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Climate change and implications for
the future distribution and management
of ungulates in Europe

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12.1 Introduction

There is little doubt that predicted changes in climate (IPCC, 2007) are of an order
of magnitude that they are likely to affect large herbivores in Europe in a number
of ways. Whichever predictive models are used, the general expectation for future
climate is for greater levels of precipitation, warmer temperatures, and perhaps
most significantly an overall increase in variability (IPCC, 2007). However, at the
regional level, both variation and uncertainty is expected to be much higher.

It is important to realise that climate in itself is not necessarily the only
limitation for the current distribution ranges of all ungulate species, whose range
may also be affected by both natural and artificial barriers, by patterns of land
use (and urbanisation), by direct management, or by the fact that they are still
colonising (Groot Bruinderink et al., 2003). This, combined with the absence of
published assessments of how the distribution of different large herbivore species
may be affected by climate, make our attempt here a risky business in terms of
accuracy of predictions. However, with that said, what might we nevertheless
expect? We focus, in the following, mainly on global distribution patterns.

In general, large herbivores can be both directly and indirectly affected by
climate. Direct effects of climate are mainly related to thermoregulation
either due to extreme heat or cold (Parker and Robbins, 1985), water limitation
(Wallach et al., 2007), and costs of moving in snow (Parker et al., 1984).
Indirect effects are largely mediated through access to forage (snow or ice) or
actual vegetational productivity and quality (e.g. Hebblewhite et al., 2008).
Climate does not in general affect distribution ranges directly. Global
climatic conditions in any given regional area interact with factors such as

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topography to determine the local weather, which is what may influence the individual. Individual responses of behaviour or physiology in turn affect the life history and thereby the demography and population dynamics of a given species.

Changes in distribution of any animal species are influenced by the dynamics of local populations as well as the pattern of movement of individuals (Maurer and Taper, 2002). Variation in population growth rates of ungulates will mainly be influenced by how summer foraging conditions affect productivity and recruitment. how many animals survive the winter, and, in populations so large that demographic stochasticity can be ignored, how environmental variability may affect temporal fluctuations in population growth rates. Such changes determine whether or not any individual local population is growing or declining. No population can persist if the expected population growth rate is less than zero. In the face of climate change, environmental conditions necessary to allow positive long-term population growth rates of most species (i.e. the niche) will be moved in space (Holt et al., 2005).

Due to local declines or extinctions, together with increases in productivity of yet other populations in different areas, overall distributional range may change through time. More immediately, distributional ranges may be altered if animals shift their home ranges through time in response to altered environmental conditions, gradually abandoning areas which are becoming less favourable and directly colonising areas whose suitability is increasing. The rate of this response in distributional range will, however, also be dependent on the magnitude of the demographic stochasticity (Holt and Keitt, 2005).

Future distribution of large herbivores, within individual countries and within their European range, will result from whether they are able to persist in their historical distribution ranges or move to new ranges. They may persist in the historical ranges if the new conditions still allow positive expected population growth rates. This may be facilitated by plastic responses in demography or by developing evolutionary adaptations to the new environmental conditions. Most studies of climate effects derive from single populations, and we have a fair understanding of how climate variability affects large herbivores in a given area (reviews in Sæther, 1997; Gaillard et al., 2000; Veladji et al., 2002; Mysterud et al., 2003). This background enables us to assess the local dynamics and thus likelihood of continued persistence within historical ranges. The behavioural ecology of the species (mainly dispersal) interacting with geographic barriers will determine if the species is capable of moving to previously hostile environments that become suitable habitat during climate change.
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Within this general framework, one of the particular factors which puts a special constraint on large herbivore populations in temperate latitudes is seasonality (mainly by affecting the timing and duration of plant growth). It is fairly clear that large herbivores at the northern distribution limits face different challenges from those at the southern distribution limits, which can be related to differing seasonal limitations. We will therefore review climate factors known to affect the population dynamics during winter and summer separately.

In this chapter, we aim to highlight what we regard as the most likely climate components to affect distribution ranges of ungulates. At northern latitudes, these are mainly changes in snow depth (a lowering will increase range size) and more frequent icing events (an increase may reduce range size) during winter. At the southern limits, increased frequencies of droughts may similarly restrict range sizes.

We are less certain about how the overall seasonal structure might affect ranges. We do know that the growing season will be extended in many areas, but this positive effect may be countered by increased summer heat. The strict division of northern and southern distributions can be questioned, as the relative role of different seasonal limitations for a given area may change in the future. For one of the best studied populations of large herbivores, the Soay sheep, winter conditions have been regarded as the critical period with a limited effect of summer conditions (Clutton-Brock et al., 1997). However, the first ever summer drought appeared in summer 2008, becoming a new, potentially important factor for future dynamics (T. Coulson, pers. comm.). The appearance of new population-limiting factors make any population prediction uncertain (Coulson et al., 2001b; Festa-Bianchet et al., 2006).

There are a number of limiting factors in addition to climate that will determine the future distribution of large herbivore populations. These include large carnivores, diseases, land use, habitat loss and, not the least, human management. These factors may increase or decrease the effect of future climate changes, and they may frequently interact. Climate may increase likelihood of diseases and parasites, which are increasingly becoming apparent as a very important field of which we know little (Murray et al., 2006; Brooks and Hoberg, 2008; Chapter 11 of this volume). Large carnivores are also expanding in much of Europe (Enserink and Vogel, 2006), and the effects of predation often depend on climate interactions (Cederlund and Lindström, 1983; Hebblewhite, 2005; see also Chapter 10, this volume). These interactions will undoubtedly be important for prediction of how the future distribution ranges of large herbivores will be affected by the expected changes in climate.
Let us then review what we do know, and try to identify the possible climate winners and losers - which ones are likely to be correlated with the possibility of expanding or restricting their distributional ranges.

12.2 Global climate, local weather and regional variation

In Europe, much of the climate variation, especially during winter, can be linked to the state of an atmospheric phenomenon across the North Atlantic Ocean called the North Atlantic Oscillation (NAO; Hurrell, 1995; Hurrell et al., 2003). During high phases of the NAO, there is lowered surface pressure over the Arctic and increased surface pressure over the subtropical North Atlantic. This pressure configuration causes a northward shift in the Atlantic storm activity, with stronger westerly winds from southern Greenland across Iceland into northern Europe (especially Scandinavia) and a modest decrease in activity towards the south. This leads in turn to increased precipitation and temperatures occurring over Iceland and Scandinavia, and drier conditions over much of central and southern Europe, the Mediterranean and parts of the Middle East (Stenseth et al., 2003). During low phases of the NAO, fewer winter storms hit northern Europe, resulting in drier and colder conditions in the north, but wetter conditions in the Mediterranean region. To enable more accurate predictions of large herbivore distribution with climate change in Europe, we need to know the relationship between the NAO and climate change and between the NAO and regional variation in local weather in Europe. The link between the NAO and climate change is complicated (review in Gillett et al., 2003). However, most climate models suggest some increase in the winter NAO index in response to increasing concentrations of greenhouse gases (Gillett et al., 2003).

The NAO as a pressure system can be indexed in several different ways and for different periods. The simplest NAO index (the so-called ‘station-based index’) quantifies the average deviation from the long-term mean sea-level surface pressure difference between Lisbon in Portugal and Stykkisholmur in Iceland. The reason for using a simple index is to get a long time series (back to 1864), but the problem is that small variations in the exact situation of the Arctic or subtropical pressure centres can have very large effects on the index if based on only two locations. More recent indices (which can be calculated from raw data available from 1899) use the first axis of a principal component analysis (PCA-based, equivalent to EOF-based; Gillett et al., 2003) of sea-level pressure anomalies over the Atlantic sector (20°-80° N, 90° W-40° E). The latter indices are more optimal representations of the full NAO spatial pattern and better capture the NAO dynamics on an annual scale (Stenseth et al., 2003).
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The NAO index most commonly used is for the months of December through March, but the index for spring has also found to be linked to local temperature and precipitation and to have an effect on large herbivores (Pettorelli et al., 2005a; Mysterud et al., 2008). The NAO is interesting due to its simplicity, and that a single index of the NAO can say something about the state of climate in much of Europe. It happens to capture variation of climate in time and space at a scale relevant in many ecological studies (Hallett et al., 2004, Stenseth and Mysterud, 2005). However, there is large regional variation in the impact of the NAO in Europe – related to altitude, latitude, topography and distance to coast (continentality), to name the most important axes of variation (Beniston, 2006).

On the west coast of Norway, the NAO is positively correlated with temperature and precipitation during winter. However, since temperatures in this region often are around 0°C during winter, the relationship between the NAO and snow depth depends on altitude (Mysterud et al., 2000). During high phases of the NAO, there is more snow at high altitude and less at low altitude, due to both increased precipitation and warmer temperature, and since it is colder at higher altitude. In the Alps, a higher NAO in contrast tends to give below-average levels of precipitation, but above-average temperatures (Beniston and Jungo, 2002; Beniston, 2006).

There is a much lower impact of the NAO for inland areas in Europe. In inland locations in Poland (Mysterud et al., 2007), PCA-based indices of local weather outperformed the NAO in predicting population dynamics of European bison. Population (harvest) growth rates of roe deer in Norway, most of them in more inland locations, were positively related to the NAO in 94.7% of the populations, but local indices of snow depth explained more of the variation (Grøtan et al., 2005). No effect of the NAO has been reported for body mass variation of moose in Estonia (Veerkoja et al., 2008) or roe deer in Sweden and France (Kjellander et al., 2006). The NAO therefore does not capture the most relevant climate variability for all of Europe. There has also been suggested a so-called phase shift in the link between a given value of the NAO and local weather; that is, the correlation between the NAO and local weather might change over decadal scales (Mysterud et al., 2003; Durant et al., 2004), which will limit the predictive value. This issue is controversial and not all climatologists are convinced this is the case (Gillett et al., 2003).

It is therefore likely that the NAO will be a useful starting point to give some expectation towards what regional patterns to expect in large herbivore dynamics as well as in scale of regional synchrony. So far, there have been few studies looking at spatial synchrony in the effects of climate on large
herbivore populations. According to the Moran effect (Moran, 1953) we would expect this correlation to be equal to the spatial autocorrelation in the environmental noise, provided that the density regulation is loglinear and of similar strength in all populations (Engen and Sæther, 2005).

The population sizes of Soay sheep on two islands 3.5 km apart in the St Kilda archipelago was remarkably synchronised over a 40-year period (Grenfell et al., 1998; Blasius and Stone, 2000). For roe deer in Norway, the density dynamic was synchronous up to a scale of about 200 km (Grotan et al., 2005). For Svalbard reindeer, only two neighbouring populations were synchronised, but not a population situated about 140 km north-west of the other two areas (Aanes et al., 2003). The dynamics of caribou and musk oxen on each side of Greenland were reported to be highly synchronised from a minimum of 1000 km up to about 1700 km (Post and Forchhammer, 2002), but this result is controversial (Vik et al., 2004). This indicates that climate covariation is able to induce spatial synchrony in the population fluctuations of ungulate populations over quite large distances (but see Grotan et al., 2008).

There is a considerable effort among climatologists in downscaling the global climate predictions to scales relevant for large herbivores. This has so far been done for the Alps (N.G. Yoccoz, pers. comm.), and will likely be available for most of Europe in the near future, allowing for much more accurate and relevant predictions of the effects of climate change on large herbivore populations.

12.3 Winter limitation at northern distribution ranges: snow depth and icing

There is a large literature from northern areas of what climatic conditions might limit large herbivore populations (reviews Sæther, 1997; Weladji et al., 2002; Mysterud et al., 2003). In a classical study, Formozow (1946) stated that northern distribution ranges of large herbivores are mainly limited by snow depth and duration of snow cover. Though cold temperature and strong winds add a negative factor to the energy budget, later quantitative research also shows that snow is the main problem (Sæther et al., 1996; Grotan et al., 2005).

Severe winters increase loss of body mass (Sæther and Gravem, 1988; Cederlund et al., 1991; Herfindal et al., 2006a), which results mainly in reduced survival of calves (Cederlund and Lindström, 1983; Loison and Langvatn, 1998). Climatic conditions during gestation (i.e. late winter) was the most important period to red deer (Sims et al., 2007). The future snow depth maps will therefore be decisive for large herbivore distribution at northern latitudes and at high altitude. As stated above, since both temperature and
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Precipitation will increase at northern latitudes, temperature at time of precipitation will be critical and determine whether or not snow depths are likely to increase or decrease. At present, maximum snow depths in the mountains of Norway are increasing, though the duration of snow cover has decreased (Kausrud et al., 2008). One can therefore expect that with future stronger warming, it may also begin to rain more in the mountains.

A higher frequency of alternating warm and cold spells (Shabbar and Bonsal, 2003) can cause problems for grazers, especially, by ‘locking pastures’. The importance of icing events can most clearly be seen in the ungulate species inhabiting the most extreme environment in Europe, the Svalbard reindeer living at 80°N. Occasional winters induce massive die-offs due to winter rains and subsequent freezing (Aanes et al., 2002; Putkonen and Roe, 2003; Kohler and Aanes, 2004; Grenfell and Putkonen, 2008). The mortality may reach levels as high as 60% of the total population.

Snow depth, quality and duration of snow cover are therefore the most likely drivers of northern distribution ranges. Decreased snow depth and cover are likely to increase northern distribution ranges of roe deer, red deer, fallow deer, wild boar, and possibly also the mouflon (depending on management action) in Sweden. Changes in the spatial distribution of snow are also likely to affect the distribution patterns of alpine ungulate species in Central Europe such as the ibex and chamois (Sæther et al., 2002; Jacobson et al., 2004; Grøtan et al., 2008). These processes are already ongoing, though there are no case studies documenting a direct link of distribution range increase to climate.

12.4 Changes in growing season length and indirect effects of snow depth

The productivity of large herbivores will also be affected by summer range conditions, but it is less clear whether it will yield changed distribution ranges. The length of growing season is probably important, and together with timing of the onset of spring defines the critical period for productivity. Early spring conditions indexed by the Normalised Difference Vegetation Index (NDVI), a measure of photosynthetic activity (often based on sensing from satellites; Petorelli et al., 2005b), was the most important predictor for individual performance (body mass) of roe deer in France (Petorelli et al., 2006).

Early plant growth is determined mainly by spring temperature, but for alpine and northern populations also by snow accumulation patterns during winter (Petorelli et al., 2005a). Duration of snow can impact plant phenology and quality for the rest of the grazing season (Borner et al., 2008; Cebrian et al., 2008). Effects of the winter NAO operating through snow depths
(Mysterud et al., 2000) are shown to affect soil moisture (Kettlewell et al., 2006) and in turn plant phenology, as shown directly on plant first-flowering dates (Post and Stenseth, 1999; Aanes et al., 2000) or indirectly with NDVI (Pettorelli et al., 2005a; 2005c, 2006; Herfindal et al., 2006b). A variable plant phenology is predicted to be favourable to most large herbivores, at least grazing species, due to an extended period with access to young, high-quality forage (Albon and Langvatn, 1992; Mysterud et al., 2001a; Hebblewhite et al., 2008).

In heterogeneous, mountainous landscapes, phenology has so far become more variable with recent warming favouring red deer in Norway (Pettorelli et al., 2005a). In contrast, less variable plant phenology was reported in the more flat landscape on Greenland, likely detrimental to caribou (Post and Forchhammer, 2008; Post et al., 2008). With increased warming, less snow will result also at higher elevation.

These same factors seem important also for continental Europe. For chamois in the Alps and the closely related isard in the eastern Pyrenees, survival decreased following high phases of the NAO and low spring degree-days (Loison et al., 1999b). There was no direct impact of winter weather, so global changes in the NAO seemed also here to operate indirectly through plants. Lower snow cover as predicted, especially below 1700–2400 m a.s.l., would therefore affect populations negatively (Loison et al., 1999b). The study suggested opposite effects of increased spring temperature in the two populations. As adult survival was affected, having a large impact on dynamics (Gaillard et al., 1998), this may have severe consequences. For alpine and northern populations, decreased amount of snow fields during summer may speed up plant phenology, reducing production markedly. Whether the beneficial effect of lower snow depth during winter may be countered or enhanced by the indirect effect of snow on plant growth during summer will likely depend on topography. Accordingly, although large snow depth during late winter generally affects the population growth of the Swiss ibex negatively (Sæther et al., 2002; Jacobson et al., 2004), large differences were found over short geographical distances in the relative impact on the population dynamics of the same climate variable (Grotan et al., 2008). This is also likely to affect grazers more than browsers.

12.5 Summer/spring limitations: drought and southern distribution ranges

When moving from north to south, the factors limiting plant growth are changing (Loe et al., 2005). In the north, the main limitation is low temperature and a very short growing season, while precipitation takes over as the most important factor further south. For example, while red deer in Norway
and Scotland decrease in mass during winter and grow from May–June until plant material senesces in late autumn (around October), Spanish red deer can grow during autumn and winter, but often do not grow during summer due to drought (Martínez-Jauregui et al., 2009). Similarly, water becomes a clear limitation for roe deer habitat selection in the southern distribution ranges of Europe (Tellier and Virgos, 1997; Virgos and Tellier, 1998; Wallach et al., 2007). At lower latitudes, summer drought may become more important, and may be a key factor to future distribution of large herbivores in southern Europe even in the mountains. A severe drought hit southern Europe in 2003 (Ciais et al., 2005). The mortality of lambs in the mouflon population of Caroux-Espinouse in southern France increased markedly, from < 10% to 25.7% (Garel et al., 2004). Survival depended on the amount of rainfall recorded at a given 14 day period and in the previous 14–21 day period, but was not influenced by the exceptionally high mean daily temperature recorded.

12.6 Buffering of (winter) climate effects: morphology and behaviour

Ungulate species differ greatly in their adaptations. Some of them are much more prone to severe conditions, and it may affect which season is the more limiting. An old paradigm for large herbivores is that the winter season determines number of animals, while summer foraging conditions determine body condition and thus quality (Klein, 1965; Sæther and Heim, 1993; Pettorelli et al., 2005c). A few studies report interspecific synchrony in body mass for a given location. In Norway, annual variation in body mass of domestic sheep (grazing during summer only) were synchronised with body mass of moose (Sæther, 1985), red deer (Mysterud et al., 2001b) and reindeer (Weladji et al., 2003b). These studies at least indicate consistent interspecific responses to summer foraging conditions.

A comparative framework for species’ ability to cope with snowy conditions was derived for North American species (Telfer and Kelsall, 1984). The ability to cope with snow was suggested to be related to both morphological factors and behavioural strategies. The chest height and foot loading were used to derive a morphological index, while a behavioural index included scoring use of trails, specific habitat selection, feeding below or above snow, cratering, migration and technique of locomotion (Telfer and Kelsall, 1984). No formal comparative work has been done at a population level to see whether such a scheme works well to predict stability of large herbivore populations facing severe climate conditions. The comparative work of Gaillard et al. (2000) found no link between annual pattern of age-specific survival and body size, but was not season specific.
12.6.1 Morphology

The single most important factor is body size; the larger, the better the chances of winter survival. Due to surface-volume ratios, larger animals need less energy per unit of body size, larger ruminants can survive on a lower quality diet, which is termed the Jarman–Bell principle (Demment and Van Soest, 1985). Since plant quality is overall lower during winter, and since the fat reserves are too small to last the entire winter, this is an extremely critical component for large herbivores. The fur and fat reserves are also regarded as important. Larger deer have fat reserves to survive longer periods than smaller deer, since fat reserves scale approximately isometrically with size (Calder, 1984), while energy use per kilogram body mass is lower for larger deer (Demment and Van Soest, 1985). The higher and more variable mortality of male compared with female ungulates likely results from exhaustion of males' fat reserves due to rutting just prior to winter (Toigo and Gaillard, 2003). Direct empirical data on the importance of the fat reserves are limited and body mass is most often the index used. For roe deer, dynamics was best explained by variation in November snowfall, indicating that duration of winter (and fat reserves) might be decisive (Groten et al., 2005). Climate change is expected to shorten duration of snow cover, which will benefit roe deer and other small ungulates with limited fat reserves.

12.6.2 Behaviour

Behaviour is a key factor in buffering climate impacts (review in Moen, 1973; Telfer and Kelsall, 1984). The single most important behavioural buffer for climate effects is migration to lower elevation by northern large herbivores (references in Fryxell and Sinclair, 1988; Mysterud, 1999). This is a widespread phenomenon, as lower elevation areas have lower snow depths, though snow quality may be similar (Lundmark and Ball, 2008). Any factor reducing the possibility for migration may thus reduce the animals' ability to buffer such effects of climate change. Building of infrastructures at low elevation can have a negative effect (Andersen, 1991); also, building of railways and major roads can either cut off migration routes completely (fences) or lead to increased number of traffic accidents if they are built in the animals' main wintering areas. Indeed, increased numbers of moose–vehicle collisions are found in harsh winters (Gundersen and Andreassen, 1998).

There is also a challenge related to how the behavioural strategies to buffer climate effects may be influenced by predation (Hebblewhite et al., 2008). Predators may frequently lead to suboptimal use of plants by large herbivores
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(c.g. Fortin et al., 2005), and moose and reindeer, having calves that are more prone to predation, may be deterred from migrating to areas with the best foraging conditions (Edwards, 1983; Bergerud et al., 1984). Therefore, both building of human infrastructure and recolonisation of large carnivores can reduce the behavioural buffering of climate effects (see also below regarding dispersal).

12.7 Likely demographic consequences of increased frequency of extreme climatic events

Due to large body size and limited time for offspring to grow sufficiently large to meet the winter conditions, annual reproduction by large herbivores is the rule with few exceptions (such as wild boar in some cases). All large herbivore species are iteroparous, and the key to female fitness is thought to be mainly related to number of reproductive attempts (Weladji et al., 2006). A general feature of the life history is thus that adult females are conservative in their resource use (Gaillard and Yoccoz, 2003). Females will decrease reproductive effort rather than risking their own survival if there is an unusually poor year (fewer resources available for reproduction). Female reindeer forced to breed late raised offspring that were smaller in autumn, but maintained the same body condition as females breeding at normal times (Holand et al., 2006). Similarly, many adult female red deer in Scotland fail to breed at all in years of low resource availability (Mitchell, 1973; Ratcliffe, 1984).

A general pattern resulting from such a conservative life history strategy of adult females, is that juvenile survival is generally lower and much more variable than adult survival (Putman et al., 1996; Gaillard et al., 1998). Adult survival is therefore usually above 90% per year in areas with no large predators or hunting, and with very low variation between years (e.g. Toigo et al., 1997). At very high density and in poor habitat, particularly harsh years may have a slight penalty even on adult survival (Albon et al., 2000). The adult stage is typically between 2 and 7 years of age; older individuals again have higher mortality (Loison et al., 1999a). There is thus a fairly predictable sequence of traits affected as climate gets more severe (Eberhardt, 2002). This conservative life history strategy has important implications for predicting future plastic responses to climate changes (Morris et al., 2008).

The resulting demographic pattern of mortality is typically that the young and very old die under extreme climatic conditions (Gaillard et al., 1998), most clearly shown for the Soay sheep in the St Kilda archipelago off Scotland (Coulson et al., 2001a). Massive die-offs of young result in cohort effects that are indeed widespread in ungulates (red deer: Albon et al., 1992;
Post et al., 1997; Mysterud et al., 2002; moose: Solberg et al., 2004, 2007; roe deer: Kjellander et al., 2006), affecting both the quantity and quality of offspring produced (review in Gaillard et al., 2003). Animals from poor cohorts typically delay onset of maturation by a year, causing lagged effects (Solberg et al., 1999; Langvatn et al., 2004).

Clearly, therefore, the frequency of extreme events will be important for population persistence; a single extreme year is not enough to drive most populations to extinction (Reed et al., 2003). High values of the NAO will lead to a higher frequency of cold and warm spells in the Arctic (Shabbar and Bonsal, 2003). Exactly how frequent such years must be to be a threat to persistence has not been modelled: it will also depend on the level of mortality rates and also on the reproductive potential of the species. Several of the alpine bovids have rather low population growth rates, and may therefore be particularly vulnerable.

12.8 Interactions with other limiting factors may buffer or increase climate effects

It is now well documented that the effects of severe winter climate are more pronounced at high population density (Sauer and Boyce, 1983; Coulson et al., 2001a), as shown for Svalbard reindeer (Aanes et al., 2000; Solberg et al., 2001), red deer (Albon et al., 2000) and ibex (Sæther et al., 2002; Jacobson et al., 2004). In comparison, there is only one study (on moose) reporting an interaction between summer climate and density (Herfindal et al., 2006a), suggesting climate and density interaction to be somewhat less important during summer (Mobaek et al., 2009). Lower effects of climate at low population density are likely to buffer effects of climate change on large herbivore distributions to some extent (see, for example, Hallett et al., 2004).

Apart from the effects of local population density, however, there are a number of other factors that will strongly affect the outcome of climate change on large herbivore numbers and distribution patterns. These factors – disease, predators and competitors – may buffer or increase the effects of climate change. In addition, land use changes may have a marked impact on some species, for example if new crops are grown. We have no overview of such changes at the present time. One feature that we regard as particularly compelling is the possible link between climate and disease (see Chapter 11 and Box 11.2). In Minnesota in the USA, the lowered food quality available after increased warming resulted in increased infestation of parasites, and this caused a decline in the moose population (Murray et al., 2006). This potential influence of changes in disease risk may thus mean that even slight
changes in temperature can affect large herbivore populations to a much larger degree than anticipated if, for example, effects were operating through plant quality alone.

In Norway there has been growing concern regarding an increased frequency of tick-borne diseases, and the recent spread of deer ked to moose. In reindeer, the largest effects of summer climate are expected to be linked to activity of both flies and warble flies (Hagemoen and Reimers, 2002; Weladji et al., 2003a). The infestations of warble flies are negatively correlated with density (Fauchois et al., 2007), so that if populations decline, increased effects can be expected. Also, reindeer typically use snow fields during insect harassment, which may melt away giving no refuge. In the Alps, chamois fecundity was affected by bacterial infections, which in turn was related to climate (negatively to the NAO, more after cold and snowy winters: Pioz et al., 2008).

More severe winters can also lead to higher rates of predation, as shown for red fox predation on roe deer (Cederlund and Lindström, 1983) and wolves for moose (Vucetich and Peterson, 2004). Predators can therefore, in combination with winter, set the northern distribution limits at lower latitudes than if climate alone was operating. Though not well documented, roe deer seem to have reduced the extent of their distribution in the north of Norway after recolonisation of lynx in recent decades. It has also been argued that wolf predation in Russia causes roe deer to have a lower northern distribution range than expected based on snow depth alone, but here human hunting also played a role (Danilkin, 1996).

Another indirect way in which climate change may influence ungulate populations is through competition (Case et al., 2005). For birds, it has been shown that climate can affect the balance of interspecific competition (Setre et al., 1999). More generally it is well established that in any competitive interaction, competitive advantage is greatly influenced by environmental conditions. If climatic change is likely to affect the balance of competition amongst ungulate species, competitive relationships may be altered even among species which already have overlapping distributions. In addition, if some species increase their distributional range, they may become sympatric with new species or species combinations with which they have to establish new competitive relationships, with unpredictable outcome. Animals forced into suboptimal habitat through competition may subsequently be more vulnerable to other effects of climate change. In Spain, the Iberian ibex is forced into suboptimal habitat by goats (Acevedo et al., 2008a) and possibly the invasive exotic aoudad (Cassinello et al., 2004; Acevedo et al., 2008b). In the UK, the red deer seem to be competitively superior to the roe deer (Latham et al., 1996, 1997; reviews in Putman, 1996; Latham, 1999).
At northern latitudes, there is also competition between rodents and larger herbivores in peak rodent years (Steen et al., 2005). The fading of the cyclic dynamics of voles and lemmings due to climate change (review in Ims et al., 2008) may relieve competition with alpine reindeer. However, in forested areas in Sweden, the generalist red fox predates more on roe deer fawns during years with a low abundance of rodents (Kjellander and Nordström, 2003). Consistent low populations of rodents might therefore markedly elevate predation rates on roe and thus lower population productivity in roe deer. Indeed, such ecosystem effects might be strong, but are often difficult to predict.

12.9 What role will evolution play?

A central focus in the literature on climate effects on animals in general is whether animals are sufficiently phenotypically plastic to respond or whether evolution will be rapid enough to track changes in the environment (e.g. Przybylo et al., 2000; Nussey et al., 2005c; Skelly et al., 2007; Charmentier et al., 2008). Theories for evolution of quantitative characters (Lande 1982) have shown that the response to selection in the mean of the life history trait $z_i$ is

$$
\frac{dz_i}{dt} = \sum_{j=1}^{n} G_{ij} \frac{\partial r}{\partial z_j},
$$

where $G_{ij}$ is the genetic variance-covariance between characters $i$ and $j$ and $\frac{\partial r}{\partial z_j}$ is the selection gradient of the $j$'th character. This means that the rate of evolution of the mean life history equals approximately the additive variance-covariance matrix of the characters, times the selection gradient, which is a gradient vector of the intrinsic rate of increase of the population with respect to changes in the mean history. Thus, rapid evolutionary responses can only occur in characters under strong selection gradient with a substantial additive genetic variance or covariance component. Several studies have in fact indicated significant heritability components on life history traits of large herbivores (e.g. Rèale et al., 1999; Rèale and Festa-Bianchet, 2000; Pelletier et al., 2007a, 2007b) and relative strong selection (Coulson et al., 2003; Pelletier et al., 2007a, 2007b, but see Wilson et al., 2006).

These evolutionary responses can be especially important to consider when understanding how the demography and thus changes in distributions will be affected by changes in climate. The life history of large herbivores is adapted to the timing of plant growth and aims to target the most energy-demanding
period of lactation to periods with rapid plant growth to ensure high-quality food for the neonates (Klein, 1965; Sæther, 1997). For example, red deer in France rut in September so that calves are born in April, while red deer at northern latitudes in Norway, with a later spring, are rutting in October and giving birth in May (Loc et al., 2005, see also Fletcher, 1974). Similar geographical gradients in the timing of ovulation are also found in the moose (Garel et al., 2009).

We also know that the phenological development of plants is likely to change with climate. Thus, since large herbivores appear to use cues to initiate reproduction well in advance of the actual time of birth, a change in the relationship between the cue and the plant can severely affect the populations and induce strong selection on the timing of birth. According to this mismatch hypothesis (Cushing, 1990; Visser et al., 1998; Stenseth and Mysterud, 2002), the key point is that there are adaptations to the seasonal cycle of plant growth that can be broken down with the expected changes in climate. With advancing spring emergence of plants occurring with climate change (Post and Stenseth, 1999), the question arises of whether large herbivores are able to track these changes with appropriate changes in mating dates to advance birth dates.

Will ungulates adapt to these changes in spring flowering? Data are limited to studies of red deer on the Isle of Rum, Scotland (Coulson et al., 2003; Nussey et al., 2005a, 2005b). Here, the effect of spring temperature on birth mass of offspring was for individual females dependent on whether or not they had experienced high density early in life. Only females born at low population density showed any plasticity for these traits (Nussey et al., 2005a, 2005b). Birth date had become 10 days earlier (0.37 days/year), which was suggested to be due to selection (Coulson et al., 2003). Based on these analyses it would seem likely that there will be selection with future climate change. These are probably not the only aspects in which evolutionary change might happen. Examples are, however, few. Different genotypes of red deer on Rum, Scotland, survived better under different climatic conditions (Coulson et al., 1998). In locations with more severe snow conditions, moose had significantly larger hooves and longer legs than would be expected from their size (Lundmark, 2008). We suspect the limited focus on these issues to date is likely to alter in the near future, and in particular there may be more research on how evolutionary change might interact with the way we manage these populations.

Many species of large herbivores are subject to intense harvesting over larger parts of their distributional ranges. The rate of evolution of adaptive life history variation to climate changes may in those species be closely related
to choice of harvest strategies. Theoretical studies have shown that rate of change in the effective population size, which determines the rate of genetic drift (Wright, 1931), in harvested populations increases rapidly with a sex-biased harvest and small harvest rates of calves (Sæther et al., 2009). Thus, the probability of fixation of a slightly advantageous mutation, which can contribute to adaptations to a changing climate, may be affected by the choice of harvest strategy.

12.10 Conclusion

The impending climate change will undoubtedly bring about changes in the potential distribution ranges of large ungulates, which is the main focus of our review above. Large herbivores are a rather wide taxonomic group and differ greatly in their adaptations. This makes some of them much more susceptible to severe climatic conditions, and it may influence which climatic season is the more limiting. A few studies report interspecific synchrony in body mass for a given location. In Norway, annual variations in body mass of domestic sheep (grazing during summer only) were synchronised with body mass of moose (Sæther, 1985), red deer (Mysterud et al., 2001b) and reindeer (Weladji et al., 2003b). These studies at least indicate consistent interspecific responses to summer foraging conditions, and that good and poor years might be so both for browsers and mixed-feeders/grazers. Highly specialised species are likely more affected by severe climate than generalists, but empirical evidence is absent. Species with a high reproductive output have a more variable annual survival (Gaillard et al., 2000), suggesting they react more to severe conditions, but by contrast they are likely to recover more quickly as well. Formal comparative analysis to understand climate susceptibility in more detail is clearly needed.

For some large herbivore species in Europe to persist under the coming climate change, some of them might have to colonise new areas. Also, climate change opens possibilities for range expansion for species limited in particular by snow depth, quality and duration. Large herbivores are mobile species compared with many other taxonomic groups, and should therefore be less susceptible to climate change compared with plants and insects, although even some birds have tracked recent climate change in Europe (albeit with a time lag) (Devictor et al., 2008). How soon will changes in large herbivore distribution happen? Habitat persistence is a major determinant for the evolution of dispersal (Travis and Dytham, 1999). In cervids, a comparative analysis suggested that those species evolved for utilising less stable habitats (typically forest opened by fire or storm) have larger litter sizes and greater
rate of genetic sex-...in the focus of...more climatic...reindeer...specific...or years...centralised...it...empir...a more...more...quickly as...coming...climate...particular...species...be less...although...it...with a...herbivore...t...for the...apprative...habitats...id greater

inherent propensity to disperse (Liberg and Wahlström, 1995). For Europe, these are roe deer and moose, and the best documented case of colonisation speed in large herbivores comes from the recolonisation of Scandinavia by roe deer from 1850 onwards. The speed was up to 20–30 km a year in low quality habitat and 2–3 km a year in good habitat (Andersen et al., 2004). Dispersal in roe deer at the yearling stage is similar among the sexes, density independent and often long distance (Wahlström and Liberg, 1995; Gaillard et al., 2008). Colonisation speed of sika deer in Argyll, Scotland, was 3–5 km a year (Ratcliffe, 1987).

The behavioural ecology of the species plays a key role in determining colonisation speed. Male-biased dispersal is the rule for most large, polygynous herbivores, making colonisation a slower process since a dispersing male is less likely to encounter a partner, which will increase the demographic stochasticity and reduce the growth rate of the recolonising populations (Engen et al., 2003). Typical examples of this are red deer (Clutton-Brock et al., 2002) and chamois (Loison et al., 2008). Climate variation can also affect dispersal rates, but not to a large degree (Clutton-Brock et al., 2002).

For large herbivores encountering more or less continuous ranges, moving their range is not likely to be problematic, in the sense that climate change is not so rapid that they will be extinct before moving. Also, many species already have a wide distribution, and it is unlikely that climate change will affect conditions other than at the margin of current ranges. For these species, it is fairly easy to predict range expansion further north (and up in elevation), due to reduced snow depths and duration of snow cover, and contraction in the south due to summer droughts. These processes are already ongoing.

But while roe deer, red deer, wild boar and fallow deer show more or less continuous distributions, most species of ungulates do not (Groot Bruinderink et al., 2003). Alpine populations such as those of reindeer, ibex, chamois and mouflon face some of the same limiting factors as northern large herbivore populations in general. However, many alpine ranges are fairly isolated, making dispersal difficult. Reindeer in Norway are already fragmented in 23 populations, partly due to natural mountain borders, partly due to infrastructure. Southern populations of alpine species may therefore be particularly vulnerable.

Habitat destruction together with climate changes may further limit possibilities for colonisation (Travis, 2003). Deer around the world face challenges related to habitat loss through forest cutting or agricultural expansion (Klein, 1992). On a global scale, there are reported problems for migratory species of ungulates (Berger, 2004; Bolger et al., 2008), and protecting migration
corridors is considered important (Berger et al., 2008). The extension of cities, farmland and infrastructure has resulted in increasingly fragmented landscapes in Europe. Small populations in isolated habitats are at a higher risk of extinction due to stochastic demographic and environmental variation. Habitat networks will be important for future distribution of large herbivores in Europe (Groot Bruinderink et al., 2003). Or do we need to adopt a framework for assisted colonisation for large herbivores in Europe to mitigate effects of future climate change (Hoegh-Guldeberg et al., 2008)?

The history of large herbivores in Europe shows many examples of successful reintroductions following extinction due to overhunting etc. (Chapter 2). It is also clear that future, reduced or increased, productivity can perhaps, at least to some extent, be buffered with changes in human harvesting off-take.

References

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