a highly significant positive correlation between cross-species population synchrony and the magnitude of the effect of the NAO on cross-species pairs of populations (Fig. 3). As Moran's<sup>1</sup> analyses and reiterations of it have shown<sup>24</sup>, the degree of pairwise correlation between any two populations synchronized by climate should scale with the degree of correlation between local weather variables influencing the dynamics of those populations. Because the NAO has opposing influences on the local weather in the regions inhabited by the focal species studied here, relating the degree of pairwise population synchrony to



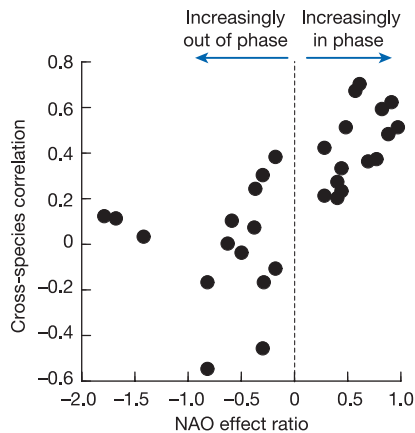
**Figure 2** Distance-dependent population synchrony and weather correlations. **a**, The spatial dimension of within-species synchrony between pairs of populations of caribou (green dots;  $r = -0.59$ ,  $P = 0.01$ ) and musk oxen (red dots;  $r = -0.60$ ,  $P = 0.03$ ), and of cross-species synchrony between caribou and musk oxen populations on opposite coasts of Greenland (black dots;  $r = -0.79$ ,  $P < 0.001$ ). Shown are all possible lag-0 Pearson correlation coefficients between caribou and musk oxen populations located in Fig. 1a plotted against the euclidean distance (Methods) between populations. **b**, Distance-dependent correlation in local winter temperatures on opposite coasts of Greenland. Shown are all possible pairs of lag-0 Pearson correlation coefficients between weather stations versus the euclidean distance between stations ( $r = -0.65$ ,  $P < 0.001$ ). Horizontal dotted line indicates zero correlation; open circles represent the correlations including the two populations that are not influenced by the NAO (Methods); inclusion of these populations resulted in the following correlations: caribou,  $r = -0.21$ ,  $P > 0.20$ ; musk oxen,  $r = -0.85$ ,  $P < 0.001$ ; cross-species,  $r = -0.73$ ,  $P < 0.001$ .

pairwise weather correlation is not meaningful. Therefore, we plotted, for each pair of cross-species populations, their correlation coefficient against the ratio of the coefficients quantifying the influence of the NAO on the dynamics of each population<sup>18</sup>.

The NAO effect ratio explains 42% of the variation in the degree of cross-species correlation, and a scatter plot of this relationship indicates that the more similar the strength of the effect of the NAO on any pair of populations, the more highly correlated are their dynamics (Fig. 3). Notably, as the magnitude of the effect of the NAO on any pair of populations diverges, so does the magnitude of their correlation with each other (Fig. 3). In the extreme, populations influenced by the NAO in opposing directions (resulting in a negative NAO effect ratio) are increasingly out of phase with each other (Fig. 3).

Because the influence of the NAO on the dynamics of populations in each species varies with latitude<sup>18</sup>, we also investigated the influence of latitudinal differences between pairs of caribou–musk oxen populations on cross-species synchrony in a multivariate regression model. This analysis explained an additional 32% of the variation in cross-species population correlation (total  $R^2 = 0.74$ ,  $P < 0.001$ ) and indicated that populations at proximate latitudes are more highly correlated than those at distant latitudes. We propose that this effect may reflect the influences of latitudinal gradients in plant phenology or forage productivity on population dynamics, but currently lack data to test these hypotheses.

Spatial coupling of widely distributed populations by large-scale climate systems as documented here indicates that climate change can influence, and already might be influencing, the dynamics of several populations and several species simultaneously. Indeed, it is difficult to explain the correlated dynamics of caribou and musk oxen that are separated by a continent-wide ice cap by means other than climate. Likewise, the concordance of the correlations between synchrony in each species and the NAO index (Fig. 1b) with the correlations between local winter temperatures and the NAO index within the range of each species (Fig. 1a) seems to implicate the NAO as the large-scale climate system that underlies population synchrony in this case. Although it may seem that the results of our analyses are particular to the climatic conditions of Greenland, the NAO does not appear to explain more of the variance in interannual density fluctuations of these populations than those of other, temperate populations of large mammals<sup>12–14,18</sup>. Further analyses will help discern the ubiquity of the role of the NAO, or other large-scale climate systems, in cross-species synchrony. □



**Figure 3** Relation between the degree of pairwise cross-correlation between caribou and musk oxen populations and the ratio of the effect of the NAO on the dynamics of each population ( $r = 0.65$ ,  $P < 0.001$ ).  $x$ -axis data were calculated from the coefficients of the terms quantifying the strength of the influence of the NAO on the dynamics of each population, according to the most parsimonious autoregressive models<sup>18</sup>.

## Methods

### Population data

Population indices were derived for the two focal species from harvest data compiled by the Greenlandic Ministry of Denmark for caribou (1908–1981) throughout west Greenland<sup>25</sup>, and survey data on local musk oxen densities (1960–1988) throughout northeast Greenland compiled by the Danish Sirius patrol<sup>19</sup>. The caribou data derive from seven geographically isolated locales separated by fjords and ice fields along the whole west coast of Greenland, whereas the musk oxen data derive from six similarly isolated locales along the northeast coast of Greenland (Fig. 1a). The spatio-temporal extent of these data is thus comparable to that of the Hudson Bay fur trading data on Canada lynx, mink and muskrat, which have been important in theoretical and statistical modelling of spatial synchrony<sup>8,16,26,27</sup>. We assume that the harvest data provide an index of caribou populations that scales roughly linearly with population size but, in the absence of independent data on actual censuses, we cannot be certain that this is the case.

### NAO influence on populations

As Moran specified<sup>1</sup>, if two populations showing similar intrinsic dynamics are both influenced by climate, then the degree of correlation between them should scale with the correlation in weather variables influencing their respective dynamics. Hence, in the interest of investigating the contribution of the NAO climate signal to spatial synchrony, the focus of our analysis is the 11 populations (6 caribou and 5 musk oxen) in which density fluctuations are influenced by the NAO. An influence of the NAO was identified in five of six caribou populations<sup>18</sup>; we analysed the dynamics of the remaining caribou population (Qeqertarsuatsiaat)<sup>25</sup> using the approach used previously<sup>18</sup> and found a one-year delayed effect of the NAO. We present results of analyses of all 13 populations for comparison.

### Population synchrony

To assess spatial patterns of synchrony in the caribou and musk oxen data, as well as cross-species synchrony, we calculated all possible pairs of lag-0 cross-correlation among populations of caribou, musk oxen and the two combined. These were then plotted against the euclidean distance between pairs of populations, estimated using a web-based surface distance calculator (<http://www.vsv.slu.se/johnb/java/lat-long.htm>). Latitude–longitude coordinates were taken at the centre of the geographical distribution of each population. We used weather station data on annual (1967–1994) values of mean winter temperatures, available from nine stations at or near the focal populations, to assess similar spatial patterns in local weather. These data show strong correlation with the NAO index (see ref. 18).

To analyse temporal fluctuations in spatial synchrony in relation to temporal fluctuations in climate, we developed a time series on synchrony among populations in each species. We used the inverse of the coefficient of variation of the log<sub>e</sub> (ln)-scale data, calculated each year, as an index of synchrony<sup>28</sup>. This was regressed against the NAO winter index (<http://www.cgd.ucar.edu/~jhurrell/nao.html>) in linear and quadratic models (the latter to test for possible nonlinear relations between the NAO and synchrony). To avoid spurious correlations owing to temporal trends in the caribou time series<sup>25</sup>, we included ‘year’ as an independent variable in the analysis of synchrony in caribou. No temporal trend is evident in the musk oxen data<sup>19</sup>. For caribou adding a quadratic term did not improve the fit over the linear model ( $R^2_{\text{linear}} = 0.43$ ;  $R^2_{\text{quadratic}} = 0.43$ ), whereas for musk oxen adding a quadratic term improved the fit of the model ( $R^2_{\text{linear}} = 0.35$ ;  $R^2_{\text{quadratic}} = 0.45$ ), which implies that the underlying relation between the NAO and spatial synchrony in musk oxen may be nonlinear. Inclusion of the two populations that are not influenced by the NAO resulted in a poorer model for both caribou ( $R^2 = 0.30$ ) and musk oxen ( $R^2 = 0.07$ ).

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## Selective habituation shapes acoustic predator recognition in harbour seals

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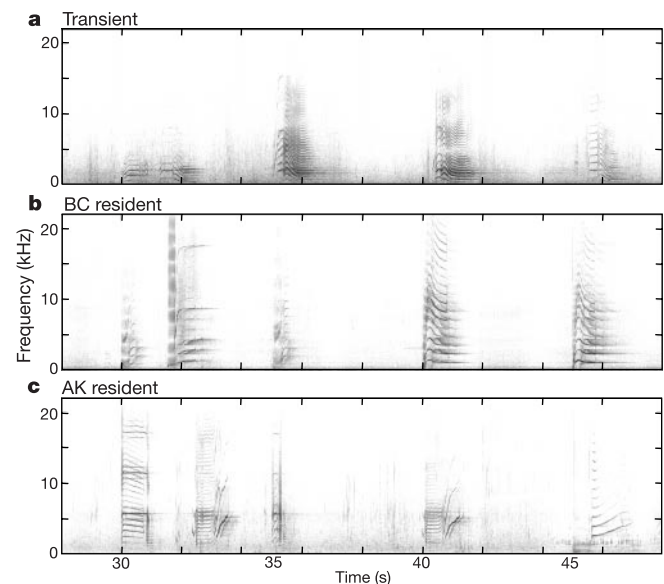
Predation is a major force in shaping the behaviour of animals<sup>1–3</sup>, so that precise identification of predators will confer substantial selective advantages on animals that serve as food to others. Because experience with a predator can be lethal, early researchers studying birds suggested that predator recognition does not require learning<sup>4,5</sup>. However, a predator image that can be modified by learning and experience will be advantageous in situations where cues associated with the predator are highly variable or change over time. In this study, we investigated the response of harbour seals (*Phoca vitulina*) to the underwater calls of different populations of killer whales (*Orcinus orca*). We found that the seals responded strongly to the calls of mammal-eating killer whales and unfamiliar fish-eating killer whales but not to the familiar calls of the local fish-eating population. This demon-

strates that wild harbour seals are capable of complex acoustic discrimination and that they modify their predator image by selectively habituating to the calls of harmless killer whales. Fear in these animals is therefore focused on local threats by learning and experience.

The northeastern Pacific Ocean is home to two distinct forms of killer whales. Resident killer whales live in large stable groups and feed exclusively on fish. Transient killer whales live in smaller social groups and prey only on marine mammals<sup>6,7</sup>. The two different forms do not interbreed and rarely interact. Resident killer whales along the west coast of North America fall into three distinct communities with adjacent home ranges (Alaskan residents, northern residents and southern residents). Transients, on the other hand, form a continuous population from northern California to southeastern Alaska<sup>8–11</sup>.

Resident and transient killer whales show striking differences in their vocal behaviour. Residents frequently emit echolocation clicks and communicative calls whereas transients are usually silent<sup>12,13</sup>. Resident killer whales have a complex system of vocal dialects: different social groups have repertoires of 7–17 structurally distinct stereotyped call types (see Fig. 1b and c). The degree of sharing of call types between groups within a community varies from no shared call types to complete sharing of the repertoire<sup>14,15</sup>, and the structure of stereotyped call types slowly changes with time<sup>16</sup>. In contrast, all members of the transient population share most of their call types. No call types are shared among members of different resident communities or between residents and transients.

Harbour seals are the most commonly taken prey of transient killer whales in the coastal waters of British Columbia, Canada<sup>6</sup>, and predation from transients is likely to be a significant source of mortality. Because harbour seals have good underwater hearing at the frequencies of killer whale vocal communication<sup>17</sup>, and because underwater calls of killer whales can be heard over long distances<sup>18</sup>, it would be beneficial for harbour seals to respond to the calls of transients with anti-predator behaviour. When the salmon migrate through these waters, groups of resident killer whales, which pose no predatory threat to seals, will often spend several weeks in a



**Figure 1** Playback sequences for experiment 2. Spectrograms of sections ( $t = 28$  s to  $t = 48$  s) of playback sequences illustrating the differences between the calls of mammal-eating killer whales (transients), familiar fish-eating killer whales (British Columbia (BC) residents) and unfamiliar fish-eating killer whales (Alaskan (AK) residents). Several (four transient, seven BC resident and four AK resident) sequences were used for each playback type.