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Landscape Heterogeneity and Ungulate Dynamics: What Spatial Scales Are Important?

MONICA G. TURNER, SCOTT M. PEARSON, WILLIAM H. ROMME, and LINDA L. WALLACE

13.1 Introduction

Ungulates make foraging choices at a variety of spatial scales, but the environmental parameters that are most important at various scales are not well known. Clearly, the spatial arrangement and density of vegetation influences the success of herbivores in finding food (Kareiva 1983, Risch et al. 1983, Stanton 1983, Cain 1985, Bell 1991). Theoretical studies suggest that organisms must operate at larger spatial scales (i.e., search a larger area) as resources become scarce and clumped across a landscape (O'Neill et al. 1988, Turner et al. 1993). In addition, the effectiveness of different foraging tactics may vary with the spatial distribution of resources (e.g., Cain 1985, Roese et al. 1991). However, understanding the responses of animals to spatial pattern at multiple scales is in its infancy (Kotliar and Wiens 1990, Kareiva 1990, Hyman et al. 1991, Ward and Saltz 1994) and remains a high priority for ecology (Lubchenco et al. 1991, Levin 1992). In this chapter, we synthesize results from three studies of winter foraging by

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elk (*Cervus elaphus*) and bison (*Bison bison*) in northern Yellowstone National Park in which we explored scale-dependent foraging patterns.

During winter, foraging ungulates seek resources that are highly variable in space and time and which vary across multiple scales. Spatially, forage may vary in abundance and in quality across a landscape as a function of plant species composition, moisture, soil fertility, and topography. This spatial variability ranges from meter-by-meter variation in forage quality or quantity to between-habitat variation over a scale of kilometers (O'Neill et al. 1989, 1991a, 1991b, S. Turner et al. 1991). The spatial pattern of winter forage also is modified by the distribution of snow, which may reduce or even eliminate potential foraging sites. Temporally, forage resources change daily as the resource is depleted by grazing and as snow conditions change. While depletion by grazing is gradual and patchy, a major snow event can rapidly change the distribution of forage availability across an entire landscape. Ungulates respond to this variability in space and time by making foraging decisions hierarchically (Senft et al. 1987, Kotliar and Wiens 1990, Danell et al. 1991, Schmidt 1993), but the scales at which decisions are made and the cues at each scale are not well understood.

Highly mobile animals such as ungulates are capable of first choosing a large area that is likely to contain suitable foraging conditions and then making additional decisions at finer and finer scales eventually to position individual foraging efforts. The scale of these choices is bounded at the broadest scale by the movement capability of the organism and at the finest scale by the spatial and temporal extent of an individual foraging event. The resulting pattern of foraging depends on the organism's foraging choices and the spatial heterogeneity of forage (Morse and Fritz 1982). It has been suggested that large ungulates make decisions at scales ranging from choosing a position in the landscape (e.g., a geographic region or watershed) for feeding down to selecting a specific portion of a plant to be eaten (Senft et al. 1987). Indeed, a variety of authors (e.g., Addicott et al. 1987, Wiens 1976, 1989, Kotliar and Wiens 1990, Orians and Wittenberger 1991, Bergin 1992, Russell et al. 1992, Pearson 1993, Pearson et al. 1995) have suggested that animals make scale-dependent choices in habitat use and/or foraging.

By creating heterogeneity, natural events (e.g., fires, storms, and droughts) provide valuable opportunities to study ungulate responses to landscape heterogeneity. The 1988 fires in Yellowstone National Park (YNP), unusual in both size and heterogeneity (Christensen et al. 1989, Knight and Wallace 1989, Turner et al. 1994a) created such an opportunity. From 1989 to 1991, we studied the effects of fire size and pattern on the foraging patterns and survival of wintering elk and bison in YNP. As part of this work, we examined the spatial scales at which ungulates appeared to respond to heterogeneity in the Yellowstone landscape. In this chapter, we synthesize our results to suggest the spatial scales that might be most

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13.2 Study Area

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Natural fires have influence
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important for wintering ungulates. We organize the chapter by the scale of heterogeneity and response explored: (1) fine-scale (within 900 m^2) foraging patterns, (2) broad-scale (150 to 500 ha) foraging patterns, and (3) foraging patterns and ungulate survival with alternative scales of heterogeneity across the entire winter range landscape (78,000 ha).

13.2 Study Area

Yellowstone National Park (YNP) was established in 1872 and encompasses 9000 km^2 in the northwest corner of Wyoming and adjacent parts of Montana and Idaho. Elevations in the park range from 1500 to more than 3000 m, and much of the area is covered by Quaternary volcanic deposits that underwent at least three extensive glaciations (Houston 1982). General descriptions can be found for park geology (Keefer 1972); and for physiography, soils, and vegetation (Meagher 1973, Barmore 1980, Houston 1982, Despain 1991). The climate of YNP is characterized by long, cold winters and short, cool summers (Diaz 1979, Dirks and Martner 1982). Our study focused on the northern 20% of the park, which is primarily a lower elevation grassland or sagebrush steppe (Figure 13.1). The northern Yellowstone elk and bison migrate seasonally between a high-elevation summer range and this lower elevation winter range (Craighead et al. 1972, Barmore 1980, Houston 1982).

The northern range extends about 80 km down the Lamar, Yellowstone, and Gardner River drainages (Houston 1982). Approximately 83% of the winter range for elk is included within YNP (Houston 1982), comprising nearly 80,000 ha; it has a warmer, drier climate than the rest of the park (Diaz 1979, Dirks and Martner 1982). We focused solely on the winter range within the park boundaries. Most of the soils derive from glacial till deposited during the Pinedale glaciation (Houston 1982) and tend to be higher in silt, clay, and organic matter than soils derived from rhyolite, the parent rock of most YNP (Despain 1991). The drier grasslands are dominated by big sagebrush (*Artemisia tridentata*), bluebunch wheatgrass (*Agropyron spicatum*), and Idaho fescue (*Festuca idahoensis*). Wet sites are dominated by bearded wheatgrass (*Agropyron caninum*), sedges (*Carex* spp.), and introduced graminoids such as Kentucky bluegrass (*Poa pratensis*). More continuous forest occurs at high elevations and on north slopes (see detailed descriptions in Houston 1982 and Despain 1991). At lower elevations, the sagebrush grasslands are interspersed with coniferous forest, primarily Douglas fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta* var. *latifolia*); aspen groves (*Populus tremuloides*); and riparian willow communities.

Natural fires have influenced plant succession on the winter range for a long time (Houston 1973). Tree-ring evidence suggests that 8 to 10 extensive fires occurred in the area during the last 300 to 400 years, but no large

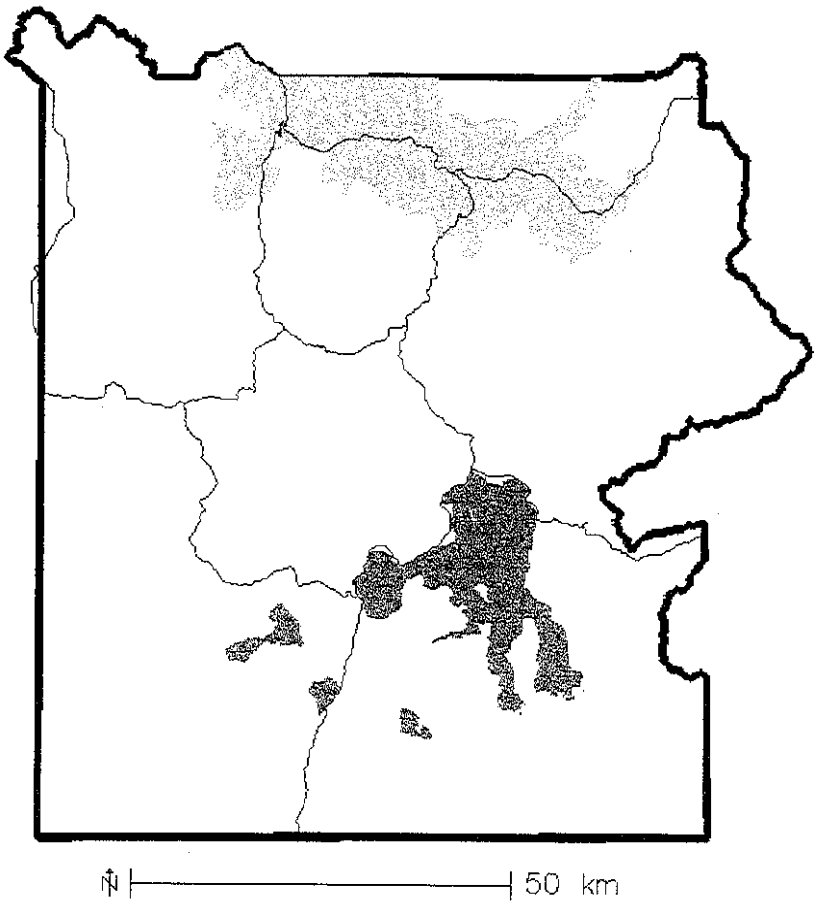

FIGURE 13.1. Map of Yellowstone National Park (YNP) showing the 78,000-ha northern winter range study area in light gray and large lakes in dark gray. Solid lines indicate major park roads.

fires have occurred previously in this century (Houston 1973). Approximately 34% of the winter range burned during the 1988 fires, including 22% of the grasslands (Despain et al. 1989). The vegetation has been dynamic during the past century (Houston 1982). Forest cover has increased, mostly on north slopes, and forests have recolonized burned areas, although aspen appears to have declined from 4–6% to 2–3% of the winter range. Sagebrush increased in extent on many slopes and exposures. Willows and associated riparian vegetation have shown a net decrease. The production of herbaceous vegetation on the northern range shows substantial annual fluctuations resulting from varied growing conditions, primarily precipitation (Houston 1982, Merrill et al. 1993).

13.3 Fine-Scale Feeding

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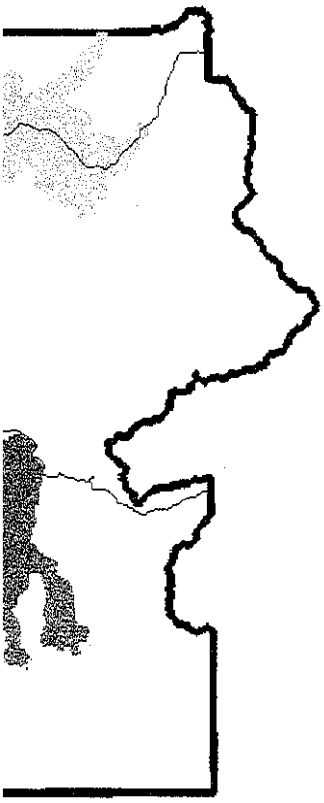

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13.3 Fine-Scale Feeding Patterns

Ungulate feeding patches (i.e., a bounded area where animals invested time and energy in finding food) are easily detectable in winter. Elk dig craters to access snow-covered forage, and bison "till" a foraging area by using head swings. Feeding craters are particularly useful indicators of foraging activity. Studies of cratering by reindeer have shown that crater area is linearly related to duration of cratering activity and the number of digging strokes of the leg (Collins and Smith 1991). Thus, crater area offers a rough index of the amount of time and energy invested in obtaining forage in a patch. Craters are visited only once by a forager simply because disturbance of the snow causes a manyfold increase in its hardness, which thereby precludes animals from reusing previously excavated areas (Pruitt 1959, Collins and Smith 1991). Because crater area is roughly proportional to foraging effort, feeding patches can be functionally identified independent of any a priori definition of patches on the landscape.

To explore fine-scale winter foraging patterns, we examined the distribution of individual feeding stations (i.e., craters) within sites of high feeding activity on the northern winter range of YNP during the 1989 and 1990 winters to address two questions (Wallace et al. 1995): (1) are the locations of ungulate feeding stations within a site predictable based upon an underlying fine-scale pattern in forage vegetation at that site? and (2) does the location of ungulate foraging sites across the landscape reflect broad-scale patterns of winter forage quantity and quality? The 30-m × 30-m study sites each encompassed a feeding patch. Feeding stations were mapped by recording *x*/*y* coordinates of each feeding crater within eight sites during the winter of 1988–1989. Forage abundance was mapped by imposing a regular 15 × 15 grid of sampling points spaced at 2-m intervals (n = 225 point samples per site) at six sites during October 1990. Sites mapped in 1990 were nearby and visually similar to sites in which feeding stations were mapped during 1988–1989. Although an a priori measurement of biomass distributions would have been optimal, it is not possible to predict exactly where ungulates will forage during any given winter.

Results demonstrated that both forage biomass and the distribution of feeding craters were spatially random within the feeding patches, except when a relatively large area was devoid of vegetation, e.g., with a large rock covering a substantial portion of the feeding patch. Thus, ungulates appeared to select feeding stations at random within a feeding patch as long as biomass was present. Ungulates apparently did not differentiate between areas with low and high biomass at the scale of selection of individual feeding stations. By simulating the use of a "smart" feeding strategy, in which an ungulate was assumed to have knowledge of the underlying distribution of biomass and could select feeding stations that would yield the most biomass, we observed that ungulates could potentially double their forage intake compared to use of a random feeding strategy (Wallace et al. 1995).

Mean forage biomass differed more than twofold among the sampling grids. To further examine the variability in forage biomass abundance across the northern-range landscape, forage biomass abundance was determined at 38 locations within nine general community types (Wallace et al. 1995). There were large differences in forage abundance between habitats. Mesic grasslands that had burned in 1988 had ~3 times the biomass observed in comparable unburned areas (170.5 and 63.3 $g\,m^{-2}$, respectively). Biomass also increased along a moisture gradient, with dry areas having low biomass (e.g., 34 $g\,m^{-2}$) and wet grasslands having high biomass (>200 $g\,m^{-2}$). This landscape-scale variability in forage abundance suggests that ungulates could respond to this broader-scaled spatial pattern by selecting feeding patches that would generally yield more resources, even though they might crater at random within the patches. These broad-scale patterns are addressed next.

13.4 Broad-Scale Foraging Patterns

The distribution of feeding patches across the landscape provides a snapshot of the patterns and intensity of ungulate foraging activity. Broad-scale estimates of foraging dynamics can be inferred by monitoring these patterns through time. Spatial patterns of winter foraging by elk and bison in northern YNP were studied in 15 study areas encompassing 7500 ha of winter range during 1991 and 1992 (Pearson et al. 1995). This study was designed to determine whether ungulates preferentially used burned areas of the landscape in which forage quantity and/or quality might be enhanced during the first few years following fire. The study also examined whether ungulates preferentially used particular habitats or landscape positions for feeding, whether the geographic pattern of habitat use changed through the winter, and whether the use of burned areas was influenced by the spatial pattern of burning. Finally, we analyzed the environmental data at four spatial scales to explore the scale(s) at which most of the variation in cumulative grazing intensity during each winter was explained; these results are summarized here.

Field studies were established in January 1991 by using a vegetation classification generated with data from YNP stored in a geographic information system (GIS) to assure that all habitats were represented in our sampling (Pearson et al. 1995). Each of the 15 study areas provided a view of several hundred hectares of the northern range from a fixed position of relatively high elevation. These 15 viewing areas encompassed approximately 10% of the northern range. The boundaries of each area were demarcated on topographic maps and digitized in a GIS. Each viewing area was visited at two-week intervals from mid-January through late March during 1991 and 1992. At each visit, the location of feeding patches (i.e.,

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contiguous area within which animals have grazed with the same level of intensity as indicated by the abundance of feeding craters) was mapped, and grazing intensity was measured as the percentage in 20% increments of the area cratered or tilled. The minimum mapping unit for feeding patches was 1 ha. Cumulative grazing intensity for each 1-ha grid cell over each winter was determined by summing the biweekly data in the GIS.

To test whether ungulate grazing intensity measured at the scale of 1 ha might be influenced by environmental variation at several scales, multiple regression was used to explore the relationship between cumulative grazing intensity and environmental characteristics at scale ≥1 ha (Pearson et al. 1995). Grazing data were first subsampled to remove the effect of spatial autocorrelation in cumulative grazing intensity. Based upon semivariance analysis, grid cells used in the regression were separated by a distance of 600 m. Factor analysis was used to identify the covariance structure of the environmental data and to reduce the data to a smaller number of "factors." Six environmental variables were reduced to three factors: (1) grassland habitat, precipitation, and elevation; (2) slope and aspect; and (3) burn status. To quantify the characteristics of the 1-ha cells and the surrounding landscape, environmental factor scores were measured at four spatial scales: 1, 9, 81, and 225 ha for each cell. At the 1-ha scale, environmental factor scores were used directly from the appropriate 1-ha map cell. To measure habitat at scales >1 ha, a square was centered on the sampling point (e.g., a 3×3 cell square for 9 ha) and the mean score of all cells in the square was calculated to represent habitat at a particular scale. Thus, a total of 12 variables was used in the regression analysis describing habitat variability due to three factors at four spatial scales. In addition, distance to cover, which may influence ungulate feeding-site selection (Grover and Thompson 1986) was used in the regression.

Results indicated that broad-scale measurements of environmental variables were more useful for statistically predicting cumulative grazing intensity on a per-grid-cell basis than fine-scale measurements (Table 13.1). Burn status (Factor 3) and slope and aspect (Factor 2) were important at the broadest scale (225 ha) for both years during mid- and late winter. Burn status at the scale of 1 ha was significant for mid- and late winter in 1991, but its explanatory power was low. Elevation, precipitation, and grassland habitat type (Factor 1) were significant at finer scales (1 to 9 ha) during both years. Interestingly, environmental characteristics were not useful for predicting ungulate foraging during early winter, a time when resources are less limited. Overall, ungulates appeared to respond strongly in mid- to late winter to broad-scale variation (225 ha) in topography and the presence of burning and to fine-scale variation (1 ha) in grassland habitat type.

The importance of broad-scale environmental heterogeneity in predicting ungulate grazing intensity might result for several reasons. Ungulates

TABLE 13.1. Results from stepwise regression of cumulative grazing intensity. Independent variables included distance to cover and factor scores for environmental parameters at four spatial scales: 1, 9, 81, and 225 ha. Factor 1 represents elevation, precipitation, and grassland habitat type. Factor 2 includes slope and aspect. Factor 3 is burn status. Analyses were conducted for three observation periods in 1991 (early, mid- and late winter) and two periods (early and late winter) in 1992. Only the factors that were significant in the model are listed. From Pearson et al. (1995)

Variable	Partial r^2	P	Coefficient	N
		1991		
Early winter				
Factor 2—1 ha	0.020	0.055	2.50	174
Model total	0.020			
Midwinter				
Factor 3—225 ha	0.191	0.0001	3.51	140
Factor 2—225 ha	0.109	0.001	4.35	
Distance to cover	0.028	0.018	−15.50	
Factor 1—9 ha	0.016	0.071	4.10	
Model total	0.344			
Late winter				
Factor 3—225 ha	0.135	0.0001	5.08	135
Factor 1—1 ha	0.038	0.026	−2.07	
Factor 2—225 ha	0.050	0.004	1.99	
Factor 3—1 ha	0.020	0.069	−1.24	
Model total	0.243			
		1992		
Early winter				
Factor 3—225 ha	0.050	0.038	5.23	86
Model total	0.050	0.038		
Late winter				
Factor 3—225 ha	0.153	0.0001	10.97	101
Factor 2—225 ha	0.027	0.074	5.07	
Factor 1—1 ha	0.034	0.042	−4.62	
Model total	0.214			

may actually be making foraging choices based on landscape cues that are apparent at broad spatial scales. Snow may obscure fine-scale cues that might be used to select the most profitable foraging sites during other seasons, and features like topography might be good indicators of areas most suitable for foraging. Ungulates may also increase the duration of time and number of foraging bouts in areas, such as burned sites, that contain greater biomass. Finally, because our study was of relatively coarse temporal grain (two-week intervals rather than observations over minutes to hours), and broader scale environmental patterns could become more influential as the temporal scale of observation increases. Clearly, however, our results suggest that interpreting or predicting ungulate grazing at any given location requires an understanding of the environmental heterogeneity of the surrounding landscape, not simply a description of local site attributes.

13.5 Landscape Hetero
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	5.23	86
	10.97	101
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13.5 Landscape Heterogeneity Within and Between Habitats

Experimentation, or even field observation, at the scale of an entire landscape is often logistically infeasible. For example, in the northern range of YNP, researchers could not impose alternative scales of heterogeneity across the landscape, then observe ungulate foraging responses. Simulation models, when combined with empirical studies, are valuable tools for exploring the implications of alternative scenarios. An individual-based, spatially explicit simulation model (NOYELP) of winter foraging by ungulates in northern YNP (Turner et al. 1994b) was used to examine the effects of heterogeneity at various spatial scales on winter habitat use and survival of elk and bison. Spatial heterogeneity in the distribution of biomass and snow across the landscape were varied in the simulations (Turner and O'Neill 1995).

The Northern Yellowstone Park (NOYELP) model simulates the search, movement, and foraging activities of individuals or small groups of elk and bison (Turner et al. 1994b). The model was developed to explore the effects of fire scale and pattern on the winter foraging dynamics and survival of these free-ranging ungulates in northern YNP. The 77,020-ha landscape is represented as a gridded irregular polygon with a spatial resolution of 1 ha. The model simulates daily forage intake as a function of an animal's initial body weight, the absolute amount of forage available on a site, and the depth and density of snow. Energy balances are computed daily, with energy gain a function of forage intake and energy cost a function of baseline metabolic costs and travel costs. When the energy expenditures of an animal exceed the energy gained during a day, the animal's endogenous reserves are reduced to offset the deficits. Simulations are conducted with a one-day time step for a duration of 180 days, approximately November 1 through April 30. The model has been used to examine the effects on ungulate survival and habitat use of fire size, fire pattern, winter weather conditions, and initial ungulate numbers (Turner et al. 1994b).

Simulation experiments were designed to assess effects of forage heterogeneity at multiple scales (Turner and O'Neill 1995). The model includes six different vegetation classes, each of which can be either burned or unburned. The initial biomass present on a grid cell at the beginning of winter is determined by the vegetation class and burn status by using the mean and 95% confidence interval obtained from field data (Wallace et al. 1995); mean forage abundance within each habitat type matches the mean obtained from the field data, but any individual grid cell within a habitat type has a forage value assigned from the distribution. We refer to this as within-habitat variability. For the simulations reported here, we used the winter of 1988–1989. Because the fires occurred in the summer of 1988,

areas of the northern range that were burned had no forage biomass present during the first winter following the fires.

To explore the effects of aggregating across this spatial heterogeneity, a series of three successive aggregations was conducted (Figure 13.2). In all cases, the total forage biomass available across the landscape was held constant. First, the within-habitat heterogeneity was removed by assigning to each grid cell the mean forage biomass for its habitat type. Second, the between-habitat heterogeneity was removed by assigning to each vegetated

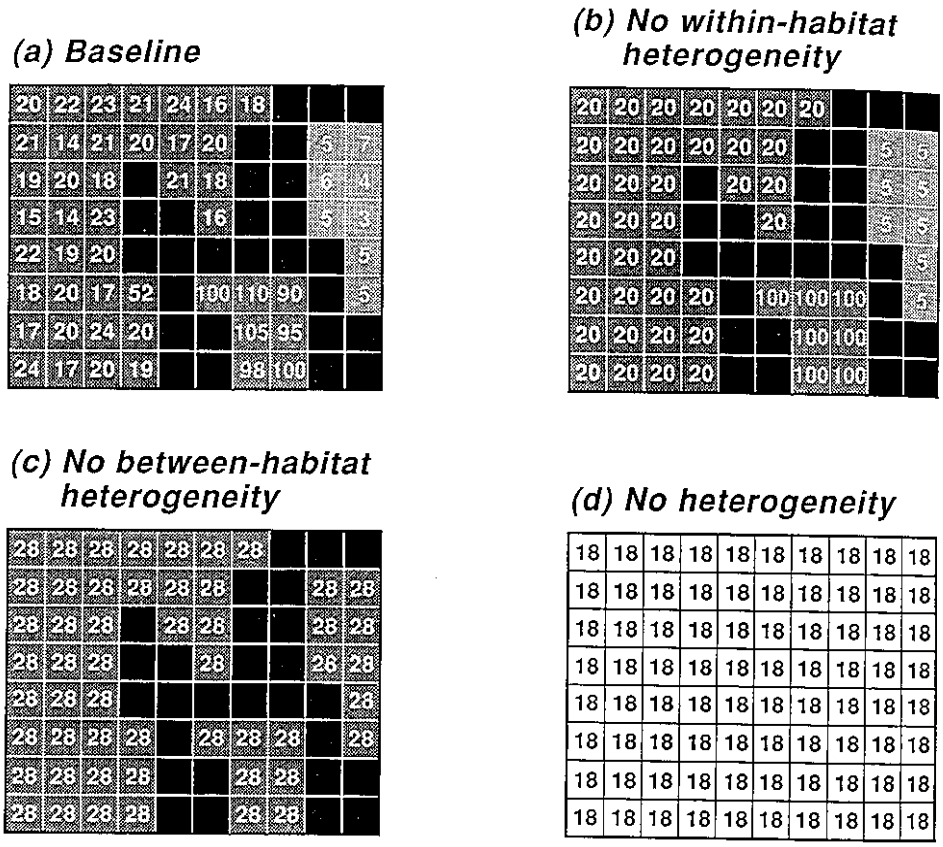

FIGURE 13.2. Schematic representation of aggregation across three scales of forage heterogeneity simulated in a spatially explicit individual-based model. The initial map with three habitat types is shown in (a). Burned areas, which have no forage, are in solid black, and forage abundance is indicated with numbers for the three habitats. When within-habitat heterogeneity is removed (b), each grid cell in a given habitat class has the same forage. When between-habitat heterogeneity is removed (c), each grid cell in one of the three habitats has the same forage. Finally, when no heterogeneity is present, all grid cells have equal forage. In all cases, total forage across the map remains constant.

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by another 20%. These results
lates of maintaining coarse-sca
tion across the landscape of
enhances ungulate survival. Si
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and O'Neill 1995); maintenar
especially the presence of are
tant for winter ungulate survi

13.6 Discussion

Winter foraging patterns of
with spatial scale. Ungulates
landscape and appear to sele
patches) based on environn
255 ha). Cues appear to be re
winters we studied, whether
snow-covered feeding patche
pears to occur at random as
random pattern is typically e
as for most herbaceous winte
1990).

At a fine spatial scale (90
aggregate response pattern p
or nutrient intake would be n
effort at a site is proportio
occurs when the foraging ef
and overmatching would oc
tional to resource profitabil
tance. First, Abrahams (198
discriminate between resour
forage biomass or quality un
site, leading to an undermat
sources. Furthermore, an inc
the degree of undermatchin

grid cell the mean biomass present across the landscape, obtained by dividing the total landscape biomass by the number of unburned grid cells; burned areas continued to have zero biomass. Finally, all spatial heterogeneity was eliminated, and each grid cell was assigned an average value for the entire landscape.

The removal of within-habitat heterogeneity had little effect on elk survival, but aggregating habitats such that between-habitat heterogeneity was eliminated reduced winter ungulate survival by 30%. Removal of all spatial heterogeneity in forage abundance across the landscape reduced survival by another 20%. These results illustrate the importance for wintering ungulates of maintaining coarse-scale variability in forage biomass. The distribution across the landscape of areas of high and low biomass substantially enhances ungulate survival. Similar results were obtained when the heterogeneity of snow depth and density across the landscape was varied (Turner and O'Neill 1995); maintenance of spatial variability in snow conditions, especially the presence of areas with reduced snow mass, was also important for winter ungulate survival.

13.6 Discussion

Winter foraging patterns of elk and bison in northern YNP clearly differ with spatial scale. Ungulates respond to relatively coarse variability in the landscape and appear to select general locations for feeding (i.e., feeding patches) based on environmental heterogeneity at broad scales (81 to 255 ha). Cues appear to be related to topography, habitat type, and, for the winters we studied, whether a site was burned. Once positioned within snow-covered feeding patches, however, selection of feeding stations appears to occur at random as long as some forage biomass is present. This random pattern is typically expected when forage quality is generally low, as for most herbaceous winter forage (Wickstrom et al. 1984, Klein and Bay 1990).

At a fine spatial scale (900 m^2), we did not observe the overmatching aggregate response pattern predicted by Senft et al. (1987) in which forage or nutrient intake would be maximized. Matching occurs when the foraging effort at a site is proportional to resource profitability. Undermatching occurs when the foraging effort is less than proportional to the resource, and overmatching would occur if foraging effort was greater than proportional to resource profitability. Two factors may be of particular importance. First, Abrahams (1986) suggests that when an organism is unable to discriminate between resource profitabilities (e.g., an elk unable to predict forage biomass or quality under snow), it will allocate itself randomly to a site, leading to an undermatching relationship between organisms and resources. Furthermore, an increase in the number of organisms will increase the degree of undermatching. Second, prewinter forage abundance within

:ned had no forage biomass
fires.
:s this spatial heterogeneity, a
onducted (Figure 13.2). In all
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ity was removed by assigning
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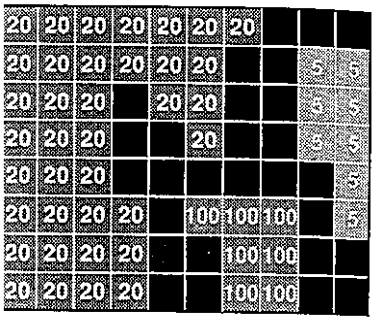
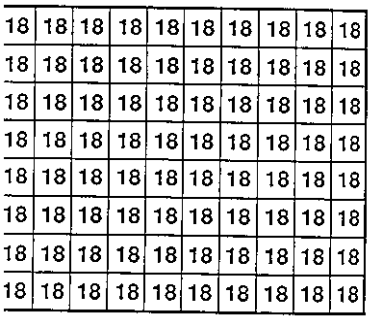
(b) No within-habitat heterogeneity



(d) No heterogeneity



ion across three scales of forage
vidual-based model. The initial
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)ved (b), each grid cell in a given
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e same forage. Finally, when no
'orage. In all cases, total forage

our study area spans an order of magnitude (5×10^2 to 2×10^3 kg/ha), but the costs associated with obtaining forage in snow can potentially range much more broadly. Parker et al. (1984) found that the energy costs of traveling in snow increased exponentially as a function of snow density and relative sinking depth as compared to the no-snow condition. Foraging theory suggests that as the next patch becomes more difficult to reach, the forager should tolerate a smaller likelihood that the present patch is good before leaving (Stephens and Krebs 1986, p. 93). Therefore, as foraging conditions deteriorate due to accumulated snow mass, the energetic costs associated with moving to another feeding site increase, and animals should spend a greater amount of time at a given site before moving elsewhere.

Interpreting ungulate grazing at a specific location requires understanding heterogeneity in the surrounding landscape. Our work supports the notion that the landscape matrix must be considered when the conservation and management of populations are considered (e.g., Franklin 1993, Andren 1994, Wiens 1997). Other studies have also demonstrated an important influence of landscape context on populations at a given site. Pearson (1993) found that the structure of the surrounding landscape explained as much as 74% of the variance in habitat occupancy of some wintering bird species in the Georgia Piedmont. Lindenmayer and Nix (1993) found that the occupancy of corridors by arboreal marsupials in Australia could not be predicted by habitat features within the corridor; information on the composition of the surrounding landscape was required. However, landscape controls over foraging patterns and movements of ungulates have not received much study.

Foraging theory has made a large set of predictions about when animals should abandon one resource patch for another (e.g., Charnov 1976, Belovsky 1984, Real and Caraco 1986, Stephens and Krebs 1986, Mangel and Clark 1988, Belovsky et al. 1989, Dannell et al. 1991, McNamara and Houston 1992, Laca et al. 1994, and many others). Most of these predictions consider the resource availability within the landscape to be fixed. However, resources across the winter landscape change dramatically as snow and previous grazing modify resource availability. Predicting ungulate foraging patterns in a large, spatially heterogeneous landscape in which resource availability (abundance and spatial pattern) can change dramatically in a matter of days remains a challenge that requires a linkage between population and landscape ecology. Furthermore, the linkage between the decisions of individual animals and the landscape-scale dynamics of an entire population are not well known. Development of models and empirical studies that consider these complex spatio-temporal dynamics would greatly enhance our understanding of ungulate dynamics.

Revealing the causes and consequences of spatial heterogeneity in natural systems has emerged as a fundamental challenge for contemporary ecologists (Turner 1989, Kareiva 1990, Kolasa and Pickett 1991, Levin 1992, Kareiva 1994). An important aspect of this challenge is understanding the

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13.7 Summary

Ungulates make foraging
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ways that consumers create and respond to heterogeneity in the resources they use. Large, mobile herbivores discriminate among spatially variable food resources, thereby altering the structure of plant communities and the rates of ecosystem processes. Improving our knowledge of the responses of large herbivores to spatial heterogeneity can contribute to understanding the workings of many other ecological processes.

Ecologists have come to recognize that many of the patterns and processes they study are scale dependent, that what happens at one scale of observation does not necessarily translate into the same thing at other scales (Wiens 1996). We make no contentions that the observations reported here for particular scales (both grain and extent) will hold for other scales not yet examined. Rather, we hope that these results will stimulate the development of studies that explicitly link the scales of heterogeneity in the environment with the decisions of individuals and the dynamics of populations in dynamic landscapes.

13.7 Summary

Ungulates make foraging choices at a variety of spatial scales, but the environmental parameters that are most important at various scales are not well known. In this chapter, results from three studies of winter foraging by elk and bison in northern Yellowstone National Park are synthesized to explore scale-dependent foraging patterns. Measurements of forage abundance and feeding station distribution within 30-m × 30-m plots suggested that the spatial pattern of foraging by ungulates was random within feeding patches. Ungulates appeared to select feeding stations at random within a feeding patch as long as biomass was present. However, large differences in forage abundance across the landscape suggested that ungulates might make choices at broader spatial scales. Analyses of grazing intensity in a set of 15 study areas encompassing 7500 ha of the northern range revealed that grazing intensity on a per-hectare basis could best be predicted by environmental variability at broad scales (100 to 500 ha) rather than by per-hectare environmental variability. A spatially explicit, individual-based simulation model of elk and bison foraging on the northern range was also used to explore scale-dependent foraging. Simulation experiments designed to assess the effects of forage heterogeneity at multiple spatial scales revealed strong responses in ungulate survival to removal of between-habitat variation in forage abundance but not within-habitat variation, and also indicated that snow heterogeneity enhanced ungulate survival. Our field and modeling results suggest strong effects of resource heterogeneity and environmental cues at broad scales on ungulate habitat use and survival. Interpreting or predicting ungulate grazing at any given location requires an understanding of the environmental heterogeneity of the surrounding landscape, not simply a description of local site attributes. Future studies that

explicitly link the scales of heterogeneity in the environment with the decisions of individuals and the dynamics of populations in dynamic landscapes represent an important research need.

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14
The Influenc on the Mana Bighorn Shee

PAUL R. KRAUSMAN

14.1 Introduction

Historically, there were *californiana*, *O.c. mexica* desert mountain ranges o today. Seton (1929) estim sheep in the contiguous desert bighorn sheep (Bue (1988) doubted that wild America. Bighorn sheep a were not distributed unifo America. However, in re alteration and destruction herds, and in 1991 appro isolated populations scatt Krausman, in press). De United States and Mexi impacts. Desert bighorns America and have been Chihuahua and Coahuila reestablishing populatio

Paul R. Krausman is Profes Renewable Natural Resour interests have centered aro recreation, military overfligh habitats and the relationsl Krausman teaches classes ir methodology at the gradua Director of the Arizona Ag search administered by the southwestern United States that is examining the influe