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# How does landscape heterogeneity shape dynamics of large herbivore populations?

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A central challenge in ecology seeks to understand the dynamics of populations. It is clear that the abundance of organisms varies over time and space in response to two broad sets of processes: those that operate within populations and those that are external to them. Internal controls on dynamics include feedbacks from the current state of the population to its future state; for example, demography and population density shape rates of population growth. External controls on dynamics, particularly weather and its effect on resources, include conditions that are not influenced by characteristics of the population. Efforts to describe the role of these controls on population dynamics have dominated ecological inquiry for decades (Kingsland 1985).

Until recently, virtually all simple models of herbivore population dynamics have ignored trophic interactions entirely (i.e., Chapter 2) or have borrowed from abstractions of predator–prey interactions, representing feedbacks from plants to herbivores based on a functional response of

heterogeneous environments influence population dynamics, and we review empirical evidence for the operation of these mechanisms. We close by considering how global change may affect ungulate populations by limiting the access of individuals to heterogeneity in resources.

## 6.1 What is spatial heterogeneity?

Ecologists use the term “heterogeneity” with a bewildering diversity of meanings (Kolasa and Rollo 1991, Hobbs 2003), so we begin by offering an operational definition. Adler et al. (2001) pointed out that when spatial heterogeneity is measured using aspatial statistics, it is synonymous with spatial variability, but when it is measured with spatially explicit statistics, it implies spatial dependence or spatial pattern. Thus, heterogeneity, taken to mean variability over space, can be evaluated with standard deviations or coefficients of variation, while heterogeneity, taken to mean spatial dependence, must be measured by spatially explicit statistics like spatial autocorrelation or geostatistics (e.g., Pastor et al. 1998, Pastor et al. 1999). Although there is a growing literature on responses of individual foragers to spatial pattern (Hobbs 1999, Hobbs et al. 2003, Searle et al. 2005, Searle et al. 2006), little is known about the ways whereby spatial pattern influences population dynamics. Thus, for the purposes here, heterogeneity can be equated with variability over space, facilitating comparisons with variability measured over time. We will use the standard deviation or coefficient of variation of resources taken from samples arrayed over space (e.g., pixels in a landscape) as an operational measure of heterogeneity. There will be cases where autocorrelation in time or space will be important and we will be careful to highlight these instances. However, throughout this chapter, our use of heterogeneity will imply the following: a system that is spatially heterogeneous will show high coefficients of variation in a variable of interest (for example, plant biomass, plant nitrogen content) sampled from many locations, while a spatially homogeneous system will show low coefficients of variation. Here, we are referring to heterogeneity at the landscape scale comprising variation between habitats in resource attributes. For our purposes, we will use the term landscape to mean the area used by a population.

## 6.2 How does spatial heterogeneity influence ungulate population dynamics?

Consider two landscapes with similar levels of net primary production. One of these landscapes is spatially heterogeneous – it contains a varied array

of resources in the quantity or quality of plants available to them (Post et al. 2002, Caughley 1976, Caughley and Lawton 1981, Caughley 1982, Schmitz 1993, Blatt et al. 2001). Variance in plant resources, particularly variation in plant quality, has been usually ignored in these models despite the clear importance of spatial heterogeneity in shaping dynamics of predator–prey and host–parasitoid systems (see reviews of Hassell 1980, Hassell and Pacala 1990, Holt and Hassell, 1993). Because variation in quality and quantity are characteristic of the foods consumed by herbivores, it follows that mathematical theory on plant–herbivore interactions may fail to represent critical controls on herbivore population dynamics (but see delislein-Keshet 1986, Owen-Smith 2002a, b).

The preponderance of empirical studies of population dynamics has also overlooked spatial variation in plant resources. Investigations of population responses to resources have most often focused on how the total or average quantity of resources mediates population dynamics by constraining equilibrium population size or influencing population growth rate (Merrill and Joyce 1991, Fabricius 1994, Kiker 1998, Mduma et al. 1999, Weisberg et al. 2002). Moreover, although many time-series analyses have studied effects of weather and population covariates on population behavior (Putman et al. 1996, Forchhammer et al. 1998, Myrsterud et al. 2000, Jacobson et al. 2004, Myrsterud and Ostbye 2006, Colchero et al. 2009), most of these studies focused exclusively on explaining variation in time, averaging over the heterogeneity that exists in space.

Population dynamics of large herbivores unfold in a spatial context. In this chapter, we explore recent work revealing how populations of ungulate herbivores respond to spatial heterogeneity in resources, particularly heterogeneity in plant quality. We depart from earlier studies in an important way. Historically, investigations of the effect of spatial heterogeneity on herbivores have focused on the ways whereby individual foraging animals discriminate among spatially variable resources arrayed across a range of spatial scales (see reviews of Senft et al. 1987, Laca and Demment 1991, Bailey et al. 1996, Hobbs 1999). Although individual choices clearly aggregate to influence populations, population-level responses of large herbivores to spatial heterogeneity in resources have not been described until recently (Illius and O'Connor 2000, Wang et al. 2006, Leblewhite et al. 2008, Post and Forchhammer 2008, Post et al. 2008, Wang et al. 2009). Here, we consider the ways that differences in the levels of heterogeneity within landscapes influence population dynamics and we propose mechanisms explaining these influences.

Our chapter will be organized as follows. We begin by delineating some terms. Next, we summarize theoretical and empirical evidence showing that population trajectories of ungulates are shaped by spatial

this heterogeneity. How will herbivore populations respond to these different spatial contexts? Answering this question empirically is challenging because doing so requires observations of population trajectories on each landscape. Simply observing each population at a few points in time in each location will not suffice. Understanding how a population responds to "variation in spatial variation" is even more difficult because we need to observe population behavior over a range of landscape types varying in their levels of spatial heterogeneity. As a result of these difficulties, empirical studies of responses of populations to landscape heterogeneity have been infrequent. However, despite these difficulties, emerging evidence suggests that spatial heterogeneity in landscapes enhances performance of populations of large herbivores.

### 6.2.1 Results from analytical and simulation models

The formidable challenges of assembling data on effects of heterogeneity on population performance has not deterred a rich set of modeling efforts focused on understanding these effects. With few exceptions, these models have relied on relatively detailed, species-specific simulations; analytically based findings are less common. Predictions emerging from these models include the following:

- 1 Heterogeneity in resources that buffer against shortages during the dormant season can increase the long-term, average abundance of herbivore populations (Illius and O'Connor 2000, Owen-Smith 2002b).
- 2 These buffering resources can enhance the long-term stability of populations (Illius and O'Connor 2000, Owen-Smith 2002a, b, 2004). Whether such resources are stabilizing depends on their quality and on critical thresholds for herbivore starvation (Owen-Smith 2002a, b, 2004). In particular, the buffering resources must be of intermediate quality. In this case, animals do not starve during periods of resource scarcity but simply lose condition, thereby limiting reproduction and reducing the tendency of the population to overshoot its equilibrium (Illius 2006).
- 3 Movement of large herbivores among patches of resources within landscapes, patches that vary over time and space, can enhance population growth rates (Fryxell et al. 2005), increase supportable densities of animals (Boone and Hobbs 2004, Underwood 2004, Boone et al. 2005, Boone 2007), and promote persistence of populations that in the absence of spatial heterogeneity would go extinct (Fryxell et al. 2005). These effects depend on low spatial autocorrelation in patch quality and

herbivore mobility (Fryxell et al. 2005). In spatial autocorrelation is high or mobility is restricted, enhancing effects of resource heterogeneity on population performance are lost.

- 4 Effects of heterogeneity depend on overall levels of resource abundance. Resource heterogeneity exerts its greatest effect at intermediate levels of resource abundance (Boone 2007).
- 5 Heterogeneity in resource types can foster coexistence among animals differing in body mass and feeding style, and, so doing, enhance the diversity of herbivore communities and increase secondary production (Owen-Smith 2002b).
- 6 Spatial variation in the resources can enhance the abundance of consumers (predators or herbivores), whenever feedbacks from consumers to resource production are weak, and relationships between consumer abundance and the quantity of resources are nonlinear (Doncaster 2001). The enhancing effect of heterogeneity on consumer abundance is opposed by density dependence in the exploitation of resources created by interference competition. It may be dampened or reversed when efficiency of exploitation of resources by consumers is high, when there are strong feedbacks to resource production, or when the relationship between consumer abundance and resource quantity is linear (Doncaster 2001).
- 7 Feedbacks from herbivores to the distribution of forage quality can create density dependence apart from any effects of herbivores on forage quantity (Edelstein-Keshet 1986).

Clearly, none of these predictions would emerge from simple models of herbivore population dynamics (Chapter 2) that fail to represent heterogeneity in plant quantity and quality. However, although these predictions are new and offer useful motivation for empirical tests, they have not yet been formed into a comprehensive, integrated theory on responses of herbivore populations to heterogeneity, but rather provide a series of vignettes where a plausible set of premises leads by induction to a set of outcomes. These outcomes clearly add to our understanding of herbivore population dynamics, but they have not yet been brought together in a comprehensive theory.

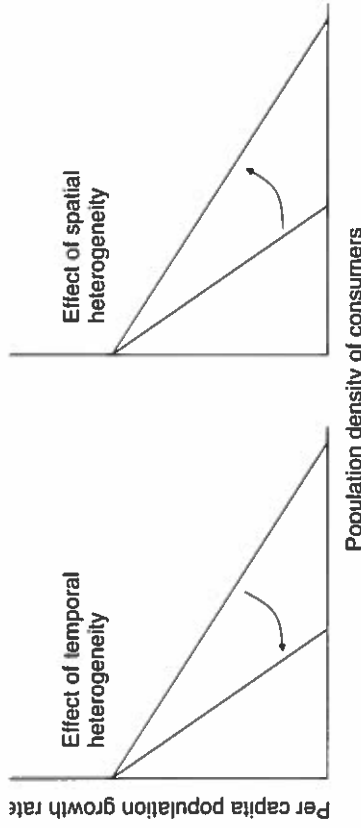
Some of these models, notably the metaphysiological models of Owen-Smith (2002b), are justified as alternatives to far simpler models, like the logistic and Ricker equations and others that model the approach of populations to equilibrium (Chapter 2). This appears to be a false comparison, because the purposes of the types of models are fundamentally different – a model cannot simultaneously be simple and, therefore, general, and at the same time, be more detailed and, therefore, specific (Levins 1966).

provide greater fidelity to specific conditions, they do so at a price. For detailed models, it remains uncertain whether the outcomes are constrained by the specific set of parameter values chosen for the simulations, and the extent to which the “generalities” that emerge are limited to the specific systems motivating the choice of those values.

## 6.2.2 Empirical results

Some of the predictions of models have been corroborated by empirical studies. Wang et al. (2006) examined time series of estimates of abundance of elk and bison in western North America and evaluated the strength of density dependence operating in each population. Strength of density dependence was estimated from the slope of annual per capita growth rate as a function of annual estimates of population size in a discrete time, Gompertz model of population growth. Increasingly negative slopes indicated stronger feedbacks from population density to population growth rate. The authors developed indices of temporal heterogeneity using the coefficient of variation in winter temperatures and developed indices of spatial heterogeneity using the coefficient of variation in the Normalized Difference Vegetation Index (NDVI). Temporal heterogeneity in winter weather amplified feedbacks from population density to population growth rate, strengthening density dependence, but spatial heterogeneity in NDVI weakened these feedbacks. Because the x-intercept of the slope of per capita population growth rate on population size estimates the potential population density at equilibrium, the result of Wang et al. (2006) implied that spatially heterogeneous landscapes could support greater densities of animals at equilibrium than landscapes that were less heterogeneous. In the same way, temporal heterogeneity reduced the equilibrium population size. Thus, a pivotal result emerging from this work was that heterogeneity in time and space acted in ways that were diametrically opposed (Fig. 6.1).

Similarly, Wang et al. (2009) estimated the strength of density dependence in populations of ungulates in Europe and North America occupying landscapes with different levels of spatial variance in elevation. They observed a negative correlation between spatial heterogeneity in altitude and the strength of density dependence, reinforcing their earlier findings. Average elevation was unrelated to strength of density dependence, leading to the conclusion that variation in resources along altitudinal gradients, rather than main effects of altitude, were responsible for effects on population dynamics. Wang et al. (2009) surmised that variation in altitude offered a surrogate for variation in plant phenology, which,



**Figure 6.1** Opposing effects of temporal and spatial heterogeneity on productivity of populations of ungulates observed by Wang et al. (2006). Arrows represent influence of increasing heterogeneity. Changes in the slopes of the lines represent effects on the strength of density-dependent feedback to population growth – steeper slopes mean stronger feedback. Because the x-intercept of the lines is landscape-carrying capacity, these hypothesized relationships predict that temporal heterogeneity reduces the number of consumers that can be supported, while spatial heterogeneity increases it.

in turn, enhanced nutritional status of individuals as described in the subsequent section.

Post and Stenseth (1999) studied reproductive performance of female red deer in relation to spatial heterogeneity in the number of calves born during years with spatial heterogeneity in date of flowering of vegetation. Females born in years when spatial variation in flowering date was high were about 25% more likely to bear calves as 2-year olds than were females born when heterogeneity in flowering was low (Post and Stenseth 1999). Langvatn et al. (1996) found that age of first reproduction in red deer in Norway and on the Isle of Rum, Scotland was influenced by spring temperatures: warm temperatures were associated with delayed reproduction, cool springs with accelerated reproduction. The authors attributed this effect to slowing of plant phenology by cold weather and consequent increased spatial variation in plant age. This variation, in turn, was believed to allow greater opportunity for females to feed on highly nutritious plant tissue by expanding the window of time when animals could consume plant tissue of peak quality.

Offspring production by caribou increased in direct proportion to spatial variation in plant phenology at 1–100 m scales in West Greenland (Post et al. 2008) and was inversely related to the extent of asynchrony between the timing of peak calf production and the timing of peak emergence in plants (i.e. “trophic mismatch,” Post and Forchhammer 2008,

Reductions in landscape heterogeneity or reductions in herbivore mobility among habitats compress the interval of time over which animals can

in their phenological response are arrayed along a spatial gradient, then animals should migrate along the phenological gradient, maintaining maximum nutrient intake rate (Fig. 6.2b, c). When plants are senescent, biomass and quality become effectively uncoupled – because plant tissue is of similar quality in all habitats. In this case, animals should be expected to migrate up the biomass gradient, because high biomass forage supplies can withstand higher levels of grazing before they become depleted. These kinds of movements also create buffering resources by assuring that some biomass remains unconsumed, a phenomenon described in the next section.

### 6.3.2 *Spatially heterogeneous landscapes contain buffering resources*

Virtually all populations of large herbivores experience periodic shortages in resources when plants are dormant, during the dry season in tropical environments and during the winter in temperate ones. Moreover, the total amount of edible biomass that is produced during any single growing season can vary enormously among years. Annual and seasonal variation in the availability of resources has the potential to cause dramatic fluctuations in animal numbers in the absence of resources that remain stable among seasons and years (e.g., Caughley et al. 1985, Ellis and Swift 1988, Fletcher et al. 1990, Owen-Smith 2004).

Heterogeneous landscapes contain a diversity of soil types, hydrologic features, and topographic positions, which, in turn, create spatial variation in standing crop biomass and vegetative composition. This diversity often includes landscape positions where plant biomass remains available for consumption by herbivores even when shortages prevail in other areas of the landscape. For example, tall grasslands in the northern Serengeti of East Africa provide biomass during the dry season when southern short grasslands are largely depleted (McNaughton 1983, Boone et al. 2006). In north-temperate ecosystems, habitats at low elevation remain largely snow free when high elevation habitats offer virtually no food because of deep snow (Wallmo et al. 1977, Frank 1998). In addition, heterogeneous landscapes contain a diversity of plant species and growth forms that respond to temporal variation in weather in different ways. Deeply rooted shrubs can persist through droughts, providing leaves when the herb layer fails to grow as a result of moisture stress (Scholes and Archer 1997). Plants with erect growth forms protrude above accumulated snow when prostrate ones are completely covered (Johnson et al. 2001, Nordengren et al. 2003). Such resources can permit herbivores to survive resource

shortages, buffering populations from temporal heterogeneity in plant production and availability (Hobbs 1989, Illius and O'Connor 2000).

A key part of this buffering is spatial variation in plant quality that allows animals to forgo consumption of low-quality resources when overall resource abundance is high (Owen-Smith 2002a, b, 2004, Illius 2006). If herbivores avoid consuming low-quality plants when high-quality ones are abundant, then low-quality biomass can accumulate to offset episodes of resource shortage. However, these accumulating resources must be of sufficient quality to prevent starvation during the dormant season. The phenomena of buffering may be common along productivity gradients. For the reasons described above, there is an inverse relationship between nutritional quality and plant biomass. Thus, landscapes with gradients in moisture often create opposing gradients in plant nutritional quality and biomass. The high productivity end of these gradients offers buffering resources that are avoided when high-quality resources are abundant and exploited when high-quality resources are rare.

## 6.4 *Influences from high-quality resources*

Enhancing access to nutritious forage forms an important selective force in the evolution of migration in large herbivores (Fryxell et al. 1988, Myerud et al. 2001a). Spatiotemporal variation in plant phenology entrains movements of large herbivores in ecosystems throughout the world, movements that are qualitatively consistent with mechanism 1. There is a common trend over time and space – animals migrate down phenological gradients during the growing season, tracking biomass and quality optima, and then move to areas of low quality, high biomass during periods of plant dormancy (McNaughton 1979, 1990).

In the Serengeti region of East Africa, zebra and wildebeest migrate over a distance spanning 200 km, following a rainfall gradient that shapes plant phenology and quality (McNaughton 1979, 1990, Boone et al. 2006). Similar patterns of movement along moisture/phenology gradients have been observed for wild and domestic ruminants in other African ecosystems (Bremner and Wit 1983, Sinclair and Fryxell 1985, Fryxell and Sinclair 1988). Models of movement of wildebeest in the Serengeti (Boone et al. 2006, Holdo et al. 2009) were able to mimic observed migration patterns of wildebeest on the basis of spatial variation in rainfall, gradients in plant nutritional quality, and availability of young, growing vegetation. Simple models predicting that animals will maximize their energy intake by tracking phenologically young patches of grass in the Serengeti have successfully explained the spatial distribution of wildebeest





(McNaughton 1989, Jefferies et al. 1994), thereby amplifying intraspecific competition for resources (Murray and Illius 2000).

The operation of this trade-off may depend on temporal heterogeneity in weather; for example, increasing effects of NAO on snow cover in Greenland appear to dictate the spatial dispersion of muskoxen (Forchhammer et al. 2005). High, positive NAO winters were associated with reduced snow accumulation during winter which increased the average annual plant biomass and the degree of spatial synchrony in plant growth in the following summer. This increased spatial synchrony in plant growth reduced aggregation of muskoxen relative to years when biomass and spatial synchrony were low. Spatial dispersion of individuals across landscapes during high NAO years may allow muskoxen to reduce competition for food while maintaining access to large quantities of high-quality forage (Forchhammer et al. 2005). Thus, although benefits of spatial heterogeneity induced by asynchronous phenology to the individual forager are clear, these benefits become less certain when animals forage in groups. It follows that understanding effects of spatial heterogeneity at levels of organization above the individual will involve aggregated consumer demand and its effects on resource supply and renewal. This empirical result is the first to represent the theoretical prediction of Doncaster (2001), that benefits of heterogeneity are opposed by intraspecific competition for resources.

## 6.5 Influences from buffer resources

In both tropical and temperate ecosystems, herbivores have been shown to move from consuming high-quality resources during the growing season into habitats that contain more abundant resources during the dry or dormant season. These habitats tend not to be used in the growing season because their vegetation is of lower quality than that available in other habitats. This movement may be localized or small scale (Bell 1971, Gordon 1989) or may involve migration such as in the case of wildebeest moving from the short grass plains in the Serengeti used in the wet season to the high biomass grasslands of the Masai Mara in the dry season (Fryxell et al. 2004).

At the vegetation community scale, Gordon (1989) found that cattle and ponies on the Isle of Rum selected for vegetation communities that contained high-quality vegetation during the growing season, but moved off these communities onto vegetation communities containing higher biomasses of lower quality vegetation during the winter. The smaller

bodied goats and red deer within this guild foraged on higher quality vegetation throughout the year. This indicates that the extent to which species use alternative resources in the growing season and the dormant season depends on the species body size and digestive system. Large-bodied species and those with a hindgut fermentation system can deal with poorer quality plant material and have high total intake requirements (Illius and Gordon 1991, 1992) and, therefore, move off higher quality resources earlier than small-bodied species (also driven by competition; Illius and Gordon 1987). Similarly, Bell (1971) showed that the guild of herbivores in the Serengeti (zebra, wildebeest, and Thompson's gazelle) moved up and down a catena gradient, using the upper part of the catena during the wet season when highly nutritious grasses and forbs were available and moved down to the lower, wetter parts of the catena to feed on more abundant, lower quality grasses during the dry season.

In western North America and Northern Europe, native ungulates used high-elevation habitats during the growing season and low-elevation habitats during winter (Garrott et al. 1987, Loft et al. 1989, Albon and Langvatn 1992, Mysterud et al. 2001a). The ability to migrate among these habitats is critical to population performance because snow accumulation during winter can make forage on productive summer ranges inaccessible, reducing their ability to support animals to virtually zero (Wallmo et al. 1977). Systems like these illustrate the operation of stabilizing heterogeneity (sensu Owen-Smith 2002a, b, 2004). Because production is low and forage quality tends to decline rapidly in low-elevation systems, they are avoided by large herbivores during the growing season. However, during most winters, they offer forage of sufficient amount and quality to largely prevent starvation of adults, and reduce starvation of young animals (Hobbs 1989).

## 6.6 Global change and access to heterogeneity by large herbivores

We have developed the case that access to spatial heterogeneity in plants influences population dynamics of large herbivores by expanding their options for selective foraging. Two aspects of global change, habitat fragmentation and climate change, may dramatically constrain these options.

Habitat fragmentation, the splitting of intact landscapes into spatially isolated parts, has emerged as a fundamentally important source of environmental change worldwide (Galvin et al. 2008, Hobbs et al. 2008, Wilcove and Wikelski 2008). Historically, the term habitat fragmentation was used to describe two effects that occur simultaneously – habitat loss that



isolation that occurs as movement of organisms among patches of habitat becomes increasingly restricted (Fahrig 2002). In order to separate the often confounded effects of isolation and habitat loss, contemporary landscape ecologists reserve the term *fragmentation* to refer specifically to the isolating effects of changes in landscapes in the absence of a reduction in habitat area (Fahrig 2002). We will use fragmentation in this sense.

A key, unresolved question in landscape ecology asks, "Does the effect of habitat fragmentation add to the effect of habitat loss?" This question can be usefully rephrased as follows: if a landscape is subdivided into a set of isolated parts, with no change in the area of habitat within the landscape, what effect should we expect for individual organisms and for populations? In the preceding sections, we showed that access to heterogeneity in resources in landscapes offers nutritional benefits to individual herbivores, benefits that appear to translate into enhanced performance of herbivore populations. These benefits occur because mobility allows herbivores to track peaks in potential maximum energy intake that occur at different times and locations across the landscape. In addition, mobility allows herbivores to exploit resources that are stable in time during episodes of resource shortage. An overlooked effect of fragmentation on organisms is that it compresses the scale of interaction between consumers and resources; that is, consumers that occupy fragmented landscapes have restricted access to the full range of temporal and spatial variation in resources that is available in intact landscapes (Hobbs et al. 2008). The theoretical framework we developed illustrates that fragmentation of habitats can lead to fundamentally important changes in population performance, even when the total area and quality of habitat remains unchanged. If habitat fragmentation reduces this mobility, then animals are compelled to consume forages that diminish in quality with time. Fryxell et al. (2005) and Iwen-Smith (2004) showed that reducing the scale at which herbivores interact with resources that vary over time and space can have profound consequences for population viability, even for an abundant species.

A warming climate and increased climate variability accompany habitat fragmentation as a prevailing source of human-caused change in the global environment. At landscape scales, climate warming appears to amplify spatial heterogeneity in plant growth, and in this way potentially enhances access to high quality forage by large herbivores (Post and Iwantsch 1999, Post et al. 2003). However, the increase in heterogeneity over the landscape can be counteracted by reduced heterogeneity in a suite of plant characteristics at finer scales (Post et al. 2008). The reduction in heterogeneity at the spatial scales most relevant to daily foraging as

a consequence of warmer temperature conditions was associated with lowered offspring production by female caribou in Greenland (Post et al. 2008). This result suggests that climate warming may reduce heterogeneity in phenology at the scales that are most relevant to daily foraging by herbivores. This reduction is associated with reduced reproduction by caribou (Post et al. 2008).

In addition, climate warming appears to create asynchrony between the time of maximum phenological heterogeneity and timing of the peak of reproduction by temperate herbivores. In Greenland, caribou synchronize their reproduction with the onset and progression of plant growth, timing their spring migrations such that they arrive on calving grounds when plants are emerging from dormancy (Post et al. 2003). Spatial heterogeneity in plant maturity created by variation in elevation, slope, and aspect allows these animals to prolong the period of peak energy and nutrient intake as depicted in Fig. 6.2. However, climate warming causes earlier initiation of plant growth, which, in turn, creates a mismatch between caribou migration and plant phenology (Post and Forchhammer 2008, Post et al. 2008). This asynchrony compresses the time interval during which animals can obtain maximum intake rates, and, in so doing, harms reproductive success. Grave consequences could arise from the combined effects of fragmentation, which compresses the spatial scale of interaction between herbivores and plant communities and climate warming, which compresses the temporal scale of that interaction.

## 6.7 Conclusions: the importance of spatial context for population dynamics

Understanding the causes and consequences of temporal variation in factors shaping population dynamics has formed a dominant theme in population ecology for decades (Kingsland 1985). Efforts to understand the role of the spatial context, particularly as it interacts with time, form a much more recent endeavor. We reviewed findings to show that heterogeneity in resources over space may be as important as the total amount of resources in shaping dynamics of populations of mobile herbivores. The temporal trajectory of plant growth and senescence creates trade-offs between quality and quantity of forage resources for herbivores. These trade-offs have fundamental implications for herbivore condition and population performance. Moreover, heterogeneous landscapes may contain patches of resources that remain stable in time despite fluctuations in the average or total amount of the resource. In so doing, heterogeneity can stabilize dynamics of ungulate populations.

interactions in models of herbivore population dynamics, progress that offers insight well beyond traditional formulations (Chapter 2). However, there is still a need for models that achieve theoretical generality while also including measurable state variables and parameters. Many of the models viewed here depend on representing the biology of specific species, which limits their generality. The more general models (i.e., Owen-Smith 2002a, 2004) rely on a representation of heterogeneity in forage quality that cannot be measured. A promising approach to representing heterogeneity in a simple, yet observable way, is developing statistical distribution functions relating plant nutritional quality to biomass (Denmmet and Van Soest 1985, Hobbs and Swift 1985, Edelstein-Keshet 1986). Future modeling efforts might usefully exploit these distributions.

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# Towards an ecology of population dynamics

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The working group “Dynamics of large herbivore populations in changing environments” that was established at the National Center for Environmental Analysis and Synthesis in 2001 had two basic aims:

- 1 To challenge prevalent population models using existing data on the dynamics of large herbivore populations
- 2 To develop alternative population models better able to accommodate the effects of environmental variability

My task in this final chapter is to outline the forms that these alternative models might take in the light of the factual information and concepts reviewed in the preceding chapters.

Weather influences have been revealed as pervasive, affecting forage production and its seasonal availability as well as imposing physiological stress (Chapter 3). Nevertheless, the magnitude of the mortality imposed depends on the population density, as well as predation and hunting pressure, influencing the effective resource availability. The birth mass and subsequent growth of the juvenile segment is most sensitive to resource limitations, affecting survival in this stage as well as the age at which females first reproduce (Chapter 4). Prime-aged females are most resistant to these influences, conferring population resilience, but with susceptibility to mortality decreasing with advancing senescence. Conditions in the year of birth may have a lasting effect on reproductive success at a