University of Nevada, Reno

Effects of Population Density on Selection of Resources by North American Elk

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By

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Abstract

Population density of large mammals effects life-history characteristics as well as use of resources, but little research has been done to show this effect directly. I analyzed resource selection in female North American Elk (*Cervus elaphus*) in relation to density dependent processes across an experimental landscape in Starkey Experimental Forest and Range of the United States Forest Service. I hypothesized that selection of resources would vary for different population densities of elk resulting from differential levels of intraspecific competition as well as varying availability of resources at different densities. Selection by elk varied significantly at different densities for slope and elevation. At higher densities, elk selected for higher elevations and steeper slopes and at lower densities elk selected for lower elevations and shallower slopes. This use of resources indicates that at times of peak foraging, elk are trading off between locations of higher forage quality and higher availability due to increased intraspecific competition at higher densities. These results indicate that when evaluating resource selection by ungulates, population density relative to ecological carrying capacity should be included in those evaluations.

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Introduction

Large mammals exhibit life-history characteristics that change markedly with population density (McCullough 1979, 1999; Kie and Bowyer 1999; Kie et al 2003; Reimers et al. 2005; Stewart et al. 2005, 2006). This density dependence in population dynamics results from feedbacks associated with changes in intraspecific competition that affect rates of survival and reproduction (McCullough 1979, 1999; Kie et al. 2003; Stewart et al. 2005). Broadly defined, density dependence is how intraspecific competition, or competition between individuals of the same species, affects changes in birth, death, immigration and emigration rates within a population (Hess 1997). More specifically density dependence is a negative relationship between a population's growth rate and a population's size relative to ecological carrying capacity (McCullough 1979, 1990, Kie et al 2003). Carrying capacity (*K*) is an equilibrium point where the number of animals on a landscape are at or near equilibrium with their food supply (equilibrium point where births = deaths, Kie et al. 2003). As large mammals exceed available food resources, density-dependent feedbacks on their survival, physical condition, and reproduction are intensified and growth of the population reaches equilibrium (e.g. births = deaths). Thus, growth approaches 0 as the population approaches the carrying capacity of the ecosystem. Certain life-history characteristics are typified by species whose populations show strong density dependence in their population ecology. Those life-history characteristics include large body size, long lifespan, strong competitive ability, low reproduction rate, and high maternal investment (McCullough 1979, 1999; Kie and Bowyer 1999; Gaillard et al. 2000; Kie et al 2003; Reimers et al. 2005; Stewart et al. 2005, 2006). Numerous studies of large herbivores have demonstrated the role that density dependence plays in the dynamics and regulation of populations, although detecting density dependence is neither simple nor straightforward (Klein

1968; Caughley 1970; Kie and Bowyer 1999; Kie et al. 2003; Stewart et al. 2005, 2006). Thus, documenting effects of those processes on demography is difficult because of interactions with other variables, such as harvest and climate (Aanes et al. 2000; Bowyer et al. 1999; Stewart et al. 2005).

Intraspecific competition is known to mediate density-dependent processes through food availability, and the consequent effects of nutrition on reproduction, recruitment, and survival (Keech et al. 2000; McCullough 1979; Stewart et al. 2005). Because many ungulate populations exist at high densities much of the time, there is strong competition within populations leading to increases in differentiation among individuals (McCullough 1999). Such individual variation leads to more intense competition at higher densities, and an increased use of lower quality resources as high-quality forage declines in availability, compared with stronger selection for higher quality resources at lower densities (Mobaek et al. 2009). A lack of necessary nutrients can have important effects on a population because females are less likely to reproduce when their body condition is poor (McCullough 1979; Stewart et al. 2005). Density-dependent mechanisms have been shown to increase the age at first reproduction in large herbivores due to increased competition and poor physical condition, delaying growth to maturity in juveniles (Clutton-Brock et al. 1987; Houston and Stevens 1988; Kie and White 1985; McCullough 1979; Stewart et al. 2005; Van Vuren and Bray 1986). Stewart et al. (2005) reported that at high densities North American elk (*Cervus elaphus*) had poorer physical condition and lower reproductive rates than what was seen at lower densities. Higher densities of females also cause age-specific pregnancy rates to be lower (Stewart et al. 2005). This result is likely in response to more competition for summer forage containing the necessary nutrients to build body stores (Mautz 1978, Stewart et al. 2005).

Resources including food, water, and shelter, affect survival and recruitment of large mammals, making their use by individuals and populations of great importance (Kie et al. 2003). Changes in resource use based on population density are important for understanding population dynamics and for managing populations. High heterogeneity of forages in a landscape allows ungulates to have different diets with varying quality among individuals at different densities (McCullough 1999). Spatial heterogeneity allows individuals to select for resources that vary over space, which compensates for the variation seen over time (Frank and McNaughton 1992; Fryxell et al. 2004; Mysterud et al. 2001; Wang et al. 2009). Effects of density dependence on population growth may be lessened when ungulates have the ability to exploit spatial heterogeneity in availability of resources. The ability to move from location to location with higher quality resources extends the period that forage can be obtained (Albon and Langvatn 1992; Frank and McNaughton 1992; Mysterud et al. 2001; Wang et al. 2009). For example, topographic variation causes plants to reach maturity at different times due to a temperature gradient where lower elevations are warmer than higher elevations. Lower elevations reach temperatures necessary for plant growth and maturity earlier than higher elevations. This variation allows large herbivores to move along the gradient and consume forage at peak quality for a longer period of time (Frank and McNaughtion 1993; Wilmshurt et al. 1999; Wang et al. 2006).

We define selection of resources to be when the use of a particular resource is greater than its availability in an ecosystem (Boyce et al. 2002; Krebs 1999). Resource selection functions (RSF) are an analytical tool that biologists use to determine the use of a resource by individuals in a population relative to the availability of that resource (Boyce et al. 2002; Manly et al. 1993). McLoughlin et al. (2010) states that RSF's that do not include population density

may represent one statistical instance of resource selection, which may differ at different population densities. When quality and quantity of resources are variable, selection and availability of resources are affected by population density (Hobbs and Hanley 1990). At high population densities, high quality resources may be less abundant per individual than at low densities, thus fewer resources are available per individual. More abundant resources of lower quality may be used by individuals in high density populations, but increased use of resources, especially food, of low quality will result in a reduced reproductive output because of lower nutritional condition of individuals in the population (Vanhorne 1983). Understanding the role of population density in resource selection shows that quantity or availability of resources, in addition to quality, are important components of how resources are selected by individuals (Schantz 1981; States 1976).

North American elk are an especially good model to examine the effects of population density on resource selection because their life-history strategies are consistent with species that exhibit strong density dependence (Stewart et al. 2005). Moreover, elk are widely distributed, have large home ranges, and make resource choices over large spatial scales; thus they are also a well-suited species for evaluating how selection of resources is affected by population density (Coe et al. 2011; Kie et al. 2003). My objective with this research was to determine how intraspecific competition and availability of resources is affected by population density of elk. I hypothesized that selection of resources varies among population densities resulting from differences in intraspecific competition and variation in availability of resources. Based on that hypothesis, I predict that at low population density and less intraspecific competition individuals will have a greater ability to partition resources so resource selection will be stronger. I also

predict that at high densities resource selection will be weaker resulting from increased intraspecific competition and a lower availability of resources on the landscape.

Study Area

Stewart et al. (2005, 2006) conducted research from 1999 to 2001 on the Starkey Experimental Forest and Range (hereafter Starkey) of the United States Forest Service (Figure 1, Rowland et al. 1997). Starkey is located in the Blue Maintains of northeastern Oregon and southeastern Washington, where elevations range from 1,120 to 1,500m. Stewart et al. (2005, 2006) experimentally created 2 populations of elk in the northeast portion of Starkey, which is comprised of 1,452 ha and surrounded by a high fence from the rest of the study area (Stewart et al. 2005, 2006). The fence restricts large herbivore immigration and emigration as well as movement to traditional winter ranges. The same fencing was used to divide the study area into two parts, the east (842ha) and the west (610ha), to create two populations at different densities for analysis of effects of density on resource selection (Stewart et al. 2006). The areas were divided so that plant communities were in proportion with each other. The size of the study areas was appropriate for population density research because it accommodated for natural movements of large herbivores (Hirth 1977; McCullough 1979; Stewart et al. 2002).

The study area contained four prominent plant communities: (1) mesic forest, (2) xeric forest, (3) xeric grassland, and (4) logged forest (Stewart et al. 2002, 2006; Figures 2 & 3). Plant nomenclature follows Hitchcock and Cronquist (1996). The mesic forest areas were primarily on north facing slopes and contained an overstory dominated by grand fir (*Abies grandis*; Stewart et al. 2002). The understory of mesic forests was primarily forbs and shrubs with a few grasses (Stewart et al. 2002). The xeric forests were generally located on south and east facing slopes

(Stewart et al. 2002). The overstory was primarily ponderosa pine (*Pinus ponderosa*) and the understory was dominated by elk sedge (*Carex geyeri*; Stewart et al. 2002). Xeric grasslands were found on primarily south and east facing slopes and were dominated by a few grasses and forbs (Stewart et al. 2002). Logged forest areas were characterized as such because timber was harvested from them from 1991 to 1992, after which the areas were seeded with several grass species (Stewart et al. 2002).

Methods

Stewart et al. (2005, 2006) created two populations of elk. They created areas of high density (20.1 elk/km²) in the east and low density (4.1 elk/km²) in the west (Figures 1 & 2). The high density value was aimed to be near to ecological carrying capacity and low density designed to be consistent with a low-density, rapidly increasing population below maximum sustained yield (sensu McCullough 1979) based on previous research conducted at Starkey (Rowland et al. 1997). They set their high density population at 20.1 elk/km², approaching ecological carrying capacity (K, McCullough 1979), but unhunted elk populations have been known to attain densities as high as 33 elk/km² (Hobbs et al. 1996; Houston 1982; Stewart et al. 2006). Due to fences inhibiting large herbivores from moving to traditional winter ranges, elk were held on a feed ground and fed a maintenance diet of alfalfa from early December to late April (Rowland et al. 1997). The study began in 1999 with moderate densities in each study area, 6.6 elk/km^2 in low density area and 10.8 elk/km^2 in the high density area (Stewart et al. 2005, 2006). During 2000 and 2001, they had high densities (20.1 elk/km^2) and low densities (4.1 elk/km^2). For complete details of the study design and implementation see Stewart et al. (2005, 2006).

Stewart et al. (2005, 2006) fitted radiotransmitters on 8 females in the east and west study areas respectively, each year of the experiment so that precise animal locations could be identified (total = 48 individuals, Stewart et al. 2006). Females were used because of the polygamous nature of elk and because males segregate from females except during mating (Bowyer 1981; McCullough 1999). Locations of radiocollared elk were obtained with a rebroadcast civilian long range navigation (LORAN-C) system during the study (Stewart et al. 2006). The mean location error of the telemetry system was 52.8 ± 5.87m (Rowland et al. 1997). They located each animal approximately every 1.5h throughout the diel cycle from May to early November each year (Rowland et al. 1997; Stewart et al. 2002). We restricted analyses to locations occurring during crepuscular periods (±1.5h before and after sunset and sunrise) to identify localities during periods when animals were actively foraging (Bowyer 1981; Stewart et al. 2002, 2006).

Stewart et al. (2005, 2006) obtained locations of each animal in each study area from radio collar data. Because of the large number of data points, we took a random subset to represent one location of an animal per week (n=1251 in the west study area, n= 1258 in the east study area). We used multi-response permutation procedures (MRPP, Slausen et al. 1991) for each study area to determine if observed locations (n=125 in the west study area, n=1258 in the east study area) differed from random locations (n=1000 per study area). MRPP are powerful, distribution free statistics, and results from MRPP indicate if distributions of animal locations differed from random (Cade and Richards 2005). We also used randomly located points (n=1000 per study area) to characterize availability of habitat components including: habitat type, distance to water, distance to roads, slope, elevation, and aspect, in each study area. We surrounded each animal and random location with a buffer of 50 m radius to account for error in the telemetry

system. We input those data into a Geographical Information System (GIS) to calculate landscape metrics expected to influence selection of resources at a 10m by 10m resolution within those buffers (ESRI 2008). We determined abiotic characteristics of habitats using a digital elevation model and habitat maps maintained by the Starkey Project (Rowland et al. 1997; Sappington et al. 2007). We calculated distance to the nearest source of water and nearest road from the centroid of the buffered points (Table 1). We calculated zonal statistics to determine the mean elevation, slope, and aspect of each buffered location (Table 1). In addition, we calculated the proportion of each vegetation community in each buffered area. We transformed aspect, a circular variable to cosine and sine, creating two new variables (Zar 1999, Table 1). Sine of aspect indicates selection or avoidance of east or west facing slopes and cosine indicates selection or avoidance of north or south facing slopes (Zar 1999). We standardized all variables (Proc STANDARD, SAS institute 2002) prior to analysis.

We developed a resource selection function (RSF) to determine if resources were used disproportionately to availability in each study area (Manley et al. 2002). In this study we were not interested in building a predictive map of resource use, but in testing the hypothesis that elk select resources differently at different population densities. We developed a set of a priori models and incorporated the effect of individual variation on resource selection by using a mixed model logistic regression with the individual animal as a random effect (Proc NLMIXED, SAS Institute 2002) to evaluate the validity of the hypothesized relationships among model parameters (Boyce et al. 2003; Duchesne et al. 2010; Fortin et al. 2009). We calculated and used habitat parameters known to be meaningful in resource selection based on previous research conducted at Starkey and incorporated interaction terms with each habitat character and population density to determine if elk selected resources differently by population density (Coe

et al. 2011; Johnson 2000; Long et al. 2009; Stewart et al. 2002). I used Akaike's Information Criterion (AIC) to evaluate model support, such that models with the lowest AIC score were designated as the most parsimonious, I calculated AIC weights to further evaluate those models (Akaike 1973; Anderson et al. 2000). Using AIC scores were appropriate because they follow the principle of parsimony, allowing for selection of a model that takes into account the most variation in the data with the least amount of variables (Boyce et al. 2002). Parameter estimates (β_i) from top-ranked models of resource selection were used to determine selection (positive value) or avoidance (negative value) and the magnitude of influence of those parameters. I determined the significance of those parameter estimates by evaluating 95% confidence intervals, such that intervals that did not overlap zero were considered to be significant (Anderson et al. 2000). We conducted an overall mixed model analysis of variance (ANOVA, Zar 1999) to determine if random variation was affected by population density, causing the significant interactions with population density seen in our best model. Individual elk was included as the random variable in the mixed model (Zar 1999). We used ANOVA with pairwise comparisons to determine the significance of use - available selection indices, construed from significant interactions in our best logistic model, compared with population density.

Results

MRPP indicated significant differences in the distributions of animal and random locations in the low density ($P \leq 0.0001$) and high density ($P = 0.0460$) study areas. The strength of selection was stronger in the low density area compared with the high density area. These results support the null model that some selection of resources occurred in each of the two study areas.

I incorporated variables likely to be selected or avoided in our models of selection by elk (Table 1). The top ranked model (Rank 1) of resource selection, determined by the lowest AIC score, contained effects of population density, elevation, slope, mesic forest, xeric grassland, logged forest as well as interactions between population density with distance to water, slope, elevation, and cosine aspect (Table 2). The top ranked model (Rank 1) also included interactions between elevation and slope as well as elevation with mesic forest (Table 2). The second ranked model (Rank 2) as well as the only other model containing support for the data, included an additive effect of distance to water but the evaluation of the parameter estimate indicates that distance to water did not play a substantial role in resource selection (β_i = 0.02467, 95% CI = -0.1183–0.1677, Table 2). Models containing the interactions of population density and distance to road (ΔAICc = 38.4), sine of aspect (ΔAICc = 38.4), and the habitat types mesic forest (ΔAICc = 25.1), logged forest (ΔAICc = 25.1), and xeric grassland (ΔAICc = 25.1) were not supported by the data as seen from their lack of inclusion in top ranked models (Table 2). Our hypothesis that elk differed in selection of resources at different population densities was supported by the interaction between population density and slope (β_i = 0.03264, 95% CI 0.02129–0.04398) as well as population density with elevation (β_i =0.133, 95% CI=0.1197–0.1463) indicating that selection for slope and elevation differed among population densities. Our top ranked model includes interactions between population density and distance to water (β_i = -0.004695, 95% CI = -0.00933–0.001729) as well as population density and the cosine of aspect (β_i = 0.004695, 95% CI = -0.00338–0.01277) but the confidence intervals overlapped 0 indicating that those variables did not have significant effects on resource selection (Table 3). This was also the case for the parameter representing an additive effect of population density (β_i = -0.00549, 95% CI = -0.02183–0.01084).

Elk strongly selected for mesic forests (β_i = 1.1258, 95% CI= 0.9041–1.3476) and xeric grasslands (βi = 1.0305, 95% CI = 0.802–1.2589) and moderately selected for logged forests (β_i = 0.5644, 95% CI = 0.3547–0.7740). Estimates for mean slope (β_i = -0.5355, 95% CI = -0.6822– -0.3889) and mean elevation (β_i = -1.7464, 95% CI = -1.9432– -1.5496) indicate that elk select for locations which were less than the landscape mean, signifying selection for lower elevations and shallower slopes (Table 3). The parameter representing the random effect of individuals (β_i = 0.16751, 95% CI = 0.00744–0.1276) was significant, therefore using a mixed model was appropriate for those analyses (Table 3).

The overall mixed model ANOVA showed a significant interaction between location (used, random) and population density for elevation ($F_{3,37}$ = 8.41, P < 0.0001) and slope ($F_{3,37}$ = 246.30, P < 0.0001) indicating differences in selection by population density. In our pairwise comparison ANOVA's comparing use-availability of elevation ($F_{3,3}$ = 71.21, P < 0.0001) and slope ($F_{3,3}$ = 4.41, P = 0.0086) with population density both parameters were significant (Figure 4). Elk in the low density population selected for lower elevations than elk in the high density populations (Figure 4A). The results for slope indicated that elk in the low density population selected for shallower slopes than elk in the high density population (Figure 4B).

Discussion

My hypothesis that selection of resources by elk differed among population densities was supported. The interactions in our non-linear mixed models between population density with elevation and population density with slope indicated that population density affected how elk selected resources and used the landscape (Table 3). In addition, pairwise comparisons indicated that at lower densities, elk select for lower elevations and shallower slopes than did elk in the

high density population (Figure 4A and B). This evidence suggests that landscape heterogeneity allows animals to select resources which vary spatially (Frank and McNaughton 1992; Fryxel et al. 2004; Mysterud et al. 2001; Wang et al. 2009) and that density plays a role in how animals select resources and use the landscape.

At lower densities, where there is low intraspecific competition for resources especially food and elk select for lower elevations and shallower slopes (Figure 4A & B). Use of lower elevations and shallower slopes, e.g. less rugged terrain, requires less energy expenditure than more rugged terrain. Stewart et al. (2002) reported that when elk were faced with less interspecific competition, from cattle and mule deer (*Odocoileus hemionus*) they used lower elevations, and when competition was increased, elk moved to higher elevations. Low population densities at low elevations allow individuals to take advantage of the most profitable resources available without greatly reducing availability and with less energy expenditure. This effect allows individuals to remain at lower elevations where an abundance of high-quality forage remains available to them as opposed to moving higher in elevation and expending a greater amount of energy.

At higher densities elk select for more rugged terrain, higher elevations and steeper slopes, possibly because of increased intraspecific competition leading to a strong effect of resource partitioning among individuals. High quality forage is quickly depleted at lower elevations when populations are at high densities, so it is likely that animals move to higher elevations and steeper slopes likely utilizing lower quality forages or accessing similar forages in more difficult to reach areas with greater availability. Perhaps elk used more difficult terrain and spent more time searching to obtain forage in the higher density area, which required greater overall expenditure of energy (Murray 1991), leading to use of more rugged terrain and lower

physical condition over the summer. This result may be indicative of shallower slopes and lower elevations requiring less energy to obtain forage and less intraspecific competition allowing animals to remain at locations for greater periods of time, thus exploiting greater availability of high quality forages (WallisDeVries 1996).

In addition, as population densities increase animals are more likely to partition space at finer spatial scales, and increase frequency of use of habitats that require greater energy expenditures. Stewart et al. (2005) reported lower nutritional condition and reproduction in the high-density elk population compared to the low density population, although species compositions in the diets were similar across density treatments (Stewart et al. 2011). Similar composition of the diets indicates that elk foraged for similar species of plants even at higher population density. Moreover, Stewart et al. (2006) reported that at low densities, forbs, shrubs, and grasses were more productive than at high density, thus increasing availability of forages for elk. Thus, elk would be able to spend less time searching, and use forages in more gentle terrain that are greater in availability than in the area with high population density (Bunnell and Gillingham 1985). Forage resources would be exploited less intensively with low density populations because of fewer animals on the landscape with low intraspecific competition (Healy 1997), and greater productivity of plants allowing those individuals to exploit the highest quality resources for a longer time period (Frank and McNaughton 1992; Stewart et al. 2006). At high density elk used steeper slopes and higher elevations. Those results likely are indicative of more intense competition for resources leading to rapid exploitation of high-quality food (WallisDeVries 1996), as well as decreased production of biomass by plants (Stewart et al. 2006). Search time for palatable forages may be longer at higher densities and the use of steeper slopes may lead to an overall reduction in competition for resources.

Our results are indicative of an optimal foraging strategy, particularly the marginal value theorem (Charnov 1976; Jiang and Hudson 1993). Individuals at low population densities take advantage of the highest quality forage available to them in locations requiring the least amount of energy (low elevations and shallow slopes) while individuals at high population densities move from one patch of forage to another more frequently, utilizing resources until they are depleted to the point of becoming less beneficial. At high densities patches are exploited much more rapidly requiring elk to spend more time moving to other suitable patches found in less ideal habitat (higher elevation and steeper slopes) and requiring greater use of energy (WallisDeVries 1996). Increased movements and energy expenditure as well as over exploitation of forage, results in the reduced intake of nutrients by individuals and lower body condition (Bowyer et al. 1999; Gaillard et al. 2000; Kie and Drawe 1983; Kie and White 1985; McCullough 1979; Stewart et al. 2005).

These results indicate very strongly that intraspecific competition affects how animals select resources and use the landscape. Increased intraspecific competition at high population densities can lead to a depletion of high quality forage, requiring individuals to use lower quality resources (Mobaek 2009) in more rugged terrain to obtain necessary nutrients. Density-dependent processes have extensive effects on populations of large mammals and population density relative to carrying capacity needs to be addressed when examining demography and ecological processes associated with these unique mammals. Density-dependent processes influence survival and reproduction, factors important to population dynamics as well as management strategies, causing population density relative to carrying capacity to be a necessary factor when doing population level analyses (McCullough 1999, 1990). In addition, models of resource selection for large mammals should incorporate population density relative to

ecological carrying capacity and its influence on how animals select and use available resources in different ecosystems (McLoughlin et al. 2010). My research is one example of how population density may influence selection of resources. Different populations as well as species may be more or less affected by density-dependent processes, necessitating the inclusion of population density into resources selection functions to better understand why and how individuals select for particular resources.

Management Implications

We demonstrate that the inclusion of population density in resource selection functions can determine significant differences in the use of resources at different densities. When populations vary in their relationship with carrying capacity, appropriate courses of management must differ. Thus, density-dependent processes and their corresponding effects on life-history traits, including survival and reproduction, must be considered when determining how animals select resources and use the landscape. Understanding how individuals use landscapes and how this use differs among population densities allows biologists to more effectively manage populations and habitats. Depending on the population density that managers are charged with maintaining populations, management strategies likely will differ. For example, our research shows that to manage a small population of elk relative to carrying capacity, it would be very important to protect areas at lower elevation and with shallower slopes. Our research shows that at higher population densities more space would likely be required for protection due to individuals moving more frequently to locate forage as well as using less suitable habitat (higher elevations, steeper slopes). Understanding landscape use will allow managers to make more effective decisions regarding populations. Many managers use resource selection models to

determine which components of habitats are important for a particular species. Those data indicate that population density affects how animals select habitat components and use the landscape, and those indices vary with population density. For instance our low density populations selected for shallower slopes versus high density populations selected for steeper slopes. Therefore when managing habitats for elk, population density may cause a complete shift in which aspects of habitat are important. Without considering how population density affects selection and use of resources a detrimental or ineffective management plan may be implemented, simply as an effect of misunderstanding the effects of density dependence.

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Table 1. Descriptive statistics for variables used in mixed models for used (animal locations) and available (random points) in both the high and low density study areas on the Starkey Experimental Forest and Range, 1999-2001.

Parameter	Low-Population Density						High-Population Density					
	Random			Animal			Random			Animal		
	n	Mean	Std Dev	n	Mean	Std Dev	n	Mean	Std Dev	n	Mean	Std Dev
Distance to water	1000	262.69	175.96	1251	279.66	161.84	1000	252.77	192.87	1258	257.65	180.59
Distance to roads	1000	106.49	80.61	1251	96.41	71.63	1000	99.49	81.47	1258	100.80	77.49
Aspect	1000	141.91	74.98	1251	127.03	71.39	1000	126.46	67.75	1258	136.50	68.85
Slope	1000	55.43	23.30	1251	51.29	22.99	1000	49.79	23.40	1258	50.86	22.69
Elevation	1000	4322.67	144.76	1251	4178.82	178.83	1000	4064.48	140.20	1258	4179.14	183.39
% Logged forest	1000	18.14	30.89	1249	21.93	33.32	1000	14.93	25.83	1257	18.74	30.55
% Mesic forest	1000	24.32	30.58	1249	35.27	34.58	1000	23.15	29.74	1257	31.75	34.79
% Xeric grassland	1000	12.95	23.64	1249	11.79	21.10	1000	11.74	19.48	1257	15.29	23.97
% Xeric forest	1000	3.19	12.66	1249	2.01	9.50	1000	3.27	10.22	1257	4.46	14.46

Table 2. Results of model selection 5 top mixed models for 41 adult females addressing resource selection at different population densities by North American elk, on the Starkey Experimental Forest and Range, 1999-2001.

Rank	Models	No. Parameters	AICc	ΔAICc	wAIC
1	-INT - POP - ELEV - SLOPE + MES_FOR + LOG_FOR + XER_GRS – POP*DIST_WAT + POP*SLOPE_MN + POP*ELEV_MN + POP*COS_ASP + ELEV*SLOPE + ELEV*MES_FOR	14	4642.1	0	0.721
2	-INT - POP + WAT - ELEV - SLOPE + MES_FOR + LOG_FOR + XER_GRS - POP*DIST_WAT + POP*SLOPE_MN + POP*ELEV_MN + POP*COS_ASP + ELEV*SLOPE + ELEV*MES_FOR	15	4644.0	1.9	0.279
3	-INT + POP - ELEV + MES_FOR + LOG_FOR + XER_GRS + POP*SLOPE_MN + POP*ELEV_MN - POP*MES_FOR + POP*LOG_FOR - POP*XER_GRS + POP*COS_ASP + ELEV*SLOPE - SLOPE*MES_FOR - SLOPE*LOG_FOR	16	4667.2	25.1	<0.0001
4	-INT - POP + WAT - SLOPE + COS_ASP + SIN_ASP - ELEV + MES_FOR + LOG_FOR + XER_GRS - POP*WAT - POP*COS_ASP + POP*SLOPE + POP*ELEV	15	4671.9	29.8	<0.0001
5	-INT + POP - SLOPE - ELEV + MES_FOR + LOG_FOR + XER_GRS + POP*SLOPE + POP*ELEV - POP*MES_FOR + POP*LOG_CUT - POP*XER_GRS + POP*COS_ASP	14	4672.8	30.7	<0.0001

Table 3. Parameter estimates from top ranked model describing resource selection by different densities of North American elk on the Starkey Experimental Forest and Range, 1999-2001.

Parameter	Estimate	SE	95% Confidence Interval
Intercept	0.4795	0.1382	-0.7598 to -0.1994
Population Density	-0.00549	-0.00549	-0.02183 to 0.01084
Mean slope	-0.5355	0.07237	-0.6822 to -0.3889
Mean Elevation	-1.7464	0.09714	-1.9432 to -1.5496
Mesic Forest	1.1258	0.1094	0.9041 to 1.3476
Logged Forest	0.5644	0.1035	0.3547 to 0.7740
Grasslands	1.0305	0.1127	0.802 to 1.2589
Population Density*Distance to Water	-0.004695	0.002728	-0.00933 to 0.001729
Population Density*Cosine Aspect	0.004695	0.003986	-0.00338 to 0.01277
Population Density*Mean Slope	0.03264	0.005601	0.02129 to 0.04398
Population Density* Mean Elevation	0.133	0.006552	0.1197 to 0.1463
Mean Slope*Mean Elevation	0.1679	0.04754	0.07158 to 0.2642
Mean Elevation *Mesic Forest	0.4426	0.1004	0.2392 to 0.6459
Random Effect	0.16751	0.02964	0.00744 to 0.1276

Figure 1. Location and map of the Starkey Experimental Forest and Range, Eastern Oregon, USA (Rowland et al. 1997).

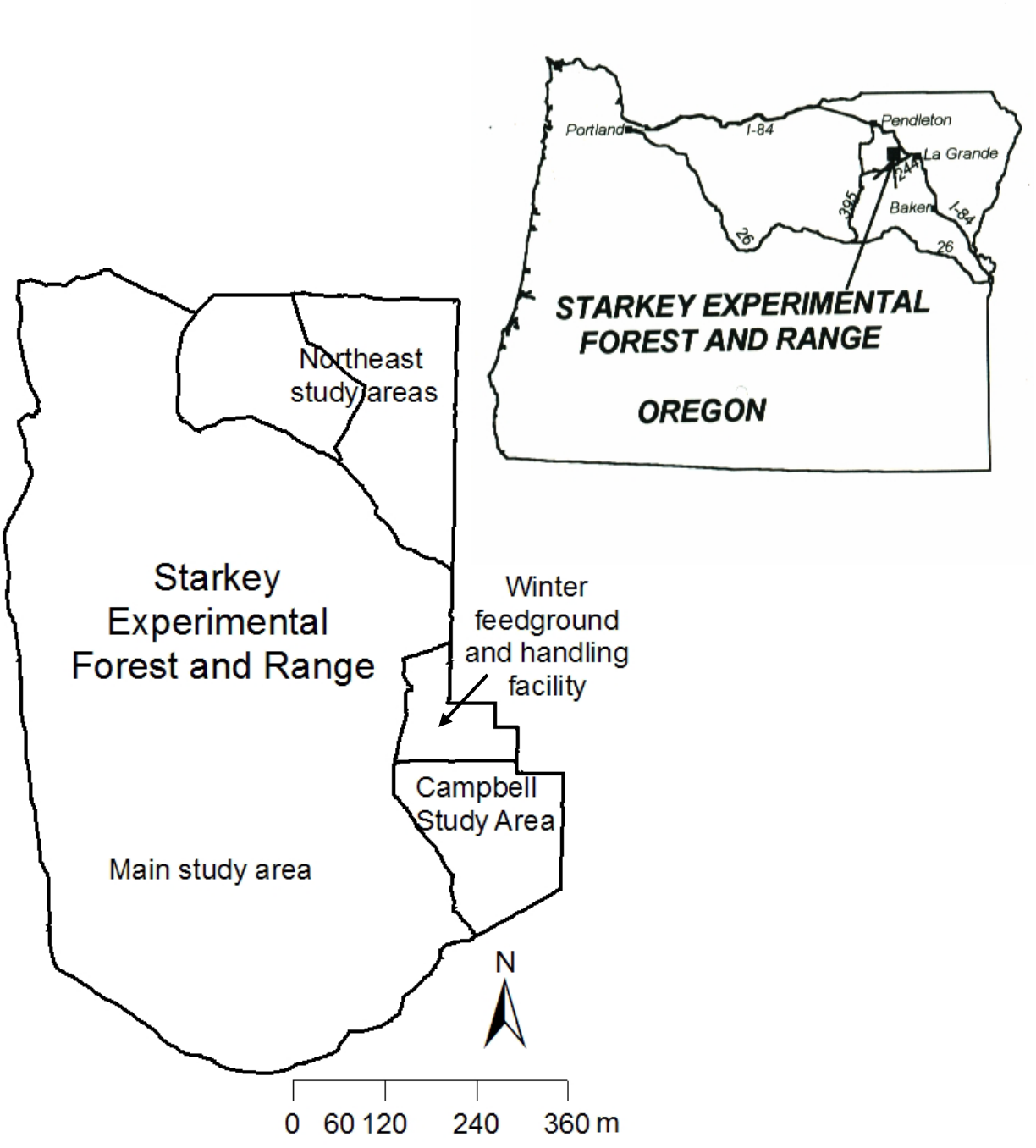

Figure 2. Habitats, fences, and streams in the Northeast study area on the Starkey Experimental Forest and Range, Eastern Oregon, USA.

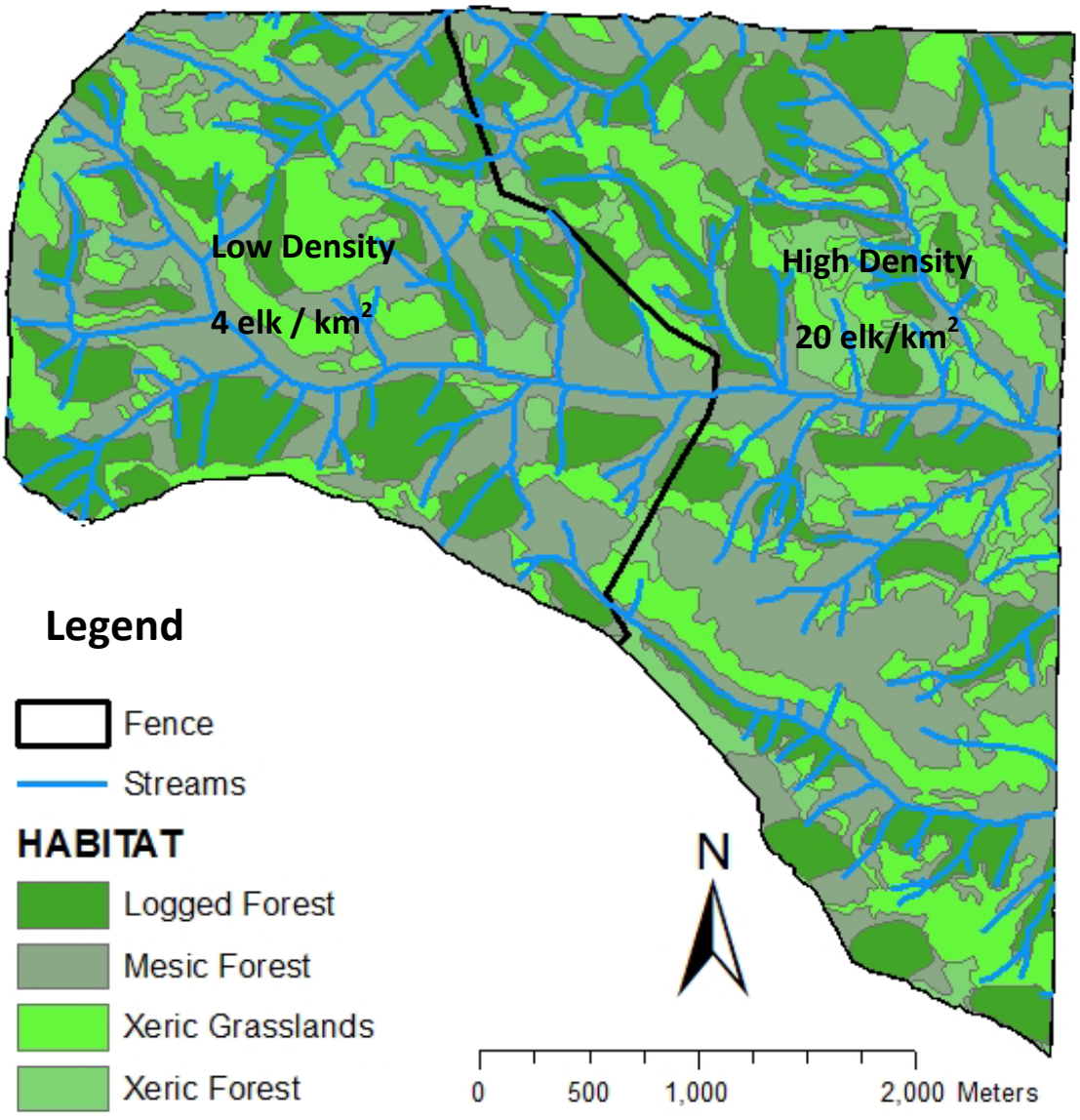

Figure 3. Topography, roads, and streams on the Northeast study area on the Starkey Experimental Foreat and Range, Eastern Oregon, USA.

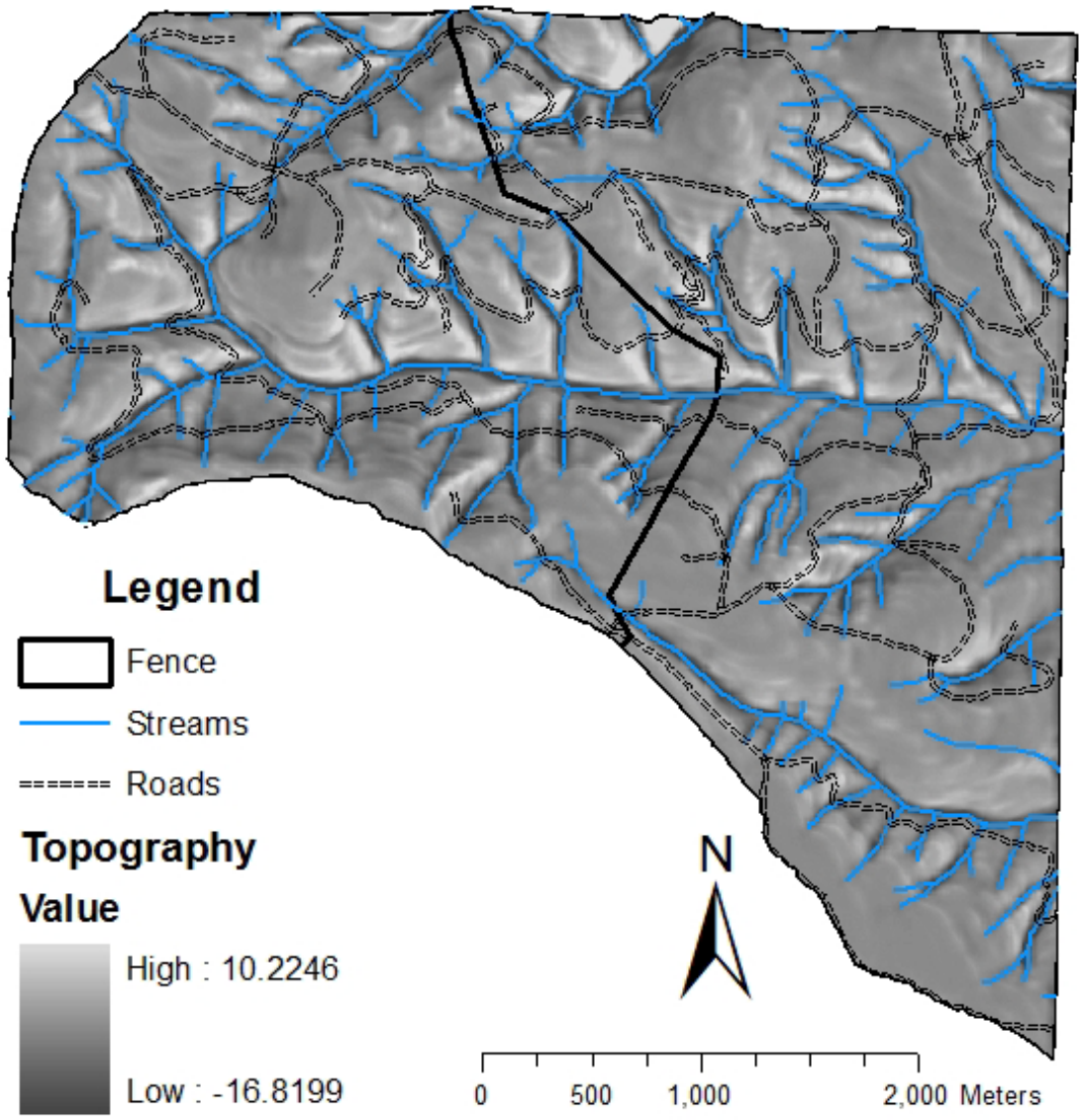

Figure 4. Results of pairwise comparisons for selection of elevation (A) and slope (B) by adult female elk on the Starkey Experimental Forest and Range. Letters over the bars indicate the results of pairwise compaisions where different letters indicate significant ($P < 0.05$) differences in selection of those resources.