ASSESSING SEXUAL SEGREGATION IN DEER

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Abstract: Sexual segregation in temperate and arctic ruminants is defined as the differential use of space by the sexes outside the mating season. This phenomenon is widespread among taxa, and is especially prevalent among sexually dimorphic deer (Cervidae). Understanding how different genders are distributed across the landscape and how to assess these spatial patterns is of theoretical and applied importance. We developed a simple model to evaluate effects of landscape grain (i.e., patch characteristics), sampling scale, and population density of deer on detection of sexual segregation. We created landscape maps of 2 areas in which landscape grain was changed while other landscape metrics (e.g., area, shape, and diversity) were held relatively constant. We created a high-density population of deer to emulate conditions near ecological carrying capacity (K), and a low-density population at $<K/2$. Sexes of deer were assigned to 4 habitats based on differences in habitat selection derived from an ideal-free distribution, which created spatial separation of the sexes similar to observations in empirical studies. We sampled this pattern of sexual segregation for both areas at large and small scales of measurement using quadrats arranged systematically. We also compared the degree of sexual segregation for the coarse-grained landscape, where the sexes used habitats differently, with a null model in which habitat preferences were identical for each gender of deer. The null model emulated conditions during rut when the sexes were aggregated. Sexual segregation was significantly greater where habitat use differed between sexes, indicating that our model was correct and that the degree of spatial segregation was not an artifact of patch configuration, sampling scale, or population density. Logistic regression revealed that population density and the size of the sample unit significantly affected our ability to assess differences in the spatial distributions of male and female deer where differential use of habitats occurred. Variation in landscape grain, however, did not influence the detection of sexual segregation. Results from our model emphasize the importance of evaluating effects of population density and especially sampling scale on assessing spatial separation of the sexes. Failure to do so may result in not recognizing patterns of sexual segregation on the landscape, or in misinterpreting that phenomenon, which clearly holds consequences for those managing large herbivores or their habitats.

Key words: Cervidae, deer, landscape metrics, population density, sampling scale, sexual segregation.

Sexual segregation is prevalent among a variety of taxa, including plants (Freeman et al. 1976), fish (Keast 1977), birds (Selander 1966), small mammals (Bowers and Smith 1979), and large herbivorous mammals (Main et al. 1996, Bleich et al. 1997, Kie and Bowyer 1999, Barboza and Bowyer 2001). This phenomenon, which is defined in temperate and arctic mammals as the differential use of space by the sexes outside the mating season (Bleich et al. 1997, Barboza and Bowyer 2000), is common among polygynous, dimorphic ruminants. Deer (Cervidae) are among the most sexually dimorphic of all mammals (Ralls 1977, Weckerly 1998, Spaeth et al. 2001). Indeed, sexes of polygynous deer aggregate during the mating season (rut) and often

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segregate in winter and during the birthing season (Cameron and Whitten 1979, Bowyer 1984, McCullough et al. 1989, Miquelle et al. 1992, Main and Coblentz 1996).

Important allometric and physiological differences exist between sexes of dimorphic deer that may cause them to select different habitats or foods contained therein (Bowyer 1984, Beier 1987, Weckerly 1993, Jenks et al. 1994, Barboza and Bowyer 2000). Risk of predation, as it relates to life-history strategies of sexes, can promote their spatial segregation (Main et al. 1996, Bleich et al. 1997, Bowyer et al. 1997). Ample empirical evidence exists of such relationships for deer (Bowyer 1984, Beier 1987, McCullough et al. 1989, Miquelle et al. 1992, Kie and Bowyer 1999).

Sexual segregation likely is most affected by habitat heterogeneity because variable landscapes can accommodate the different needs of the sexes (Miquelle et al. 1992, Bleich et al. 1997, Kie and Bowyer 1999). Other landscape characteristics (e.g., area, patch, and shape metrics) also may play a role in determining how the genders partition habitat space. Spatial separation of the sexes in ungulates can be extremely variable and ranges from differences in the use of small (1 ha) areas (McCullough et al. 1989) to differential use of separate mountain ranges (Bleich et al. 1997). Such marked variation in patterns of segregation upon the landscape present difficulties when sampling this spatial phenomenon.

Li and Reynolds (1994) described habitat heterogeneity in terms of number of patch types, proportion of each type, spatial arrangement of patches, patch shape, and contrast between patches. Spatial heterogeneity, including many attributes of patches, has important effects on ecological processes within landscapes and on life-history characteristics of animals that inhabit them (O'Neill et al. 1988, 1989; Turner 1989; Kie et al. 2002). Such landscape metrics also hold the potential to bias measures related to evaluating ecological and behavioral attributes. Indeed, ecologists have had a long-standing interest in effects of quadrat size on measures of association (Kershaw 1964, Noy-Meir et al. 1970, Upton and Fingleton 1985). Many aspects of ecology are thought to be scale dependent (Dale and MacIsaac 1989, O'Neill et al. 1991, Levin and Pacala 1997, Gardner 1998, Kie et al. 2002). Thus, landscape features that affect the ecology of sexes of deer likewise may lead to biases in the manner in which sexual segregation is measured and interpreted.

The ability to assess the degree of sexual segregation in deer, then, should relate to landscape grain and the measurement scale at which segregation is sampled. Bowyer et al. (1996) reported that size of sampling units had a profound effect on the likelihood of detecting sexual segregation. There is no single correct scale for ecological studies (Wiens 1989); sexual segregation is notably scale sensitive (Bowyer et al. 1996, Kie and Bowyer 1999), implying that analysis at >1 scale will be necessary to derive general results (Morris 1987, Wiens 1989, Orians and Wittenberger 1991, Powell 1994). Population density also is thought to affect the degree of sexual segregation in ungulates (Clutton-Brock et al. 1987, Conradt et al. 1999, Kie and Bowyer 1999). Again, population density, relative to patch dynamics and scale of measurement, can influence detection of the ecological process for which it is, in part, responsible.

Although attempts have been made to investigate effects of habitat heterogeneity (Miquelle et al. 1992, Bleich et al. 1997), population density (Clutton-Brock et al. 1987, Conradt et al. 1999, Kie and Bowyer 1999), and sampling scale (Bowyer et al. 1996) on sexual segregation in ruminants, no studies have considered combined effects of those variables on the ability to assess spatial separation of the sexes. Indeed, sorting the influence of those complex variables for free-ranging deer would be difficult under natural conditions. Nonetheless, understanding those relationships has implications for sampling sexual segregation and has considerable theoretical (Barboza and Bowyer 2000, 2001) and applied (Bleich et al. 1997, Kie and Bowyer 1999, Bowyer et al. 2001) importance. Kie and Bowyer (1999) suggested that the niche requirements of male and female white-tailed deer (*Odocoileus virginianus*) were so different that they should be managed as if they were separate species, and Bowyer et al. (2001) noted that habitat manipulation to benefit moose (*Alces alces*) held the potential to benefit 1 sex, possibly to the detriment of the other. Tests of theory related to why the sexes spatially segregate, as well as subsequent management of wildlife and their habitats based on those conclusions, require sound sampling designs.

Consequently, we developed a simple landscape model to explore effects of landscape grain, sampling scale, and population density of deer on assessing sexual segregation, while holding other characteristics of habitat heterogeneity relatively constant. We also compared our model for segre-
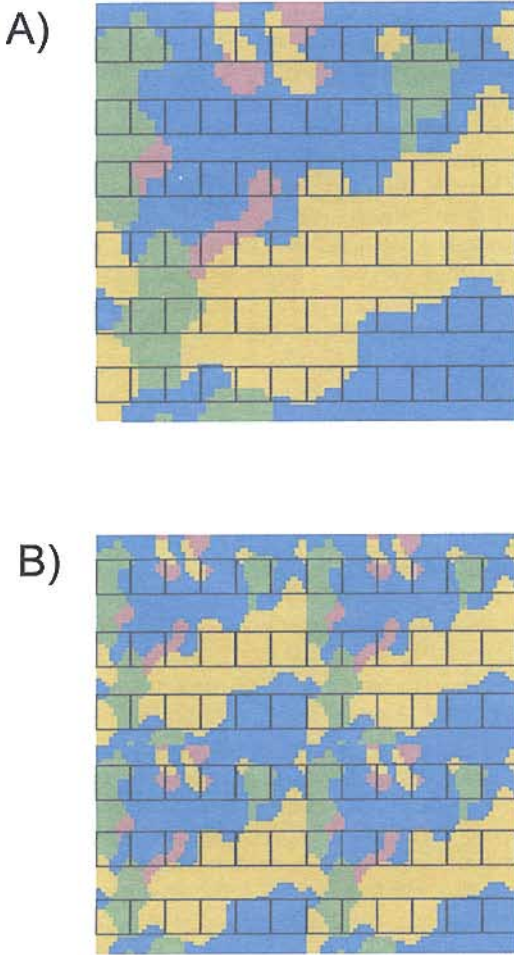
A)

B)

Fig. 1. Coarse- (A) and fine-grained (B) landscape images composed of 4 habitats (habitat 1 = brown, habitat 2 = green, habitat 3 = yellow, habitat 4 = blue) used to sample sexual segregation in deer. Small quadrats, shown in black, were 6 ha; large quadrats, consisting of 3 adjacent small quadrats, were combined into contiguous large areas totaling 18 ha. Both landscapes encompass 1,000 ha.

gation with a null model to evaluate potential affects of sampling scale and population density on our interpretations. Our purpose was to understand how to measure sexual segregation.

METHODS

We determined effects of landscape grain on assessing sexual segregation in deer while holding other characteristics of landscape heterogeneity relatively constant. We produced a coarse-grained raster map (60 × 60 cells) of a landscape containing 4 habitats, each with at least 4 patches, by simplifying and manipulating a geographic information

system (GIS) database obtained from Nicholson et al. (1997) with ARC/INFO (ESRI, Redlands, California, USA). To achieve a total map area of 1,000 ha, we arbitrarily set the size of each cell to 52.7 m. We then created a fine-grained landscape by reducing the coarse-grained image to 25% of original size and combining 4 copies of the resulting image into a single map (Fig. 1). Resolution remained constant in both images: 52.7-m cell size, 60 × 60 cells, and 1,000 ha total for each landscape.

From the perspective of the animal, grain is the smallest scale at which an organism perceives and responds to patch structure (Kotliar and Weins 1990). From the human viewpoint, grain represents biotic and abiotic discontinuities in landscapes depicted in a map format (Milne 1991). Neither of these approaches provides a workable definition of grain for our model, although we assume that animals perceive and respond to differences in our landscape (Fig. 1). Thus, for our purposes, mosaics containing patches that are large relative to the landscape are referred to as coarse-grained, whereas those with small patches in relation to total area are termed fine-grained landscapes (Forman and Godron 1986, Norton and Lord 1990).

We evaluated and quantified the 2 landscape maps (Fig. 1) using FRAGSTATS (McGarigal and Marks 1995). We included selected landscape measurements related to area, patch, shape, diversity, and contagion metrics (McGarigal and Marks 1995). Patch metrics, especially mean size, are important components of landscapes (Forman and Godron 1986, Turner 1989, Norton and Lord 1990, Kie et al. 2002).

We populated coarse- and fine-grained landscapes (Fig. 1) with deer by using a simple set of rules for how adult males and adult females select habitats when spatially separated (Table 1). Our rules for habitat selection do not incorporate all casual mechanisms but emulate their result—the sexes of deer select some habitats differently (Table 1). That differential use of habitats by the sexes will cause sexual segregation upon the landscape is axiomatic; only the degree of their spatial separation is in question. Our approach allowed a relatively unambiguous assessment of the roles of population density, landscape grain, and sampling scale on our ability to detect spatial segregation of the sexes.

We varied ecological carrying capacity (*K*) of each habitat, and preferences of sexes for types of habitats (Table 1). We assumed differing requirements for resources by sexes. Habitats 1 (brown) and 2 (green) were ranked as most pre-

Table 1. Carrying capacity and preference ranks for habitats and total area used to develop a model to evaluate effects of landscape grain, population density, and scale of measurement on detection of sexual segregation in deer.

Variable	Habitat 1 (brown)	Habitat 2 (green)	Habitat 3 (yellow)	Habitat 4 (blue)	Landscape average
Carrying capacity (deer/ha)	1.00	0.50	0.14	0.07	0.20
Male preference rank	1	2	3	4	–
Female preference rank	2	1	3	4	–

ferred by males (habitat 1) or females (habitat 2); the 2 remaining habitats, 3 (yellow) and 4 (blue), were given equal but lower rankings of preference for the sexes (3 and 4, respectively; Table 1). We assumed that different preference rankings would result in a differing density of deer at K for each habitat, and altered density accordingly (Table 1). Based on these rules, we obtained high-density populations of deer at K of 200 animals/1,000 ha, and arbitrarily designated low-density populations as 75 deer/1,000 ha. Densities of deer were affected by the sex ratio of adult males to adult females, which was set at 35:100 for both low-density and high-density populations. Such sex ratios are reasonable for nonhunted populations of polygynous deer, where mortality of males is exacerbated by strenuous rutting activities (Bowyer 1981, 1991; Kie and Bowyer 1999).

We filled habitats with deer using the same rules and conditions for each treatment (coarse- and fine-grained landscapes, high- and low-density populations) to avoid potential biases from differing initial conditions (King 1997). To begin, we randomly selected individual deer of either sex and randomly placed each animal into an available patch of the highest habitat preference (Table 1), with probability proportional to patch size. If a randomly selected patch was full (i.e., the K of that patch for deer had been reached previously), then another patch of the same habitat was selected. If all patches for a particular type of habitat were full, then we moved deer to the next lower-ranking patch based on preferences of each sex (Table 1). Some movement of deer across the landscape is reasonable given their vagility (Nicholson et al. 1997). The spatial pattern we modeled reflects density-dependent resource selection under an ideal-free distribution (Fretwell 1972), although for the low-density population, some patches of less-preferred habitat would not be used. We continued this process until the landscape was filled with deer (i.e., K was attained for high-density populations), or

until a predetermined number of deer was reached for low-density populations.

Following placement of deer on the 2 landscapes, we systematically located quadrats across both landscapes (Fig. 1). We subdivided quadrats into 2 scales: small (6 ha) and large (18 ha) by combining 3 contiguous small quadrats into 1 large quadrat. Herein we use the term scale exclusively to mean the type of measurement scale (Schneider 1994). We avoided potential problems with placement and interspersion of samples on the landscape by requiring that both small and large quadrats sample identical locations. This method resulted in our sampling 43.2% of each landscape. Some lack of statistical independence occurred between our comparisons of sampling scales because the same areas were sampled with both large and small quadrats.

We calculated the area of each habitat patch within a quadrat and used the proportion of that patch to determine the number and sex of deer that were present (from the number of animals in that patch). When a quadrat contained areas from >2 habitat patches, we summed the proportional areas within the quadrat, and thereby determined the number and sex of deer from the proportion of the patch area to the total area of the quadrat. We assumed that once assigned to a patch, deer could not move, and that no differences in our ability to detect deer occurred among habitats or between sexes.

Following Bowyer et al. (1996) and Kie and Bowyer (1999), we defined a quadrat as sexually segregated if it contained ≥90% of either sex. This threshold is somewhat arbitrary, but helps avoid a potential bias from the sex ratio of deer—which was skewed (74.1% females)—in assessing degree of sexual segregation. Thus, quadrats would not be classified as segregated simply because they contained the skewed sex ratio representative of the overall population. Quadrats that did not contain deer were not included in analyses (Bowyer et al. 1996, Kie and Bowyer 1999).

Table 2. Metrics for landscape map images (coarse and fine) for modeling effects of landscape grain, population density, and scale of measurement on detection of sexual segregation in deer (McGarigal and Marks 1995).

Landscape metric	Coarse image	Fine image
Number of patches (*n*)	22	70
$\bar{x}$ patch size (ha)	45.4	14.3
Patch size coefficient of variation (%)	185.3	245.3
Patch density (*n*/100 ha)	2.2	7.0
Double log fractal dimension	1.20	1.30
Mean shape index	1.43	1.41
Shannon's diversity index	1.15	1.16
Contagion index	45.8	36.8

We repeated our analysis using identical preferences for habitats by the genders of deer (e.g., habitats 1, 2, 3, 4 in descending order of preference) to develop a null model (Gotelli and Graves 1996). This null model also emulates conditions during rut when the sexes are aggregated. We compared our model of segregation with the null model for the coarse-grained landscape only. We evaluated differences in the spatial separation of the sexes from those 2 models using a 2-sample *z*-test for proportions (Remington and Schork 1970) for large and small sampling quadrats, and high and low population densities. We adjusted alpha for making multiple comparisons with a sequential Bonferroni correction (Rice 1989).

We used logistic regression (PROC LOGISTIC; SAS Institute 1987) to model the probability that a quadrat would be sexually segregated. The binomial dependent variable was coded "0" if deer were not sexually segregated, and "1" if sexual segregation occurred on a particular quadrat. We created dummy independent variables (Agresti 1990), including sampling scale (large and small quadrats), landscape grain (coarse and fine), and population density (high and low) and tested for interactions among those independent variables. We evaluated our model with a Pearson test for goodness-of-fit. We also examined the percent concordance, based on a jackknifed reclassification, which evaluated whether observations were consistent with predictions from the model (Agresti 1990). We determined that our sampling design yielded adequate sample sizes to evaluate sexual segregation by examining a reduction in variance of mean values for quadrats that were segregated with increasing cumulative sample size (Kershaw 1964). We arbitrarily set $\alpha = 0.03$ to compensate for a potential lack of statistical independence between samples obtained from large and small quadrats.

RESULTS

The 2 landscape images (Fig. 1) contained identical proportions for each of the 4 habitats: habitat 1 (brown) = 4.6%, habitat 2 (green) = 14.6%, habitat 3 (yellow) = 35.8%, and habitat 4 (blue) = 45.0%. Likewise, differences in shape (double log fractal dimension, mean shape index), and diversity (Shannon's index) were similar between coarse- and fine-grained images (Table 2). Metrics related to landscape grain, however, varied markedly between images. Number of patches, coefficient of variation (CV) of patch size, and patch density were greatest in the fine-grained image, whereas mean patch size was largest in the coarse-grained image (Table 2). The contagion index was larger in coarse than in fine-grained landscapes (Table 2).

Patch size is a critical component of landscape grain. Therefore, we evaluated that metric for individual habitats. Mean (± SE) patch size for the 4 habitats in the coarse-grained landscape was habitat 1 = 7.5 ± 2.54 ha, habitat 2 = 29.3 ± 9.95 ha, habitat 3 = 52.0 ± 38.18 ha, and habitat 4 = 111.1 ± 60.4 ha. That same metric for the fine-grained landscape was habitat 1 = 2.0 ± 0.32 ha, habitat 2 = 9.2 ± 1.19 ha, habitat 3 = 16.3 ± 5.97 ha, and habitat 4 = 55.8 ± 28.04 ha. Although habitat 4 (blue) possessed the largest patch sizes at both landscape grains (Fig. 1), some patches of habitat 4 in both images were too small to hold deer because of the low carrying capacity of that habitat (Table 1).

The mean patch size of habitats 1 (brown) and 2 (green), which were preferred most by males and females, respectively, were sufficiently large that they did not occur in the same quadrats repeatedly. Co-occurrence of those preferred habitats in numerous quadrats could cause an underestimate of the degree of sexual segregation (e.g., sampling scale was too coarse). For the fine-grained image, habitats 1 and 2 co-occurred in 11% of small quadrats and 33% of large ones; in the coarse-grained image, those values were 4% and 8%, respectively (Fig. 1).

We accomplished our goal of producing sexual segregation on our landscapes. Degree of sexual segregation (percentage of quadrats with ≥90% of either sex) varied (8.3–96.4%) across landscapes and treatments (Table 3). Sexual segregation ($\bar{x} \pm$ SE) was greater at low population density (84.5 ± 0.47%) than at high density (14.6 ± 0.42%), and greater at a small sampling scale (56.9 ± 3.10%)

Table 3. Degree of sexual segregation in deer resulting from sampling quadrats in 2 landscape grains, 2 population densities, and 2 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).

Grain	Population density	Sample quadrat size (ha)	Quadrats with deer (n)	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

than a large sampling scale (42.2 ± 4.38%); less difference existed between coarse- (51.2 ± 3.91%) and fine-grained (48.1 ± 3.17%) landscapes (Table 3).

We compared degree of sexual segregation for the coarse-grained landscape, in which the sexes selected habitats differently (Table 3), with a null model in which habitat selection was identical for the genders of deer. Some sexual segregation occurred in our null model. Nonetheless, spatial segregation of the sexes was uniformly greater ($P = 0.05$ following sequential Bonferroni correction of z-tests) where habitat selection differed between the sexes than for the null model: large quadrats (34.2% vs. 9.0%), small quadrats (38.0% vs. 10.7%), high population density (13.5% vs. 4.2%), and low population density (90.5% vs. 25.0%).

We further evaluated effects of deer population density, scale of measurement, and grain of landscape on sexual segregation in a single logistic-regression mode (Table 4). A Pearson test of fit indicated that our model was apt ($P = 0.91$). The overall model (79% concordance) was highly significant, with population density and sampling scale contributing most to that outcome. Landscape grain, however, did not have a significant effect on our ability to assess the degree of sexual segregation and did not interact with sampling scale or population density (Table 4). Because landscape grain did not have a significant effect on our ability to detect sexual segregation (Table 4), we did not test the segregation model against a null model for the fine-grained landscape.

DISCUSSION

We implemented modeling rules that resulted in realistic outcomes for deer and their habitats, including configuration of patches within landscapes (Nicholson et al. 1997), deer densities and sex ratios (Bowyer 1984, 1991; Kie and Bowyer 1999), and quadrat sizes used to sample sexual segregation (Bowyer et al. 1996). Our model produced sexual segregation upon the landscape outside the mating season so that we could evaluate effects of landscape grain, sampling scale, and population density on assessing segregation of the sexes. Empirical evidence exists to document that sexual segregation outside the mating season is a biological phenomenon and not a sampling artifact, including tests against null models for differences in habitat selection between the sexes, and effects of a skewed sex ratio (Bowyer et al. 1996, Bleich et al. 1997, Kie and Bowyer 1999). Thus, numerous permutations and simulations with the model were not necessary. We acknowledge that other potential methods exist for locating deer on the landscape. Nonetheless, our procedure was successful in altering population density and degree of sexual segregation in an appropriate manner for coarse- and fine-grained environments. Hence, other methods would have a limited effect on conclusions about how best to sample sexual segregation. Indeed, comparisons of degree of sexual segregation (Table 2) against our null model, where habitat selection by the genders of deer was identical, indicated that degree of spatial segregation in our model was not an artifact of patch configuration, sampling scale, or population density.

Population density affects patterns of sexual segregation across the landscape in deer (Clutton-Brock et al. 1987, Kie and Bowyer 1999). Biological processes related to avoiding intersexual competition likely are involved in the partitioning of space by the sexes outside the mating sea-

Table 4. Results from logistic regression relating effects of landscape grain (coarse and fine), population density (high and low), and sampling scale (large and small quadrats) on detection of sexual segregation in deer; $n = 278$ quadrats.

Variable	df	Parameter estimate	SE	P
Intercept	1	2.6400	0.6626	0.0001
Landscape grain	1	0.7252	0.9177	0.4294
Population density	1	−3.7338	0.6990	0.0001
Sampling scale	1	−2.0320	0.7917	0.0103
Grain × density	1	−1.3514	0.9160	0.1401
Grain × scale	1	0.3337	0.8004	0.6767
Density × scale	1	1.4968	0.8809	0.0893

son (Kie and Bowyer 1999). Rules for habitat selection by the sexes (Table 1) were sufficient to cause marked differences in sexual segregation at differing population densities (Table 3). Moreover, our model indicated that the ability to assess the degree of sexual segregation was dependent on population density (Table 4). Clearly, the failure to consider population densities of deer could bias measurement and thereby interpretation of results. A sufficiently low density of deer, however, holds the potential to produce segregation of the sexes independent of differential habitat use and sampling scales based on chance alone. Comparisons against our null model indicated that potential bias did not influence our conclusions markedly. In practice, this is not a serious consideration because a significant difference in spatial separation of the sexes must exist between periods of segregation and aggregation (i.e., the mating season) to infer that this phenomenon occurred (Bowyer 1984, Bleich et al. 1997, Kie and Bowyer 1999). Our model of spatial separation includes only the period in which the sexes are segregated, although our null model provides a realistic approximation of periods of aggregation because the sexes selected habitat in an identical fashion.

The strong effect of sampling scale (quadrat size) on our ability to measure sexual segregation (Table 4) also has been reported in empirical studies of deer (Bowyer et al. 1996, Kie and Bowyer 1999). Indeed, Bowyer et al. (1996) observed >50% decline in the number of quadrats that were sexually segregated with increasing scale of measurement. Those authors recommended using a runs test to determine an optimum-sized quadrat when sampling units were aligned along transects, and the contagion index (Li and Reynolds 1993) when quadrats could not be combined into sequentially larger areas. No previous study, however, has evaluated effects of population density and sampling scale because of the difficulty of assessing those variables simultaneously under field conditions. Although both population density of deer and quadrat size were influential in determining our ability to detect sexual segregation, their interaction was not significant (Table 4).

Surprisingly, landscape grain did not affect our ability to measure sexual segregation in deer (Table 4), at least for the landscape grains and measurement scales at which we sampled. A bias in detecting spatial separation of the sexes might occur if habitats preferred by males and females

were both clustered and small relative to the size of our sampling quadrats; the result would be relatively few quadrats that were sexually segregated. For our model, however, a nearly equal percentage of quadrats in both fine- and coarse-grained images were segregated, probably because differences in habitat selection by the sexes were held constant. Finally, we failed to identify interactions of landscape grain with either sampling scale or population density in our logistic-regression model (Table 4).

Results from our model of sexual segregation do not mean that habitat heterogeneity is unimportant in causing spatial separation of the sexes. Several empirical studies strongly indicate that heterogeneity plays a major role in sexual segregation of some ungulates (Miquelle et al. 1992, Bleich et al. 1997, Kie and Bowyer 1999, Bowyer et al. 2001). Also, recall that our model manipulates only 1 (grain) of many attributes of landscape heterogeneity (Li and Reynolds 1994). We suggest only that landscape grain is less likely to bias measures of sexual segregation than scale of measurement (quadrat size) or population density. Kie et al. (2002) demonstrated that other characteristics of landscapes, which we held relatively constant in our models (Table 2), could have a profound effect on spatial distribution of deer.

Sampling scale and population density affected our ability to measure sexual segregation; such outcomes have been reported previously (Bowyer et al. 1996, Kie and Bowyer 1999). Consideration of such variables is required in designing studies of sexual segregation, yet few researchers have done so (Bowyer et al. 1996, Kie and Bowyer 1999). Moreover, failure to consider sampling scale and population density prevents meaningful comparisons among studies or species in the degree of sexual segregation exhibited by large herbivores. Clearly, future research on sexual segregation requires designs to address those biases in measurement we demonstrated (Table 4). The observation that landscape grain failed to affect our ability to detect sexual segregation, however, was unexpected, as was the absence of interactions with sampling scale and population density—conclusions that are only possible using our modeling approach.

We succeeded in varying landscape grain, while holding other aspects of habitat heterogeneity (Li and Reynolds 1994) relatively constant (Table 2). Our method of reducing and combining habitat images holds promise for understanding landscape processes where randomizing patch types,

sizes, and shapes leads to confounding effects from simultaneously varying a myriad of landscape metrics. Although habitat patches on the edge of the original image may tend to form slightly bigger patches when combined (e.g., habitat 4; Fig. 1), our procedure should be useful in modeling numerous landscape characteristics while controlling for effects of landscape grain.

MANAGEMENT IMPLICATIONS

Results from field studies seldom are as clearly interpretable as outputs from models, and often are not amenable to simultaneous alteration of important patterns on the landscape. Our model outputs offer insights into how landscape grain, sampling scale, and population density of deer may affect measurement of sexual segregation. Such an outcome should be of value to others studying associations of organisms across a landscape. We recommend that biologists investigate potential effects of sampling scale and population density on the detection of sexual segregation, or other spatial associations of organisms, when designing field experiments. Our method of combining landscape images in a manner that affects primarily landscape grain will be useful in other models of landscape heterogeneity.

Assessing patterns of spatial separation of the sexes may be difficult (Bowyer et al. 1996), and failure to consider how and why the sexes segregate may lead to management errors, especially in manipulating habitat (Bowyer et al. 2001). Our modeling approach offers insights into how best to design studies to address these problems. Nonetheless, additional research on how other landscape metrics affect sampling designs is warranted.

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