

# Are local weather, NDVI and NAO consistent determinants of red deer weight across three contrasting European countries?

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## Abstract

There are multiple paths via which environmental variation can impact herbivore ecology and this makes the identification of drivers challenging. Researchers have used diverse approaches to describe the association between environmental variation and ecology, including local weather, large-scale patterns of climate, and satellite imagery reflecting plant productivity and phenology. However, it is unclear to what extent it is possible to find a single measure that captures climatic effects over broad spatial scales. There may, in fact, be no *a priori* reason to expect populations of the same species living in different areas to respond in the same way to climate as their population may experience limiting factors at different times of the year, and the forms of regulation may differ among populations. Here, we examine whether the same environmental indices [seasonal Real Bioclimatic Index (RBI), seasonal Normalized Difference Vegetation Index (NDVI) and winter North Atlantic Oscillation (NAO)] influence body size in different populations of a large ungulate living in Mediterranean Spain, Western Scotland and Norway. We found substantial differences in the pattern of weight change over time in adult female red deer among study areas as well as different environmental drivers associated with variation in weight. The lack of general patterns for a given species at a continental scale suggest that detailed knowledge regarding the way climate affects local populations is often necessary to successfully predict climate impact. We caution against extrapolation of results from localized climate–population studies to broad spatial scales.

**Keywords:** ecology, environment, local weather, NAO, NDVI, seasonal indices

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## Introduction

Climatic variation influences demography and population dynamics of herbivores by influencing plant productivity and more directly by imposing energetic demands or behavioral constraints (Saether, 1997; Ottersen *et al.*, 2001; Stenseth *et al.*, 2002; Forchhammer

& Post, 2004). For example, during hot periods many ungulate species seek shade to reduce water loss and this limits opportunities to feed (Owen-Smith, 1998). The multiple paths via which environmental variation can impact herbivore ecology can complicate the identification of environmental drivers. While examining the association between environmental variation and animal ecology, researchers have traditionally used local weather variables including winter snow depth, total precipitation or mean temperature over a period of

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time [Picton (1984) as an example]. In the 1990s, climatic indices that describe larger-scale patterns of weather than local variables became available and this led to a proliferation of studies reporting associations between indices like the North Atlantic Oscillation (NAO) and the El Niño Southern Oscillation (ENSO) and population performance (Ottersen *et al.*, 2001; Stenseth *et al.*, 2002, 2003; Forchhammer & Post, 2004). More recently still, satellite imagery describing the productivity of vegetation [Normalized Difference Vegetation Index (NDVI)] has been used to assess the impact of climate on aspects of population ecology via food availability (Pettorelli *et al.*, 2005b). However, which measures typically perform best? Can any general rules be elucidated? Certainly, most climate envelope models typically assume global relationships between climate variables and species rather than allowing these relationships to vary with space (e.g., Iverson & Prasad, 1998; Thuiller, 2003; Thomas *et al.*, 2004).

In some systems, the identification of climatic factors is relatively straightforward. For example, in many Polar regions snow fall and the degree of 'icing', which increases movement costs for large herbivores (Parker *et al.*, 1984) and prevents animals from foraging on vegetation hidden underneath the snow (Mysterud *et al.*, 1997), has been shown to have a strong effect on ungulate and small mammal demography (e.g., Helle & Kojola, 2008). However, in other systems, identifying the climatic drivers can be more challenging. For example, do they operate directly on the animal by imposing energetic stresses or indirectly by influencing food supply? What time of year is likely to be important climatically? How will such complexities, if they are important, impact on our ability to make generalizations about the role of climate across species, or even across populations of the same species in different places?

There are a growing number of comparative studies where the role of a single environmental driver on population dynamics is examined. Some of these studies have concluded that the same climatic variable influences aspects of the population dynamics in different ways in different places (Post & Stenseth, 1999; Ginnett & Young, 2000; Steinheim *et al.*, 2004; Hebblewhite, 2005; Loe *et al.*, 2005; Nussey *et al.*, 2005; Pettorelli *et al.*, 2005a, 2006; Kjellander *et al.*, 2006). These results show that some populations of a species might be influenced by one environmental driver whereas in other populations, the species' ecology is apparently independent of the driver. Does this mean that the species is unaffected by environmental variation at one site, or that the ecology of the species differs among sites? The fact that environmental conditions can differ markedly among populations over large spatial scales is widely documented. It should perhaps not be surpris-

ing that populations of the same species in different areas are influenced in contrasting ways by the same environmental driver, or that different environmental drivers may influence different populations (Ginnett & Young, 2000). However, despite this, extrapolations based on an association between a single environmental driver and aspects of a species' ecology are frequently conducted to predict responses to climate change (e.g., Iverson & Prasad, 1998; Thuiller, 2003; Thomas *et al.*, 2004). The objective of this paper is to examine whether the assumption of a geographically invariant response of deer ecology to climate change is appropriate.

Red deer (*Cervus elaphus* L.) is an ungulate with a large range, extending in Europe to as far North as Scandinavia and as far South as Spain (Putman, 1988). The global distribution of *C. elaphus* extends to most of Europe, Central Asia and North Africa. It has been also introduced in New Zealand, Australia and South America. Our study areas, therefore, represent fairly close to the center of the species global range. Although there is some variation in the phenology of red deer among Spain, Scotland and Norway, the rut is always in the autumn, and calves are born in late spring (Loe *et al.*, 2005). Red deer are well studied in northern environments where food availability is lowest during the winter months (Post & Stenseth, 1999). In contrast, food availability is most limiting during the summer months in southern, as opposed to northern, environments (Fernández-Olalla *et al.*, 2006). We, consequently, may not expect the same variables to influence the population ecology of red deer in Northern and Southern Europe. In this paper, we examine red deer culling data from three contrasting environments, Spain, Scotland and Norway, to test whether NDVI, NAO or the Real Bioclimatic Index (RBI), an integrated measure of local weather, provide a universal predictor of variation in red deer mass and, therefore, whether environment influences body weight in different populations of the same species in a similar manner.

## Material and methods

### *Study area and deer data*

We used data on harvested female red deer collected from Quintos de Mora, Los Yébenes, Central Spain, between 1988 and 2003; from the Isle of Rum, Western Scotland, between 1982 and 1997; from Kvinnherad, Southwest Norway, between 1983 and 2002; and from Snillfjord, mid-Norway, between 1984 and 2003. Further details of the study areas are given in Table 1. In Quintos de Mora, red deer are harvested in a variety of ways with the hunting method influencing the weights (Martínez *et al.*, 2005). In this analysis, we only

**Table 1** Characteristics of each study area

	Quintos de Mora (Spain)	Isle of Rum (Scotland)	Kvinnherad (Norway)	Snillfjord (Norway)
Latitude	39°26'N	57°0'N	60°12'N	63°29'N
Longitude	4°2'W	6°20'W	6°29'E	9°35'E
Surface	6864 ha fenced	Island of 16 684 ha	Open system of 113 720 ha	Open system of 51 200 ha
Climatic characteristics	Mediterranean and continental: Drought in summer; cold in winter; big interannual variability	Oceanic climate with mild wet and windy weather for much of the year. No drought periods; mild summers and winters; low interannual variability	Oceanic and coast: No drought periods but snowy and fairly cold in winter; far milder than in Snillfjord	Oceanic and coast: No drought periods but snowy and cold in winter
Soils	Poor soil	Poor soil		
Red deer resources available	Evergreen trees and shrubs and their fruits during the autumn. Withering herbaceous pastures are present during the summer. Poor growth occurs during winter	No tree stratum; <i>Calluna</i> heath constitutes nearly 80% of the Island vegetation. Poor growth occurs during winter	Deciduous and pine ( <i>Pinus sylvestris</i> ) forests. Rich in herbaceous species during summer; feeding also on pasture during winter	Birch, pine and spruce ( <i>Picea abies</i> ) forests. Rich in herbaceous species during summer; feeding also on pasture during winter
Management	Hunting and cropping oats, barley, rye and clover to contribute to red deer food supply	14% annual cull	Hunting with sex and age-specific quotas	Hunting with sex and age-specific quotas
Hunting period	Mainly between September and February	Mainly between September and January	Mainly between September and November	Mainly between September and November

use individuals shot in management culls. On the Isle of Rum, animals were killed as part of an annual 14% management cull, and were not selected for body size. In both Southern and mid-Norway, animals were shot by hunters under licenses issued by local management boards (Myrsterud *et al.*, 2001a). All females considered were 2 years of age or older.

We compiled a dataset for each study that contained the following data on culled individuals:

- Month and year at death. The data were unbalanced as different numbers of individuals were shot in different months and years (see Appendix S1). However, month was always included in the model as a factor, and we had sufficient data in each month-year group to estimate parameters.
- Age estimated from tooth rings (Lowe, 1967) (information about the age structure of the population used in the analysis is given in Appendix S2).
- Weight in kilograms. The way the weight data was collected differed slightly among studies. In Spain, the weight of the entire animal was recorded. On Rum, weight was measured after the rumen had been removed. In Norway, weight is dressed mass (i.e., live mass minus head, skin, viscera, bleedable blood and metapodials; about 58% of live mass) (Myrsterud *et al.*, 2001a).
- Reproductive status recorded as a binary variable. Reproductive status describes whether a female was lactating or not. This variable was not available for Norway.
- Pregnancy status as a binary variable. Pregnancy status describes whether a female is pregnant or not. This variable was not available for Norway.
- Population density. In Spain and Scotland, this was estimated from censuses whereas in Norway, estimates were obtained from the number of animals harvested relative to the area of red deer habitat (Myrsterud *et al.*, 2001c). The Norwegian population estimates might be subject to greater uncertainties and biases than the Spanish or Scottish estimates. However, we would expect density dependence to operate in a similar manner in all study areas, and all density indices have been found to explain significant amounts of variation in other studies of these populations (Myrsterud *et al.*, 2001c). Scottish data had similar densities among years.

The dataset for each study also contained the following environmental data.

- Winter NAO index: We chose this variable because it is widely used in the large mammal ecology literature as a broad-scale measure of weather (Ottersen *et al.*, 2001; Stenseth *et al.*, 2003; Forchhammer & Post, 2004). We used a winter index of the NAO (December to February) calculated as the difference in normalized sea level pressures (SLP) between Ponta Delgada (Azores) and Stykkisholmur (Reykjavik, Iceland) weather stations (Hurrell, 1995). This index is corrected for anomalies at each station and is available from <http://www.cgd.ucar.edu/cas/jhurrell/indices.html> from 1965 to 2003. The December–March index, which is frequently used in ecological studies [but see Hurrell *et al.* (2003); Gallego *et al.* (2005)], was not used to allow comparison with the other seasonal environmental measures available for us in this study. Note that the NAO measured December to February and the NAO measured December to March are strongly correlated over this period (Pearson correlation coefficient,  $r = 0.85$ ).
- NDVI: The Normalized Difference Vegetation Index is a vegetation index derived from satellite imagery that measures the vegetation greenness; it is widely used in ecology (e.g., Pettorelli *et al.*, 2005b). Here, we used the NDVI calculated by the Global Inventory Modelling and Mapping Studies (GIMMS) (Tucker *et al.*, 2005). The GIMMS-NDVI is a bi-monthly index (consisting of 15-day composites) with  $8 \times 8 \text{ km}^2$  spatial resolution. It is freely available from <http://gimms.gsfc.nasa.gov/>. We extracted one GIMMS-NDVI pixel value from close to the center of each study area using ENVI software (ENVI 4.2 RSI, USA). The exception was Rum, where we selected the three pixels that included the whole island and averaged across these. In all, the study areas proximal pixels were examined to ensure they provided similar information to the focal pixels. The exception was Rum where neighboring pixels consisted almost entirely of water. In this case, we compared the pixels from Rum with pixels from the adjacent island of Skye. In all the cases, the focal and comparison pixels gave nearly identical information. The values used in the analysis were a monthly NDVI calculated as the average of the two 15-day GIMMS-NDVI values within each month.
- RBI index data: We also used an index based on Ombrothermic diagrams (Gaussen, 1955) that was developed by Montero de Burgos & González-Rebollar (1974) to describe vegetation growing conditions. The index is referred to as the RBI and

estimates vegetation productivity based on local climatic and geographic processes including topography. It is a function of local weather and incorporates an estimator of the soil water content and the evapotranspiration of the vegetation (Appendix S3). We used monthly RBI estimates and seasonal estimates which were simply the sum of the monthly values. We used seasonal RBI as it provides an estimate of local growing conditions summarized over many local weather data. The RBI index is a summary of extreme weather including frozen periods and droughts. Larger values are associated with good conditions for vegetation growth. Negative values characterize periods when vegetation growth stops because of low temperatures or limited water availability.

- Seasonal weather covariates were defined as the sum of the monthly values before culling: winter (December + January + February), spring (March + April + May), summer (June + July + August) and autumn (September + October + November).

#### Statistical analysis

The objectives of our statistical analyses were to identify environmental factors associated with body mass in each of the three populations of red deer and then to compare results across systems. We describe our approach in detail below, but first describe our strategy for identifying effects.

1. We first examined graphically how each of our environmental drivers varied over time within each of the study areas, and looked for correlations among environmental drivers.
2. Our next objective was to provide an estimate of the contribution of each of our environmental drivers to temporal variation in body weight in each study area. We did this by comparing models including environmental drivers with those that did not include them. We considered environmental drivers fitted alone or additively.
3. To decide on the most appropriate form of association between the dependent variable and each of the independent variables (e.g., linear, nonlinear, parametric, nonparametric) we initially fitted nonparametric splines. In cases where there was no evidence of nonlinearity in associations, we simplified these to linear fits. Hence, we report results from two types of models: general additive models when there was evidence of nonlinear associations and general linear models.
4. We finally compared the performance between the best-fit model containing environmental drivers with

the equivalent model excluding them. We used evidence ratios [which is the probability that one model is more likely to be to be correct than another, defined as  $1/(\exp(-0.5 \times \Delta\text{AIC}))$ , where AIC is Akaike's information criterion] to assess whether environmental drivers should be included in final models (Crawley, 2007).

#### *Graphical examination of pattern*

We graphically characterized the monthly environmental indicators (RBI and NDVI) in each study area. Correlations were then calculated among the three different environmental indices within each study area. Variables were not sufficiently strongly correlated to prevent them being fitted into the same multiple regression analyses of weight (Appendix S4). This suggests that the different climatic variables summarize different aspects of local weather in each study area. This analysis also demonstrated that there was considerable spatiotemporal variation in the environmental drivers we selected.

#### *General additive and general linear models*

We fitted models of body weight using Generalized Additive Models with smoothing splines (Gaussian family and identity link function) for each study area using library MGCV in R.2.3.1 (R Development Core Team, 2006; Wood, 2006). Model fits were assessed graphically (Mysterud *et al.*, 2001b). We compared different models fit with *F*-tests, choosing the best model following the principle of parsimony. In general, age and month were associated nonlinearly with weight, while the environmental variables we considered were linearly associated (see Table 2). In some cases, mostly in the Spanish study area, we did find evidence of nonlinear climatic effects. However, these were typically due to individual outliers. In these cases, we again simplified the nonparametric functions to linear functions. These results suggest that the associations between our climatic variables and body weight are well described with linear models. This simplified our remaining analyses.

#### *The effects of environmental drivers*

Next, we fitted linear models to each study area with all our environmental variables included. We focused on additive effects because, in general, plots of the environmental driver and density showed that there were often cases where the parameter space was not adequately covered, for example, no cases of low NAO and high density. Then we removed nonsignificant variables

one at a time. Once the most appropriate models were identified, the contribution of environmental drivers was examined by comparing the fit of models including and excluding environmental drivers. Separate analyses were conducted for each study area (Table 2): we report models that do not contain environmental covariates, and models incorporating significant seasonal environmental covariates (four seasonal RBI variables, four seasonal NDVI variables and the December–February NAO variable). Models were compared using AIC,  $\Delta\text{AIC}$  and the evidence ratio. Models between different countries were not quantitatively comparable using this approach as they were fitted to different datasets. However, the evidence ratio can be used to compare the rankings of the different models between the different populations analyzed in our study areas (Crawley, 2007).

## **Results**

### *Description of environmental variables*

Monthly and annual NDVI and RBI time series are shown in Figs 1 and 2 for each study area. There are markedly different patterns between the Northern and Mediterranean study populations. There was little correlation between the environmental indicators within the study areas (Fig. 3, Appendix S4).

The RBI curve for Quintos de Mora shows a maximum in spring, a minimum in summer due to drought, and a second minimum in winter caused by cold temperatures. In contrast, the NDVI curve for Quintos de Mora varies little over the year due to the presence of evergreen trees and shrub species. The spring maximum is due to the growth of herbaceous vegetation. In the northern study areas, there is one long harsh period in winter, with maximum vegetation growth occurring in summer. As expected, both the NDVI and RBI indices capture the seasonal variation in vegetation productivity that increases with latitude. Figures 1 and 2 also both show the interannual variability in RBI and NDVI, respectively. In Quintos de Mora, the RBI shows large variability among years, especially in those months (late spring and late summer) when lack of rainfall leads to summer droughts. In Norway, both RBI and NDVI describe some interannual variability of winter and summer temperatures. There is little interannual variability for both environmental measures in Scotland.

### *Seasonal patterns in female red deer weight across three contrasting European countries*

We found evidence of different seasonal trends in age-corrected weight at different times of year across study

**Table 2** Subset, variables introduced in full models, significance and direction of the significant environmental variables (positive or negative) of the separate models fitted for every study area

GAM	Quintos de Mora	Isle of Rum	Kvinnherad	Snillfjord
Country	Spain	Scotland	Norway	Norway
Years	1988–2003	1982–1997	1983–2002	1984–2003
Number of data	1294	716	1252	598
<b>Subset</b>				
Density	No subset	Blocks 1,2,3 pre-91 and Block 2 up to 99	No subset	No subset
Hunting months	October–February	October–January	September–December	September–November
<b>Nonenvironmental variables</b>				
s (age)	*	*	*	*
Density index	*	NO	*	*
Status†	‡	*	NO	NO
Pregnancy†	*	*	NO	NO
Month†	*	*	*	*
AIC	<b>9229</b>	<b>4608</b>	<b>8461</b>	<b>3995</b>
<b>Environmental seasonal approach</b>				
s (age)	*	*	*	*
Density index	*	NO	*	*
Status†	‡	*	NO	NO
Pregnancy†	*	*	NO	NO
Month†	*	*	*	*
Winter RBI	‡	‡	‡	‡
Spring RBI	*(-2.16 ± 0.58)	*(-1.36 ± 0.67)	*(+1.68 ± 0.56)	*(-1.19 ± 0.47)
Summer RBI	‡	‡	*(-0.71 ± 0.34)	‡
Autumn RBI	*(+1.81 ± 0.32)	‡	‡	‡
Winter NDVI	‡	‡	‡	‡
Spring NDVI	*(+28.10 ± 4.99)	‡	‡	‡
Summer NDVI	‡	‡	‡	‡
Autumn NDVI	‡	‡	‡	‡
Winter NAO	‡	*(+0.93 ± 0.13)	‡	‡
AIC	<b>9157</b>	<b>4563</b>	<b>8452</b>	<b>3991</b>
ΔAIC§	72	45	9	4
Evidence ratio	4.3E + 15	5.9E + 9	90	7

Two different environmental approaches are shown for every study area: (i) without environmental variables, (ii) seasonal environmental approach. All models were fitted using GAM with smoothing splines. Different country models are not comparable because the same subset and data are required. Comparison of the more likely model for each country is possible using the AIC and the evidence ratio.

NO: variables not included in the full models.

\*Significance ( $\alpha = 0.05$ ). Estimate and standard error of the coefficients are given in brackets.

†Variables are considered as factor.

‡Variables not included in the simplified final models.

§Calculated between model 1 and 2 in each study area.

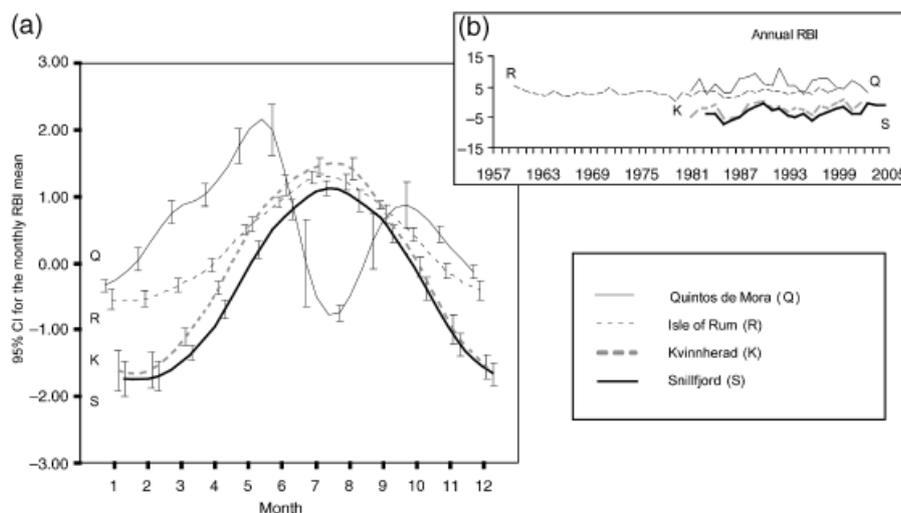
RBI, Real Bioclimatic Index; NDVI, Normalized Difference Vegetation Index; NAO, North Atlantic Oscillation; AIC, Akaike's information criterion.

areas (Fig. 4). Females in Quintos de Mora had a minimum weight in November before increasing in size significantly until February ( $P < 0.001$ ); females on Rum decreased in weight significantly between October and January ( $P = 0.0015$ ); Norway-Kvinnherad female's weight showed a nonsignificant decline from October to December ( $P = 0.7392$ ) and Norway-Snillfjord female's weight decreased significantly from September

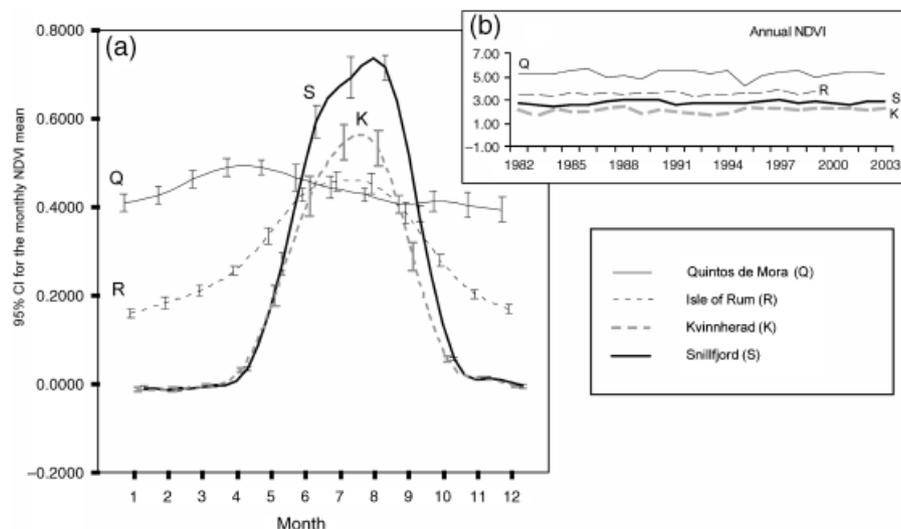
to November; this relationship is well described with a linear fit ( $P = 0.0015$ ).

#### *Associations between female red deer weight and environmental indices*

Table 2 shows the results of the analyses between weight and independent variables for the eight different



**Fig. 1** Pattern of Real Bioclimatic Index (RBI) variation across study areas. (a) Average and 95% confidence intervals of the monthly RBI in each study area. (b) Annual values of RBI in each study area.

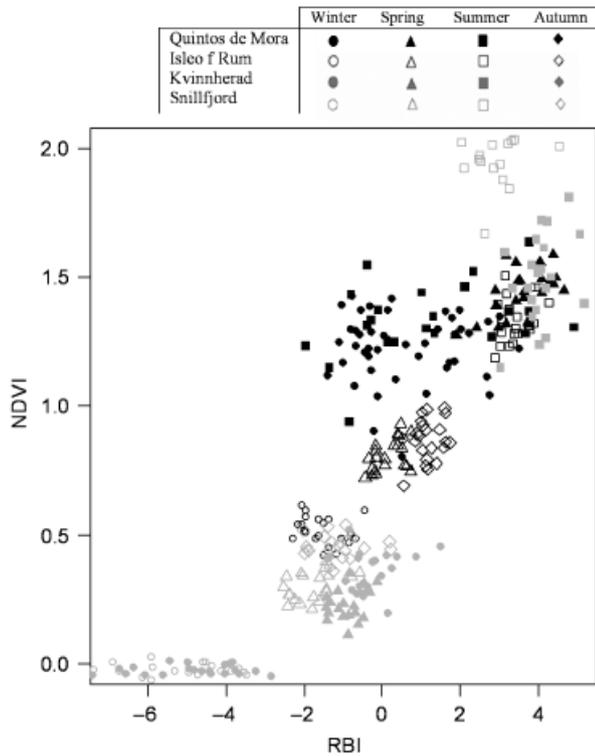


**Fig. 2** Pattern of Normalized Vegetation Index (NDVI) variation across study areas. (a) Average and 95% confidence interval of the monthly NDVI in each study area. (b) Annual values of NDVI in every study area.

models: (1) one model for each study area, containing no climatic indices; (2) and another four models containing seasonal indices (seasonal RBI and NDVI variables and winter NAO). Weight was influenced by different covariates, and in different ways, in different study areas.

Based on the evidence ratios, models containing seasonal indices were substantially better than those fitted without considering environmental variables. A significant amount of variation in weight is consequently explained by climatic variation, but different climatic drivers explain this variation in different study areas. At Quintos de Mora, there were three significant

climate-weight associations. Weight was negatively associated with spring RBI ( $P < 0.001$ ), and positively associated with autumn RBI ( $P < 0.001$ ) and spring NDVI ( $P < 0.001$ ). The analyses revealed different patterns between Rum and Quintos de Mora. On Rum, weights increased with increasing winter NAO ( $P < 0.001$ ) and decreased with increasing spring RBI ( $P = 0.012$ ). None of the environmental variables improved model fit in either of the Norwegian study sites to the same extent as they did for the other two study sites. However, weights did significantly vary over time, which may suggest we failed to identify the appropriate climatic index. Although evidence ratios



**Fig. 3** Correlation between environmental variables. Scatter plot of monthly Normalized Vegetation Index (NDVI) against monthly Real Bioclimatic Index (RBI). Study areas and seasons are distinguished with different symbols.

did not provide support for the retention of environmental variables in the models for Norway, we still report the direction of the significant effects. In the model containing seasonal climatic covariates, weights increased with increasing spring RBI ( $P = 0.003$ ) and with decreasing summer RBI ( $P = 0.039$ ) in Kvinnherad. In Snillfjord, we found a significant negative effect of spring RBI ( $P = 0.015$ ) in the seasonal model.

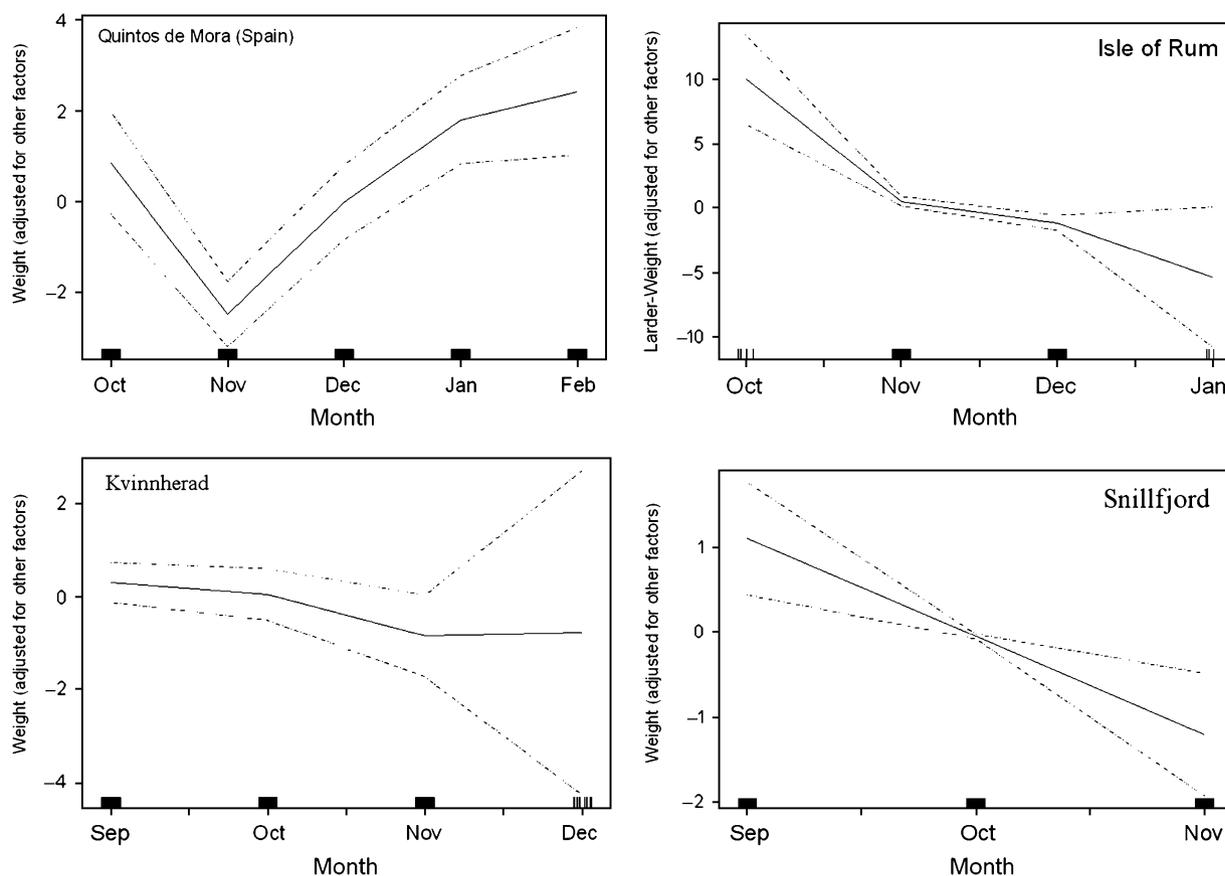
## Discussion

We found substantial differences in the pattern of weight change over time in adult female red deer between study areas as well as compelling evidence that different environmental drivers were associated with variation in weight in different parts of Europe. We conclude that it is difficult to identify general patterns which would allow us to make predictions about which climatic drivers might influence red deer populations elsewhere. Unsurprisingly the most striking differences we observed were between the Iberian population in Quintos de Mora and the more Northerly populations in Scotland and Norway. However, the comparisons between the Rum population and the

Norwegian populations were illuminating. The effects of individual attributes and climate were less substantial, but still present, in Norway compared with Scotland. This is consistent with a hypothesis that Norwegian red deer may be better buffered against climatic variation, perhaps because their seasonal migration between altitudinal ranges reduces competition for resources (Mysterud *et al.*, 2001a). Alternatively, it is possible that none of our environmental drivers captured the path via which climate impacts on Norwegian red deer. Certainly, climate effects have been reported to influence other ecological and life history variation within these populations (Mysterud *et al.*, 2001a, 2008). There are likely to be other ecological factors that differ between the four populations including hunting management, predators, competitors or parasites. Usually, these differences may also complicate the comparison of the results of different studies and could be a major cause of difference in climatic drivers across our populations. In the absence of any evidence, we make the simplifying assumption that these differences act additively on body weight rather than through an interaction with weather variables, but this may not necessarily be correct. Clearly, further work examining the *modus operandi* of climatic variation on body weight in these populations is desirable. Until this question is addressed, we caution against the use of extrapolation from a climate–ecology association from one population to larger spatial scales or to different populations of the same species living in different locations.

### *Associations between female red deer weight and environmental indices*

We found that one climatic covariate may explain large amounts of variation in a trait in one area and very little variation elsewhere. Most variation in body weight was explained by climatic variation in Spain, with the association weakening with increasing latitude. It is entirely possible that a different set of climatic drivers – including, for example, measures defining the onset of spring – would provide a contrary picture. Although we can explain substantial variation in the temporal pattern of body mass within each population, an understanding from one population may contribute little to understanding patterns in other populations. This suggests that we need specific details from each study area and a good understanding of the underlying ecology in order to understand how climatic variation influences a species' biology. Our results also suggest that an *a priori* understanding about the way climate is likely to influence population processes may help when selecting an appropriate environmental indicator for analysis (Burnham & Anderson, 2001). These are important insights



**Fig. 4** Temporal variation in female red deer weight in each study area (Quintos de Mora, Isle of Rum, Kvinnherad and Snillfjord) after correcting for age, density, status, pregnancy and environmental factors. Model fits and the 95% confidence intervals presented are from generalized additive models.

that underline the need to conduct studies of multiple populations spread widely over the species range, if we are to understand the general patterns of life history trait variation in relation to climate changes.

One striking feature of our results is that the signs of associations are not easy to interpret. For example, on Rum there is a positive association between NAO in the winter before culling occurs and body weights. However, previous research has shown that positive values of the NAO provide poor conditions for ungulates living in the west of Scotland; on Rum, survival rates decrease with increasing NAO (Coulson *et al.*, 2001). We are confident that the positive correlation is a result of lighter individuals dying in harsh winters (Coulson *et al.*, 1998) before the year before the cull, but we only believe this because of a very detailed long-term study on part of the island (Clutton-Brock & Albon, 1989). If the association had gone the other way, and we did not have the understanding of the system that we do, we could have argued that poor winters had previously reduced the condition of individuals and that they had not regained weight before the cull.

#### *Seasonal patterns in female red deer weight across three contrasting European countries*

Because we have time series of body weights of culled deer in each month of the hunting period in every year, we are in a position to further explore why we see the associations between climate and body weight that we do by looking at weight changes during the year. This aspect of our study further demonstrates that an understanding of the local ecology can help in identifying climate–ecology associations.

As expected, populations of the same species living in areas with different characteristics show different growth trajectories associated with the environments they experience (Langvatn *et al.*, 1996; Post & Stenseth, 1999; Loe *et al.*, 2005; Kjellander *et al.*, 2006; Pettorelli *et al.*, 2006). Adult female red deer from Los Quintos de Mora increased their body weight in autumn and the beginning of winter following a period of summer drought. This increase in weight is caused by the availability of acorns and new vegetation growth at this time of year (Bugalho & Milne, 2003). Summer is

expected to be dry and winters are cold, so spring and autumn are key periods in Mediterranean ecosystems that show large interannual variability.

In Norway there is very strong seasonality. Food is plentiful in summer, while in winter it is limiting with no vegetation growth during the winter months due to low temperatures (Loe *et al.*, 2005). Because of this strong seasonality, the identification of climatic drivers in Norway is relatively straightforward and has focused on variables that measure the onset of spring like NDVI on May 1 (Pettorelli *et al.*, 2005a) and measures of winter harshness like the December–March NAO (Mysterud *et al.*, 2003, 2008).

In Scotland, seasonality is less pronounced compared with Norway and the timing of spring is possibly less important than in Norway; this is why previous analyses have found that weather during winter most strongly influences ungulate ecology (Kruuk *et al.*, 1999; Catchpole *et al.*, 2000; Coulson *et al.*, 2001; Hallett *et al.*, 2004). Winter food production and availability are likely to be as important on Rum as the length of the winter season.

These differences in the *modus operandi* of climate between the three study areas begs the question as to why did we not use local weather variables for each study area? We chose the variables we did because our objective was to search for drivers that influence red deer mass across a range of environments – the sort of variables that are chosen while conducting large-scale comparative studies. We were unable to find an environmental driver that explained substantial variation in an important aspect of deer ecology in all three populations. This suggests that extrapolating from one climate–ecology association in one population to other populations may not always succeed in providing useful predictions about the consequences of climate change.

At one level, it is obvious that weather differs at different places on the globe, and that these differences are likely to influence the ecology of the same species in different ways at different places. However, large-scale analyses of ecological patterns focusing on static relationships between climate variables and species are widespread (e.g., Iverson & Prasad, 1998; Thuiller, 2003; Thomas *et al.*, 2004). Taken together, these observations suggest that a detailed analysis of the relative contribution of different climatic variables on ecology of the same species in different places is warranted.

Are there likely to be important unmeasured factors that influence changes in body weight in our study populations that could undermine our interpretation of our results? There are differences among our study areas other than the climate. Deer in the isle of Rum and Quintos de Mora populations are unable to migrate

in the way that they do in Norway. This is because in our Scottish study area, deer are restricted to the Island of Rum, and in Spain they are kept enclosed within the state. They are free to roam further afield in Norway, and show seasonal patterns of altitudinal migration (Mysterud *et al.*, 2001a). Furthermore, as discussed above, other ecological factors differ among the four populations including differences in harvesting selectivity, predators, competitors or parasites (Martínez *et al.*, 2005; Mysterud *et al.*, 2006).

Ecological and management differences similar to those mentioned above are likely to exist among most populations of the same species living in different places (e.g., Wimberly *et al.*, 2008). It is possible that these processes do influence the association between a population's ecology and environmental drivers. However, these differences help to reinforce our point: subtle differences between ecologies in different parts of the globe make it likely that large-scale, predictable associations between a single climatic driver and aspects of the ecology of a species are not necessarily to be expected other than at very crude scales – for example, a certain level of rainfall is necessary for a species to persist in an area. Predictions of the more subtle ecological consequences of climate change should acknowledge a role for such ecological variation, and predictions from simple climate–ecology associations obtained locally should be interpreted with care.

## Conclusion

It is straightforward to generate climate–ecology hypotheses whenever a significant association is identified – even if the association is apparently counterintuitive. To really understand the link between climate and body weight, and in general climate and ecology, we need a solid understanding of the details of the system. Which is the dominant path via which climate influences ecology? Does the path remain constant over time, or does it vary within and between years? And does climate influence ecology in the same way over large spatial areas? Given that climate is rapidly changing as a result of anthropogenic activities, and that we wish to understand the likely consequences of this change, we suggest that it is important for population biologists to report climate–phenotype effects but that great care should be taken when making biological inference. In order to obtain a more robust mechanistic link between climate and ecology, good local climatic information is probably required, as are data on the suspected *modus operandi* of climate. For example, if climate is believed to influence body weight of an herbivore via food availability, ideally good measurements are required on

vegetation productivity, biomass and composition, as well as repeated measures on marked individuals.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Sample sizes of the number of individuals harvested in each study site and each year

**Appendix S2.** Percentage of the number of females at different ages in the data used in analyses.

**Appendix S3.** Summary of Montero de Burgos & González-Rebollar (1974) methodology for calculating Real Bioclimatic Index (RBI).

**Appendix S4.** Correlation matrix among the environmental indices used in this study in each country. The values are Pearson correlation coefficients.

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