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# Ungulate migration, plant phenology, and large carnivores: The times they are a-changin'

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Those of us living in a strongly seasonal environment at northern latitudes know how to appreciate longer days and a warming sun after months of winter cold. We can only barely grasp how an ungulate must feel when the spring flush of new green, protein-rich grass emerges after months of starvation and misery. It is no wonder that many ungulates wish to prolong this period of access to fresh spring vegetation by migrating. How will migratory animals cope with changes in plant dynamics due to climate change? What are the consequences of expanding large-carnivore populations in these systems? Why do some individuals remain stationary in nearly all populations of migratory animals? The study by Middleton et al. (2013) shed light on all these issues, without giving a definite answer to the relative role of each process.

## THE BASICS OF NORTHERN UNGULATE MIGRATION

At a basic level, animal migration is due to seasonal variation in factors limiting population growth (Bolger et al. 2008). Snow was identified a long time ago as the main driver of altitudinal migration of northern ungulates (Brazda 1953, LeResche 1974, Pulliainen 1974). Snow alone is sufficient to provoke migration, as areas of suitable habitat shrink from summer to winter because of increasing snow cover. These gradients are most frequently created by altitudinal variation in mountainous landscapes, and vertical movements from low-elevation winter ranges to high-elevation summer ranges is the most typical migration pattern (Mysterud 1999). A recent study comparing roe deer (*Capreolus capreolus*) populations spanning a wide range of latitudes in Europe clearly documented that migratory behavior increased with increasing seasonality and duration of snow cover (Cagnacci et al. 2011).

A rule-of-thumb in ungulate ecology is that winter forage conditions determine population density, while summer foraging conditions determine the size and body condition of individuals (Klein 1965). Since ungulates typically gather in low-elevation areas in valley bottoms

with shallow snow during winter, the interaction of landscape characteristics with snow creates strong seasonal variation in habitat suitability. We therefore see two end points of a continuum for populations that are not strongly limited by predation: (1) In flat landscapes, the whole area is suitable year-round. This leads to the build up of dense, mostly nonmigratory populations consisting of small individuals, because of density dependence and of a short period of access to fresh spring vegetation. (2) In mountainous landscapes, population density is limited by the small wintering areas, leading to low density on the summer ranges, which are often larger than winter ranges (Mysterud et al. 2011). Individuals in these migratory populations are often larger than those in nonmigratory populations, because of weaker density-dependent effects on growth and a prolonged period of access to fresh spring vegetation as animals migrate along a green-up gradient. The Clarks Ford elk (*Cervus elaphus*) clearly fall in the latter category, and the historical dominance of migratory animals points to an additional and strong nutritional benefit of migration, at least before wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) were present in current numbers (Middleton et al. 2013). Why is the migratory strategy no longer equally beneficial?

## MIGRATION AND PLANT DYNAMICS: PHENOLOGY AND BEYOND

Numerous processes might contribute to the altitudinal expansion of populations during summer relative to winter (Mysterud et al. 2011). The most prominent among these are clearly the forage maturation hypothesis, which formalizes how access to a more continuous supply of highly nutritious, newly emergent forage is a driving force of migration in large herbivores (Fryxell and Sinclair 1988, Hebblewhite et al. 2008). In climate effects studies, changing phenology has been a core theme for studies of migration in fish (Cushing 1990), birds (Visser et al. 1998), as well as ungulates (Pettorelli et al. 2005). Several closely linked themes connect migration and new patterns of plant dynamics under climate change: (1) the timing of spring peak in food (Visser et al. 1998), (2) changes in abundance (Durant et al. 2005), (3) duration of the spring peak in forage

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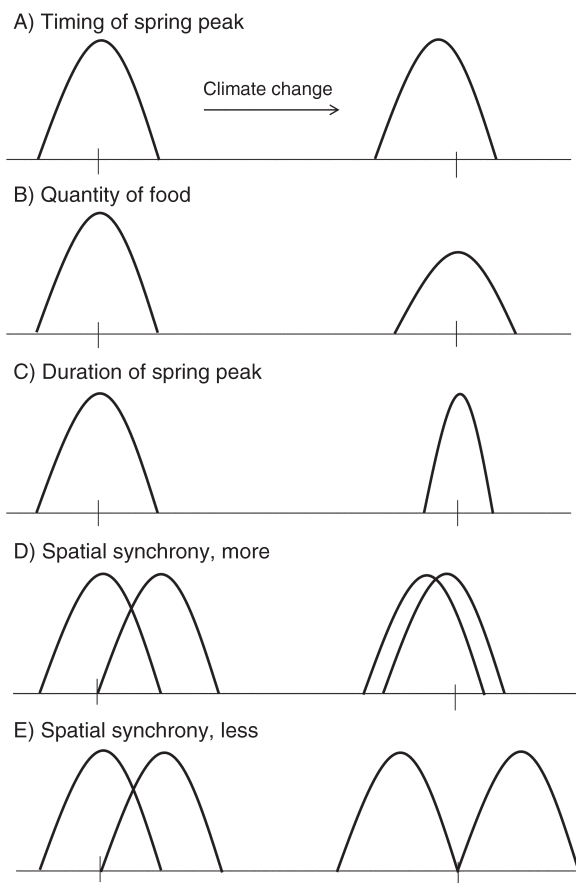


FIG. 1. Climate change may affect (A) the timing of spring peak, (B) the quantity of food, (C) the duration of the spring peak, and whether the peak becomes (D) more or (E) less synchronous in space.

nutritional quality, and (4 and 5) spatial synchrony of spring (more or less; Fig. 1).

The so-called match–mismatch hypothesis focuses on how long-distance migrators initiate migration based on cues in their winter range to optimally time their arrival in the summer range. If spring occurs earlier in the summer range, but the cue does not change (e.g., daylight duration or temperature in winter range), the animal will arrive in the summer range too late relative to peak food availability (Visser et al. 1998, Visser and Holleman 2001, Stenseth and Mysterud 2002). Timing of migration is plastic in ungulates, where it varies depending on spring conditions each year, as shown for red deer (*Cervus elaphus*; Pettorelli et al. 2005) and mule deer (*Odocoileus hemionus*; Monteith et al. 2011). However, the timing of parturition is less plastic, and it is therefore likely that there will be selection for earlier calving, as documented for red deer on Rum (Coulson et al. 2003). Short-term studies provide little basis for inference in this respect (Post and Forchhammer 2008).

#### DURATION OF SPRING AND SPATIAL SYNCHRONY: ALTITUDE IS KEY

The duration and spatial synchrony of spring can have multiple effects on migratory ungulates (Fig. 1C–E). At high altitude, deeper snow and lower temperature delay the timing of spring and forage development during summer. The consequences of global warming are predicted to differ dramatically with altitude. In the Alps, a 4°C increase in average summer temperature will shorten the period with snow cover by 50% at 2000 m above sea level (asl) and by 95% at 1000 m asl (Christensen et al. 2007). At low altitudes, climate warming is resulting in longer growing season, earlier migrations, and earlier reproduction in several taxa (Stenseth et al. 2002). A contrasting pattern emerged at high altitude in the Colorado Rocky Mountains over a 25-year period (Inouye et al. 2000). At higher altitudes, the average date of snowmelt had not changed despite warmer spring temperatures, likely because of increased winter precipitation falling as snow at high elevation (Inouye et al. 2000). There was no evidence for an effect of global warming on the timing of flowering at high altitudes (as in Fig. 1E). Similarly, in Norway, with increasing temperatures and increased precipitation, there was less snow at low elevation and more snow at high elevation (Mysterud et al. 2000). That led to increased spatial variation in plant phenology when comparing over a range of altitudes, and thus increased duration of spring in mountainous landscapes for migratory ungulates (Fig. 1E; Pettorelli et al. 2005).

A key issue is, therefore, whether a given landscape would retain sufficient variation in snow accumulation to prolong the duration of the spring flush under global warming. A recent study suggests decreased spatial synchrony with recent warming in a flat landscape at small spatial scales (Fig. 1D; Post and Forchhammer 2008, Post et al. 2008). The study by Middleton et al. (2013) is worrisome, as it provides the first case of a decrease in duration of spring in a mountainous landscape. There was apparently not sufficient snow falling at high elevation to counter the effect of increased temperatures. The benefits of migration therefore weaken, but is this the most likely explanation of the reduced recruitment of migratory elk?

#### WHY BE FASTER THAN THE SPEED OF SPRING?

According to the forage maturation hypothesis, a migratory ungulate should follow the uphill gradient of spring green-up. While there is clear evidence that ungulates benefit from migration (Hebblewhite et al. 2008), a recent study suggests they could do even better. Red deer move quickly between the winter and the summer home range; they are green-wave jumpers at a coarse scale (Bischof et al. 2012). During migration, small-scale foraging decisions may be overruled by other decisions operating at larger scales. Deviations from optimal surfing of the spring green wave may be due to trade-offs between energy intake and predator risk

(Festa-Bianchet 1988) or other constraints on space use such as avoidance of competition in the winter range (Myserud et al. 2011). Similarly, elk (*Cervus elaphus*) in the Canadian Rockies migrated rapidly, likely because during migration they were exposed to 1.7 times higher predation risk than nonmigratory elk (Hebblewhite and Merrill 2007, Hebblewhite and Merrill 2009).

#### DROUGHT OR NONLETHAL EFFECTS OF PREDATION?

The dynamics and behavior of ungulates are set to change dramatically as large carnivores recolonize parts of North America and Europe. Migration is often considered as a strategy to relieve predation (Bergerud et al. 1990, Barten et al. 2001). Predation risk by wolves on summer ranges of migrant elk was 70% lower than that experienced by nonmigratory elk in the Canadian Rockies (Hebblewhite and Merrill 2007, Hebblewhite and Merrill 2009). On Isle Royale, Michigan, moose (*Alces alces*) cows with calves remained resident on the small, wolf-free islands during the whole growing season, while moose without offspring later in the growing season moved onto the main island with wolf because of higher forage quality (Edwards 1983). Though these moose were not marked or followed over the entire year, there seems to be no general rule that migration relieves predation. In line with this, the decline of migratory strategy reported by Middleton et al. (2013) seems partly due to being exposed to four times as many grizzly bears and wolves as resident elk.

Drought may increase mortality of alpine ungulates (Garel et al. 2004), but the scale of decline in recruitment of migratory elk of Yellowstone is of a magnitude rarely achieved by other means than predation (Middleton et al. 2013). The unexpectedly low pregnancy rates of lactating migratory elk are based on a rather small sample size. If real, either drought effects are dramatic, or nonlethal effects of predation are fierce. And are the very low pregnancy rates sufficient to yield such a dramatic decline in recruitment? When several processes contribute to a pattern, it is often helpful to use a model to determine the contribution of each. For elk in Yellowstone, I lack an attempt to quantitatively model the relative contribution of reduced condition (and pregnancy) and offspring survival to the reported declines in recruitment. Are the lower pregnancy and survival rates sufficiently large to explain the 70% decline in recruitment over 21 years? To establish annual data on vital rates in the long term are clearly challenging. The study by Middleton et al. (2013) is important in this respect, providing a call for further research action.

#### STAYING BEHIND: AGRICULTURAL SUBSIDIES AND THE HUMAN SHIELD

Some individuals remain stationary in most populations with migratory ungulates (termed partial migration), but surprisingly little is known as to why both strategies persist over time. Theoretical models of partial

migration points to a central role of density dependence and competition (Kokko and Lundberg 2001, Guttal and Couzin 2010). There is a trade-off between staying outside of the smaller winter range for as long a time as possible in fall due to dense populations and likely high levels of resource competition, and the risk of being trapped in deep snow in the summer range. Mule deer (*Odocoileus hemionus*) in good condition were more risk prone, and delayed fall migration (Monteith et al. 2011). Indeed, facultative migration has been observed in mule deer (Nicholson et al. 1997), and anecdotal evidence for roe deer (Myserud 1999) suggest that they only return to their usual winter range if forced by snow. With decreased snow cover during winter, migration will become less common irrespective of plant phenology in these systems. That change in migratory behavior may be more marked for browsers such as mule deer, white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), and roe deer, for which the forage maturation hypothesis is less relevant than it is for grazers. How quick can such changes appear? Individuals most often follow the same migration pattern every year, as for elk in Yellowstone (Middleton et al. 2013). Although it is often argued that offspring inherit their mothers migration pattern (Sweaner and Sandegren 1988), the most thorough study of the development of migration clearly showed a between-generation switch between strategies (Nelson 1998).

Unfortunately, we know little about the overall fitness of resident and migratory individuals. Similar adult and juvenile survival was documented for migratory and nonmigratory elk in the Canadian Rockies (Hebblewhite and Merrill 2011), partly because nonmigratory elk reduced predation risk by selecting areas close to humans, the so-called human shield (Berger 2007). Middleton et al. (2013) suggest that agricultural subsidies could favor the nonmigratory strategy. I argue that this is a highly underrated factor for species prone to using agricultural pastures. Agricultural subsidies may explain why differences in body mass between migratory and nonmigratory animals tend to be small (Albon and Langvatn 1992). Silage production would produce a secondary peak in diet quality after the first harvest in July (Albon and Langvatn 1992), and red deer in the Alps (Zweifel-Schielly et al. 2012) and in Norway (Godvik et al. 2009) made extensive use of pastures. Staying at low elevation close to humans may both reduce predation and provide access to protein-rich agricultural forage, contributing to the persistence of partial migration. Clearly, we are facing new possibilities of studying the development of individual migratory strategies and why both strategies co-exist, now that “the times they are a-changin’”, yielding new balances in the relative benefits of migration.

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## Assessing fitness consequences of migratory tactics requires long-term individually based monitoring

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Migration is a behavioral response of individuals to the spatiotemporal variability of their environment across large spatial scales (Fryxell and Sinclair 1988). Migration has been reported in many vertebrate species living in seasonal environments and is interpreted as a tactic to maximize Darwinian fitness (Swingland and Greenwood 1983). By migrating, ungulates can both benefit from greater access to high-quality forage and escape from predators. For instance, Fryxell et al. (1988) observed that migratory ungulates outnumbered residents in savanna ecosystems of Africa mostly by escaping predation by large carnivores, while Hebblewhite et al. (2008) found that migrant elk (*Cervus elaphus canadensis*) had higher fecal nitrogen levels than residents. If such benefits indeed translate into fitness advantages, migrating should be the rule among ungulate populations in seasonal environments. However, in most populations of large herbivores studied so far, only a proportion of individuals migrate, whereas others remain resident. The role of environmental factors and individual attributes in shaping such partial migration is currently attracting attention among ecologists (Chapman et al. 2011). During the last decade, several studies have reported increasing threats to migrants. These threats include overhunting and restricted access to water or forage generated by habitat loss, competition with livestock, or fencing (Harris et al. 2009). Both a marked decrease in the propensity to

migrate and rapid population collapse have been reported (Bolger et al. 2008).

Middleton et al. (2013; hereafter referred to as Middleton et al.) studied an elk population where migrants winter in wilderness areas and summer 40–60 km away in Yellowstone National Park (USA), all areas not subject to human disturbance. Despite the lack of habitat degradation or physical barriers caused by human activities, the proportion of migrants decreased from 81% in the late 1970s to the early 1980s to 47.5% in recent years. In parallel, the productivity of migratory females decreased over the last 20 years. Compared to resident females, young and lactating females engaging into migration had a lower reproductive output than their nonmigratory counterparts in recent years. The authors concluded that deterioration of summer range habitat induced by climate change and high predation by wolves (*Canis lupus*) and grizzly bears (*Ursus arctos horribilis*) in summer range account for the patterns observed. While this case study improves our understanding of ungulate migratory tactics by providing clear evidence for lower pregnancy rates of migrants compared to residents in the absence of human disturbance, it fails to either quantify fitness differences between migrant and residents or identify the contribution of factors involved in such differences. Three major limitations, common to most studies of fitness consequences of migratory tactics in ungulates, likely account for these shortcomings: high heterogeneity in data quality and temporal scale, strong assumptions, and the lack of long-term individually based data.

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