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Asynchrony, fragmentation, and scale determine benefits of landscape heterogeneity to mobile herbivores

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Abstract Understanding the ways that resource heterogeneity shapes the performance of individuals and the dynamics of populations offers a central challenge in contemporary ecology. Emerging evidence shows that herbivores track heterogeneity in nutritional quality of vegetation by responding to phenological differences in plants, differences that result from spatial and temporal variation in conditions favoring plant growth. Theory predicts that when spatial variation in temperature, nutrients, or moisture results in spatially asynchronous pulses of plant growth, herbivores are able to prolong the period during which they have access to forage of peak nutritional value. Although this idea has substantial support from observational and modeling studies, it has not been examined experimentally. We hypothesized that access to asynchronous resources enhances nutritional status and growth of herbivores and that the magnitude of this effect depends on the scale of access relative to the grain of resources. We tested these hypotheses in mesocosm experiment using the migratory grasshopper, *Melanoplus sanguinipes*, feeding on young wheat and protein-rich bran as a model system. We demonstrated access to asynchronous pulses in resources enhanced the efficiency of use of high quality resource use and increased growth of individuals by 13%. Disruption of this mechanism when landscapes were fragmented lowered efficiency of resource use and caused growth of individuals to decline by 15%. However, the strength of the effects of fragmentation on herbivore performance depended on the spatial extent of fragmentation relative to the spatial and temporal grain of resource emergence. Our findings add experimental support to modeling and observational studies that have linked herbivore performance to spatial and temporal variation in plant phenology. We also offer evidence that fragmentation can impair herbivore performance, even when the total amount and quality of resources on landscapes remains unchanged.

Keywords Consumer–resource dynamics · Habitat fragmentation · Phenology · Resource heterogeneity · Resource tracking

Introduction

An ongoing challenge in ecology seeks to understand the biotic consequences of environmental variation expressed over space and time. Recent studies of large herbivores in seasonal environments have offered powerful new insight into the ways that individuals and populations respond to spatial and temporal heterogeneity (reviewed by Hobbs and Gordon 2010). The ability of landscapes to support herbivores is ultimately limited by the total amount of aboveground net-primary production (ANPP) available for consumption (Cebrian and Lartigue 2004; McNaughton et al. 1989). However, emerging evidence suggests that limits set by ANPP can be modified by the spatial pattern and timing of plant growth. In particular, there is evidence that heterogeneity in plant communities expressed over

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space, particularly heterogeneity that induces variation in time by influencing plant phenology, offers fundamentally important nutritional benefits to foraging herbivores, benefits that enhance the performance of their populations. This finding means that access to heterogeneity can be a critically important feature of habitats for large mobile herbivores (Fryxell et al. 2005; Hobbs et al. 2008; Owen-Smith 2004).

These new lines of evidence have emerged from temperate and tropical systems alike, as well as from empirical and modeling studies. Wang et al. (2006) found that spatial heterogeneity in the normalized difference vegetation index (NDVI) within habitats of North American ungulates was negatively correlated with the strength of density dependent feedbacks between population density and population growth rate. This suggests that, all other things being equal, spatially heterogeneous landscapes had higher carrying capacities than homogeneous ones (Wang et al. 2006). A similar relationship was discovered between heterogeneity in elevation (linked to variation in plant phenology) and population growth for ungulates in Europe and North America (Wang et al. 2009). Simulation modeling revealed that the viability of populations of Thompson's gazelle on the Serengeti plains of East Africa depended on access to patches of grasses with phenologies that were asynchronous in time as a result of spatial heterogeneity in rainfall, topography, and soils (Fryxell et al. 2005). The effect of asynchrony depended on the area accessible for foraging; populations could persist in the face of spatially auto-correlated resources only if they had access to sufficiently large areas of landscape (Fryxell et al. 2005). Similarly, ecosystem models revealed that supportable densities of cattle were reduced when access to landscape heterogeneity was reduced by habitat fragmentation (Boone 2007; Boone and Hobbs 2004), but this effect depended on the scale of fragmentation relative to the grain of heterogeneity (Boone 2007). These last two results point to the potential for an important driving mechanism linking herbivore response to habitat fragmentation with access to heterogeneity, determined by the contrasting scales of animal movement and resource distribution.

Enhanced population performance in environments offering spatially heterogeneous resources appears to result from the ability of foraging herbivores to prolong the period during which they can exploit patches of immature plants, patches that offer maximum nutritional benefits (Pettorelli et al. 2005a, 2007). Hobbs and Gordon (2010) summarized mechanisms leading to this result, and offered a general, graphical model summarizing why spatial heterogeneity promotes herbivore nutrition (Fig. 1). In brief, this mechanism operates as follows. There is a well-established inverse relationship between plant biomass and plant nutritional quality, a relationship that is explained by the thickening of plant cell walls that is required to support an expanding canopy against gravity as plants mature (Mattson 1980; Van Soest 1994). This relationship is important because instantaneous intake rate is accelerated when herbivores feed in patches with high biomass, but daily intake rate is diminished when animals feed in patches of low nutritional quality. Consequently, plant patches of intermediate biomass offer the greatest nutritional benefits to grazing herbivores (Wilmshurst et al. 1995, 2000) (Fig. 1).

Heterogeneous landscapes promote access to patches with intermediate biomass by reducing spatial and temporal autocorrelation in plant growth. Spatial heterogeneity in a wide range of abiotic features (elevation, aspect, soil type, rainfall patterns, snow accumulation) can cause plants on different areas of the landscape to initiate growth at different times, thereby prolonging the window of time during which patches of optimum biomass can be found somewhere on the landscape (Fig. 1). In the absence of spatial heterogeneity in conditions controlling the initiation of plant growth, plant phenology becomes synchronized over space and the window of time during which animals can find patches of optimum biomass is compressed (Fig. 1) because all pulses occur at once. Synchronicity in plant growth is analogous to synchronized reproduction by prey (Ims 1990)—in both cases, synchronized pulses of production at lower trophic levels limits the ability of consumers to exploit the synchronized resource. There is ample evidence that large herbivores respond to landscape-level asynchrony by altering their distribution to coincide with the distribution of patches with rapid plant growth (Boone et al. 2006; Fryxell et al. 2004; Hebblewhite et al. 2008; Holdo et al. 2009; Mueller et al. 2008; Mysterud et al. 2001; Wilmshurst et al. 1999), and this response has been show to enhance herbivore nutrition and growth (Hebblewhite et al. 2008; Mysterud et al. 2001; Pettorelli et al. 2005b).

Although these observations have emerged from diverse ecosystems all over the world, they share features in common. In all instances, herbivores forage on landscapes with abundant low quality food where high quality food appears in pulses that appear and disappear as plants initiate growth and mature (Fig. 1). Access to these high quality pulses strongly influences herbivore nutritional status and growth. If these pulses were to appear simultaneously, that is, if phenology were perfectly synchronized, then there would be more primary production than the herbivores could consume. These shared features motivate the following general predictions:

1. *The asynchrony hypothesis* resource asynchrony enhances nutritional status and growth of herbivores feeding on pulsed resources.

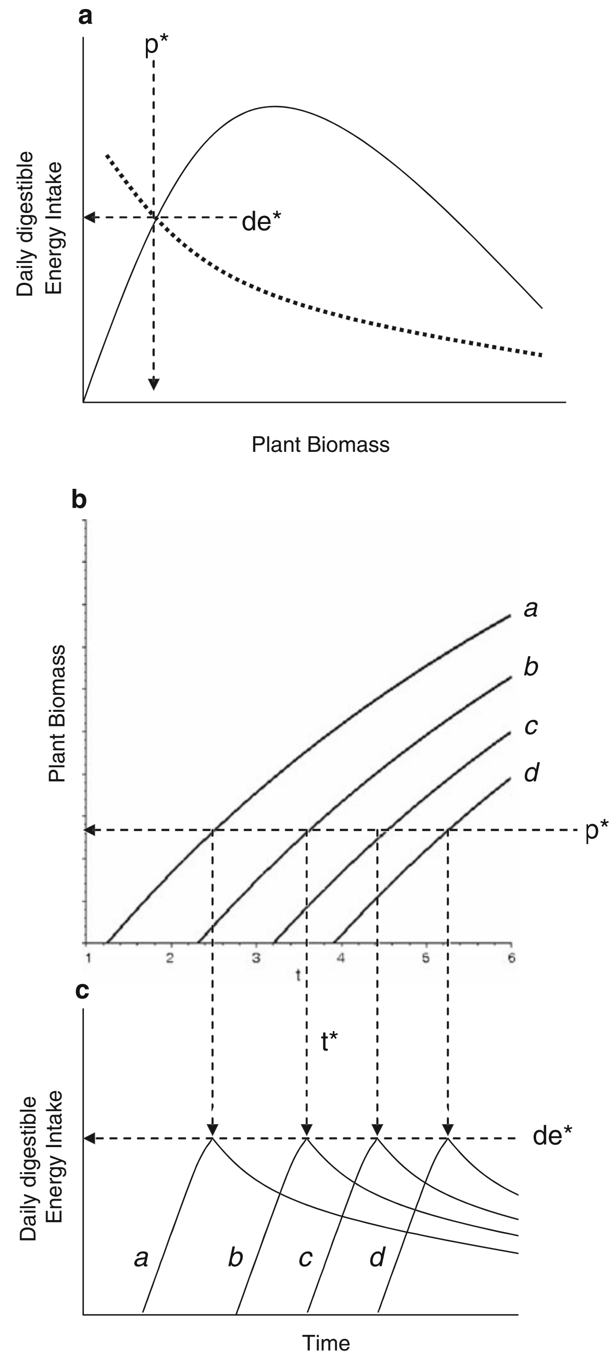

Fig. 1 **a** Daily digestible energy (*de*) intake is limited by foraging (*solid line*) or digestion (*dotted line*), whichever is less. There is a biomass of plants (*p**) that provides the maximum daily de intake due to quality/quantity trade-offs as plants mature. **b** Consider four habitats (*a*–*d*) with asynchronous phenology caused by variation in the initiation of plant growth with habitat *a* being earliest and *d* latest. Heterogeneity in phenology means that *p** occurs at different times in different locations. **c** As a result, the limiting portions of the foraging and digestion constraint curves show peaks (*de**) at different times. These differences expand the time interval (*t**) when herbivores can obtain maximum digestible energy. When plant growth is synchronous, the growth curves in plan (**b**) move closer together, compressing *t**. Adapted from Hobbs and Gordon 2010

2. *The fragmentation hypothesis* restricting access of herbivores to resources that are asynchronously produced over space, for example, by habitat fragmentation, will harm their nutritional status and growth even when the total amount and quality of production remains unchanged.
3. *The scale hypothesis* the outcome of the fragmentation prediction depends on the spatial pattern of resource pulses and the scale of restriction of access. If resource pulses are sufficiently fine-grained relative to the scale of restriction of movement, then fragmentation will not affect herbivore nutrition and growth.

These predictions follow logically from the empirical observations and modeling results described above; however, they have never been tested experimentally. Here, we report a mesocosm experiment designed to test the asynchrony, fragmentation, and scale hypotheses.

Materials and methods

Mesocosm design

We sought to understand how the growth of individual herbivores responded to the timing and spatial pattern of pulses of high quality food on a landscape. To do so, we created a model system that mimicked conditions experienced by herbivores in landscapes offering varying degrees of spatially and temporally heterogeneous plant phenology. These landscapes represented mobile herbivores feeding in a habitat with a uniform supply of low quality food interspersed with pulses of high quality food; analogous to the forage conditions found in many grassland systems during the onset of the growing season and subsequent maturation of available forage. We manipulated the timing and pattern of the pulses within the landscape and the scale of herbivore access to the pulses to test the three hypotheses. It was important that we were able to hold the total amount of food of each type constant such that the only source of variation in herbivore growth would be induced by the timing and pattern of pulses of high quality food.

Experimental design

We conducted a fractional factorial experiment with a completely randomized design (Fig. 2). We created six landscapes, 3.0 × 1.5 m in size, and imposed synchrony, fragmentation, and scale treatments on each landscape during a 7-week experiment. The synchrony treatment was structured by timing of the addition of pulses of high quality food; the fragmentation treatment was created by imposing barriers to movement, and the scale treatment was implemented by varying the grain of spatial heterogeneity of resource pulses. The density of herbivores and the total amount of high and low quality food per individual was held constant across all treatments, as described in more detail below. To test the asynchrony hypothesis, we examined how herbivore growth changed in response to variation in timing of additions of pulses, that is, access to one pulse versus two pulses versus four pulses of resource (Fig. 2). To test the fragmentation hypothesis, we compared growth of herbivores on landscapes that contained four asynchronous pulses but that were fragmented at different levels (intact, 2 fragments, 16 fragments) to restrict individual access to heterogeneity in high quality resources. To test the scale hypothesis, we compared growth of herbivores in landscapes that were increasingly fragmented (intact, 2 fragments, 16 fragments), but that allowed individual herbivores to access the full range of heterogeneity (4 resource pulses) in all fragmentation treatments.

All landscapes were housed in a greenhouse on Colorado State University campus, Fort Collins, Colorado, maintained within a temperature range of 24.5–33.5°C. The layout of the six landscapes was randomized, and daily maximum and minimum temperatures were recorded at each landscape position to serve as correlates in statistical analysis.

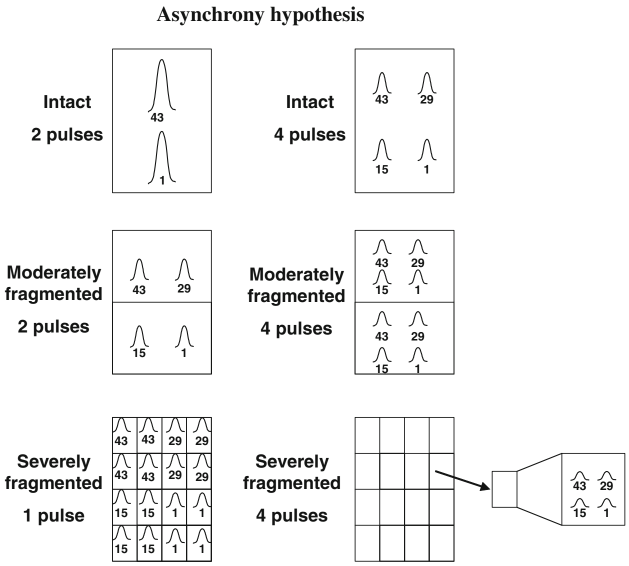

Fig. 2 To test the asynchrony hypothesis, we created six model landscapes that differed in the grain of spatial and temporal resource heterogeneity, as well as the severity of habitat fragmentation (intact, moderate, and severe). All six landscapes offered the same total biomass of resources. Resource heterogeneity was created using different spatial and temporal arrangements of a high quality resource (protein-rich bran powder) to create landscapes offering one, two, or four asynchronous resource pulses. The amount of high quality resource available per landscape fragment is represented by resource distributions, ⋀, each of which was available to consumers for 1 week. The timing of each resource pulse is identified by the *numbers* beneath each resource distribution, indicating the day at which different resource pulses were added to the landscape. We predicted that consumers with greater access to asynchronous resource pulses (*right column*) would have higher performance than those with access to more synchronous resource pulses (*left column*)

Herbivore

We used grasshoppers (*Melanoplus sanguinipes*, Fabricius) as a model herbivore. Individuals at the fourth instar stage (approx. 3 cm in length, 4 weeks old) were acquired from the USDA ARS Northern Plains Agricultural Research Laboratory in Sidney, Montana, USA. These individuals were reared under controlled, homogeneous conditions to minimize individual variation prior to the onset of the experiment. The insects were reared in 30 × 30 × 60 cm cages at 26–28°C. under a 16:8 L:D photoperiod, and fed organic Romaine lettuce, fresh cut wheat grass (*Triticum aestivum* L.), and commercial, dry wheat bran ad libitum. They were pathogen-free and reared without any antibiotics or antimicrobials. Supplementary heat was provided to the cages in the form of 100-W tungsten lamps positioned approx. 20 cm above each cage. Sixty-four grasshoppers were stocked on each landscape to achieve a density of 14 m^{-2}, at a 1:1 sex ratio. Densities corresponded to the reported economic threshold for grasshoppers in rangeland systems, estimated at 12 individuals m^{-2}; beyond this density, grasshoppers start to have economically meaningful impacts on vegetation (Davis and Skold 1996).

Growth measurements

We measured change in mass of individuals on each landscape during the 7-week experiment. All individuals were weighed on day 1. Thereafter, a sample of approximately 30 individuals from each landscape was caught and weighed weekly. The spatial distribution of sampled individuals was systematically distributed across each landscape so as to collect an even number of animals from all fragments or from the intact landscapes. Individuals were caught using a small net and transferred to plastic jars. Animals were placed in a refrigerator for approximately 15 min to reduce activity levels prior to weighing.

Food resource

Mesocosm landscapes contained identical supplies of wheat to provide abundant low quality resources. 'Hatcher' wheat (Haley et al. 2005) was used throughout the experiment, which is an awned, white-chaffed, medium maturity, semi-dwarf hard red winter wheat. Wheat was grown under homogeneous greenhouse conditions, and, after 2 weeks growth, was introduced to the experimental landscapes. Growing wheat in pots was evenly placed into each of the landscapes for 1 week, and then removed and replaced with fresh 2-week-old wheat. During each week, wheat was watered to maintain turgor and freshness. Wheat was supplied to allow individuals to maintain body mass. Hewitt and Onsager (1982) previously estimated average forage losses of 111.8 mg dm per individual per day in a northern mixed prairie. Over the course of 1 week, this equates to an estimate of approx. 0.78 g dm per individual. Given the stocking rate of 14 per m^2, a total of 50 g dm of wheat was required to meet maintenance in each landscape.

High quality resources were chosen to mimic emergence of young, nutritious forage for herbivores. They consisted of a mixture of high-calcium cricket feed and whey protein isolate. We added a total 180 g of high quality resource to each landscape in two or four pulses that lasted for 1 week. Pulses were introduced on days 1, 15, 29, or 43 according to the synchrony treatments (Fig. 2). Pre-experiment measurements quantified the consumption rates of individually housed fourth instar *M sanguinipes* over 3 weeks. Based on these measurements, we were able to ensure that some high quality resource would remain uneaten at the end of the pulse.

Mechanism

We determined the proportion of high quality resource that was consumed by herbivores in each landscape for each resource pulse. This was calculated as the ratio of the mass of high quality resource consumed over the total mass of high quality resource available in each landscape. This proportion was calculated for the final three pulses of high quality food, added on days 15, 29, and 43.

Analyses

We constructed a general linear model (GLM) to test the asynchrony hypothesis. Changes in mean mass (g) of sampled individuals from each landscape were analyzed using a GLM with level of fragmentation (intact, moderate, severe) and access to asynchronous resource pulses (four, two, one) as fixed class variables. We also included week as a fixed class variable to account for repeated measures. The mean mass of all individuals per landscape on day 1 was used as a covariate, as well as the normalized sex-ratio of sampled individuals per landscape in each week. We compared least squares means for levels of resource pulse asynchrony (four vs two vs one) averaged across levels of fragmentation; that is, the least squares mean of all landscapes with four resource pulses ($n = 3$) was compared with the least squares mean of landscapes with two resource pulses ($n = 2$) and the least squares mean of the landscape with only one resource pulse.

To test the fragmentation hypothesis, we constructed a GLM with mean mass gained (g) at each weekly interval of the 7-week experiment. Mean mass gained was the mean mass of the sampled individuals from each landscape minus the mean mass of all the individuals from each landscape on day 1. Data on mean mass were for sampled individuals in the three landscapes in which resource heterogeneity was constant but fragmentation levels varied (Fig. 3, fragmentation hypothesis). Level of fragmentation and week were used as class variables. We tested for an effect of two covariates; sex-ratio of sampled individuals, and temperature variation over each week (mean max. temperature − mean min. temperature).

We tested the scale hypothesis that increasingly fine grain in resources opposes the effect of fragmentation, using a GLM with mean mass gained (g) at each weekly interval of the experiment. Data on mean mass were for sampled individuals in the three landscapes in which the grain of resource heterogeneity progressively decreased with increasing severity of fragmentation (Fig. 3, scale hypothesis). Mean mass gained was the mean mass of the

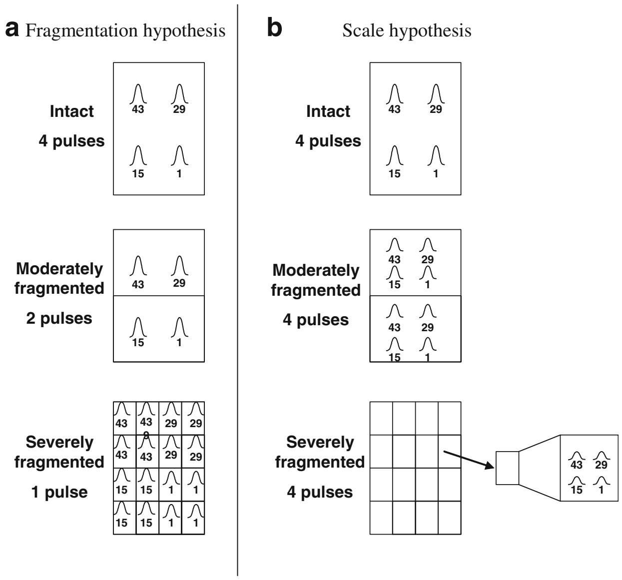

Fig. 3 Schematic of layouts of experiment used to test the fragmentation and scale hypotheses. The same amount of high quality resource was added to each landscape in pulses that were available for 1 week. Pulse size, spatial location, and timing of appearance differed among landscapes. The amount of high quality resource available per landscape fragment is represented by resource distributions. The timing of each resource pulse is identified by the numbers beneath each resource distribution, indicating the day when different resource pulses were added to the landscape. Under the fragmentation hypothesis (**a**, *left column*), we tested our prediction that increasing fragmentation would reduce consumer performance because the scale of fragmentation disrupted access to asynchronous resource pulses. Under the scale hypothesis (**b**, *right column*), we predicted that fragmentation would have no effect because it does not change access to asynchronous resource pulses

sampled individuals from each landscape minus the mean mass of all the individuals from each landscape on day 1. Level of fragmentation and week were included as class variables. We looked for significant effects of two covariates (sex-ratio of sampled individuals, temperature variation over each week).

Due to slight differences in mortality of individuals between the six landscapes, we also tested for an effect of population density in all three GLMs used to test each hypothesis. Density of individuals per landscape was estimated each week by averaging visual counts of animals made on three separate days per week.

Results

We found no significant effect of population density in any of the GLMs used to test the three hypotheses (asynchrony: $F_1 = 1.92$, $P = 0.1786$; fragmentation $F_1 = 2.29$, $P = 0.1647$; scale: $F_1 = 2.15$, $P = 0.1786$).

The asynchrony hypothesis

Increasing access to asynchronous resource pulses had a significant positive effect on average mass of herbivores (Table 1; $F_2 = 10.27$, $P = 0.0004$). Herbivores with access to only one resource pulse weighed significantly less than herbivores with access to two resource pulses (LSmeans difference −0.056 g, 95% CI −0.082 to −0.029, $P = 0.0002$), and significantly less than herbivores with access to four resource pulses (LSmeans difference −0.045 g, 95% CI −0.066 to −0.024, $P = 0.0001$). The average mass of herbivores with access to two or four resource pulses did not differ (LSmeans difference 0.011 g, 95% CI −0.003 to 0.024, $P = 0.1258$). The mean proportion of high quality food consumed by herbivores during each resource pulse declined as the number of asynchronous resource pulses available to individuals decreased (Table 2, asynchrony hypothesis).

Two of the covariates supplied to the GLM had significant effects on changes in mean mass of herbivores in all six landscapes over the duration of the experiment. The mean mass of all individuals per landscape on day one was used as a covariate ($F_1 = 17.52$, $P = 0.0002$) as well as the normalized sex-ratio of sampled individuals per landscape in each week ($F_1 = 7.58$, $P = 0.0101$). The model explained 96% of the variation in the data ($F_{12,41} = 63.63$, $P < 0.0001$).

The fragmentation hypothesis

Fragmentation had a significant negative effect on the mass gained by herbivores (Table 1; $F_{2,6} = 12.81$, $P = 0.0011$). Herbivores in the severely fragmented landscape gained significantly less mass than those in the moderately fragmented landscape ($P = 0.0005$), and significantly less mass than herbivores in the intact landscape ($P = 0.0017$). Mean mass gained by herbivores in the moderately fragmented landscape did not significantly differ from that gained by herbivores in the intact landscape ($P = 0.53$).

Table 1 Least squares means for average mass (g) of sampled individuals (asynchrony hypothesis) and average mass gain of sampled individuals (fragmentation and scale hypotheses), with associated standard error (SE) of the LSmean

	Number of periods of access to asynchronous resource pulses		
	4	2	1
Asynchrony hypothesis			
LSmean mass (SE) (g) and 95% CI	0.400 a (0.00308) (0.939–0.405)	0.410 a (0.00532) (0.400–0.421)	0.354 b (0.00926) (0.335–0.373)

	Level of fragmentation		
	Intact	Moderate	Severe
Fragmentation hypothesis			
LSmean mass gain (g) and 95% CI	0.227 a (0.00552) (0.215–0.239)	0.232 a (0.00552) (0.220–0.244)	0.196 b (0.00552) (0.184–0.208)
Scale hypothesis			
LSmean mass gain (g) and 95% CI	0.227 a (0.00459) (0.217–0.237)	0.204 b (0.00459) (0.194–0.214)	0.251 c (0.00459) (0.241–0.261)

Numbers in parentheses on second line are 95% confidence intervals from general linear models used to evaluate grasshopper response to asynchronous peaks in resource quality and landscape fragmentation. Letters denote results that are significantly different from one another ($\alpha = 0.05$)

Table 2 Observed proportion of high quality food eaten by consumers under the asynchrony, fragmentation and scale hypotheses

	Number of periods of access to asynchronous resource pulses		
	4	2	1
Asynchrony hypothesis			
Proportion of high quality food consumed (SE)	0.185 (0.026)	0.142 (0.036)	0.117 (0.035)
	Level of fragmentation		
	Intact	Moderate	Severe
Fragmentation hypothesis			
Proportion of high quality food consumed (SE)	0.209 (0.076)	0.171 (0.030)	0.117 (0.035)
Scale hypothesis			
Proportion of high quality food consumed (SE)	0.209 (0.076)	0.182 (0.032)	0.165 (0.025)

Numbers in parentheses are one standard error of the mean

Increasing fragmentation led to a steep decrease in the mean proportion of high quality food consumed per resource pulse (Table 2; fragmentation hypothesis).

No covariates proved to be significant so were not included in the final model. The model explained 95% of the variation in the data ($F_{8,20} = 26.39$, $P < 0.0001$).

The scale hypothesis

Fragmentation had a significant effect on the mass gained by herbivores (Table 1; $F_{2,6} = 26.26$, $P < 0.0001$); however, the pattern of this effect was different to that in landscapes in which the grain of resource heterogeneity did not change with degree of fragmentation. Instead, mass gained by herbivores in the severely fragmented landscape was significantly greater than that gained by herbivores in either the moderately fragmented landscape ($P < 0.0001$) or the intact landscape ($P = 0.0032$). Mass gained by herbivores in the intact landscape was significantly greater than that gained by herbivores in the moderately fragmented landscape ($P = 0.0039$). The proportion of high quality food consumed by herbivores declined slightly as the severity of fragmentation increased (Table 2, scale hypothesis), however, the decline was much less steep than in landscapes with more coarse-grained resource heterogeneity (Table 2, fragmentation hypothesis).

No covariates were significant so were not included in the final model. The model explained 97% of the variation in the data ($F_{8,20} = 49.46$, $P < 0.0001$).

Mechanism

The effect of asynchrony, fragmentation, and scale can be explained by access to resources in space and time. The pattern of differences in growth (Table 1) was matched by the pattern of the proportion of high quality food that was consumed (Table 2). When access to high quality food was brief because pulses were synchronized or because herbivores were prevented from moving freely across the landscape, more of the high quality resource remained unconsumed.

Discussion

We provide experimental evidence that herbivore growth is enhanced by asynchrony in timing of emergence of high quality food resources, that fragmentation can harm herbivore growth by preventing access to resources that vary over space and time, and that the effect of fragmentation depends on the spatial and temporal grain of resource emergence. By allowing manipulation of food resources and by controlling influences on herbivore nutrition and growth, our experimental approach filled an important void between large-scale, observational studies (Hebblewhite et al. 2008; Wang et al. 2006) and simulation modeling (Boone 2007; Fryxell et al. 2005).

We demonstrated that greater access to asynchronous resource pulses increased the growth of herbivores. A necessary condition for this result was that reduced access caused a portion of resources to go unused. Herbivores with access to only one resource pulse had significantly lower average mass than those with access to two or four resource pulses, despite the fact that the total amount of resource was the same. However, there appeared to be a threshold above which increasing access to pulses failed to enhance consumer performance. We found no difference in mass between herbivores with access to either two or four asynchronous resource pulses. It is likely that the elevation in diet quality gained from access to two asynchronous resource pulses was sufficient to increase herbivore nutritional status above a threshold, beyond which growth could not be further elevated; an effect previously demonstrated for this species (Fielding and Defoliart 2008).

An important consequence of landscape fragmentation was demonstrated: when increasingly severe fragmentation was not matched by more fine-grained resource heterogeneity, the growth of herbivores in the severely fragmented landscape was significantly lower than that of herbivores in intact landscapes, even though total resources per landscape remained unchanged. Growth of herbivores in the moderately fragmented landscape did not differ from that in the intact landscape, likely due to the threshold effect described above. However, we demonstrated that this effect of fragmentation depended on the scale of fragmentation and the grain of resource heterogeneity. When increasingly severe fragmentation was matched by an increasingly fine grain of resource heterogeneity, herbivores in the most severely fragmented landscape gained significantly more mass than herbivores in either the intact or moderately fragmented landscape.

We suspect this benefit may be due to reduced intraspecific interactions. Even though we maintained equal overall population density between the different landscapes, it is likely that crowding of individuals may have occurred in the less fragmented landscapes when high quality resource pulses were added. This type of phenomenon was reported in another fragmentation study that used an experimental model system with the beetle *Oryzaephilus surinamensis* (L.); progressively fragmented populations with constant total amounts of food had greater beetle abundance than non-fragmented populations (Bancroft and Turchin 2003). The authors attributed this finding to herbivores in more fragmented populations experiencing a release in competition for space, such that interference between individuals decreased relative to intact populations (Bancroft and Turchin 2003). This finding has relevance for applications of our concepts to large herbivores. Aggregation in large herbivores is caused in part by attraction to resources that are spatially concentrated (Fryxell 1991). This may bring benefits, as occurs when grazing lawns are formed (McNaughton 1984, 1986). However, aggregation can also increase intraspecific competition for resources (Doncaster 2001), or increase levels of harassment between individuals (Holand et al. 2006). Benefits of asynchronous phenology for large herbivores will, therefore, result from the interplay of individual behaviour and group dynamics in social species.

The importance of heterogeneity in forage resources for herbivores has been increasingly recognized, in both modeling and empirical studies. Offspring production by caribou (*Rangifer tarandus*) in Greenland and by red deer (*Cervus elpahus*) in Norway increased linearly with spatial heterogeneity in plant phenology (Post and Forchhammer 2008; Post and Stenseth 1999). Post and Stenseth (1999) demonstrated that female red deer born in years with high spatial variation in flowering date of vegetation were about 25% more likely to bear calves as 2 year olds than were females born in years of low spatial variation in flowering date. Pettorelli et al. (2005a) showed that when increases in the North Atlantic Oscillation led to a more spatially variable vegetation phenology in Norway, migratory red deer experienced an extended period of access to high quality forage and achieved higher body masses.

The mechanistic link between resource heterogeneity and large herbivore dietary and population level responses derives from behaviors that allow herbivores to dynamically match their distributions with those of resources that vary in space and time. Resource tracking, where consumers track peaks in forage quality across a landscape, is known as a crucial mechanism by which large herbivores, whose food is typically abundant but of low quality (Mattson 1980), can elevate diet quality and enhance individual and population level performance (Albon and Langvatn 1992; Frank and McNaughton 1992; Hebblewhite et al. 2008; Mysterud et al. 2001; Pettorelli et al. 2005a; Wilmshurst et al. 1999). The forage maturation hypothesis (FMH) proposes that migratory ungulates are driven by selection for high forage quality to follow phenological gradients during the growing season (Fryxell 1991; McNaughton 1985). A seminal study of resident and migratory elk in the Canadian Rocky Mountains demonstrated that migration by ungulates led to greater access to higher quality forage, and consequently higher diet digestibility, relative to nonmigratory conspecifics (Hebblewhite et al. 2008). In tropical ecosystems, ungulates migrate across regions spanning hundreds of kilometers to follow a rainfall gradient that drives patterns in plant phenology and quality (Boone et al. 2006; Fryxell and Sinclair 1988; McNaughton 1979, 1990). Modeling has shown that movement patterns can be successfully predicted when animals are assumed to track phenological variation in plants in heterogeneous landscapes (Boone et al. 2006; McNaughton 1990; Wilmshurst et al. 1999), and that these resource tracking movements serve to enhance diet quality, nutritional status, and increase population densities (Hebblewhite et al. 2008; Pettorelli et al. 2005a; Wang et al. 2006). In a broader ecological sense, this phenomenon is just one strand in a common thread that links spatio-temporal consumer–resource interactions across many different taxa and ecosystems. It is analogous to the concepts of habitat and resource complementation and supplementation, which have been empirically demonstrated in both terrestrial and aquatic systems (Dunning et al. 1992; Tilman 1982).

Our empirical results are in line with previous modeling work that demonstrated important consequences for population abundance and viability when the scale at which an herbivore interacts with a key resource was compressed (Boone 2007; Boone et al. 2005; Fryxell et al. 2005; Owen-Smith 2004). Fragmentation studies have offered conflicting conclusions; both empirical and modeling studies have concluded that fragmentation can have positive or negative effects on species (e.g., compare Bancroft and Turchin 2003 and Caley et al. 2001 with Rosenberg et al. 1999 and van Nouhuys 2005). There are many different mechanisms that can drive positive and negative responses to fragmentation; however, many of these mechanisms depend upon the interaction between temporal and spatial variation in one or more resources, such as food or shelter, and the scale over which those resources are available, a scale set by the size of habitat fragments (Hobbs et al. 2008). Ultimately, consumer performance is determined by access to critical resources (Dunning et al. 1992; Durant et al. 2005; Illius and O'Connor 2000), and this access depends on the ability of consumers to match their distribution with the distribution of these resources (Hobbs et al. 2008). Our results have shown that the compressing effect of fragmentation on the scale of interaction between consumers and resources offers a general mechanism translating effect of landscape pattern into population responses. By limiting the mobility of consumers, fragmentation restricts access to resources that vary over space and time, and in so doing reduces the efficiency of resource use by consumers. By interfering with the ability of consumers to track resources, fragmentation can harm their diet quality, nutritional status, and growth, even when total resource production remains unchanged.

These findings show that access to spatial heterogeneity in resources enhances nutrition of herbivores, adding empirical support to modeling studies that have obtained similar results (Boone 2007; Boone et al. 2005; Boone and Hobbs 2004; Fryxell et al. 2005). Our results support the thesis that the interaction between fragmentation and resource heterogeneity influences herbivore condition by determining their ability to track temporally and spatially variable resource pulses. These results also show that fragmentation can harm herbivore performance even when the total amount and quality of resources remains unchanged.

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