



# Effects of scale on interpreting life-history characteristics of ungulates and carnivores

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## ABSTRACT

Many life-history characteristics of large mammals are scale sensitive. We provide examples where varying temporal and spatial scales can affect interpretation of data concerning life-history characteristics in large herbivores and carnivores and offer recommendations for selecting the most appropriate sampling scale or scales. We also document that some animals make decisions concerning their spatial distribution at scales well beyond the size of the home range. Conversely, other decisions involving sexual segregation of sexes, or where to give birth, may be made at scales below the level of the habitat patch. Such differences in behaviour affect our understanding of habitat selection in large herbivores, and interpreting tradeoffs between acquiring essential resources and avoiding predators. Moreover, some landscape attributes may be selected at one scale, whereas other characteristics of the environment may be selected at another. We argue that even sophisticated models for explaining the ecology and behaviour of mammals benefit from framing specific hypotheses that are related to the life-history characteristics of those animals. We also believe that the failure to consider and select the most appropriate scale, or suite of scales, may lead to the mismanagement of critical natural resources. We forge relationships among scale, life-history characteristics of mammals, and biodiversity. Finally, we synthesize the literature on scale for large mammals and make recommendations for future research.

## Keywords

Habitat selection, large mammals, life-history characteristics, scale, sexual segregation.

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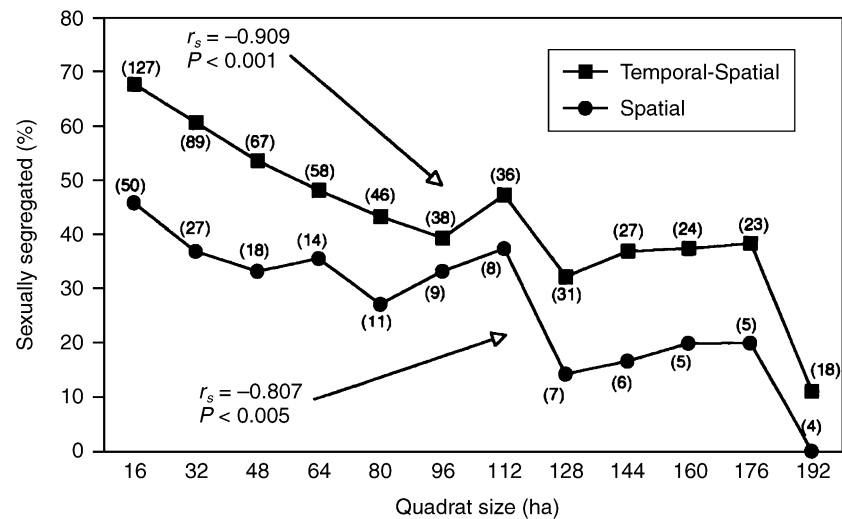
## INTRODUCTION

Problems related to scaling are central to ecological theory (Levin & Pacala, 1997). The portrayal of an ecological system relies on the spatial, temporal, and organizational perspectives selected. Consequently, there is a pressing need to understand how ecological patterns and dynamics vary with scale, and how patterns at one scale may be related to processes operating at other scales. Moreover, each species experiences and reacts to its environment at potentially unique and multiple scales, including interactions with other flora and fauna that can result in distinct assemblages of organisms (Levin & Pacala, 1997). Coexisting assemblages thus link scale and biodiversity. Nonetheless, developing an evolutionary perspective and forging a causal relationship between scale and biodiversity require a more complete knowledge of precisely how life-history characteristics of species are related to variation in temporal and spatial scales. Such information is also critical for setting conservation priorities. Lima and Zollner (1996) emphasized that a major problem in

applying concepts of behavioural ecology to landscape processes was that ecologists and behaviourists tended to work at different spatial scales. Indeed, there may be no single scale for investigating ecological phenomena; systems may show variability over a range of spatial, temporal, and organizational scales (Levin, 1992). In addition, there is a need to incorporate unique life-history information in ecological modelling to produce realistic models (Dostalkova *et al.*, 2002), and models developed for smaller animals may not incorporate appropriate life-history characteristics for larger ones (Bowyer *et al.*, 2005).

Large herbivores and carnivores present an opportunity to understand better effects of scale on their ecology and behaviour; these mammals possess unique life-history traits that are well described, including a comparatively long life span, large body size, iteroparity, extended care of young, and strong density-dependent mechanisms that differ markedly from other, smaller species (Stearns, 1977; Kie, 1999; McCullough, 1999; Stewart *et al.*, 2005). Understanding the effects of scale on the ecology of smaller species may not suffice for larger ones.

**Figure 1** Effects of temporal and spatial scales on measures of sexual segregation in black-tailed deer based on percentage of quadrats of varying size containing = 90% of a single sex, northern California, USA, July 1992 (from Bowyer *et al.*, 1996). The temporal-spatial scale was analysed by week and, consequently, contains more quadrats, whereas the spatial scale combines weeks. Number of quadrats sampled is in parentheses. Note that degree of sexual segregation is increased by shortening sample intervals or reducing quadrat size.



Moreover, some of these large mammals can alter ecosystem structure and function, thereby influencing biodiversity (reviewed by Kie *et al.*, 2003; Bowyer *et al.*, 2005).

Our purpose is to investigate how spatial and temporal scales affect ecological patterns observed for large, terrestrial mammals, to seek links between those patterns and the life-history characteristics of those mammals, and to discuss potential problems in analyses involving habitat selection and scale (both extent and grain size). We also develop a rationale for understanding how scale relates to biodiversity. We use a series of case histories to examine scale in relation to the life-history traits of large herbivores and carnivores, relying heavily on our own research. We then examine the relevant literature to identify potential problems of resource selection involving scale, and to forge links between scale, the ecology and behaviour of large mammals, and biodiversity. Finally, we synthesize much of the literature on scale and life-history characteristics of large, terrestrial mammals and make recommendations for future research.

## POTENTIAL PATTERNS FROM VARYING SCALES

### Outcomes vary with spatial or temporal scales

One potential problem with interpreting life-history traits for large mammals is that some of these characteristics are extremely scale sensitive. For instance, Bowyer *et al.* (1996) assessed the degree of sexual segregation in a population of black-tailed deer (*Odocoileus hemionus columbianus*) inhabiting the Trinity Alps of northern California, USA. In that study, the size of sampling quadrats was increased from 16 to 192 ha by sequentially combining adjacent quadrats along a 9-km transect during the period when sexes of deer spatially segregated from one another. Bowyer *et al.* (1996) also varied the temporal scale by examining quadrats weekly or combining quadrats over 5 weeks. The outcome was that larger quadrats were more likely to contain adult male and adult female deer and, therefore, be categorized as aggregated (i.e. not segregated), whereas smaller quadrats tended to contain mostly one sex (= 90%) and, consequently,

were categorized as segregated (Fig. 1). Similarly, the longer sampling period resulted in less segregation than the shorter one (Fig. 1). More importantly, this pattern of sexual segregation by deer was clinal, and almost any degree of sexual segregation could be obtained by varying the size of sampling quadrats. Indeed, sampling at an inappropriate scale can prevent detection of sexual segregation as noted by Kie and Bowyer (1999) for white-tailed deer (*Odocoileus virginianus*). Bowyer *et al.* (1996) offered a method to help select the most appropriate scale for assessing sexual segregation, but the specific solution likely would be unique to the species and environment under study (Bowyer, 2004). Many studies of sexual segregation fail to evaluate sampling scale or even indicate at what scale data were collected, making comparative studies of sexual segregation problematic, and limiting the usefulness of some tests for why the sexes of large ruminants remain apart for much of the year (Bowyer, 2004).

Another potential problem is that other factors may have additive effects on sampling scale or interact with scale to produce unexpected outcomes. Bowyer *et al.* (2002) developed a landscape map from a study of mule deer (*Odocoileus hemionus*) conducted in the mountains of southern California, USA, by Nicholson *et al.* (1997). Four habitats were identified, and preferences of male and female deer were assigned to each habitat, as well as the carrying capacity (*K*) for that habitat. That initial map representing 1000 ha was termed 'coarse grained'. A 'fine-grained' map was obtained by reducing pixel size in the coarse map to 25% of the original and combining the four copies of the reduced map into a new map of identical area, with each quarter of the map representing an identical, reduced image of the original. This method resulted in two maps with marked variation in many landscape variables related to grain, including patch characteristics, shape indices, and measures of diversity and contagion (Bowyer *et al.*, 2002).

High-density maps (200 deer/1000 ha) were created by assigning sexes of deer (35 males:100 females) randomly to habitat patches under an ideal-free distribution, until the *K* of a particular patch was reached. Bowyer *et al.* (2002) employed that

**Table 1** Degree of sexual segregation in deer resulting from sampling quadrats in two landscape grains, two population densities, and two scales of measurement. Twenty-four quadrats were sampled at the large scale (18 ha) and 72 quadrats were sampled at the small scale (6 ha; from Bowyer *et al.*, 2002)

Grain	Population density	Sample quadrat size (ha)	Quadrats with deer ( <i>n</i> )	Quadrats showing segregation (%)
Coarse	Low	18	13	84.6
		6	28	96.4
	High	18	24	8.3
		6	72	15.3
Fine	Low	18	14	64.3
		6	31	93.5
	High	18	24	12.5
		6	72	22.2

method a second time to create low-density (75 deer/1000 ha) maps. Finally, sampling scale was varied by examining quadrats of 6 and 18 ha for sexual segregation. This design allowed assessment of the role of landscape grain, population density of deer, and sampling scale in affecting measures of sexual segregation, which varied from 8.3 to 96.4% (Table 1). Logistic regression was used to determine which variables were influential in determining whether a particular quadrat was sexually segregated (= 90% one sex). Population density had the greatest effect on sexual segregation, followed by sampling scale. Surprisingly, grain did not significantly influence the model, perhaps because habitat selection by sexes of deer did not vary with patch size (Bowyer *et al.*, 2002). Moreover, no interactions occurred between grain, density, or scale. These outcomes indicate, however, that consideration of how scale and population density of deer influence sexual segregation should be important components of future sampling designs, and emphasize that other biological processes can either reduce or enhance scale-sensitive phenomena.

**Table 2** Pearson correlation coefficients (*r*) between ln(home range size from 95% adaptive-kernel analysis) in female mule deer and selected landscape metrics measured at different spatial scales (250, 500, 1000, and 2000 m from the centre of each deer’s home range), California, USA (from Kie *et al.*, 2002)

Type	Landscape		Spatial scale (m)			
	Metric	Description (units)	250	500	1000	2000
Patch	MPS	Mean patch size (ha)	0.38*	0.26 ns	0.09 ns	0.10 ns
	PSCV	Patch size CV (%)	-0.27 ns	0.23 ns	0.41*	0.51*
Edge	ED	Edge density (m/ha)	-0.44*	-0.49*	-0.49*	-0.52*
	MECI	Mean edge contrast index (%)	-0.13 ns	-0.04 ns	0.26 ns	0.39*
Shape	MSI	Mean shape index	-0.29 ns	-0.52*	-0.58*	-0.64*
	DLPD	Double-log fractal dimension	-0.25 ns	-0.33 ns	-0.57*	-0.60*
Proximity	MNN	Mean nearest neighbour (m)	0.28 ns	0.37*	0.33 ns	0.32 ns
Diversity	PRD	Patch richness density (no./100 ha)	-0.35*	-0.13 ns	-0.16 ns	-0.39*
Contagion	CONTAG	Contagion index	0.24 ns	0.48*	0.42*	0.37*

\**P* = 0.05, following a sequential Bonferroni correction; ‘ns’ indicates non-significance (*P* > 0.05).

Schaefer and Messier (1995) noted few changes in patterns of habitat selection in winter by muskoxen (*Ovibos moschatus*) across varying scales, which included the range of the population, travel routes, feeding sites, feeding craters, and plant species consumed. At successively smaller scales, muskoxen selected for a greater abundance of graminoids and less snow cover. Nonetheless, the general consistency in habitat selection with a changing scale of measurement was interpreted as local levels of habitat selection occurring within one scaling domain (Schaefer & Messier, 1995). Clearly, not all potential scales were measured, but this hierarchical approach was necessary to reveal the overall pattern. Moreover, there may be a temporal component to understanding hierarchical habitat selection. Schaefer *et al.* (2000) noted that at the scale of the year-round range, sedentary and migratory populations of caribou (*Rangifer tarandus*) exhibited similar patterns of philopatry. At the scale of the seasonal range, however, sedentary caribou displayed fidelity from calving to mating, whereas migratory caribou exhibited fidelity only during late autumn.

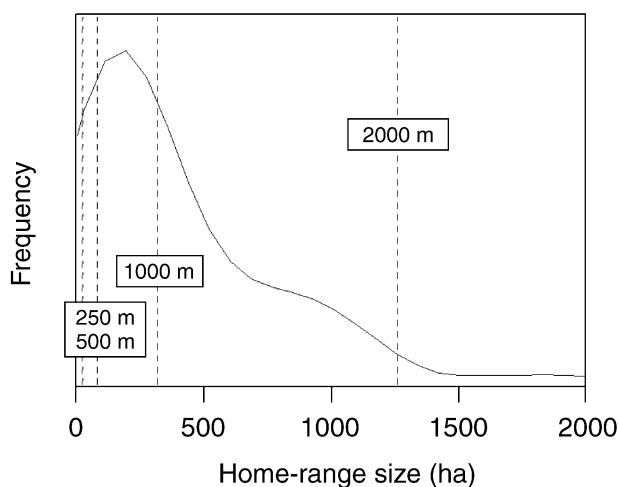
**One scale is more explanatory than others**

A convincing example in which one scale was superior to others in explaining a life-history characteristic comes from a study of home-range size in female mule deer inhabiting five study areas spanning much of California, USA (Kie *et al.*, 2002). Habitats within these study areas were organized into seven broad types: conifer, hardwood, closed shrub, open shrub, meadow-riparian, grassland, and barren. Home ranges (95% adaptive kernels) of 80 deer varied markedly among individuals across study sites (39–2878 ha). Kie *et al.* (2002) measured landscape metrics related to habitat heterogeneity in circles of increasing radii (250, 500, 1000, and 2000 m) from the centre of the home range for each deer. The authors then obtained simple correlations between home-range size for the four spatial scales for landscape metrics related to patch, edge, shape, proximity, diversity, and contagion of habitats — both strength and direction of some correlations changed with scale (Table 2). Home-range size was

**Table 3** Effects of scale on regression models of home-range size in adult female mule deer incorporating landscape metrics related to habitat spatial heterogeneity, California, USA (from Kie *et al.*, 2002)

Scale (m)	$b_0$	PRD (no./100 ha)		MNN (m)		MSI		MECI (%)		$n$	$C_p$	AIC	$R_{adj}^2$	Overall $P$
		$b_1$	$r^2$	$b_2$	$r^2$	$b_3$	$r^2$	$b_4$	$r^2$					
250	8.13	-0.66*	0.10	0.0026 ns	0.03	-1.75*	0.06	0.019 ns	0.05	65	10.04	216.50	0.16	< 0.010
500	9.00	-0.16*	0.06	0.0038 ns	0.05	-2.46***	0.21	0.019 ns	0.05	74	10.24	227.06	0.29	< 0.001
1000	9.77	-0.66**	0.11	0.0002 ns	< 0.01	-2.68***	0.36	0.030**	0.12	79	8.38	220.31	0.46	< 0.001
2000	8.06	-1.63*	0.17	0.0004 ns	< 0.01	-2.09***	0.34	0.042**	0.24	80	4.02	202.90	0.57	< 0.001

Notes: Abbreviations for landscape metrics are as follows: PRD, patch richness density; MNN, mean nearest neighbour; MSI, mean shape index; MECI, mean edge contrast index; samples are from five sites in California. Regression coefficient ( $b_i$ ) and coefficient of partial determinations ( $r^2$ ) are provided for each landscape metric; sample size ( $n$ ), Mallows's statistic ( $C_p$ ), Akaike's Information Criterion (AIC), adjusted coefficient of determination ( $R_{adj}^2$ ), and overall  $P$ -value for the full model are provided at each scale. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.0001$ ; 'ns' indicates non-significance ( $P > 0.05$ ).



**Figure 2** Smoothed frequency distribution of 95% adaptive-kernel analysis of home-range sizes for 80 female mule deer from five study sites in California. Vertical dashed reference lines have been placed at 20, 79, 314, and 1257 ha, representing the four spatial scales at which landscape metrics were measured within 250, 500, 1000, and 2000 m from the centre of each home range (from Kie *et al.*, 2002).

negatively correlated with edge density, mean shape index, and double-log fractal dimension. Those metrics were related to habitat graininess and indicated that fine-grained matrices were related to small home ranges in deer. In addition, home-range size was positively correlated with contagion (Table 2).

A multiple-regression approach identified the most explanatory scale for predicting the home-range size of mule deer. The largest scale (2000 m) yielded the highest multiple coefficient of determination ( $R_{adj}^2 = 0.57$ ) as well as the lowest AIC (Akaike Information Criterion) value (202.90), with model fit generally improving with increasing scale (Table 3). Nonetheless, Akaike weights indicated that the model at the 2000-m scale was clearly the best model ( $w_i = 0.99$ ), with other scales being extremely poor models ( $w_i < 0.01$ ).

Kie *et al.* (2002) demonstrated that one model was markedly better than the others in understanding home-range dynamics of

deer. Moreover, the failure to examine larger scales would have led to the conclusion that habitat heterogeneity had little effect on home-range dynamics in deer. Furthermore, the finding that the 2000-m scale was the most informative was not intuitive; nearly all home ranges of deer were smaller than the 2000-m scale (Fig. 2). Thus, mule deer apparently assessed areas well outside their home ranges in making decisions concerning where to establish home ranges, which also holds import for understanding the various landscape levels at which use or selection should be evaluated — a point we will return to later.

### Only one scale is explanatory — others give misleading results

Bowyer *et al.* (1999) conducted a study of birth-site selection in moose (*Alces alces*) inhabiting the foothills of the Alaska Range in interior Alaska, USA. Maternal moose were located via radio-telemetry and visual transects and their birth sites recorded over 5 years — 39 birth locations and 69 random points (unused sites) were sampled for variables related to geography, topography, climate, forage, and risk of predation (Bowyer *et al.*, 1999). This traditional calving area (~300 km<sup>2</sup>) was mapped and organized into six habitat types used by moose. Remarkably, no difference existed in the percentage of birth or random sites across six heterogeneous habitats occurring on the study area, which included forest, tall shrub, low shrub, dwarf-shrub tundra, herbaceous tundra, and river bar-dry wash (Bowyer *et al.*, 1999). This outcome was unexpected because grizzly bears (*Ursus arctos*), which were the primary predators on young moose (Bowyer *et al.*, 1998a), made extensive use of dry washes as routes of travel (Albert & Bowyer, 1991). Unfortunately, this scale was too coarse to understand why moose selected particular sites to give birth. Sampling at an even coarser scale or including additional variables, however, may have yielded a different outcome.

Bowyer *et al.* (1999) also sampled a suite of variables immediately around (50 m) birth sites and random locations. Analysis of samples collected at this fine scale with logistic regression revealed that forage abundance was a critical determinant of where moose gave birth, but that slope aspect and visibility (an

index that reflected the ability of a female to observe an approaching predator) also were significant variables (Bowyer *et al.*, 1999). Consequently, rather than avoiding a particular habitat that might reduce the likelihood of an encounter with a predator, moose selected microsites that allowed them to avoid predators while acquiring essential forage. Sampling at a large scale (the level of the vegetation type) obscured patches of willows (*Salix* spp.), which were an important forage for moose, and masked the importance of small changes in topography that allowed females an unobstructed view of approaching predators (Bowyer *et al.*, 1999).

McLoughlin *et al.* (2004) reported that tundra wolves (*Canis lupus*) exhibited selection for esker habitat at the level of the home range, but failed to link habitat selection to vegetation communities within the home range. The authors concluded that the failure to view habitat selection as a hierarchical process might lead to misconceptions concerning the value of particular habitats to animals. Indeed, Johnson (1980) first introduced the concept of hierarchical selection with scales ranging from locations of animals within their home range, to home-range selection within the study area, and finally extending selection to the geographical range of the species. Clearly, sampling at multiple scales is an important key to understanding habitat selection.

### Sampling at more than one scale is necessary to explain a pattern

Rachlow and Bowyer (1998) examined a suite of biotic and abiotic variables to understand habitat selection by female Dall's sheep (*Ovis dalli*) during the birthing season in the Alaska Range of interior Alaska, USA. They sampled at both a microscale (1 m<sup>2</sup>) and a macroscale (15–450 ha), which varied in size depending on terrain steepness, elevation, and aspect, to compare used and available sites for maternal groups of Dall's sheep. Moreover, climatic differences between study years (1988 and 1989) were marked, with a late snow storm and cool growing season in 1989, substantially delaying growth of plants, reducing the abundance and nutritional value of forage, and ultimately resulting in a comparatively short growing season.

Rachlow and Bowyer (1998) examined effects of scale on habitat selection by maternal Dall's sheep by including in a discriminant function analysis (DFA) variables at both micro- and macrosites, for locations used by sheep and for random sites. Following that analysis, the strength and direction of standardized canonical correlation coefficients were used to evaluate whether sheep selected habitats (use > available) or avoided (use < available) them (Table 4). A jackknifing procedure yielded good classifications for both study years (> 84%) for a suite of significant habitat variables (Table 4). The model for 1988 indicated strong selection for more level microsites (a negative coefficient for slope), and steep macrosites (a positive coefficient). Mothers selected large areas with steep, rugged terrain (brokenness) coupled with areas of level terrain for birthing and care of neonates (Table 4). Failing to consider microsites would have produced a model that overlooked the need for small, level areas, and

**Table 4** Standardized canonical correlation coefficients entering DFA models of habitat selection by maternal Dall's sheep in interior Alaska, USA, during spring 1988 and 1989. Percentage of sites classified correctly was evaluated with a jackknifing procedure (from Rachlow & Bowyer, 1998)

Variable	1988 model	1989 model
Distance to escape terrain	−0.421	−0.122
Percentage cover		
Grasses		0.334
Dryas		0.466
Browse		0.242
Macroaspect (E–W)	0.701	0.277
Macrobrokenness	0.664	
Microslope	−0.413	0.312
Macroslope	0.571	
Macroaspect (N–S)		
Snow presence		
Percentage classified correctly	84.3	84.6

indicated a much greater extent of potential lambing habitat that might not have been suitable.

Dall's sheep selected to be closer to escape terrain (a strong negative coefficient indicates closeness to such terrain) during both study years (Table 4). During the cool and less-productive growing season in 1989, however, females and young ventured farther from escape terrain (weaker correlation than in 1988). Coefficients for macroslope and macrobrokenness no longer were significant in 1989, cover of forages entered that model, and the coefficient for microslope weakened (Table 4). Consequently, females and neonates traded off more secure sites selected in 1988 in this predator-rich environment (Albert & Bowyer, 1991; Bowyer *et al.*, 1998a) for better foraging conditions during the cool and unproductive spring of 1998 (Table 4). Numerous studies have examined tradeoffs between acquiring forage and risk of predation for large mammals (Festa-Bianchet, 1988; Bleich *et al.*, 1997; Bowyer *et al.*, 1998b; Barten *et al.*, 2001; Corti & Shackleton, 2002; many others), but few have considered how scale might effect such interpretations — an area in dire need of more research.

Habitat use by Asiatic black bears (*Ursus thibetanus*) also required sampling at multiple scales to understand the ecology and potentially local extirpations of this large carnivore. Carr *et al.* (2002) reported that at the landscape scale, the greatest densities of bears occurred in areas with little agriculture or other human developments and with national parks. At a more local scale, the distribution of natural foods, particularly mast, affected the distribution of bears.

Another study documenting the need to consider habitat for a large mammal at multiple scales was conducted on moose in interior Alaska, USA, by Maier *et al.* (2005). Those authors investigated the density of moose in five populations distributed across the interior of Alaska by examining influences of numerous habitat variables, including potential anthropogenic effects. Moose were surveyed from the air with standardized methods on

quadrats of 15 km<sup>2</sup>, the smallest unit possible with this methodology. Habitat was evaluated in the area of the sampling region, and then was increased by 50%. This procedure was continued for six iterations, so that the edge of the sampling region would not extend beyond the most distant edge of adjacent survey units. Resultant sampling regions were 15, 23, 34, 51, 76, and 114 km<sup>2</sup> with sampling radii of 2.2, 2.7, 3.3, 4.0, 5.0, and 6.0 km, respectively.

Analyses indicated that significant relationships of most habitat variables with moose density occurred at or below the 34-km<sup>2</sup> scale (Maier *et al.*, 2005). For instance, influence of landscape variables such as patch richness density, terrain variability, and distance to towns were most evident at a scale of 34 km<sup>2</sup>, elevation and burns 11–30 years old were most evident at 23 km<sup>2</sup>, and length of rivers, slope, and several other variables were most influential at 15 km<sup>2</sup>. These outcomes indicated that moose responded to environmental variables relatively close to their sampling location (Maier *et al.*, 2005). Unfortunately, the resolution was limited to a minimum scale of 15 km<sup>2</sup> because estimates of density for female moose initially were developed at that resolution. Some of the non-significant or less-significant variables analysed in that study might become more important if analyses were conducted at a finer resolution than 15 km<sup>2</sup>. Indeed, the life-history characteristic of interest may constrain interpretation across multiple scales. For instance, moose select birth sites at an exceptionally fine scale (Bowyer *et al.*, 1999), but those microsite samples might not detect the influence of larger-scale phenomena such as burns. Although density of moose was poorly predicted at extremely large scales by Maier *et al.* (2005), multiple scales were necessary to understand the importance of some habitats such as rivers (finer scale) and terrain variability (coarser scale), and conclusions about the ‘most appropriate’ scales were not intuitive, because of varying moose density across interior Alaska. There is a clear need to sample at multiple scales to investigate ecological phenomena for large mammals.

Mysterud *et al.* (1999) reported that roe deer (*Capreolus capreolus*) also selected habitat features at multiple scales during winter. At the scale of the foraging patch, no selection occurred with regard to cover, but forage availability was greater for feeding sites than random sites. At the scale of the habitat, however, roe deer selected feeding sites with more cover, and forage availability was no longer selected.

In a study linking habitat selection by moose to limiting factors, Dussault *et al.* (2005) predicted that moose should avoid the most important limiting factor (i.e. predation) at large spatial scales (landscape), whereas the influence of less-important factors (e.g. food availability and snow depth) should be evident at a finer scale (home range). Those authors concluded that animals should attempt to minimize the most limiting factor at the large scale. Nonetheless, when risk associated with several limiting factors varied with scale, moose made tradeoffs among those factors. Dussault *et al.* (2005) demonstrated that not only was more than one scale necessary to explain the pattern, but that tradeoffs among factors at differing scales may be necessary to understand how moose respond to their environment. Indeed, O’Neill and DeAngelis (1986), Wiens, 1989), and Levin (1992)

have argued the need to sample at the scale of interest, as well as one scale above to provide context, and one scale below to examine potential mechanisms.

## RELATING SCALE TO LIFE-HISTORY CHARACTERISTICS AND BIODIVERSITY

### Scale-related problems involving habitat selection

Populations of large mammals tend to be vagile and often integrate landscape processes, such as nutrient cycling and rates of mineralization, over large areas, which have implications for understanding habitat selection (Bowyer *et al.*, 1997; Kie *et al.*, 2003). One difficulty in choosing an appropriate scale at which to measure habitat selection based on a life-history characteristic is that some desirable characteristics may vary spatially or temporally among individuals. For instance, home-range size may differ greatly even within a population of large herbivores (Nicholson *et al.*, 1997). Consequently, the use of the home range as a scale to assess habitat selection may introduce a spatial bias into that analysis (i.e. most home ranges are of different sizes and may differ in shape). Even if spatial extent of home ranges could be controlled in analyses as a covariate, differences in shapes of home ranges might still affect analyses in unexpected ways (Kie *et al.*, 2002). We recommend using a standard shape (e.g. a circle) as well as a standard size (perhaps the mean or median size of the home range) to investigate habitat selection at the scale of the home range (*sensu* Kie *et al.*, 2002). Including areas inside or outside the actual home ranges of some individuals is likely preferable to markedly varying the spatial scale or shape of the area to be sampled, because of the strong effects of scale and shape on ecological analyses (Wiens, 1989; Schneider, 1994; Gardner, 1998).

Kie *et al.* (2002) demonstrated that the location of a home range resulted from selection of habitat features occurring across a much greater area (i.e. larger scale) than the home range itself. About 95% of home ranges of 80 female mule deer were smaller than the spatial scale that best explained their size (Fig. 2). Thus, selection for or against particular landscape features already had occurred in the process of deer deciding where to locate their home ranges, and evaluating habitat selection only at the level of the home range could produce a biased and circular result. Under these circumstances, avoided (use < available) features are more likely to be outside and selected (use > available) features more likely to be within the home range than at larger scales. Such an analysis risks undervaluing critical habitat for large mammals, because the proportion of selected habitat variables within the home range already is large, which increases availability relative to use in an analysis of resource selection. In addition, difficulties may exist in simply using the relative proportion of habitats at the level of the landscape to assess availability (Katnik & Wielgus, 2005).

Another scale-related issue in analyses of resource selection at the level of the home range is the comparison of ‘core’ with ‘outlining’ areas. This analysis typically is accomplished by comparing various isopleths determined from kernel analyses of home ranges (Kie *et al.*, 1996). For example, the area within the 50%

isopleth might be defined as the core (Person & Hirth, 1991) and a comparison could be made with the remaining areas of lower use within the home range (e.g. 50–95% isopleths). Even if it is assumed that areas within these home-range contours represent habitat use by an animal, such a comparison is not technically a measure of selection (e.g. use relative to availability), but rather a comparison of use between areas. Not only are there potential biases in this analysis from differences in scale and shape of those two areas (core and outlining), but it also is assumed that the animal chose the core from the home range as a whole — that the scale of selection was known. Even this interpretation is not quite correct, the core would need to be compared against the entire home range for this to be an analysis of use relative to availability. Furthermore, we have demonstrated previously that selection for some attributes of the environment can occur at very fine scales (e.g. birth sites — Bowyer *et al.*, 1999). Under such circumstances, a comparison of use and availability within the core and within outlying areas might be most appropriate, with a subsequent comparison of selection coefficients between areas.

Long-distance movements of both ungulate prey and their primary predator (Ballard *et al.*, 1997; Pierce *et al.*, 1999) may further complicate measures of availability. Considerable thought needs to be given to the scale of sampling when designing such studies (Turner *et al.*, 1989; Dutilleul, 1998), especially as it relates to the life-history characteristic of interest, with a clear notion of hypotheses to be tested. If the scale of selection is unknown, then sampling at multiple scales probably will be necessary, including areas smaller and larger than the home range.

Aside from problems in assessing habitat selection from home-range models, it is tenuous to assume that even the most sophisticated home-range metrics represent where animals occurred. Moreover, such models assume that all habitats within the home range are available, something that may not be correct, particularly if unsuitable habitat for a particular species is contained within the home range. Deciding what is available to an animal can be complex, especially for large carnivores where the dispersal and density of prey can be a key component in the distribution of the predator (Pierce *et al.*, 2000). Although the concept of the home range has served ecologists well for many years (Hayne, 1949), we contend that it is time to move away from home-range models as a mechanism for understanding resource selection. Point sampling of use and availability already is commonplace in analyses of habitat selection (Ben-David *et al.*, 1996; Bowyer *et al.*, 1999, 2003), but results from such analyses cannot be assumed to be independent of scale. For example, as areas around points are increased to evaluate scale, the likelihood of points overlapping increases. Overlap in 'used' points or overlap in 'random' ones results in a lack of independence within those sampling categories, whereas overlap of used and random (or unused) sites reduces the power to detect resource selection, especially if that overlap is large (Imbens & Lancaster, 1996). Study areas (extent) should be of sufficient size to accommodate sampling at a scale that is likely to be relevant to the life-history characteristic of interest, something that is seldom included in research designs. Moreover, making use of used and random sites for selection analyses, as well as creating some statistical difficulties

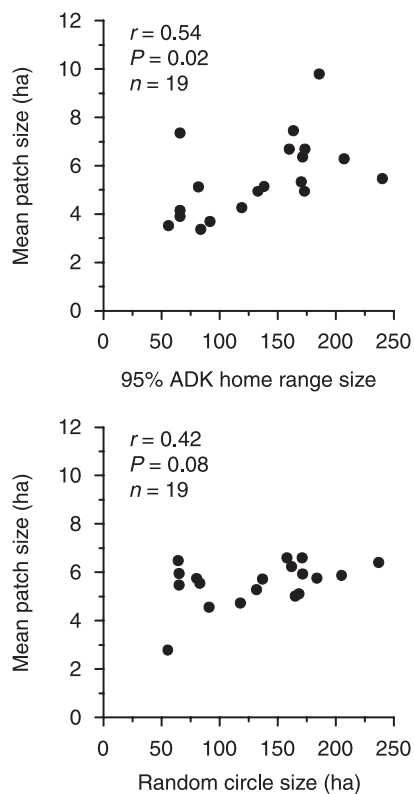
(Keating & Cherry, 2004), produces a conservative analysis, because it generally is not possible to know if a random site was used at a time when sampling did not occur, or was used by an un-sampled animal.

Analyses at the level of the home range to assess selection of habitats by animals have other limitations. Where animals must traverse surrounding habitats of lower quality to acquire resources in a preferred habitat, their use of that preferred habitat might be affected adversely by the size, shape, quality, and predation risk in those surrounding patches. An analysis of use and availability might undervalue the preferred habitat where there was a high cost to moving through surrounding, less-preferred areas. Likewise, such an analysis might overvalue patches of surrounding low-quality habitat because animals might cross them more frequently while travelling to and from a desirable habitat. Assessing surrounding arrangements, configurations, and shapes of habitats, as well as the quality and abundance of forage and predation risk associated with each patch to understand habitat selection, is not commonplace. We suggest that using movement paths of mammals (Ostro *et al.*, 1999; Johnson *et al.*, 2001, 2002a; Brilling *et al.*, 2004; Preisler *et al.*, 2004; Kie *et al.*, 2005) holds promise for resolving some of these shortcomings, but more formal research is needed to link movement paths to selection of habitat.

Use of the home range to understand ecological phenomena has other potential problems, and caution is needed in making interpretations where home-range size is variable. For instance, a plethora of metrics is now available to assess landscape configurations (Greenberg *et al.*, 2002). In our analysis of landscape features on home-range size in mule deer (Kie *et al.*, 2002), we initially observed a strong correlation between the size of the home range and the size of habitat patches contained within that area. The obvious interpretation was that large patches of habitat resulted in large home ranges for deer. Nonetheless, when we regressed home-range size against various sizes of circles placed randomly on the landscape, we obtained a similar result (Fig. 3) — larger home ranges simply could encompass larger patches of habitat. Sorting cause from effect can be difficult in problems involving scale, and considerable attention is needed to arrive at ecologically sound conclusions. We suggest that a strong hypothesis-testing approach is necessary to resolve complex questions linking life-history characteristics of mammals to the suite of landscape metrics that are available. For instance, in our study of home-range dynamics in mule deer (Kie *et al.*, 2002), examining all possible models or other methods of model selection, even with sophisticated criteria, yielded a perplexing array of outcomes that confused rather than clarified our analysis. Only when we set forth the hypothesis that habitat heterogeneity would affect home-range size in deer were we able to select the appropriate variables to test that postulate. Indeed, Guthrie *et al.*, 2005) argued that even the most sophisticated model-selection approaches require strong ecological underpinnings to be meaningful.

### Linking scale, life-history characteristics, and biodiversity

Links between scale (both extent and grain size) and the species richness of large mammals have been demonstrated for an



**Figure 3** The relationship between the mean size of a patch of habitat within the home range with increasing adaptive kernel (ADK) home-range size for mule deer (above), and that same relationship for randomly placed circles of increasing size (adapted from Kie *et al.*, 2002).

African ecosystem; not surprisingly, the relationship between mammal species richness and indices of habitat diversity was scale sensitive (Oindo *et al.*, 2003). Processes underpinning such a relationship, however, likely involve the life-history characteristics of the species involved. For instance, the population dynamics of large herbivorous mammals can profoundly influence ecosystem structure and function (reviewed by Hobbs, 1996; Bowyer *et al.*, 1997; Kie *et al.*, 2003; Coté *et al.*, 2004; Bowyer *et al.*, 2005; McShea, 2005). These large mammals do not utilize their environment uniformly (Hobbs, 1996; Kie *et al.*, 2003), and they often concentrate foraging activities and deposition of urine and faeces in localized areas (McNaughton, 1985; Etchberger *et al.*, 1988; Ruess & McNaughton, 1988; Day & Detling, 1990). The patchy nature of interactions of large herbivores with their environment (Wallis de Vries *et al.*, 1999), and their ability to move over large distances (Berger, 2004), introduces scale sensitivity into many ecosystem processes affected by large herbivores. Indeed, D'Eon and Serrouya (2005) reported that migratory mule deer exhibited little consistent selection within the scale of the home range, but substantial selection at the level of the home range.

Large herbivores can affect vegetation via trampling and compaction of soil (Packer, 1953, 1963). Likewise, at sufficiently high densities, ungulates can promote changes in successional pathways of vegetation communities (Pastor *et al.*, 1993; Wallis de

Vries, 1995) and cause ecological meltdowns with subsequent trophic cascades (Terborgh *et al.*, 2001; Ripple & Beschta, 2004; McShea, 2005) that can affect biodiversity. Nitrogen in faeces of herbivores is correlated with the quality of their diet (Hodgman & Bowyer, 1986; Leslie *et al.*, 1989). Indeed, depending on population density, these large mammals are capable of driving nutrient cycling and thereby ecosystem processes in both terrestrial and aquatic communities (Bryant *et al.*, 1983; Irons *et al.*, 1991; Molvar *et al.*, 1993; Frank & McNaughton, 1997). Primary production is strongly correlated with biodiversity in some ecosystems (Tilman *et al.*, 1996). Moreover, the density of large herbivores has been correlated with measures of biodiversity in several studies (Anderson & Loucks, 1979; Augustine & McNaughton, 1998; Fletcher *et al.*, 2001).

Population dynamics of large herbivores also hold consequences for other fauna. High densities of herbivores can have deleterious effects on birds, especially in ecosystems where large carnivores are absent or reduced in numbers (de Calesta, 1994; McShea & Rappole, 2000; Berger *et al.*, 2001). Similarly, ungulate densities affect small mammals (Flowerdew & Ellwood, 2001; Keesing & Crawford, 2001), reptiles (Beever & Brussard, 2004), and invertebrates (Suominen *et al.*, 1999a,b; Myrsterud *et al.*, 2005). Clearly, large herbivores can influence biodiversity via their disproportionate effects on ecosystem structure and function. Moreover, the dynamics of large herbivores can be strongly affected by large carnivores that prey on them (reviewed by Kie *et al.*, 2003; Bowyer *et al.*, 2005). Systems where ungulates are held at low density in relation to carrying capacity ( $K$ ) by predators (Gasaway *et al.*, 1992; Bowyer *et al.*, 1998a; Hayes *et al.*, 2003) differ markedly from those in which predators are rare or absent. Extremely deleterious consequences for ecosystems are most prevalent at high densities of ungulates (reviewed by McShea, 2005). It is axiomatic that if large carnivores affect population density of ungulates in relation to  $K$ , those predators can influence biodiversity (Bowyer *et al.*, 2005).

Links between scale and biodiversity for large mammals rely, in part, on how the density of these animals is affected by the scale at which they respond to environmental variation (Morris, 1987; O'Neill *et al.*, 1988) — changes in population density clearly can be drivers of ecosystem processes that ostensibly relate to biodiversity (Kie *et al.*, 2003; Bowyer *et al.*, 2005). Perhaps the clearest examples involve spatial separation of the sexes of large herbivores outside the mating season (Bowyer, 1984). This life-history characteristic of ruminants has its underpinnings in allometric differences between dimorphic sexes (Barboza & Bowyer, 2000, 2001), but also can be affected by risk of predation (Bleich *et al.*, 1997; Corti & Shackleton, 2002; Bowyer, 2004). In some species, such as bighorn sheep (*Ovis canadensis*), sexual segregation may involve movements into different mountain ranges that are separated by as much as 15 km (Bleich *et al.*, 1997), whereas sexes of white-tailed deer may partition space on the basis of 100–400 m (McCullough *et al.*, 1989; Kie & Bowyer, 1999; Stewart *et al.*, 2003). Because the sex ratio of dimorphic ruminants strongly favours females (Kie & Bowyer, 1999; Stewart *et al.*, 2003; Bowyer & Kie, 2004), density on ranges occupied by males typically is much lower than areas inhabited by females during

segregation. Such differences in density should affect ecosystem processes and ultimately biodiversity, but confirmation requires further study. We do know, however, that these large mammals respond in a strong density-dependent fashion to resource limitation (McCullough, 1979; Kie *et al.*, 2003; Stewart *et al.*, 2005). Moreover, the density of females rather than of males is most influential in determining recruitment of young into the population (McCullough, 1979; Kie *et al.*, 2003), although males may play some role, especially at low density (Myserud *et al.*, 2002). Female density typically is most important in determining recruitment of young because sexes are spatially segregated for much of the year (Bowyer, 2004), and females compete more intensely with other females and young than do males (McCullough, 1979). Consequently, the scale at which females select resources during segregation will affect recruitment and, ultimately, population density on those areas (Bowyer, 2004). Likewise, Farmer *et al.* (in press) linked fine-scale habitat use in male black-tailed deer (*O. h. sitkensis*) and large-scale habitat use by females to their survivorship. This study was unique in linking scale to a component of animal fitness. An explicit understanding of how fitness is related to habitat selection and scale increasingly should be a goal of researchers.

Changes in density of large herbivores have been implicated in 'herbivore optimization' whereby intermediate densities of animals yield the greatest primary productivity (reviewed by Kie *et al.*, 2003). Another large-scale effect involves seasonal migrations of large herbivores, which can concentrate animals and redistribute resources garnered in one area to another (McNaughton, 1985; Nicholson *et al.*, 1997; Berger, 2004). We hypothesize that changing density of ungulates is an important component of understanding biodiversity in many terrestrial ecosystems.

Smaller-scale phenomena also may be important. White-tailed deer and moose in north-eastern North America concentrate their winter activities in 'yards', thought to be critical for their survival (Telfer, 1976a, b, 1970). Moose also may use traditional migratory routes that are thousands of years old, thereby altering habitats along those travel routes (Andersen, 1991). Large herbivores also alter habitat at locations where they give birth and, in some species such as moose, remain at the birth site long enough to accumulate large amounts of faeces, and to deplete browse sufficiently to necessitate bark stripping of shrubs (Bowyer *et al.*, 1999). Even where such localized effects at birth sites are not obvious, the use of traditional areas for completing life-history events, such as giving birth, will concentrate animals (Rachlow & Bowyer, 1998) and may result in herbivores altering plant species composition and concentrating urine and faeces. Obviously, the scale at which birth sites, traditional birthing areas, wintering areas, or migratory routes are chosen will have potential effects on the structure of plants and perhaps other taxa.

Even the social behaviour of large herbivores may hold consequences for biodiversity. In many species of these large mammals, adult males scent urinate as part of behavioural displays during the mating season to either intimidate rivals (Bowyer & Kitchen, 1987) or to attract females (Miquelle, 1991). Ungulates

also scent post trees and shrubs by scraping away the bark and rubbing the mark with glands (Oehler *et al.*, 1995; Massei & Bowyer, 1999), which can result in death of pole-sized trees and help open the forest canopy or do other damage (Nielsen *et al.*, 1982; Bowyer *et al.*, 1994), with clear consequences for the plants and animals in those ecosystems. Such effects tend to be localized, but traditional areas often are used for mating (Bowyer *et al.*, 1994), which would produce larger-scale effects. Consequences of these social behaviours on plant communities have been documented, but more research is needed to understand their connections to biodiversity and how they might vary across spatial scales.

## SYNTHESIS

Scale has become increasingly important in studies of large mammals over the past decade. The concept of scale has been applied to gain a better understanding of the nutritional ecology of herbivores, with scales varying from landscape-level measurements to the location of individual bites of browse (Schaefer & Messier, 1995; Myserud *et al.*, 1999; Wallis de Vries *et al.*, 1999; Parker, 2003; Spaeth *et al.*, 2004). Scale also has been involved in comprehending the population dynamics of large mammals (Coulson *et al.*, 1999), their harvest (McCullough, 1996), and metapopulation dynamics (Bleich *et al.*, 1996; DeWoody *et al.*, 2005). Most studies of scale, however, have focused on habitat use and selection, with comparatively less attention given to carnivores than herbivores (Powell, 1994; Smallwood, 1999; Carr *et al.*, 2002; McLoughlin *et al.*, 2002, 2004). Indeed, such studies of scale for large herbivores abound, including publications on caribou (Rettie & Messier, 2000; Schaefer *et al.*, 2000; Apps *et al.*, 2001; Johnson *et al.*, 2001, 2002a, b, 2004), North American elk and red deer (*Cervus elaphus*; Myserud *et al.*, 2000; Boyce *et al.*, 2003; Anderson *et al.*, 2005), muskoxen (Schaefer & Messier, 1995), Dall's sheep (Rachlow & Bowyer, 1998), moose (Bowyer *et al.*, 1999), and dorcas gazelles (*Gazella dorcas*; Ward & Saltz, 1994). A recognition that scale is important for understanding the ecology of these mammals is evident, and likely to become a driving force in future studies.

The concept of hierarchical habitat selection proposed by Johnson (1980) has served biologists well for over two decades, and sampling at multiple scales has become commonplace (King, 1993). Indeed, sampling at appropriate temporal and spatial scales may be more important than replication for tests of some hypotheses (Oksanen, 2001). We suggest that many more levels of sampling scales or landscape extents than those described by Johnson (1980) are possible, and we believe there are advantages in investigating scales that are related to the life-history traits of the animal under study; as we discussed previously, many of these characteristics are scale sensitive. Moreover, there is a need to distinguish grain and extent in studies of scale (Goodwin & Fahrig, 1998). Changing the size of the sampling unit (grain) does not necessarily change the extent (spatial scale) over which the resulting data apply; confusion over scale-defined and other levels of organization are common in ecological studies (Allen & Hoekstra, 1990, 1992; O'Neill *et al.*, 1996). There

also may be unforeseen biases from varying the size and shape of sampling units for a particular life-history characteristic such as the home range. A careful and well-planned research design is required to avoid pitfalls associated with sampling at a scale that might provide an incomplete or misleading interpretation. Likewise, the myriad of landscape metrics that can be generated in studies involving multiple scales can be confusing and are open to misinterpretation (Fig. 3). We contend that a well designed, hypothesis-testing approach can help sort among landscape variables and their meaning at varying scales (*sensu* Kie *et al.*, 2002).

One unresolved problem involving scale is that it may be difficult to sort between the scales at which an animal is making decisions related to its environment, and the scales at which the biologist chooses to sample that environment. A mismatch in 'decision' and 'sampling' scales could lead to specious conclusions regarding the ecology of the animal. There probably is no single method to completely avoid this potential problem, but we suggest that linking the scale (extent and grain) to the life-history trait of interest and sampling at multiple scales might help (*sensu* Kie *et al.*, 2002).

We argue that the population dynamics of large herbivores and the carnivores that prey on them can drastically affect ecosystem structure and function, and thereby biodiversity. Accordingly, a patchy or heterogeneous environment can influence the distribution and density of large herbivores as modified by life-history traits such as sexual segregation, migration, and use of traditional areas for mating and giving birth. Many links between population density of large herbivores, nutrient cycling, and community composition of plants and other animals already have been demonstrated. An important area for future research is to address the fitness consequences (*sensu* Gaillard *et al.*, 2000) associated with habitat selection and their links to scale. Another challenge for the future is to design manipulative experiments, or engage in adaptive management, to specifically test the causal mechanisms between the density of large mammals and biodiversity. Much exciting research remains to be done.

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