

THE IMPORTANCE OF SEX AND SPATIAL SCALE WHEN EVALUATING SEXUAL SEGREGATION BY ELK IN YELLOWSTONE

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The forage-selection hypothesis (FSH) explains sexual segregation in ungulates as a function of different dietary requirements producing different levels of habitat optimality, whereas the reproductive-strategy hypothesis (RSH) explains sexual segregation as a function of different survival strategies between the sexes. Based on observations of habitat use by elk (*Cervus elaphus*) in Yellowstone National Park, Wyoming with regard to varying levels of wolf encounter risk, we found that our determination of whether the RSH or FSH best applied to sexual segregation varied by the scale at which we were measuring habitat use. At broad spatial scales we found no significant avoidance of wolves by elk. At the habitat scale we found that habitat use by elk was consistent with predictions of the reproductive strategy in that female elk used habitats that offered a balance of forage and escape terrain for themselves and calves, and that the degree to which escape terrain was present was dependent upon the risk of wolf encounter. At the scale of the habitat patch we found that differences in forage availability likely drove the differences in habitat use. Our results highlight the importance of scale when investigating habitat use, nonlethal predation effects, and sexual segregation in ungulates.

Key words: *Cervus elaphus*, elk, habitat use, landscape, noninvasive sampling, sexual segregation, Yellowstone

One of the fundamental goals of ecology is to understand the relationship animals have with their environments. An intriguing aspect of environmental interactions of ungulates is sexual segregation with regard to resource utilization (Bleich et al. 1997; Main et al. 1996). Two generalized groups of hypotheses have been put forth to explain sexual segregation among ungulates, and are generally categorized as either social or ecological (see Main [2008] for a review). Most ecological hypotheses take 1 of 2 forms: forage-selection hypotheses (FSHs) or reproductive-strategy hypotheses (RSHs—Main 2008; Main et al. 1996). FSHs, frequently referred to as gastrocentric hypotheses (Barboza and Bowyer 2000; Gross et al. 1996), explain sexual segregation as a function of allometric differences between males and females that create differences in the optimality of habitats. Alternatively, RSHs, frequently referred to as predation-risk hypotheses, explain sexual segregation as a function of differing

survival strategies between males and females (Deperno et al. 2003; Main 2008).

The scale of spatial analysis is an important consideration when exploring resource use (Johnson 1980; Weins 2001) and may be important in understanding the underlying mechanism for sexual segregation. For example, imagine a prey species for which predation risk varies by sex, and at a certain time of year males and females occur in sex-specific groups. RSHs would predict that in regions with predators, males and females would use space differently, but in regions without predators, space use would be similar (Main et al. 1996). However, because animals make resource-use decisions at different scales (Johnson 1980), if one did not measure the scale where the risk-reduction choice was occurring, these differences might not be detected. Alternatively, FSHs would predict that males and females use space differently in relation to food availability based on allometrically scaled differences in body size, regardless of varying levels of predation risk (Ruckstuhl and Neuhaus 2002). However, the decision by animals to use space may occur at 1 or more scales (e.g., landscape level, habitat level, or patch level within habitats), and depending on the scale of analysis, the conclusions may vary.

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Although it is an oversimplification to define the RSH simply as the predation-risk hypothesis, the RSH does focus on the dynamic nature of predation risk and recognizes that during different times of the year males and females likely face different levels of predation, or have different metabolic demands, or both (Main 2008; Neuhaus et al. 2005). One of the key components of the RSH is that predation risk modifies prey behaviors (e.g., space use—Brown et al. 1999; Laundre et al. 2001). For example, animals may choose food-poor habitats that reduce exposure to predation risk, which may have reproductive or survival consequences (Werner et al. 1983). Animals also may choose riskier habitats if important resources are found there (Brown et al. 1999; Lima and Dill 1990). If risk varies between sexes then we expect different choices by males and females to balance resource demands and safety, and these decisions may happen at different spatial scales. Therefore, one should simultaneously measure sex-specific space use at multiple spatial scales to accurately evaluate the mechanisms operating.

Elk (*Cervus elaphus*) in Yellowstone National Park provide a system to explore the influence of predation risk on use of space by prey, and provide insight into whether the FSH or RSH are functioning to drive the observed sexual segregation of elk. The northern range of Yellowstone National Park is home to more than 8,000 elk and currently more than 100 wolves (*Canis lupus*—Smith 2005). Wolves are the principle predators of adult elk, which comprise 90% of the wolves' diet in Yellowstone National Park (Smith et al. 2003). However, grizzly bears (*Ursus arctos horribilis*) are the primary predator of elk calves, being responsible for 60% of total calf predation (Barber et al. 2005).

Predation risk to elk also varies by sex and age. Young of the year are generally the most vulnerable to predation by both wolves and grizzly bears (Barber et al. 2005; Smith et al. 2003). Further, during the calving season predation risk to female elk is higher than to male elk (Smith 2005; White and Berger 2001). Therefore, the spring calving season on the northern range provides an opportunity to explore variation in use of space by male and female elk and relate space use to the predictions of the RSH or the FSH with regard to sexual segregation.

Previous research in Yellowstone National Park has shown that wolves alter foraging behaviors of elk (Childress and Lung 2003; Laundre et al. 2001; Liley and Creel 2008; Lung and Childress 2007) and habitat use (Fortin et al. 2005; Hernandez and Laundre 2005; Mao 2003; Ripple et al. 2001; White and Garrott 2005). At the landscape scale elk avoid areas used frequently by wolves (Hernandez and Laundre 2005), whereas within the landscape elk avoid certain habitat types such as aspen stands (*Populus tremuloides*) and low-elevation riparian corridors in areas used by wolves (Ripple et al. 2001), and open areas (Creel et al. 2005). Female elk also make greater use of burnt forests and steeper-sloped terrain when wolves are present (Mao 2003). In addition, as use by wolves increases, habitat preference of female elk switches from more open grassland-dominated habitats to closed

canopy, subalpine-fir (*Abies lasiocarpa*)–Douglas-fir (*Pseudotsuga menziesii*), forested habitats (Fortin et al. 2005). Use of forested cover by elk as an antiwolf predation mechanism also varies temporally (within hours) of wolf presence on the landscape (Creel et al. 2005).

This study expands on previous work by delineating sex differences in use of space by elk at different spatial scales. Previous studies have explored either general habitat use by elk without identifying sex (Hernandez and Laundre 2005; Ripple et al. 2001), habitat use only by female elk (Fortin et al. 2005; Mao 2003), or habitat use by elk at a single spatial scale (Fortin et al. 2005; Hernandez and Laundre 2005; Laundre et al. 2001; Liley and Creel 2008; Mao 2003; Ripple et al. 2001).

We hypothesized that at the landscape scale, both male and female elk will choose to use regions not frequently used by wolves. We hypothesized that at the habitat scale, however, habitat use by elk would be best predicted by the RSH of sexual segregation. Consequently, we expected that elk would not use all areas equally and that open habitats (steppe prairies and wet meadows), which likely represent areas of high forage quality and quantity but also high risk, would be preferred by males but not females. Conversely, forested habitats, which offer greater cover and safety but less forage availability, ought to be preferred by females. We expected that the FSH would be operant at predicting habitat use and sexual segregation by male and female elk at finer spatial scales (habitat-patch).

MATERIALS AND METHODS

Study site.—This study took place on the northern range of Yellowstone National Park, Wyoming. The northern range is an approximately 100,000-ha region of the park, encompassing an 80-km stretch of the Lamar, Yellowstone, and Gardiner river drainages (Fig. 1). Temperatures range from an average low of -13°C in January to an average high of 27°C in July. Elevations range from 1,200 to 3,300 m above sea level and precipitation varies between 50 and 205 cm annually (data summarized from the Western Regional Climate Center, Tower Falls, Wyoming, station). Vegetation on the northern range is a mixture of upland conifer forests (42%), upland steppe (27%), shrub steppe (26%), wet meadows (3%), and other (2%) vegetation types (Despain 1973; for further description of Yellowstone National Park, see Childress and Lung [2003]).

Field methods.—Using ArcInfo 9.0 (Environmental Systems Research Institute Inc., Redlands, California) and the Yellowstone National Park landcover data set (Despain 1990), we selected a 225-km² subset of the northern range containing habitat proportions representative of the northern range as a whole and including areas both inside and outside of known wolf territories (Smith 2005; Smith et al. 2003). We then used ArcInfo to systematically place points at 0.25-km² intervals across the study region and Trimble handheld global positioning system units (Trimble Navigation Limited, Sunnyvale, California) to navigate to these points. At each

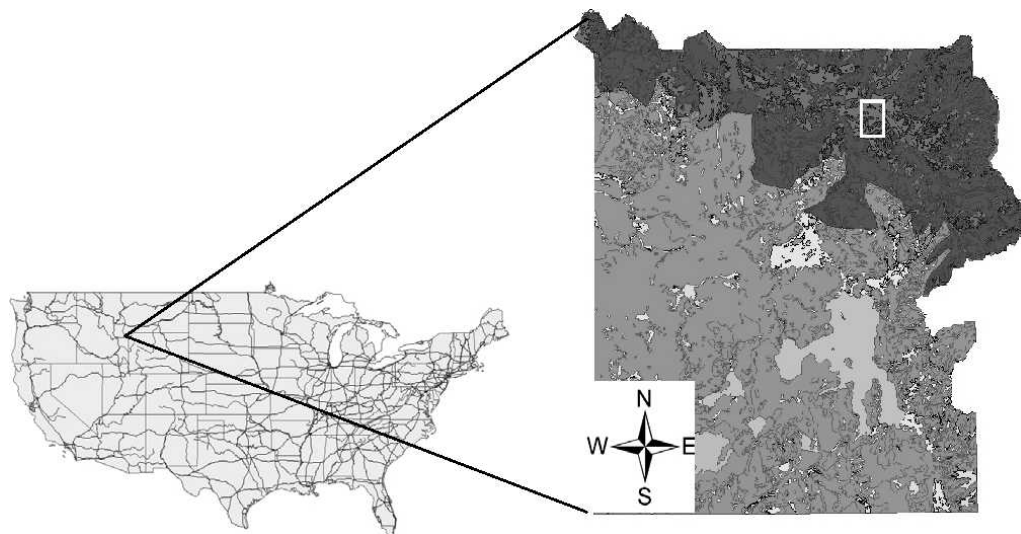


FIG. 1.—Yellowstone National Park. The northern range is highlighted in dark gray. The white box represents the location of this study on the northern range. The study site was selected to have habitat types within it occur with the same frequency as they do on the northern range as a whole.

location we established a 400-m² sample plot. This sampling scheme yielded a total of 440 sample plots across the 2 years of the study, 180 of which were sampled repeatedly in both years to test for yearly variation in elk distribution.

We used ArcInfo to assess slope, elevation, and aspect of each point and field-based assessment to measure habitat type, percent ground cover, number of elk pellet groups, vegetation height, visual obstruction, habitat complexity, and distance to nearest feature. At each plot we counted the number of elk fecal pellet groups in a 400-m² area following methods similar to those of Ripple et al. (2001) and Hernandez and Laundre (2005). Percent cover, vegetation height, and visual obstruction were measured with line-intercept sampling, Robel pole, and density boards, respectively (Noon 1981; Robel et al. 1970). Habitat complexity was assessed following the methods of Edge et al. (1987), and distance to nearest treeline, water source, and road were measured using Bushnell 800 laser-actuated range finders (Bushnell Corp., Overland Park, Kansas). Percent forage, a synthetic variable defined as the sum of the percent ground cover of grass and forbs, also was calculated for each 400-m² study plot. For a more detailed description of the field methods see Gregory (2006).

Before using elk fecal pellets we wanted to be certain their use as an index of relative habitat (Hernandez and Laundre 2005; Ripple et al. 2001) would not bias our estimates of habitat use. To ensure that fecal pellets were an accurate estimate of use of space by elk, we observed and measured elk defecation rates. Elk were observed from distances of 50–500 m continuously for 6-h intervals. We recorded the number of defecations per hour, habitat type, and behaviors when defecating. Also, to ensure that elk pellets represented temporally relevant use of space by elk, we marked fresh elk scats and observed changes in their physical characteristics as they aged. Based on these observations, pellets were divided into 5 qualitative age classes (criteria for age classes available in Gregory [2006]). Pellets in age classes 1–4 were

<6 weeks old and have an equal likelihood of yielding reliable polymerase chain reaction product (Gregory 2006). Therefore, only pellets from age classes 1–4 were counted and used in subsequent analysis.

Laboratory methods.—We used molecular determination of sex to distinguish between elk pellets from males and females. Because of financial constraints we were only able to determine sex for pellets collected from a 180-plot subset (30 from each vegetation type) of our initial 440 plots. The 180-plot subset used for molecular analysis is not the same 180-plot subset that was sampled repeatedly across years.

Elk pellets were collected in the field at each sample plot and preserved in 95% ethanol. DNA was extracted from preserved elk fecal pellets using Qiagen DNeasy ministool kits (Qiagen, Valencia, California). DNA was amplified at 2 microsatellite primers: a Y chromosome-specific marker (SRY—Wilson and White 1998), and an autosomal control marker (BMC-1009—Talbot et al. 1996). Because we were working with low-copy DNA, rigorous measures were taken to prevent contamination (Swanson and Rusz 2006), and samples were amplified via polymerase chain reaction 3 times each to reduce biochemical genotyping errors (Gregory 2006). If amplification occurred at both markers (SRY and BMC) the sample was recorded as male; if amplification occurred only at BMC in all amplifications the sample was recorded as female.

From each sample plot we extracted DNA from 3 randomly chosen elk pellet groups. Based on our observations of elk defecation rates, a sample plot was deemed to be preferred by males if all samples collected at that sample plot showed amplification at both markers, and preferred by females when amplification was successful for 2 or more samples for the BMC marker only.

Estimating wolf encounter risk.—Data on wolf locations were obtained from the Yellowstone Wolf Project (D. Smith, Yellowstone National Park, Wolf Restoration Biologist, pers. comm.). Risk of elk encountering wolves was estimated using

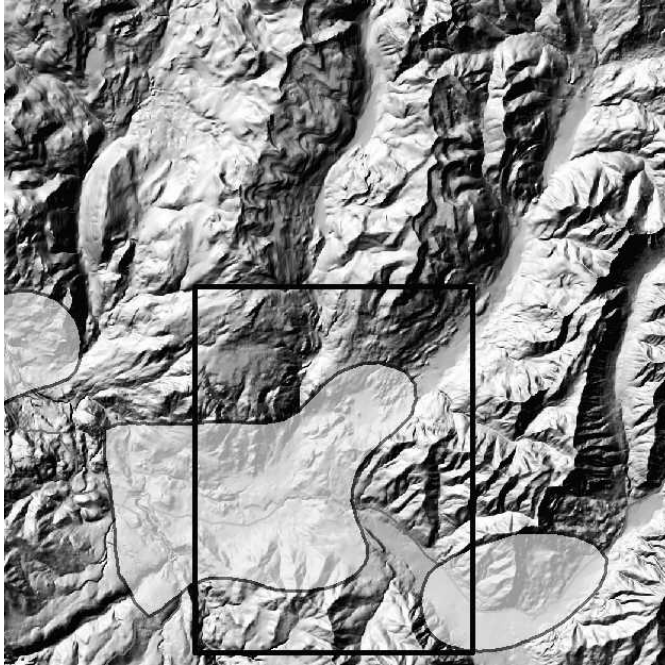


FIG. 2.—Map of the study site showing topography within the northern range of Yellowstone National Park (study area shown as black rectangle). Areas of high wolf encounter risk (50% wolf kernels) are indicated by gray polygons, whereas all other regions outside the polygons are considered areas of low wolf encounter risk (100% wolf kernels). Kernel polygons shown in this figure are from wolf telemetry data for 2004. Kernel polygons for 2005 were created from wolf telemetry data for 2005 and encompass a similar area.

telemetry data collected from April to June 2004 and 2005. Kernel estimators were used to estimate the intensity of use of an area by wolves and the likelihood of wolf–elk encounter (Worton 1989). Assuming that the intensity of use of an area by predators directly relates to encounter risk for prey, we estimated 2 levels of wolf encounter risk using kernel estimators: 50% core range (high encounter risk) and 100% kernel (low risk—Kaufmann 1962; Fig. 2). Because there was evidence that wolf distribution had changed from 2004 to 2005 (D. Smith, pers. comm.), we tested for spatial overlap between years using multiple response permutation procedures (Blossom version W2005.05.06; Ft. Collins Science Center, United States Geological Survey, Fort Collins, Colorado). Based on the results of this multiple response permutation procedure analysis we calculated encounter risk for each year independently.

Estimating intensity of use by elk.—We 1st tested for spatial autocorrelation, out to 10,000 m, between intensity of use by elk and interplot distance. We selected 10,000 m as the maximum distance to test for autocorrelation based on the maximum average daily travel distance of elk in Yellowstone National Park during seasonal migrations of 12,900 m (Irwin 2002); 10,000 m is likely a greater distance than an elk would normally travel (Cook 2002). Using the 180-plot subset for which we had molecular data, both male and female elk were observed using all habitat types. Consequently, to assess differences in effect size of various geomorphologic variables on habitat preference of elk, we divided use by elk into 3

levels of intensity (low, medium, and high use), and used ordered polytomous logistic regression. The number of scats per plot used to determine if a plot was in the low, medium, or high elk-use category was based on inflection points in the frequency histogram of the number of pellets per plot.

Statistical methods.—To test for changes in elk distribution between years we used the 180 plots sampled repeatedly each year and a paired *t*-test, testing for significant differences in number of scats counted within plots located at the same geographic coordinates between years. We observed and collected elk fecal pellets at all sample plots; consequently, at the habitat and habitat-patch scales we were dealing with selected units and for this reason statistical tests based on use verses availability were inappropriate (Johnson 1980; Manly et al. 1993). We used linear regression in SAS 9.1 (SAS Institute Inc., Cary, North Carolina) to test the influence of wolf kernel (encounter risk) on density of elk fecal pellets at the landscape scale, using data from all 440 sample plots. We used 2 different statistical analyses of the 180-plot subset for which we had molecular data for to determine habitat preference. The 1st was a chi-square goodness-of-fit test (Neu et al. 1974) used to determine if elk used space randomly. This was done to remove the potential for spurious results based on landscape composition as a result of the hierarchical nature of habitat choice (Alldredge and Griswold 2006; Johnson 1980). In our 2nd round of testing for habitat preference, we used preference rank analysis as recommended by Johnson (1980). Preference analysis uses the difference in habitat usage rank and habitat availability rank as an indicator of preference. To test for differences in preference we used a Bayesian decision rule for multiple comparisons with an odds likelihood ratio of 1:50—which is similar to a 95% confidence interval (Waller and Duncan 1969; recommended by Johnson 1980).

Within preferred habitats we tested the influence of geomorphologic features and vegetative ground cover on pellet distribution using polytomous logistic regression (North and Reynolds 1996) with an information theoretic approach to model selection (Burnham and Anderson 1998). Initially, data were collected on 18 habitat variables. In an effort to reduce model complexity, Pearson's correlation analysis was used to check for correlation, and correlated variables were eliminated. From 13 noncorrelated variables we chose 5, based on previously published data and biological inference, which we believed were most influential in determining elk use of a habitat patch (Table 1; Fortin et al. 2005; Lung and Childress 2007; Mao 2003). Interobserver reliability and sex-specific elk defecation rates were analyzed using standard frequentist statistics. All field procedures described above are consistent with guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

RESULTS

We recorded 5,093 pellet groups in 440 sample plots within a 225-km² study site over a 2-year period. The number of

TABLE 1.—Variables included in the Akaike information criterion (AIC) analyses of models predicting habitat use by male and female elk (*Cervus elaphus*).

Variable	Variable description
Forage	An estimate of forage availability at each plot obtained by summing the percent ground cover of all grass and forb species present along the line-intercept sampling transect measured at each sample plot.
Slope	The slope of the landscape in degrees as measured using ArcInfo 9.0 using a 30-m digital elevation model for Yellowstone National Park.
Predation	Categorical variable of the risk of encountering wolf (high or low) at a particular habitat patch based on kernel estimates of wolf habitat use.
Elevation	The elevation of the point in meters above sea level of the landscape.
Habitat complexity	The average distance from the center of the sample plot in each of the 4 cardinal directions at which a researcher is >50% obscured by the terrain.
Aspect	The degree measure of the aspect of the landscape measured for each habitat plot from the digital elevation model for Yellowstone National Park using ArcInfo 9.0.

pellet groups per plot ranged from 1 to 72, with a mean \pm SE of 11.78 ± 1.86 pellet groups/plot. No significant spatial autocorrelation was detected between sites and number of fecal pellets found in a site ($P = 0.34$, distance to independence ≤ 500 m). Male elk (2.19 pellet groups/h ± 0.3 SE) deposited pellets significantly more frequently than did female elk (1.06 ± 0.9 pellet groups/h; 2-sample t -test: $t = 5.42$, $d.f. = 17$, $P = 0.01$). We also found no influence of habitat type on elk defecation rates ($F = 7.41$, $d.f. = 5, 18$, $P = 0.17$).

Our analysis of only 3 pellet groups from each plot resulted in our analyzing 5–100% of the pellet groups in each plot. In 40% of the plots our sampling yielded $\geq 50\%$ of the total pellet groups in a plot, and pellets from males and females were found together in only 28 (16%) of 180 plots analyzed. We were unable to differentiate whether the plot was most frequently used by males or females in only 7 (4%) of the plots.

Landscape scale.—Of the 440 sample plots analyzed, no significant influence of wolf kernel on elk pellet distribution was detected at the landscape scale ($\beta = -0.3 \pm 0.2$, $d.f. = 439$, $P = 0.41$). Nor did we detect a change in elk distribution between years using the 180-plot subset sampled across both years of the study ($P = 0.63$).

Habitat scale.—Using the subset of 180 plots for which we had genetics data on sex we found that regardless of use of space by wolves, elk did not use habitats randomly ($\chi^2 =$

55.73 , $n = 180$, $d.f. = 5$, $P = 0.01$). Male elk did not use habitat randomly in low-intensity ($\chi^2 = 82.38$, $n = 41$, $d.f. = 5$, $P = 0.001$) or in high-intensity ($\chi^2 = 54.51$, $n = 28$, $d.f. = 4$, $P = 0.002$) wolf-use areas. The same is true of female elk, which did not use habitats randomly in low-intensity ($\chi^2 = 112.96$, $n = 36$, $d.f. = 4$, $P = 0.01$) or in high-intensity ($\chi^2 = 53.80$, $n = 32$, $d.f. = 3$, $P = 0.01$) wolf-use areas. Preference-rank analyses indicated that some habitat types were preferred over others as risk varied (Table 2). As wolf presence in an area increased, conifer forests increased in their importance to females. Conversely, as wolf presence increased, male elk tended to prefer open steppe habitats (Table 2).

Habitat-patch scale.—An independent set of candidate models was evaluated for each pairwise combination of wolf risk and elk sex and goodness-of-fit tests were conducted to evaluate model fit to the data (Hosmer et al. 1997). All models with a change in Akaike information criterion corrected for small sample size (ΔAIC_c) ≤ 4 were considered to be possible candidate models, with ΔAIC_c values < 2 indicating the most-likely models (Burnham and Anderson 1998). The top-performing models for each sex and predation-risk category, along with the global model for all elk, are listed in Table 3. The best-performing AIC_c models (highest model weight) for male elk varied with intensity of use by wolves. In areas with low wolf use, 5 models had ΔAIC_c values < 2 , and the global

TABLE 2.—Habitat preferences for male and female elk (*Cervus elaphus*) in the northern range of Yellowstone National Park, 2004 and 2005. Habitats are ordered left to right from most to least preferred. Separate analyses were conducted for males and females in areas of low and high risk of encounter with wolves. Preference analysis following the Bayesian decision rule (Waller and Duncan 1969) revealed no differences in elk preference for habitat types within a category that have the same superscripted symbol.

Female elk in areas with low risk of encounter with wolves:				
Shrub Steppe*	Burnt Forest*	Upland Steppe†	Wet Meadows†	Conifer Forest
Female elk in areas with high risk of encounter with wolves:				
Conifer Forest*	Shrub Steppe*	Burnt Forest	Upland Steppe†	Wet Meadows†
Male elk in areas with low risk of encounter with wolves:				
Burnt Forest	Conifer Forest	Shrub Steppe	Wet Meadows*	Upland Steppe*
Male elk in areas with high risk of encounter with wolves:				
Upland Steppe	Shrub Steppe	Conifer Forest*	Burnt Forest*	Wet Meadows

Habitat types within sex and risk categories that have a * or † after them indicate that within that sex and risk category there was no difference detected in preference of elk for habitat types which share a common symbol. Habitat types that lack a symbol or have a different symbol were found to differ in preference of elk for them.

TABLE 3.—Akaike information criterion corrected for small sample sizes (AIC_c) model selection for habitat variables explaining elk patch use. AIC_c model selection of geomorphological variables important in explaining elk habitat-patch use for male and female elk in each wolf predation–risk category (low or high). Models were developed from an a priori candidate set of variables likely to influence elk habitat use. For each category the full or global model is listed 1st followed by all competing models with ΔAIC_c values ≤4.0. Variables are defined as follows: Forage = percent forage within the plot, Slope = slope of the land across the sample plot, Elev = plot elevation, Complex = habitat complexity, Aspect = degree measurement of the aspect of the plot, and Pred = wolf predation category high or low. *w_i* = Akaike weight.

Model	K	AIC _c	ΔAIC _c	<i>w_i</i>	Hosmer–Lemeshow	
					C	P
Both sexes, all predation levels (<i>n</i> = 440 plots)						
Forage Slope Pred Elev Complex Aspect (global model)	11	2,965.974	127.029	—	0.55	<0.01
Forage Pred Elev	11	2,838.945	0	0.63	0.53	<0.01
Slope Pred	11	2,842.820	3.875	0.09	0.54	0.08
Forage Pred	11	2,843.302	4.357	0.07	0.53	0.02
Male elk in areas with high risk of encounter with wolves (<i>n</i> = 28 plots)						
Forage Slope Elev Complex Aspect (global model)	7	54.256	9.174	—	0.74	0.08
Aspect	7	45.082	0	0.43	0.69	0.05
Forage Aspect	7	47.393	2.311	0.14	0.73	0.78
Complex Aspect	7	47.751	2.669	0.11	0.71	0.42
Elev Aspect	7	47.781	2.699	0.11	0.70	0.05
Slope Aspect	7	47.779	2.697	0.11	0.69	0.26
Slope	7	48.078	2.996	0.10	0.54	0.08
Male elk in areas with low risk of encounter with wolves (<i>n</i> = 41 plots)						
Forage Slope Elev Complex Aspect (global model)	7	74.847	2.914	0.06	0.68	0.48
Forage	7	71.933	0	0.29	0.64	<0.01
Forage Elev Complex	7	72.852	0.919	0.18	0.68	0.33
Forage Aspect	7	73.101	1.168	0.16	0.63	0.01
Forage Slope Complex	7	73.138	1.205	0.16	0.66	0.28
Forage Slope Complex Aspect	7	73.191	1.258	0.15	0.68	0.02
Female elk in areas with high risk of encounter with wolves (<i>n</i> = 32 plots)						
Forage Slope Elev Complex Aspect (global model)	7	41.164	3.228	0.05	0.78	0.01
Slope Complex Aspect	7	37.936	0	0.27	0.79	0.01
Slope Complex	7	38.048	0.112	0.25	0.62	<0.01
Forage Slope Complex Aspect	7	38.576	0.64	0.19	0.81	0.01
Slope	7	39.559	1.623	0.12	0.52	0.08
Forage Elev Complex Aspect	7	39.645	1.709	0.11	0.63	0.44
Female elk in areas with low risk of encounter with wolves (<i>n</i> = 36 plots)						
Forage Slope Elev Complex Aspect (global model)	7	61.499	9.527	—	0.80	0.14
Slope Complex	7	51.972	0	0.31	0.74	0.06
Slope Complex Aspect	7	52.376	0.404	0.25	0.68	0.05
Slope Elev	7	52.819	0.847	0.20	0.78	0.09
Slope Elev Complex Aspect	7	53.736	1.764	0.13	0.52	0.92
Forage Slope Elev Complex	7	53.878	1.906	0.12	0.80	<0.01

model had ΔAIC_c <4. All selected models included the variable forage. Abundant elk pellets from males were found in habitat patches with high percent forage and high habitat complexity. Conversely, in areas frequented by wolves, a single model had ΔAIC_c <2, with 5 additional models having ΔAIC_c values <4. Aspect was the only variable in the top model, and was included in 4 of the 5 models we considered additional possible candidates (2 < ΔAIC_c < 4). High densities of fecal pellets from male elk were predicted by a southern aspect.

Five models for female elk in areas of high wolf use had ΔAIC_c <2, and 5 models for female elk in areas of low wolf use had ΔAIC_c <2. Slope and habitat complexity were included in 4 of the 5 selected models in areas with high wolf use, slope was included in all 5 selected models, and habitat

complexity in 4 of 5 selected models. In areas with both low and high wolf use, a high occurrence of fecal pellets was predicted at sites with high habitat complexity, moderate slopes, and southern aspect.

Among habitat types preferred by females, forage availability was not significantly different regardless of wolf predation risk (*F* = 3.54, *df.* = 4, 18, *P* = 0.14, *n* = 66 plots); the same was true for habitat types preferred by male elk (*F* = 1.98, *df.* = 4, 18, *P* = 0.37, *n* = 69 plots). However, when comparing forest habitat plots used by female elk to randomly selected forest plots, a marginally statistically significant difference in percent forage was detected (forest plots used by females: percent forage = 0.58; random forest plots: percent forage = 0.52; *P* = 0.068, *n* = 36 plots).

DISCUSSION

We found that wolf predation risk influenced use of space by male and female elk differently and that the effects varied with spatial scale. Recent studies suggest that ecological rather than social hypotheses explain why sexes of some species segregate by habitat (Main 2008). Most ecological explanations either argue in favor of a gastrocentric (FSH) hypothesis or a predation-risk (RSH) hypothesis (Gross 1998; Main 1998, 2008). Examination of our data on space use by male and female elk in Yellowstone National Park as a response to wolf predation risk suggests that RSH may be driving sexual segregation at 1 spatial scale (habitat), and that FSH may be a more tenable explanation at another spatial scale (habitat-patch). This may mean that FSH and RSH are not necessarily mutually exclusive ecological explanations, but rather a matter of the scale at which one investigates sexual segregation.

At a landscape scale elk appear to use space regardless of wolf distribution. Over the 2 years of this study we observed annual changes in wolf distribution but did not observe a similar change in use of space by elk. In part this could be due to the fact that predation risk to elk is not strictly a function of wolf distribution, because grizzly bears, which are the chief predator of elk calves, range widely throughout the northern range. Subsequently, predation risk from grizzly bears is likely ubiquitous across the northern range, but only for females with calves (Barber et al. 2005; Dahle and Swensen 2002). Conversely, wolves occur in packs of different sizes and their activities generally occur within discrete territories (Mech 2001); this is particularly true in spring when wolves den and their activities are focused close to the den site while caring for pups (Jedrzejewski et al. 2001).

At the habitat scale, we observed elk using spaces in a manner consistent with the predictions of the RSH (Main et al. 1996). As wolf encounter risk increased, habitat preference of female elk shifted from open steppe habitats to closed-canopy conifer forests. Male elk showed the opposite trend in habitat preference: as wolf encounter risk increased, male elk used the potentially more dangerous, but more forage-rich steppe habitats. Therefore, at the habitat scale it would appear that sexual segregation by elk is a function of females using space to maximize forage availability while minimizing their exposure to predation risk. This is the chief prediction of the RSH to sexual segregation (Gross 1998; Main 1998, 2008; Main et al. 1996; Neuhaus et al. 2005).

However, when we evaluated use of space by elk at fine spatial scales (habitat-patch), we found that the same set of predictor variables was able to explain patch use by female elk regardless of wolf encounter risk. The 2 top-performing models for female elk in both high and low risk of wolf encounter predicted patch characteristics of sites to all have attributes associated with risk reduction (Table 3; Creel et al. 2005; Kunkle and Pletcher 2000, 2001; Liley and Creel 2008; Mao 2003). Females choosing habitat to reduce risk makes sense in light of the combination of ubiquitous grizzly bear predation risk to elk calves paired with the regional risk of wolf predation on the northern range. These results would

appear to be additional support for the RSH, except that the attributes included in the top-performing models explaining patch use by male elk changed with regard to wolf predation risk. In areas of low risk of wolf encounter, patch use by male elk appears to be a function of forage availability, whereas in areas of high wolf encounter risk patch use by males is a function of south-facing aspects. However, the underlying reason for that choice may remain the same. In northern climates, southern and eastern slopes tend to be the 1st to show new growth of green vegetation in spring (Schwartz 1996), and are preferred by elk (Houston 1982). Additionally, throughout the northern range south-facing slopes tend to be upland steppe grasslands. Because this study took place during the spring calving season, shortly after snow-melt, it is possible that use of south-facing patches by male elk also may be directly related to forage availability.

Percent forage may not have turned up in the AIC_c model for male elk in high-wolf areas because of a 2nd-order correlation between forage and the upland steppe habitats that dominate south-facing slopes. Furthermore, at the patch scale we detected no significant difference in the percent forage available between any patches used by females or males when pooled across habitat types, but there were marginally significant differences between forest habitat patches used by males and those used by females. If there also are significant differences with regard to percent forage available between habitat patches used by males and females compared to random habitat patches, which we suspect there are, then this would argue in favor of FSH being operant in determining sexual segregation by elk at the habitat-patch scale.

Our study also highlights the power of using noninvasive molecular tools in studies of habitat preference. Because of the high costs associated with global positioning system and very-high-frequency collars, elk trapping, and staff to collect telemetry data, previous studies of resource use by elk have focused on relatively few individuals (<20) and generally only 1 sex (Fortin et al. 2005; Mao 2003). Using noninvasive sampling of pellets and subsequent molecular determination of sex, we were able to obtain large sample sizes and simultaneously evaluate sex-specific differences. In addition, the large sample sizes helped to highlight the importance of spatial scale in studies of space use and sexual segregation. This will not only help us better understand the mechanisms of sexual segregation but also will help better elucidate the multifaceted way in which predation influences prey community structure (Ripple and Beschta 2006).

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