BioOne COMPLETE

Sex and scale: implications for habitat selection by Alaskan moose Alces alces gigas

Authors: Oehlers, Susan A., Bowyer, R. Terry, Huettmann, Falk, Person, David K., and Kessler, Winifred B.

Source: Wildlife Biology, 17(1) : 67-84

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/10-039

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

Wildl. Biol. 17: 67-84 (2011)
DOI: 10.2981/10-039
© Wildlife Biology, NKV
www.wildlifebiology.com

Original article

Sex and scale: implications for habitat selection by Alaskan moose *Alces alces gigas*

Susan A. Oehlers, R. Terry Bowyer, Falk Huettmann, David K. Person & Winifred B. Kessler

We examined the roles of sex and spatial scale in habitat selection by Alaskan moose *Alces alces gigas*. We GPS-collared 11 female and seven male adult moose in the Tongass National Forest, Alaska, USA, during 2002-2004. We predicted that adult male and female moose would be spatially separated outside of the mating season, consistent with hypotheses attributing sexual segregation among sexually dimorphic ruminants to allometric differences in body and gastrointestinal size, and resulting differential needs for nutrient requirements by the sexes (the gastrocentric hypothesis), and varying risks of predation (the predation hypothesis) between sexes, especially for females with young. We predicted that habitat selection would be similar between sexes during the mating season, but dissimilar and occur at different scales during periods of late gestation and lactation. We expected that during segregation, females would select for a higher percentage of forested cover and a higher edge density than males to reduce predation risk on their young. Furthermore, we examined whether differences in scale of habitat selected between the sexes was related to home-range size. Multi-response Permutation Procedures (MRPP) analysis indicated that the spatial distributions of adult males and females differed, particularly near or during parturition. The sexes selected habitats similarly during the mating season (rut), when sexes generally were aggregated, whereas sexes exhibited differential habitat selection during spring, when sexes were segregated. Habitat selection by both sexes was best explained by vegetation and landscape composition tabulated within 1,000-m radii centered on GPS locations of moose. The sexes did not differ in the scale at which they selected habitats. Mean size of the annual home range was 76 km^2 for females and 125 km^2 for males, but size of home range was not related to scale of habitat selection by moose. Our results indicate that females were likely selecting habitat with high-quality forage while minimizing predation risk during periods of sexual segregation, whereas males were selecting habitat that allowed high forage intake, which together provide support for both the gastrocentric and the predation hypotheses.

Key words: Alaska, Alces alces, habitat selection, moose, scale, sexual segregation

Susan A. Oehlers, Yakutat Ranger District, Tongass National Forest, 712 Ocean Cape Drive, Yakutat, Alaska 99689, USA - e-mail: soehlers@fs.fed.us
R. Terry Bowyer, Department of Biological Science, Idaho State University, 921 South 8th Avenue, Stop 8007, Pocatello, Idaho 83209, USA - e-mail: bowyterr@isu.edu
Falk Huettmann, EWHALE Lab, Institute of Arctic Biology, Biology and Wildlife Department, University of Alaska-Fairbanks, Fairbanks, Alaska 99775, USA - e-mail: fhuettmann@alaska.edu
David K. Person, Division of Wildlife Conservation, Alaska Department of Fish and Game, 2030 Sea Level Drive, Ketchikan, Alaska 99901, USA - e-mail: dave.person@alaska.gov
Winifred B. Kessler, Alaska Region, USDA Forest Service, P.O. Box 21628, Juneau, Alaska 99802, USA - e-mail: winikessler@gmail.com*

* *Present address: 26700 West Fork Road, Prince George, British Columbia V2K 5L6, Canada*

Corresponding author: Susan A. Oehlers

Received 9 April 2010, accepted 17 January 2011

Associate Editor: Leif Egil Loe

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

Alaskan moose *Alces alces gigas* are sexually dimorphic in body size (Weckerly 1998), and the sexes select habitats and forage differently, leading to their spatial segregation throughout much of the year (Miquelle et al. 1992, Bowyer et al. 2001, Spaeth et al. 2004). Sexual segregation is widespread among polygynous ruminants (Bowyer 1984, Bowyer et al. 1996, Clutton-Brock et al. 1987, Bleich et al. 1997, Weckerly et al. 2001), and several competing hypotheses have been forwarded to explain this phenomenon (Main et al. 1996, Ruckstuhl & Neuhaus 2002, Bowyer 2004, Ciuti et al. 2004 for reviews). Main (2008) recently resurrected hypotheses originally proposed in Main et al. (1996) as explanations for sexual segregation. The debate continues, however, over whether the hypotheses are independent or testable (Bowyer 2004).

The gastrocentric hypothesis (Barboza & Bowyer 2000) incorporates both allometric differences in body size and annual changes in the physiology and morphology between sexes of ruminants, as related to their life-history characteristics, to explain periods of segregation and aggregation. Females undergo a remodeling of their digestive system related to late gestation and lactation to help them meet the increased nutrient demands associated with reproduction (Barboza & Bowyer 2000). These changes include increases in rumen-reticular size as well as increases in the hepatic and intestinal tissues (Barboza & Bowyer 2000, Zimmerman et al. 2006), which allows them to acquire the necessary nutrients from high-quality foods. Large males, however, undergo no similar changes in gastrointestinal morphology, but can consume abundant forages of lower quality than could be digested by reproductive females, because males possess higher digestive capacity, which permits prolonged retention time of forages and more complete digestion of bulky fibers than would be possible for reproductive females (Barboza & Bowyer 2000). This hypothesis predicts that large males will consume large quantities of low-quality, highly fibrous forages, whereas smaller-bodied females are better adapted to postruminal digestion of smaller quantities of high-quality forage to accommodate the acquisition of energy and protein necessary to support late gestation and lactation (Barboza & Bowyer 2000). Males cannot quickly adjust their diets to higher-quality forages used by females without risking bloat and rumen acidosis (Barboza & Bowyer 2000). Therefore, males and females are postulated to select different habitats which accommodate their forage requirements.

The predation hypothesis (Bleich et al. 1997) predicts that females, particularly those with young, may trade-off a high-quality diet for security from predators during periods of sexual segregation. That trade-off may be most apparent during spring and summer when young are most vulnerable to predation (Gasaway et al. 1983, Bowyer et al. 1998). Trade-offs between diet and risk of predation by female ruminants have been well documented for bovids (Festa-Bianchet 1988, Berger 1991, Rachlow & Bowyer 1998, Hamel & Côté 2007, Moe et al. 2007) and cervids, including moose (Molvar & Bowyer 1994, Barten et al. 2001). Moreover, Bowyer (2004) suggested that the gastrocentric and predation hypotheses, although not mutually exclusive, are sufficient to explain the patterns of sexual segregation that have been observed in dimorphic ruminants (i.e. either the gastrocentric or predation hypothesis alone is sufficient to explain sexual segregation, or they may both be operating simultaneously). Finally, increasing evidence indicates that body-size differences among species of ruminants proposed to explain interspecific differences in their niche dynamics do not hold for sexes in a dimorphic species (Weckerly 2010). Therefore, the body-size hypothesis proposed by Main et al. (1996) no longer offers a viable explanation for sexual segregation.

A confounding factor for studies of habitat selection and sexual segregation in ungulates is that detection of both attributes in large mammals is sensitive to scale (Bowyer et al. 1996, Mysterud et al. 1999, Bowyer et al. 2002). Several studies have provided evidence of habitat selection by moose at one scale while failing to show selection at another, or differential selection between scales (Bowyer et al. 1999, Maier et al. 2005, Månsson et al. 2007, Herfindal et al. 2009, Jiang et al. 2009, van Beest et al. 2010). Sampling at a single or inappropriate scale may fail to fully document habitat selection (Bowyer & Kie 2006, Mayor et al. 2009); this is illustrated when linking habitat with wildlife data for answering distribution questions (Huettmann & Diamond 2006). Likewise, determining whether the sexes segregate is also scale sensitive (Bowyer et al. 1996, 2002), and measuring at an inappropriate scale may fail to detect segregation (Kie & Bowyer 1999).

Sexual segregation may occur at different spatial scales for the ruminant species (Bowyer 2004); less attention has been paid, however, to effects of scale on sexual segregation (*sensu* Bowyer et al. 1996,

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

2002), or to whether the sexes might select habitat at different scales. Indeed, understanding effects of scale on how sexes make trade-offs between predation risk and habitats with essential forages are largely unstudied. Sexes of dimorphic ruminants may select habitats at different scales because of their distinct forage requirements or their dissimilar life-history strategies. In addition, Farmer et al. (2006) detected marked differences between sexes with respect to the scale at which habitat factors affecting risk of death operated in a population of Sitka black-tailed deer *Odocoileus hemionus sitkensis*. Life-history tactics of the sexes also might lead to seasonal changes in the scale of habitat selection by males and females. For instance, female moose concentrate their activities around birth sites (Bowyer et al. 1998, 1999) at the time when the degree of sexual segregation is pronounced (Miquelle et al. 1992).

We hypothesized that adult male and female moose would be spatially separated outside of the mating season because of differential nutritional requirements related to their life-history strategies (*sensu* Barboza & Bowyer 2000). We expected that habitat selection would be similar between the sexes during the times of sexual aggregation (i.e. the mating season), but dissimilar and at different scales during periods of sexual segregation (i.e. late gestation and lactation). Furthermore, we examined whether differences in scale of habitat selection between the sexes was related to home-range size.

We expected differential habitat selection by sex to be most pronounced during spring and summer because of the high risk of predation on young (Bowyer et al. 1999) and pronounced differences in gastrointestinal morphology and physiology between males and lactating females (Barboza & Bowyer 2000, Zimmerman et al. 2006). We predicted that females would select for a higher percentage of forested habitat than males during periods of segregation to reduce predation risk (Bowyer et al. 2001, Molvar & Bowyer 1994), thereby compromising their ability to select high-quality forage in the non-forested areas. Additionally, we predicted that females would select for higher edge density than males to allow for foraging in the open habitat but with proximity to forested escape cover to reduce predation risk (Molvar & Bowyer 1994). We expected that concealment cover (forested areas) would reduce the risk of predation by both gray wolves *Canis lupus* and bears *Ursus americanus* and *U. arctos* on females with young particularly during summer, whereas nonforested areas likely would provide better predator detection and escape opportunities, depending on snow conditions during winter. In addition, we predicted that females would select for higher stream densities than males during spring and summer, because of their need for access to free water to meet the increased demands of lactation (Bowyer 1984), and because of the abundant and high-quality forage in riparian areas (Collins & Helm 1997, Stephenson et al. 2006). Finally, to avoid problems of detecting habitat selection and sexual segregation because of sampling at an inappropriate spatial scale, we evaluated the factors at multiple scales. Understanding the degree of sexual segregation and the scale at which it is measured will provide additional insights into this important life-history characteristic for dimorphic ruminants.

Methods

Study area

The Yakutat Forelands (1,280 km^2) of the Tongass National Forest are located along the southeast coastline of Alaska, USA (Fig. 1). Glacier Bay National Park is located to the south and Wrangell-Saint Elias National Park to the north. Our study area included about 80 km of the coastline extending from Yakutat Bay in the north to Dry Bay in the south. Several large rivers and numerous smaller streams were distributed throughout the study area. The forelands remain a relatively intact and undisturbed ecosystem.

The terrain is relatively flat with glacial moraines rising to elevations of < 60 m near the mountains. The Yakutat Forelands are a mosaic of wetlands, shrublands and coastal temperate rainforests (Alaback 1982). Forested areas are dominated by Sitka spruce *Picea sitchensis* occasionally interspersed with black cottonwood *Populus trichocarpa*. Nonforested wetlands and shrublands are composed of graminoids, forbs and shrubs including several species of willows *Salix* spp. and Sitka alder *Alnus sinuata*.

Cloudy, cool and wet conditions occurred year-round. Mean annual temperature was 4.1°C and average total precipitation was 381 cm (combined snow and rain) from 1971 to 2000 (National Oceanic and Atmospheric Administration 2005). Mean temperature during that period was -3.4°C during January (the coldest month) and 12°C during July (the warmest month). Mean total snowfall for the

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

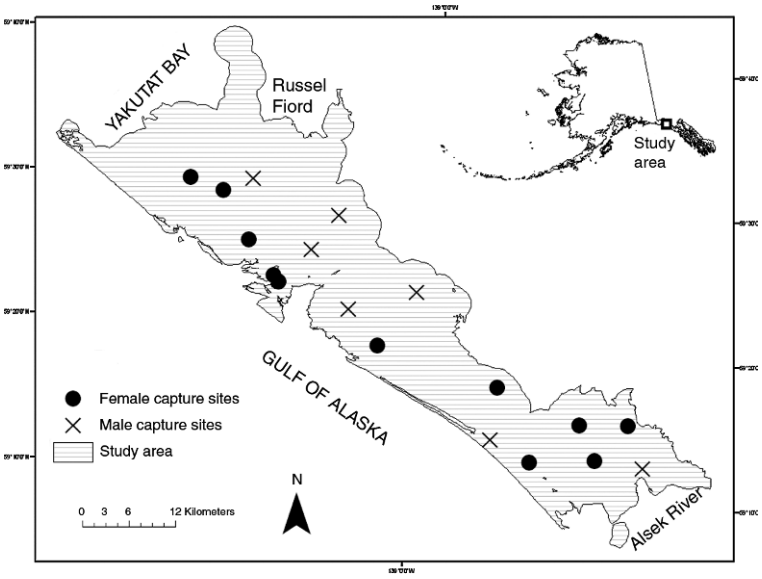

Figure 1. Area for studying habitat selection by GPS telemetry of adult male and female moose and their capture locations on the Yakutat Forelands, Alaska, USA, during 2002-2004.

two winters during our study was 218 cm; mean daily snow depth was 2.2 cm in the winter of 2002/03 and 17.1 cm during the winter of 2003/04. Maximum depth of snow in the winters of 2002/03 and 2003/04 was 23.1 and 40.6 cm, respectively. Snow was not sufficiently deep (i.e. $\geq$ 70 cm) to impede movements of moose (Coady 1974).

Moose were widely distributed throughout the forelands with a density of 0.5 moose/km^2. Predators of moose included brown bears, black bears, coyotes *Canis latrans* and gray wolves. Moose are an important part of the local subsistence economy (Schmidt et al. 2007).

Capture and handling of moose

Adult moose were captured and GPS-collared in November 2002 (12 females and one male), March 2003 (four females and four males) and in December 2003 (two males). Moose were darted from a helicopter by certified Alaska Department of Fish and Game personnel with Palmer CAP-CHUR equipment and the use of immobilizing drugs carfentanil and xylazine (Roffe et al. 2001). We attempted to distribute sites of capture across the study area (see Fig. 1). All capture and handling methods for moose followed guidelines established by the American Society of Mammalogists Animal Care and Use Committee (1998), and were approved by independent Institutional Animal Care and Use committees at the University of Alaska Fairbanks, and the Alaska Department of Fish and Game. We monitored moose for one month postcapture by aerial survey to assess capture-related mortality. Five females were subsequently removed from the data analysis due to mortality, lost telemetry signals or departure from the study area.

Data collection

We drew blood samples from the jugular vein of each moose and serum was analyzed (Bio Tracking, Moscow, Idaho, USA) for pregnancy-specific protein B (PSPB; Haung et al. 2000). A lower incisor was removed to determine age (Gasaway et al. 1978; Matson Laboratory, Milltown, Montana, USA). Animals were fitted with global position system (GPS) collars (Mod 4000, Lotek Wireless, Ontario, Canada) scheduled to record locations at 03:00, 09:00, 15:00 and 21:00 (Alaska Standard Time) each day. We downloaded GPS data remotely approximately once every two months, and when collars were recovered from the field. We tested GPS collars for differences in success rates of fixes and positional accuracy between habitat types (D'Eon et al. 2002, Di Orio et al. 2003) and seasons. Success rates for fixes averaged 99% in non-forested and 94% in forested habitats. Mean estimates for location errors were 22 m for both vegetation types. We retained all two-dimensional (2-D) and three-dimensional (3-D) fixes (D'Eon et al. 2002). The overall rate of fix success on moose was 97%. Location errors were within the resolution of our 50-m grid cells.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

Habitat classification

We classified habitats using U.S. Forest Service GIS data layers and ArcGIS 9.1 (Environmental Systems Research Institute ESRI, Redlands, California, USA). To reduce error, we used two classes, forest and nonforest, which best reflected potential forage and concealment cover for moose. Earlier successional stages, such as Alaskan shrub communities, generally produce a higher quantity (Miquelle et al. 1992, Collins & Helm 1997, Farmer et al. 2006, Stephenson et al. 2006) and quality (Bowyer et al. 1998) of browse than later successional stages. Furthermore, Molvar & Bowyer (1994) documented that the foraging efficiency of Alaskan moose declined significantly with distance from cover, likely associated with increased risk of predation. Consequently, we considered the nonforested areas to represent zones of higher forage quality (i.e. willow shrub species) and higher predation risk, and the forested areas to represent lower quality of forage and lower predation risk. We measured habitat characteristics in circles with radii of 250, 500 and 1,000 m from the center of each 50-m grid cell (Kie et al. 2002, Farmer et al. 2006). We classified aspect into nine categories, using south as the reference direction, because moose select southerly aspects (Bowyer et al. 1999).

We measured landscape and class variables at the three spatial scales (250, 500 and 1,000 m) using the raster version of FRAGSTATS 3.1 (McGarigal & Marks 1995). To avoid using intercorrelated variables, we calculated an edge-density and shape index to represent relevant landscape characteristics. In addition to initial screening for correlations, we also examined variance inflation factors (VIF; SAS Institute Inc. 2002) of covariates to further identify multicollinearity during model selection. Values of VIF < 10 were considered acceptable (Neter et al. 1996).

We placed 2-km buffers around each used location (Bleich et al. 1997) and considered all lands within that buffer up to 260 m in elevation as available habitat for moose. For each location used by moose, and at each scale, we selected a random point within the area of available habitat that did not overlap any of the radii around used locations (Bowyer & Kie 2006). We determined that a subset of 65% of our data was comparable in mean values to the full data set of used and random (available) points and used that subset for analysis and reserved 35% for model validation (Fielding & Bell 1997).

We evaluated used resources at the individual level and available resources at the population level (Manly et al. 2002), because cervids, including moose, may consider areas outside their home ranges when establishing home-range size (Kie et al. 2002, Maier et al. 2005). We compared habitat characteristics of sites used by collared moose with those at random sites for sexes and seasons. This method provided a conservative test of habitat selection (Bowyer et al. 1998). We defined biological seasons as spring-parturition (1 May - 30 June), summer-post-parturition (1 July - 24 August), autumn-rut-post-rut (25 August - 15 December), and winter (16 December - 30 April), similar to Miquelle et al. (1992).

Statistical analyses

We calculated home ranges for moose (Rodgers et al. 2005) for each sex and season, as well as the composite annual home ranges, to determine if home-range size was related to habitat selection. We created kernel home ranges using a h_{ref} (smoothing parameter) value of 1.0, then lowered or raised h_{ref} in 0.1 increments until we established a level one step above where 95% home ranges split into multiple polygons. We also calculated 95% minimum convex polygons (MCP; Rodgers et al. 2005) for comparative purposes (Hundertmark 1998). We calculated mean sizes of home ranges for each sex by season.

We examined differences in the spatial distribution of sexes of moose by season and by month with Multi-response Permutation Procedures (MRPP; Slauson et al. 1991) that analyzed Euclidean distances between moose monitored simultaneously. We report the average within-group distance, or delta value (the mean distance between all pair-wise locations of each group of moose observed: males or females), as a descriptive measure of spatial dispersion (Slauson et al. 1991). We used latitude and longitude as the response (dependent) variables and sex as the main effect (the grouping variable) and tested for spatial separation by month. We also used MRPP to test whether there was a difference in the overall spatial distribution of males and females using the excess function (Pierce et al. 2000), which tests whether a particular group could be obtained in a random draw from the joint distribution of two groups. We arbitrarily adjusted alpha to 0.02 to help limit potential problems resulting from a lack of independence from obtaining multiple locations for individual animals (Bowyer et al. 2007). We also examined existing data from aerial surveys conducted by the Alaska Department of Fish and Game

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

in 2005 to document group composition of moose among seasons.

We tested for differences in habitat selection by sexes of moose by comparing availability and use of habitats at each of the three scales (circular buffers with radii of 250, 500 and 1,000 m). We treated the individual animal as the sampling unit, because we wanted to make inferences about the population (Millspaugh & Marzluff 2001, Boyce 2006). We used conditional logistic regression (Hosmer & Lemeshow 2000, Manly et al. 2002, PROC PHREG - SAS Institute Inc. 2002), stratified by individual (Anderson et al. 2005, Boyce et al. 2003). We matched used locations with random points that represented habitat availability.

We used AIC_c criteria (Burnham & Anderson 2002) to identify the best subset of logistic-regression models explaining habitat selection by moose. We calculated each of the models separately by sex for each scale and season. We examined models for indications of overfitting, unrealistically large estimated coefficients or standard errors (Hosmer & Lemeshow 2000) and tested each model for correlations between covariates. If the covariates in a particular model exhibited a correlation of ($|r| \geq 0.7$), we eliminated that model from comparison and used the model with the next lowest AIC_c (highest AIC_c weight). We only considered models with values of $\Delta < 10$ for comparison. We compared AIC_c weights for models representing different scales to determine which scale of selection best fit data for each sex and season.

We calculated relative effects or risk ratios for covariates in all valid models to compare effect sizes of each variable (Riggs & Pollock 1992, Farmer et al. 2006). We calculated relative effects for a 10% increase in continuous covariates. In general, relative effects > 2.0 or < 0.5 indicated large effects of covariates on probability of use (Riggs & Pollock 1992).

We validated our selected models by converting them to resource selection functions (RSF; Manly et al. 2002), and compared predicted use to the withheld data set of used locations. We calculated the predicted RSF values for the withheld used locations and determined the number of used locations corresponding to each of 10 discrete numerical categories of equal size within the total range of RSF values available within the study area. We adjusted the frequency of locations within categories by the total land area of each range of RSF scores available across the landscape to account for strong selection of areas of low availability. We then compared frequencies of predicted and observed use within categories using Spearman-rank correlations (Boyce et al. 2002, Johnson et al. 2004). A model with good predictive performance should show a strong positive correlation, reflecting more used locations in higher ranked categories representative of more strongly selected habitats. We also calculated the accuracy of predicting use by assigning a threshold probability value of 0.4-0.6 to distinguish between predictions of used or available locations. For each model, we selected a threshold probability that maximized overall accuracy and the accuracy of predicting a used location (Pereira & Itami 1991). We described sensitivity and specificity (Hosmer & Lemeshow 2000, Boyce et al. 2002) for the final models. We used χ^2-analysis (Zar 1999, SAS Institute Inc. 2002) to compare the proportion of used and random (available) locations classified accurately.

Finally, we developed landscape models based on resource selection functions for each season by calculating RSFs for all 50-m pixels within our study area (ArcView, RSI, Redlands, California, USA). We used each RSF to establish cut points that allowed us to partition our study area into four categories: 1) areas most likely to be used by males; 2) areas most likely to be used by females; 3) areas most likely to be used by either sex; and 4) areas unlikely to be used by either sex.

Results

Age, pregnancy and survival

The median age of male moose was six years and ranged from three to eight years old. The median age of females was six years and ranged from three to 13 years old. All GPS-collared females in our sample survived for the duration of our study, but one male was legally harvested in October 2003. The pregnancy rate was 100% and the twinning rate was 60% for nine adult females captured in March 2003. Two females captured for collar removal in March 2005 also tested positive for pregnancy, both with PSPB values indicating twins.

Home ranges of moose

We obtained 30,825 GPS locations from 11 female and seven male moose. Sizes of home ranges were large, ranging up to 259 km^2 (Table 1). Home-range sizes for males and females combined were larger in

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

Table 1. Home-range sizes for GIS collared adult moose on the Yakutat Forelands, Alaska, USA, during 2002-2004.

	Home-range size (in km^2)					
	95% fixed kernel			95% minimum convex polygon		
Season and sex	Mean	SD	Range	Mean	SD	Range
Spring						
Males (N = 10)	64.08	74.41	8.79-258.63	34.01	25.62	5.32-92.04
Females (N = 12)	49.38	46.76	7.27-167.14	28.02	21.70	5.79-89.22
Summer						
Males (N = 10)	26.22	29.40	2.56-94.83	17.21	14.29	1.80-39.21
Females (N = 11)	40.46	33.19	11.32-119.84	24.78	16.78	4.22-53.60
Autumn						
Males (N = 7)	85.69	43.42	35.36-130.65	64.27	32.42	26.00-106.32
Females (N = 11)	65.15	31.89	27.29-141.31	39.07	16.75	13.65-69.72
Winter						
Males (N = 7)	81.62	32.93	41.39-135.23	57.04	34.51	25.35-103.77
Females (N = 13)	60.02	30.36	5.56-108.77	42.04	27.37	2.76-83.67
Annual						
Males (N = 5)	124.93	48.54	67.21-175.62	89.73	47.94	27.16-147.79
Females (N = 9)	76.01	39.92	31.81-160.34	69.81	18.35	44.19-89.93

autumn than in summer (see Table 1). Males had somewhat larger home ranges than females in all seasons except summer (see Table 1).

Spatial separation of sexes

The MRPP analyses indicated that a difference occurred between spatial distributions of males and females during all months ($P < 0.0001$). Within-group distances were higher in females than in males during all months, particularly in May and June (Fig. 2), which encompassed parturition, indicating that females were more spatially segregated from each other than were males. The distributions of males could not be obtained from a random sample of the joint distributions of the sexes ($P < 0.001$) during all months, indicating a difference in the overall spatial distribution of males and females. The distribution of females differed from the joint distribution of males and females only in March and April ($P < 0.001$). These distributions did not differ significantly for the remainder of the year ($P=0.218$-0.999).

During aerial surveys, we observed 61 groups of moose in autumn, 16 groups in winter, three groups in spring and six groups in summer. The proportion of mixed-sex groups was highest during autumn (56%), followed by winter (44%) and spring and summer (33%). Male-only groups composed the smallest proportion of groups during summer, autumn and winter (17, 10 and 19%, respectively).

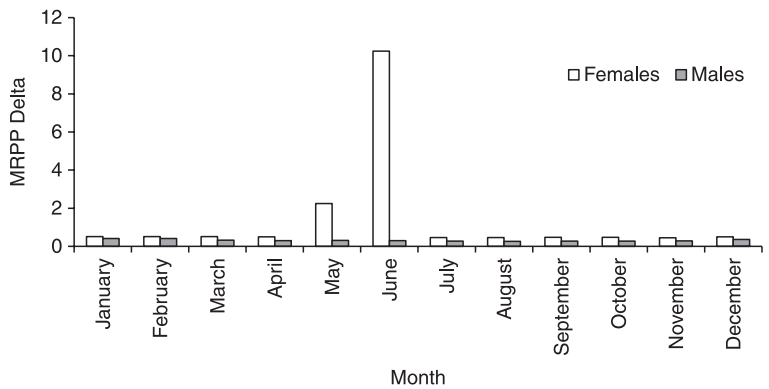

Figure 2. Multi-response permutation procedure (MRPP; within-group) values for delta by month for adult male and female moose on the Yakutat forelands, Alaska, USA, during 2002-2004. Delta values represent mean distances between individual locations within each group measured in decimal degrees.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

Few data existed on group composition during spring and summer, mostly because of low visibility of moose. By December 2005, aerial surveys revealed a ratio of only 8 young/100 females (N=633).

Seasonal habitat selection by sexes

Habitat selection based on 21 candidate models was best explained at the 1,000 m scale. Indeed, AIC weights indicated that selection models at the 1,000 m-scale, compared with 500 and 250-m scales, received overwhelming support for males and females during all seasons (Table 2). Consequently, we restricted further analyses to the 1,000-m scale. All logistic regressions at the 1,000-m scale were significant for sexes and seasons ($P < 0.001$).

Female and male moose used a variety of habitats either more or less often than their availability (Appendix I). Females selected for areas with high edge and stream density and low elevations during spring (Table 3). Males also selected for low elevations, but selected for a high percentage of forested cover (Table 4). Edge and stream density were not selected by males (see Table 4). Females selected a southerly aspect (see Table 3), whereas southwest, southeast, west and northeast aspects were selected by males (see Table 4).

During summer, percent forested cover, stream density, edge density and aspect were most influential on habitats selected by females, whereas habitat selection by males was best explained by percent

Table 2. Number of model parameters (k), differences in Akaike's Information Criterion (AIC_c) scores (Δ) and AIC_c weights (w) for candidate habitat-selection models for season and scale for male and female moose on the Yakutat forelands, Alaska, USA, during 2002-2004. The most parsimonious model for each scale is reported. A complete list of all models tested is available from the lead author.

Sex, season and scale (in m)	k	Variables	$AIC_c\Delta_i$	AIC_cw_i
Female, spring				
250	4	Edge density, stream density, elevation, aspect	62.5	0.00
500	4	Edge density, stream density, elevation, aspect	18.7	0.00
1000	4	Edge density, stream density, elevation, aspect	0.0	1.00
Female, summer				
250	5	Edge density, % forest, stream density, elevation, aspect	173.3	0.00
500	4	Edge density, % forest, stream density, aspect	76.3	0.00
1000	4	Edge density, % forest, stream density, aspect	0.0	1.00
Female, autumn				
250	4	Edge density, % forest, elevation, aspect	270.3	0.00
500	4	Edge density, % forest, elevation, aspect	211.4	0.00
1000	4	Edge density, stream density, elevation, aspect	0.0	1.00
Female, winter				
250	4	Edge density, % forest, stream density, aspect	294.6	0.00
500	4	Edge density, % forest, stream density, aspect	178.0	0.00
1000	4	Edge density, % forest, stream density, aspect	0.0	1.00
Male, spring				
250	4	Edge density, % forest, elevation, aspect	25.6	0.00
500	4	% forest, elevation, aspect	14.6	0.00
1000	4	% forest, elevation, aspect	0.0	1.00
Male, summer				
250	3	% forest, elevation, aspect	53.1	0.00
500	4	Edge density, % forest, elevation, aspect	33.4	0.00
1000	3	% forest, elevation, aspect	0.0	1.00
Male, autumn				
250	4	Edge density, stream density, elevation, aspect	62.5	0.00
500	4	Edge density, stream density, elevation, aspect	46.3	0.00
1000	4	Edge density, stream density, elevation, aspect	0.0	1.00
Male, winter				
250	4	Edge density, % forest, stream density, elevation	34.5	0.00
500	4	Edge density, % forest, stream density, elevation	6.7	0.03
1000	4	Edge density, stream density, elevation, aspect	0.0	0.97

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

Table 3. Coefficients (β), risk ratios (RR) and 95% confidence intervals (95% C.I.) for habitat selection by adult female moose at the 1,000-m scale on the Yakutat forelands, Alaska, USA, during 2002-2004. The regression coefficients for variables included in the most parsimonious model for each season are reported. Aspect categories (flat through northwest) are relative to the reference variable of south. βs indicate the direction of selection, with negative values reflecting selection against, and positive values reflecting selection for a covariate. RR > 2.0 or < 0.5 indicated large effects of covariates on the probability of use.

	Season											
	Spring			Summer			Autumn			Winter		
Covariate	β	RR[a]	95% C.I.[a]	β	RR[a]	95% C.I.[a]	β	RR[a]	95% C.I.[a]	β	RR[a]	95% C.I.[a]
Forest				0.004	1.042	1.013-1.071				-0.010	0.907	0.898-0.916
Edge (in m/ha)	0.012	1.128	1.098-1.160	0.015	1.176	1.133-1.221	0.013	1.147	1.122-1.173	-0.005	0.946	0.931-0.962
Stream density	0.011	1.050	1.025-1.075	0.033	1.157	1.120-1.194	0.015	1.069	1.050-1.089	0.025	1.119	1.104-1.134
Elevation (in m)	-0.004	0.886	0.830-0.946				-0.022	0.440	0.383-0.506			
Flat	-0.252	0.777	0.662-0.912	0.178	1.195	0.961-1.487	0.190	1.209	1.012-1.445	0.634	1.885	1.634-2.173
North[b]	-1.243	0.289	0.118-0.704	-0.500	0.607	0.247-1.496				-0.692	0.501	0.124-2.016
Northeast	-0.839	0.432	0.283-0.660	0.213	1.238	0.738-2.075	-2.310	0.099	0.025-0.401	-0.480	0.619	0.428-0.894
East	-0.198	0.820	0.534-1.260	0.075	1.078	0.640-1.815	0.523	1.686	1.254-2.267	0.863	2.371	1.949-2.884
Southeast	-0.193	0.825	0.639-1.064	0.378	1.460	1.083-1.969	0.935	2.547	2.034-3.190	0.748	2.113	1.779-2.510
Southwest	-0.057	0.945	0.796-1.121	0.315	1.371	1.085-1.732	0.010	1.010	0.819-1.246	0.165	1.179	1.000-1.390
West	-0.658	0.518	0.382-0.702	-0.004	0.996	0.739-1.344	0.742	2.101	1.682-2.624	0.421	1.523	1.280-1.812
Northwest	-0.280	0.755	0.591-0.965	-1.700	0.185	0.086-0.397	-0.569	0.566	0.393-0.816	-0.549	0.578	0.426-0.783

[a] Risk ratios and 95% confidence intervals are standardized for a 10% increase in all continuous variables.
[b] Estimate for autumn was not available due to a small sample size.

forested cover, elevation and aspect. Both sexes selected for a high percentage of forested cover (see Tables 3 and 4). Coefficients for north, northeast and east aspect for males could not be estimated because of small sample sizes, which reflected low availability of those aspects on the forelands. Females selected for flat, northeast, east, southeast and southwest aspects. During autumn, when sexes were aggregated, both sexes selected for high edge and stream density and low elevation (see Tables 3 and 4).

Table 4. Coefficients (β), risk ratios (RR) and 95% confidence intervals (95% C.I.) for habitat selection by adult male moose at the 1,000-m scale on the Yakutat forelands, Alaska, USA, during 2002-2004. The regression coefficients for variables included in the most parsimonious model for each season are reported. Aspect categories (flat through northwest) are relative to the reference variable of south. βs indicate the direction of selection, with negative values reflecting selection against, and positive values reflecting selection for a covariate. RR > 2.0 or < 0.5 indicated large effects of covariates on the probability of use.

	Season											
	Spring			Summer			Autumn			Winter		
Covariate	β	RR[a]	95% C.I.[a]	β	RR[a]	95% C.I.[a]	β	RR[a]	95% C.I.[a]	β	RR[a]	95% C.I.[a]
Forest	0.010	1.105	1.079-1.132	0.014	1.155	1.119-1.192						
Edge (in m/ha)							0.008	1.087	1.056-1.118	-0.002	0.981	0.959-1.005
Stream density							0.010	1.049	1.025-1.074	0.025	1.123	1.101-1.145
Elevation (in m)	-0.032	0.412	0.349-0.487	-0.054	0.167	0.122-0.229	-0.028	0.350	0.284-0.432	-0.018	0.551	0.483-0.628
Flat	-0.035	0.966	0.791-1.179	0.024	1.024	0.763-1.375	-0.086	0.917	0.761-1.106	0.158	1.171	1.005-1.365
North[b]	-0.284	0.753	0.379-1.500				-0.692	0.501	0.271-0.925	0.122	1.130	0.736-1.735
Northeast[b]	0.319	1.375	0.905-2.090				-0.741	0.477	0.256-0.886	-0.139	0.870	0.559-1.356
East[b]	-1.518	0.219	0.054-0.886				0.245	1.378	0.852-2.227	0.138	1.149	0.739-1.785
Southeast	0.133	1.142	0.839-1.154	-0.428	0.652	0.427-0.996	0.263	1.301	0.971-1.741	0.613	1.846	1.497-2.278
Southwest	0.271	1.312	1.062-1.620	0.071	1.074	0.757-1.522	-0.122	0.885	0.717-1.094	0.457	1.579	1.330-1.875
West	0.139	1.149	0.892-1.482	0.606	1.833	1.320-2.546	0.807	2.240	1.758-2.855	-0.195	0.823	0.661-1.024
Northwest	-0.183	0.832	0.609-1.138	0.110	1.117	0.766-1.627	0.761	2.140	1.692-2.708	0.386	1.471	1.184-1.827

[a] Risk ratios and 95% confidence intervals are standardized for a 10% increase in all continuous variables.
[b] Estimates for summer was not available due to a small sample size.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

Female moose selected flat, east, southeast and west aspects, whereas west and northwest were the only aspects selected by males (see Tables 3 and 4).

Stream density, percent forested cover, edge density and aspect were included in the best model describing habitat selection by females during winter, whereas males selected habitats based on stream density, edge density, elevation and aspect (see Table 2). In contrast to summer, females selected for a low percentage of forested cover, and in comparison with the remaining three seasons, low edge density (see Tables 2 and 3). Similar to the remaining seasons, females also selected high stream density. Males selected high stream density and low elevation. Both sexes selected flat, southeast and southwest aspects; additionally, females selected for east and west aspects and males for northwest aspects (see Tables 2, 3 and 4).

Relative effects were generally small for all continuous variables included in models for both sexes during all seasons, with the exception of elevation for females in autumn and for males during all seasons (see Tables 3 and 4). Relative effects for aspect were generally stronger than for the remaining continuous variables (see Tables 3 and 4). Our landscape surfaces illustrated that the area of overlap predicted between the sexes was largest in autumn, lower during spring and summer and smallest during winter (Fig. 3).

Model accuracy

Our selected models (1,000 m) had good classification power. Spring ($r_s = 0.93$), summer ($r_s = 0.71$), autumn ($r_s = 0.96$) and winter ($r_s = 0.94$) models had high Spearman rank correlations (r_s) for females (Appendix II). Models for spring ($r_s = 0.92$), summer ($r_s = 0.92$), autumn ($r_s = 0.86$) and winter ($r_s = 0.92$) also had high classification power for males (see Appendix II). Our best subset models had relatively high sensitivity and generally poor specificity (Appendix III). Sensitivity in 1,000-m models for females ranged from 78.8% during autumn to 99.2% during summer, whereas specificity ranged from 6.5% in summer to 48.2% during autumn (see Appendix III). Sensitivity in 1,000-m models for males ranged from 69.9% during autumn to 88.0%

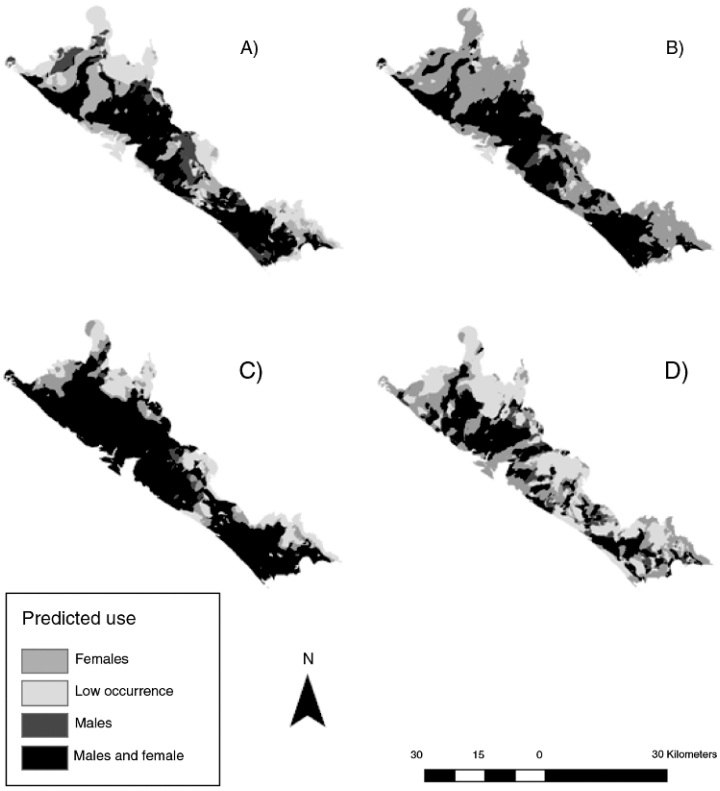

Figure 3. Relative index of occurrence predicted for adult moose on the Yakutat forelands, Alaska, USA, during 2002-2004, for spring (A), for summer (B), for autumn (C) and for winter (D). Expected use for each sex was calculated with threshold RSF values. Locations below the threshold value for either sex represent an expected relative low occurrence, and locations above the threshold value for expected high use by males and females.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

during winter, and specificity ranged from 29.1% during winter and 51.0% during summer (see Appendix III).

Discussion

Studies of sexual segregation in dimorphic ruminants must address at least two important issues related to scale. First, sampling at too large a scale may fail to detect the spatial segregation of sexes, whereas sampling at too small a scale may lead to the conclusion that segregation is ubiquitous (Bowyer et al. 1996, Bowyer & Kie 2006). Consequently, the failure of some studies to detect spatial separation of sexes may be methodological rather than reflecting a biological phenomenon (Bowyer 2004). We overcame this difficulty by using a scale-insensitive approach for assessing sexual segregation: the MRPP. The MRPP compares Euclidean distances among locations for males, females and between sexes to calculate delta values that reflect the degree to which the sexes are aggregated or segregated. This metric performed well in detecting the expected seasonality of sexual segregation upon the landscape (see Fig. 2) and eliminated scale-related problems in making this assessment.

The second potential problem was that resource selection functions are extremely sensitive to scale (Mysterud & Østbye 1999, Bowyer et al. 2002, Bowyer & Kie 2006). We used a hierarchical approach with varying scales that were appropriate for large herbivores (Kie et al. 2002, Bowyer & Kie 2006) to address this issue. The 1,000-m scale produced the best models for all seasons and sexes; however, we were unable to evaluate scales $> 1{,}000$ m, because it would result in substantial overlap in used and random locations, consequently reducing the statistical power (Bowyer & Kie 2006). Nevertheless, we believe that our sampling scale was reasonable and allowed us to detect strong patterns of resource selection by moose. Moreover, patterns of selection corresponded with our prediction that the sexes would select habitat differently when spatially segregated but not when aggregated. Although Alaskan moose are more gregarious than other subspecies and aggregate into large groups during rut (Miquelle et al. 1992, Molvar & Bowyer 1994), this did not affect the scale of, or cause marked differences in, habitat selection by males and females. We did not find evidence that the sexes selected habitat at different scales during other seasons. The presence of mixed sex groups during spring and summer indicates that habitat selection by those moose was similar during a period when the sexes were strongly spatially separated (see Fig. 2). If the occurrence of some mixed-sex groups introduced a bias into our models of habitat selection, the direction would be to reduce differences in habitat selection between sexes during the period of sexual segregation. Nonetheless, our models still detected substantial differences between the sexes (see Tables 3 and 4). When sexes overlap in space during the period of sexual segregation, the pattern is for the sexes to partition niche on another axis such as diet (Kie & Bowyer 1999, Schroeder et al. 2010).

Predicted use on the forelands by sexes of moose illustrated that spatial separation of sexes was most pronounced around the period of parturition and less evident during rut (see Fig. 3). This pattern of sexual segregation and aggregation is typical of many sexually dimorphic ruminants, including moose (Miquelle et al. 1992, Bowyer et al. 2001, Bowyer 2004). Our models for resource selection are in keeping with predictions of the gastrocentric (Barboza & Bowyer 2000) and the predation hypotheses (Bleich et al. 1997) for explaining sexual segregation. Other potential explanations for sexual segregation have been forwarded (Main 2008), but most of these have been rejected (Bleich et al. 1997, Bowyer 2004), or are not independent and, consequently, are difficult or impossible to test. Our purpose was not to test all potential explanations for sexual segregation, especially those that have been rejected repeatedly or lack predictions concerning the spatial distribution of sexes (Bleich et al. 1997, Bowyer 2004), but to determine if our data supported or contradicted two prominent hypotheses related to the ecology of moose. Long et al. (2009) and Schroeder et al. (2010) successfully followed this same approach.

Female moose selected areas with higher elevations and likely steeper slopes during spring and summer than did males (see Table 2), ostensibly to lower the risk of predation. These seasons include times when females are giving birth, nursing and have offspring at heel. In addition, females selected for higher edge density than did males during spring and summer, which supports an hypothesis of increased vulnerability of young to predators during this time period (Bowyer et al. 1998, Kunkel & Pletcher 2001, Keech et al. 2000), and the conse-

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

quent higher need for concealment cover by maternal females than for males (*sensu* Molvar & Bowyer 1994). Contrary to our hypothesis, females did not select forested cover in spring and only did so weakly in summer. The juxtaposition of forested and more open habitats, with considerably more forage, likely represents a trade-off between risk of predation (predation hypothesis) and the increased need for maternal females to acquire the resources to support the high costs of lactation (gastrocentric hypothesis). Likewise, females selected higher stream densities than did males during spring and summer, likely to meet the requirements of lactating females for free water (Bowyer 1984), but also because riparian zones have high-quality forage to meet the nutritional requirements of lactating females (Collins & Helm 1997, Stephenson et al. 2006), providing additional support for the gastrocentric hypothesis.

We overcame some statistical problems by using a design (conditional logistic regression) that allowed us to use all of our sampling locations for moose while avoiding pseudoreplication (Boyce 2006). We documented significant differences in resource selection by male and female moose during periods of spatial segregation even though the comparison of used and random locations results is a conservative test of habitat selection (Bowyer et al. 1998). Indeed, our resource selection functions should be interpreted as a relative scale or index of habitat selection rather than as an absolute statistical probability (Keating & Cherry 2004).

Another difficulty was the coarse nature of our habitat types. We knowingly traded off a greater diversity of poorly delineated vegetation types for a more accurate but simpler landscape coverage for our analyses. The use of two highly contrasting types (e.g. closed forest and more open areas) also provided a clear-cut test of habitat selection as related to predation risk and the acquisition of food. Indeed, our model accuracy was high (see Appendix II). Other investigators have used a similar approach of strongly contrasting habitats to examine resource selection by cervids (Kie et al. 2005). Dense forests clearly provide substantial concealment cover, whereas more open habitats and riparian areas offer higher-quality forage for moose. Characteristic of such studies (Manly et al. 2002), we acknowledge that we do not have direct data on forages consumed by moose in our study area. There is, however, considerable information on habitat selection and diets of moose in Alaska (Hundertmark et al. 1990, MacCracken et al. 1997, Bowyer et al. 1999, 2001, Stephenson et al. 2006). Moreover, biomass and quality of forages in various habitats are well documented, with higher quality foods in more open areas, especially those associated with riparian areas, than in closed forests (Alaback 1982, MacCracken et al. 1997, Bowyer et al. 2001, Stephenson et al. 2006). Consequently, we believe that our assumptions that moose would have had greater access to forage in most open habitats than in closed forests, and that closed forests would have provided more concealment cover than open habitat were reasonable (Molvar & Bowyer 1994, Bowyer et al. 1998). Extensive published data exist to support these assumptions concerning concealment cover and availability of forage.

Although our sample size was small, several factors indicated that our sample was representative of the population. First, captures of moose were distributed broadly across the study area (see Fig. 1). Moreover, the extremely large home ranges of these cervids (see Table 1) indicate that their distributions covered much of the landscape. Secondly, aerial surveys indicated that moose aggregated into mixed-sex groups during rut, which also was reflected in delta values from our MRPP analyses (see Fig. 2). Thirdly, resource selection functions differed for males and females during periods of segregation but not during aggregation. Finally, the accuracy of our models developed from resource selection functions and tested with a withheld portion of our data was high (see Appendix II).

Our findings are generally consistent with others regarding sexual segregation in moose (Miller & Litvaitis 1992, Miquelle et al. 1992, Bowyer et al. 2001, Spaeth et al. 2004). Moreover, previously only Miquelle et al. (1992) studied sexual segregation year-round. Those authors were able to document that the period of sexual segregation started in winter and extended into spring. Bowyer et al. (2001) provided collaborative evidence of spatial segregation of sexes for Alaskan moose during winter. Our results (see Fig. 3), however, indicated that spatial separation was most pronounced in spring and likely coincided with parturition (Bowyer et al. 1998). This pattern of sexual segregation has been reported widely in the literature (Bowyer 1984, Kie & Bowyer 1999, Bowyer 2004, Whiting et al. 2010). Reasons underpinning differences in timing and duration of sexual segregation, however, require further study.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

We have few data on predation on moose by bears and wolves; several life-history characteristics of this moose population, however, indicate that it was predator-limited. A low density of moose, high pregnancy rates and high rates of twinning but a low young-to-female ratio by autumn is consistent with a prey population experiencing top-down forcing by predators (Bowyer et al. 2005). Moreover, our supposition that female moose sought higher elevations than did males to avoid predation on neonates is supported by the literature (Bowyer et al. 1999 and references therein). We hypothesize that high-elevation sites in our study area may also provide maternal females with a good view of approaching predators. Large carnivores tend to hunt at lower elevations than those chosen by parturient females in many species of ungulates (Rachlow & Bowyer 1998, Barten et al. 2001, Kunkel & Pletscher 2001, Farmer et al. 2006). Female moose selecting areas with more edge density may have simultaneously reduced predation risk by being in close proximity to concealment cover (Molvar & Bowyer 1994), and also may have enhanced opportunities for foraging by occupying more open habitats. This circumstance would not have necessitated a trade-off between risk of predation and abundant forage (Berger 1991, Rachlow & Bowyer 1998, Bowyer et al. 1999); rather, females near edges might have followed a tactic of reducing the predation-to-forage ratio (Pierce et al. 2004).

We quantified the nature of sexual segregation in Alaskan moose in a remote temperate rainforest. Although our resource selection functions are unique to that ecosystem, we believe that our results, including prediction from the gastrocentric and predation hypotheses, will be applicable to other sexually dimorphic ruminants. Indeed, our results are in keeping with the gastrocentric and predation hypotheses for sexual segregation, and indicate that those models offer a satisfactory approach for framing and investigating questions concerning this phenomenon. Others recently have reached the same conclusion (Long et al. 2009, Schroeder et al. 2010). Understanding the pattern and scale of sexual segregation upon the landscape has critical implications for the conservation and management of large mammals (Bowyer 2004, Whiting et al. 2010); moreover, sampling at the wrong scale may preclude the detection of this pattern (Bowyer & Kie 2006). Bowyer et al. (2001), Stewart et al. (2003) and Long et al. (2009) have noted that habitat manipulations designed to enhance habitat for a particular species may inadvertently benefit one sex at the expense of the other. The marked differences in spatial patterns and habitat selection that we observed for moose associated with sexual segregation support the contention of Kie & Bowyer (1999), i.e. that the sexes of dimorphic ruminants are best managed as if they were separate species.

Acknowledgements - Our research was funded primarily by the U.S. Forest Service, with additional funding from the Department of Interior Bureau of Indian Affairs and in-kind support from the Alaska Department of Fish and Game. The Institute of Arctic Biology, Department of Biology and Wildlife, the Alaska Fish and Wildlife Cooperative Research Unit of the University of Alaska Fairbanks and the Ecological Wildlife Habitat Data Analysis for the Land and Seascape (EWHALE) laboratory all were instrumental in the development and funding of the project. Support also was provided by the Department of Biological Sciences at Idaho State University. J. Ritter helped with GIS and data analysis. E.C. Murphy provided valuable editorial review, J.G. Kie provided expertise on home-range analysis and W.G. Eastland supported our project and offered technical input. We thank T.O'Connor, C. Grove and E. Campbell of the U.S. Forest Service for their support of our project. We thank the Alaska Department of Fish and Game biologists J. Crouse, S. Jenkins, N. Barten and K. White for their expert capture and handling as well as for their technical advice. K.L. Monteith and R.A. Long provided helpful discussions concerning habitat modeling. Pilots D. Russel, L. Hartley, B. Bingham and J. Liston contributed to captures and aerial survey effort. We thank the helicopter pilots of Temsco Helicopter and U.S. Forest Service helicopter managers A. Stearns, J. Schlee and D. Andreason. We acknowledge the U.S. Forest Service personnel N. Catterson, K. Schaberg, B. Lucey, D. Gillikin, S. Mehalick, M. Moran and C. Wiseman for their field and logistical support. This article constitutes EWHALE Lab publication #103.

References

Alaback, P.B. 1982: Dynamics of understory biomass in Sitka spruce-western hemlock forests of Southeast Alaska. - Ecology 63: 1932-1948.

American Society of Mammalogists Animal Care and Use Committee 1998: Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. - Journal of Mammalogy 79: 1416-1431.

Anderson, D.P., Forester, J.D., Turner, M.G., Frair, J.L.,

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

Merrill, E.H., Fortin, D., Mao, J.S. & Boyce, M.S. 2005: Factors influencing home range sizes in elk (*Cervus elaphus*) in North American landscapes. - Landscape Ecology 20: 257-271.

Barboza, P.S. & Bowyer, R.T. 2000: Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. - Journal of Mammalogy 81: 473-489.

Barten, N.L., Bowyer, R.T. & Jenkins, K.J. 2001: Habitat use by female caribou: tradeoffs associated with parturition. - Journal of Mammalogy 65: 77-92.

Berger, J. 1991: Pregnancy incentives, predation constraints, and habitat shifts: experimental and field evidence for wild bighorn sheep. - Animal Behaviour 41: 61-77.

Bleich, V.C., Bowyer, R.T. & Wehausen, J.D. 1997: Sexual segregation in mountain sheep: resources or predation? - Wildlife Monographs 134: 1-50.

Bowyer, R.T. 1984: Sexual segregation in southern mule deer. - Journal of Mammalogy 65: 410-417.

Bowyer, R.T. 2004: Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation. - Journal of Mammalogy 85: 1039-1052.

Bowyer, R.T., Bleich, V.C., Manteca, X., Whiting, J.C. & Stewart, K.M. 2007: Sociality, mate choice, and timing of mating in American bison (*Bison bison*): effects of large males. - Ethology 113: 1048-1060.

Bowyer, R.T. & Kie, J.G. 2006: Effects of scale on interpreting life-history characteristics of ungulates and carnivores. - Diversity and Distributions 12: 244-257.

Bowyer, R.T., Kie, J.G. & Van Ballenberghe, V. 1996: Sexual segregation in black-tailed deer: effects of scale. - Journal of Wildlife Management 60: 10-17.

Bowyer, R.T., Person, D.K. & Pierce, B.M. 2005: Detecting top-down versus bottom-up regulation of ungulates by large carnivores: implications for conservation of biodiversity. - In: Ray, J.C., Redford, K.H., Steneck, R.S. & Berger, J. (Eds.); Large carnivores and the conservation of biodiversity. Island Press, Covelo, USA, pp. 342-361.

Bowyer, R.T., Pierce, B.M., Duffy, L.K. & Haggstrom, D.A. 2001: Sexual segregation in moose: effects of habitat manipulation. - Alces 37: 109-122.

Bowyer, R.T., Stewart, K.M., Wolfe, S.A., Blundell, G.M., Lehmkuhl, K.L., Joy, P.J., McDonough, T.J. & Kie, J.G. 2002: Assessing sexual segregation in deer. - Journal of Wildlife Management 66: 536-544.

Bowyer, R.T., Van Ballenberghe, V. & Kie, J.G. 1998: Timing and synchrony of parturition in Alaskan moose: long-terms versus proximal effects of climate. - Journal of Mammalogy 79: 1332-1344.

Bowyer, R.T., Van Ballenberghe, V., Kie, J.G. & Maier, J.A.K. 1999: Birth-site selection in Alaskan moose: maternal strategies for coping with a risky environment. - Journal of Mammalogy 80: 1070-1083.

Boyce, M.S. 2006: Scale for resource selection functions. - Diversity and Distributions 12: 269-276.

Boyce, M.S., Turner, M.G., Fryxell, J. & Turchin, P. 2003: Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. - Écoscience 10: 421-431.

Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K.A. 2002: Evaluating resource selection functions. - Ecological Modeling 157: 281-300.

Burnham, K.P. & Anderson, D.R. 2002: Model selection and inference: a practical information-theoretic approach. 2nd edition. - Springer-Verlag Inc., New York, USA, 496 pp.

Clutton-Brock, T.H., Iason, G.R. & Guinness, F.E. 1987: Sexual segregation and density-related changes in habitat use in male and female red deer (*Cervus elaphus*). - Journal of Zoology (London) 211: 275-289.

Coady, J.W. 1974: Influence of snow on behavior of moose. - Naturaliste Canadian 101: 417-436.

Collins, W.B. & Helm, D.J. 1997: Moose, *Alces alces,* habitat relative to riparian succession in the boreal forest, Susitna River, Alaska. - Canadian Field-Naturalist 111: 567-574.

Ciuti, S., Davini, S., Luccarini, S. & Apollonio, M. 2004: Could the predation risk hypothesis explain large-scale spatial sexual segregation in fallow deer (*Dama dama*)? - Behavioral Ecology and Sociobiology 56: 552-564.

D'Eon, R.G., Serrouya, R.G., Smith, G. & Kochanny, C.O. 2002: GPS radiotelemetry error and bias in mountainous terrain. - Wildlife Society Bulletin 30: 430-439

Di Orio, A.P., Callas, R. & Schaefer, R.J. 2003: Performance of GPS telemetry collars under different habitat conditions. - Wildlife Society Bulletin 31: 372-379.

Farmer, C.F., Person, D.K. & Bowyer, R.T. 2006: Risk factors and survivorship of black-tailed deer in a managed forest landscape. - Journal of Wildlife Management 70: 1403-1415.

Festa-Bianchet, M. 1988: Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. - Oecologia 75: 580-586.

Fielding, A.H. & Bell, J.F. 1997: A review of methods for the assessment of prediction errors in conservation presence/absence models. - Environmental Conservation 24: 38-49.

Gasaway, W.C., Harkness, D.B. & Rausch, R.A. 1978: Accuracy of moose age determination from incisor cementum layers. - Journal of Wildlife Management 42: 558-563.

Gasaway, W.C., Stephenson, R.O., Davis, J.L., Shepherd, P.E.K. & Burris, O.E. 1983: Interrelationships of wolves, prey, and man in interior Alaska. - Wildlife Monographs 84: 1-50.

Hamel, S. & Côté, S.D. 2007: Habitat use patterns in relation to escape terrain: are alpine ungulate females trading off better foraging sites for safety? - Canadian Journal of Zoology 85: 933-943.

Haung, F.D., Cockrell, C., Stephenson, T.R., Noyes, J.H. & Sasser, R.G. 2000: A serum pregnancy test with a specific radioimmunoassay for moose and elk pregnan-

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

cy-specific protein B. - Journal of Wildlife Management 64: 492-499.

Herfindal, I., Tremblay, J-P., Hansen, B.B., Solberg, E.J., Heim, M. & Sæther, B-E. 2009: Scale dependency and functional response in moose habitat selection. - Ecography 32: 849-859.

Hosmer, D.W. & Lemeshow, S. 2000: Applied logistic regression. 2nd edition. - John Wiley and Sons, New York, USA, 392 pp.

Huettmann, F. & Diamond, A.W. 2006: Large-scale effects on the spatial distribution of seabirds in the Northwest Atlantic. - Landscape Ecology 21: 1089-1108.

Hundertmark, K.J. 1998: Home range, dispersal and migration. - In: Franzmann, A.W. & Schwartz, C.C. (Eds.); Ecology and management of the North American moose. Smithsonian Institution Press, Washington, D.C., USA, pp. 303-335.

Hundertmark, K.J., Eberhardt, W.L. & Ball, R.E. 1990: Winter habitat use by moose in southeastern Alaska: implications for forest management. - Alces 26: 108-114.

Jiang, G., Ma, J., Zang, M. & Scott, P. 2009: Multiple spatial-scale resource selection function models in relation to human disturbance for moose in northeastern China. - Ecological Research 24: 423-440.

Johnson, C.J., Seip, D.R. & Boyce, M.S. 2004: A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple scales. - Journal of Applied Ecology 41: 238-251.

Keating, K.A. & Cherry, S. 2004: Use and interpretation of logistic regression in habitat selection studies. - Journal of Wildlife Management 68: 774-789.

Keech, M.A., Bowyer, R.T., Ver Hoef, J.M., Boertje, R.D., Dale, B.W. & Stephenson, T.R. 2000: Life-history consequences of maternal condition in Alaskan moose. - Journal of Wildlife Management 64: 450-462.

Kie, J.G., Ager, A.A. & Bowyer, R.T. 2005: Landscape-level movements of North American elk (*Cervus elaphus*): effects of habitat patch structure and topography. - Landscape Ecology 20: 289-300.

Kie, J.G. & Bowyer, R.T. 1999: Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. - Journal of Mammalogy 80: 1004-1020.

Kie, J.G., Bowyer, R.T., Nicholson, M.C., Boroski, B.B. & Loft, E.R. 2002: Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. - Ecology 83: 530-544.

Kunkel, K.E. & Pletscher, D.H. 2001: Winter hunting patterns of wolves in and near Glacier National Park, Montana. - Journal of Wildlife Management 65: 520-530.

Long, R.A., Rachlow, J.L. & Kie, J.G. 2009: Sex-specific responses of North American elk to habitat manipulation. - Journal of Mammalogy 90: 423-432.

MacCracken, J.G., Van Ballenberghe, V. & Peek, J.M. 1997: Habitat relationships of moose on the Copper River Delta in coastal south-central Alaska. - Wildlife Monographs 136: 1-52.

Maier, J.A.K., Ver Hoef, J., McGuire, A.D., Bowyer, R.T., Saperstein, L. & Maier, H.A. 2005: Distribution and density of moose in relation to landscape characteristics: effects of scale. - Canadian Journal of Forest Research 35: 2233-2243.

Main, M.B. 2008: Reconciling competing ecological explanations for sexual segregation in ungulates. - Ecology 89: 693-704.

Main, M.B., Weckerly, F.W. & Bleich, V.C. 1996: Sexual segregation in ungulates: new directions for research. - Journal of Mammalogy 77: 449-461.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. 2002: Resource selection by animals: statistical design and analysis for field studies. 2nd edition. - Kluwer Academic, Dordrecht, The Netherlands, 240 pp.

Månsson, J., Andrén, H., Pehrson, A. & Bergström, R. 2007: Moose browsing and forage availability: a scale-dependent relationship? - Canadian Journal of Zoology 85: 372-380.

Mayor, S.J., Schneider, D.C., Schaefer, J.A. & Mahoney, S.P. 2009: Habitat selection at multiple scales. - Écoscience 16: 238-247.

McGarigal, K. & Marks, B.J. 1995: FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. - US Forest Service, GTR-PNW-GTR-351, 141 pp.

Miller, B.K. & Litvaitis, J.A. 1992: Sexual segregation by moose in a boreal forest ecotone. - Acta Theriologica 37: 41-50.

Millspaugh, J.J. & Marzluff, J.M. 2001: Radio-tracking and animal populations. - Academic Press, San Diego, USA, 474 pp.

Miquelle, D.G., Peek, J.M. & Van Ballenberghe, V. 1992: Sexual segregation in Alaskan moose. - Wildlife Monographs 122: 1-57.

Moe, S.R., Rutina, L.P. & du Toit, J.T. 2007: Trade-off between resource seasonality and predation risk explains reproductive chronology in impala. - Journal of Zoology (London) 273: 237-243.

Molvar, E.M. & Bowyer, RT 1994: Costs and benefits of group living in a recently social ungulate: the Alaskan moose. - Journal of Mammalogy 75: 621-630.

Mysterud, A. & Østbye, E. 1999: Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. - Wildlife Society Bulletin 27: 385-394.

Mysterud, A., Lian, L.-B. & Hjermann, D.Ø 1999: Scale-dependent trade-off in foraging by European roe deer (*Capreolus capreolus*) during winter. - Canadian Journal of Zoology 77: 1486-1493.

National Oceanic and Atmospheric Administration (NOAA) 2005: Local climatological data. - Available at: http://cdo.ncdc.noaa.gov. (Last accessed on 8 May 2007).

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

Neter, J.W., Kutner, M.H., Nachtsheim, C.J. & Wasserman, W. 1996: Applied linear statistical models. 4th edition. - McGraw-Hill Companies, Inc., Boston, USA, 1408 pp.

Pereira, J.M.C. & Itami, R.M. 1991: GIS-based habitat modeling using logistic regression: a study of the Mt. Graham red squirrel. - Photogrammetric Engineering and Remote Sensing 57: 1475-1486.

Pierce, B.M., Bleich, V.C. & Bowyer, R.T. 2000: Social organization of mountain lions: does a land-tenure system regulate population size? - Ecology 81: 1533-1543.

Pierce, B.M., Bowyer, R.T. & Bleich, V.C. 2004: Habitat selection by mule deer: forage benefits or risk of predation? - Journal of Wildlife Management 68: 533-541.

Rachlow, J.L. & Bowyer, R.T. 1998: Habitat selection by Dall's sheep (*Ovis dalli*): maternal trade-offs. - Journal of Zoology (London) 245: 457-465.

Riggs, M.R. & Pollock, K.H. 1992: A risk ratio approach to multivariable analysis of survival in longitudinal studies of wildlife populations. - In: McCullough, D.R. & Barrett, R.H. (Eds.); Wildlife 2001: Populations. Elsevier Applied Science, New York, USA, pp. 74-89.

Rodgers, A.R., Carr, A.P., Smith, L. & Kie, J.G. 2005: HRT: home range tools for ArcGIS. - Ontario Ministry of Natural Resources, Central Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

Roffe, T.J., Coffin, K. & Berger, J. 2001: Survival and immobilizing moose with carfentanil and xylazine. - Wildlife Society Bulletin 29: 1140-1146.

Ruckstuhl, K.E. & Neuhaus, P. 2002: Sexual segregation in ungulates: a comparative test of three hypotheses. - Biological Review 77: 77-96.

SAS Institute Inc. 2002: SAS/STAT user's guide. - Release 9.1. SAS Institute, Inc., Cary, North Carolina, USA. Available at: http://support.sas.com/documentation/onlinedoc/stat/chapters91.html (Last accessed on 1 May 2007).

Schmidt, J.I., Ver Hoef, J.M. & Bowyer, R.T. 2007: Antler size of Alaskan moose: effects of population density, harvest intensity, and use of guides. - Wildlife Biology 13(1): 53-65.

Schroeder, C.A., Bowyer, R.T., Bleich, V.C. & Stephenson, T.R. 2010: Sexual segregation in Sierra Nevada bighorn sheep, *Ovis canadensis sierrae*: ramifications for conservation. - Arctic, Antarctic, and Alpine Research 42: 476-489.

Slauson, W.L., Cade, B.S. & Richards, J.D. 1991: Users manual for BLOSSOM statistical software. - United States Fish & Wildlife Service, National Ecology Research Center, Fort Collins, Colorado, USA, 111 pp.

Spaeth, D.F., Bowyer, R.T., Stephenson, T.R. & Barboza, P.S. 2004: Sexual segregation in moose *Alces alces:* an experimental manipulation of foraging behaviour. - Wildlife Biology 10(1): 59-72.

Stephenson, T.R., Van Ballenberghe, V., Peek, J.M. & MacCracken, J.G. 2006: Spatio-temporal constraints on moose habitat and carrying capacity in coastal Alaska: vegetation succession and climate. - Range Ecology and Management 59: 359-372.

Stewart, K.M., Fulbright, T.E., Drawe, D.L. & Bowyer, R.T. 2003: Sexual segregation in white-tailed deer: responses to habitat manipulations. - Wildlife Society Bulletin 31: 1210-1217.

van Beest, F.M., Mysterud, A., Loe, L.E. & Milner, J.M. 2010: Forage quantity, quality and depletion as scale-dependent mechanisms drive habitat selection of a large browsing herbivore. - Journal of Animal Ecology 79: 910-922.

Weckerly, F.W. 1998: Sexual size dimorphism: influence of mass and mating systems in the most dimorphic mammals. - Journal of Mammalogy 79: 33-52.

Weckerly, F.W. 2010: Allometric scaling of rumen-reticulum capacity in white-tailed deer. - Journal of Zoology (London) 280: 41-48.

Weckerly, F.W., Ricca, M.A. & Meyer, K.P. 2001: Sexual segregation in Roosevelt elk: cropping rates and aggression in mixed sex groups. - Journal of Mammalogy 82: 825-835.

Whiting, J.C., Bowyer, R.T., Flinders, J.T., Bleich, V.C. & Kie, J.G. 2010: Sexual segregation and use of water by bighorn sheep: implications for conservation. - Animal Conservation 13: 541-548.

Zar, J.H. 1999: Biostatistical analysis. 3rd edition. - Prentice Hall, Upper Saddle River, New Jersey, USA, 718 pp.

Zimmerman, T.J., Jenks, J.A. & Leslie, D.M., Jr. 2006: Gastrointestinal morphology of female white-tailed and mule deer: effects of fire, reproduction, and feeding type. - Journal of Mammalogy 87: 598-605.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

Appendix I.
Summary statistics for habitat characteristics used by and available (random sites) to A) female and B) male moose by season, Yakutat Forelands, Alaska, USA, during 2002-2004.

Season	Spring				Summer				Autumn				Winter			
	Used		Random		Used		Random		Used		Random		Used		Random	
Covariate	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
A) Females																
Forest (%)	59.7	23.6	62.61	29.79	59.8	22.7	62.63	29.69	49.1	24.8	62.54	29.67	47.0	28.7	62.28	29.86
Edge (in m/ha)	36.4	16.1	25.57	20.14	37.3	16.4	25.25	20.68	34.4	16.4	25.57	20.24	27.7	16.7	25.51	20.62
Stream density (in m/ha)	19.8	8.1	15.88	9.41	21.4	7.8	15.84	9.48	20.6	8.9	16.26	9.52	19.5	9.8	15.91	9.59
Elevation (in m)	18.4	30.5	24.37	31.29	16.7	18.4	25.69	32.50	13.5	14.5	23.76	29.33	16.3	17.6	24.63	32.04
Aspect																
Flat (%)	55.8		49.32		57.8		47.11		70.5		51.15		71.1		49.25	
North (%)	0.2		1.00		0.4		1.39		0.0		0.96		0.0		0.86	
Northeast (%)	1.2		2.07		1.2		2.85		0.1		2.35		0.6		2.46	
East (%)	1.1		1.00		1.2		1.67		2.5		1.24		3.6		1.39	
Southeast (%)	4.2		5.89		6.1		5.01		6.7		5.08		6.4		6.04	
South (%)	9.9		8.70		7.6		10.44		4.2		8.80		3.4		9.06	
Southwest (%)	19.9		19.51		18.9		17.68		8.6		16.57		8.0		17.33	
West (%)	2.5		7.62		6.4		8.35		6.3		8.8		6.0		8.30	
Northwest (%)	5.1		4.94		0.5		5.50		1.2		5.05		0.9		5.30	
B) Males																
Forest (%)	70.1	21.9	62.09	30.12	68.9	19.3	61.55	28.90	59.4	25.1	62.53	30.38	55.8	26.3	62.63	24.49
Edge (in m/ha)	29.2	17.9	25.64	19.91	33.3	17.7	25.63	20.47	31.2	18.9	24.43	19.93	29.8	18.5	25.95	20.51
Stream density (in m/ha)	19.6	8.0	16.75	9.70	20.8	7.8	16.55	9.81	18.4	10.1	16.05	9.34	21.2	9.5	16.13	9.69
Elevation (in m)	14.7	11.6	24.40	29.06	11.7	7.5	24.35	32.77	14.4	11.9	26.06	35.06	14.7	13.4	24.55	30.64
Aspect																
Flat (%)	52.3		47.73		63.5		51.68		52.2		49.40		56.8		48.44	
North (%)	0.6		1.07		0.0		1.42		0.7		1.20		0.9		1.05	
Northeast (%)	1.8		2.21		0.0		2.65		0.6		2.67		0.8		1.96	
East (%)	0.1		1.54		0.0		1.15		1.1		1.20		0.8		1.49	
Southeast (%)	4.1		4.95		3.5		6.37		3.4		5.72		5.6		5.98	
South (%)	10.8		9.89		5.4		7.70		7.5		8.50		8.8		9.35	
Southwest (%)	18.6		18.11		7.3		16.28		16.5		17.92		15.7		18.09	
West (%)	8.6		8.96		14.3		8.76		8.4		8.99		5.1		8.92	
Northwest (%)	3.9		5.55		6.0		3.98		9.2		4.41		5.6		4.71	

Appendix II.
Spearman rank correlations (r_s) between area-adjusted categories and withheld used locations for 1,000-m seasonal models of habitat selection by adult male and female moose on the Yakutat forelands, Alaska, USA, during 2002-2004. We calculated indices of relative occurrence for our withheld locations and divided the range of these values into 10 categories of equal intervals. We adjusted the frequency of locations falling into each category by the area of each range of RSF scores available across the landscape.

	Female			Male		
Season	N	r_s	P	N	r_s	P
Spring	1027	0.927	0.0001	824	0.915	0.0002
Summer	705	0.709	0.021	601	0.915	0.0002
Autumn	1721	0.964	< 0.0001	956	0.855	0.002
Winter	3055	0.939	< 0.0001	1506	0.915	0.0002

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use

Appendix III.
Accuracy of habitat-selection models for adult moose on the Yakutat forelands, Alaska, USA, during 2002-2004. All Ps for χ^2-analysis were < 0.0001.

	Model prediction accuracy									
	Female					Male				
Season	N	Value[a]	Used[b]	Random[c]	Total[d]	N	Value[a]	Used[b]	Random[c]	Total[d]
Spring	1027	0.5	87.34	35.93	61.64	824	0.5	84.10	43.52	63.81
Summer	707	0.6	99.15	6.50	52.82	601	0.5	85.36	51.00	68.18
Autumn	1721	0.4	78.79	48.17	63.48	956	0.4	69.87	50.57	60.22
Winter	3055	0.5	83.37	44.86	64.12	1506	0.6	87.98	29.08	58.53

[a] Value indicates the threshold probability value used to distinguish classification of used vs available points (i.e. a threshold value of 0.5 indicates that a point with a probability of ≥ 0.5 would be classified as a used point, whereas a point < 0.5 would be classified as random).
[b] Used indicates percentage of withheld used locations classified as used (sensitivity).
[c] Random indicates percentage of random locations classified as random (specificity).
[d] Total indicates the overall accuracy; i.e. the average of used and random.

Downloaded From: https://bioone.org/journals/Wildlife-Biology on 29 Apr 2024
Terms of Use: https://bioone.org/terms-of-use