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Research Article

# Evaluating Dall's Sheep Habitat Use via Camera Traps

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**ABSTRACT** Anthropogenic disturbances, such as military training, potentially affect mountain ungulate populations. Assessing the spatiotemporal occupancy or habitat use of a wildlife population can assist with planning of potentially disrupting activities. Currently, military training is expanding into potential Dall's sheep (*Ovis dalli dalli*) habitat within 2 training areas of Fort Wainwright, Alaska. The 2 study areas included Molybdenum Ridge, a 10-km long geologically isolated granite ridgeline on the northern periphery of the Alaska Range and Black Rapids Training Area, a steeper and smaller area within the mountain range and bordered by the Delta River. The United States Army requires a better understanding of sheep habitat use in these 2 areas to identify how training could affect the population and to reduce overlap of training and high sheep occupancy. We used an array of 54 spatially balanced camera traps, taking triggered and hourly time lapse images, to determine Dall's sheep habitat use based on seasonal and site covariates. Camera traps operated for a continuous 15-month sampling period and captured nearly 8,000 images of sheep. Our occupancy models indicated that abiotic covariates such as slope, snow depth, and distance to escape terrain were the most important factors determining habitat use. Seasonal differences in habitat use indicated higher use during winter and spring for Molybdenum Ridge, and higher habitat use during the summer for Black Rapids Training Area. Detection probabilities were constant temporally and were higher if the camera was positioned on a wildlife trail versus off trail. Our results suggest that the best opportunity to minimize training interactions with Dall's sheep is to conduct training in early-July to early-September, specifically in areas with <60% slope and >500 m from escape terrain. © 2017 The Wildlife Society.

look ←  
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can see on  
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areas  
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**KEY WORDS** Alaska, camera traps, Dall's sheep, habitat use, military lands, occupancy models, *Ovis dalli dalli*.

Analyzing the spatiotemporal occupancy or habitat use of a wildlife species is increasingly important to assess if a population may be affected by human activities (Karanth et al. 2011). Anthropogenic disturbance of wildlife is a concern for the conservation of species because disturbance can affect wildlife behavior and physiology (Walker et al. 2006). Military installations are often centers of large-scale human movements and disturbance but have been increasingly recognized for their availability of wildlife habitat (Joselyn 1965, Stein et al. 2008). Potential effects of military

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actions on wildlife is a growing concern and focus of research interest (Krausman et al. 2004, Telesco and Van Manen 2006, Barron et al. 2012), especially in the United States because military lands under the United States Department of Defense must conform to federal environmental legislation (e.g., National Environmental Policy Act, Endangered Species Act).

Aircraft overflights and military training effects on ungulates have shown differing results including increased dispersal distances (Bleich et al. 1994, Côté 1996), moderate physiological effects (Krausman et al. 1998), and limited behavioral responses (Lawler et al. 2004, 2005). However, limited work has occurred on the effects of military ground operations on the occupancy of mountain sheep. Therefore, understanding the spatiotemporal occupancy of mountain

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ungulates on military lands is an important consideration for military planners to balance the conservation of these species with the overall training mission.

Mountain sheep species occupy military lands in the western United States and Alaska. Dall's sheep (*Ovis dalli dalli*) inhabit areas on, and adjacent to, military lands of interior Alaska. Current expansion of ground-based operations in these training areas could overlap with Dall's sheep occupancy. Previous research of these central Alaska Range populations provided evidence for winter dispersals into lower elevation military lands (Spiers and Heimer 1990); however, estimates of spatiotemporal occupancy by Dall's sheep is required to better inform management decisions.

Dall's sheep typically migrate between seasonal ranges throughout the year because of the dynamic nature of the climate and habitat in which the sheep reside. Dall's sheep spend the majority of the year on winter ranges, preferably on wind-swept slopes where snow depth is shallow and forage is more readily available (Geist 1971). Adult males (i.e., males >2 years old), move away from female bands after the rut. Female bands (i.e., groups including parturient and non-parturient females, lambs, and young males <2 years old) remain on the same range through winter; thus, we predicted constant occupancy of individuals in female bands during the winter to lambing seasons.

Proximity to escape terrain, forage availability, and adequate visibility are the predominate features dictating preferred sheep habitat (Risenhoover and Bailey 1985, Wakelyn 1987, Nichols and Bunnell 1999, Walker et al. 2007). Occupancy is also affected by physiology and demographics of sheep. Rachlow and Bowyer (1998) reported a significant difference between the habitats selected by females before and during the lambing period at a study area in Denali National Park, Alaska. Before lambing, females selected areas of greater forage and less snow cover. During lambing, pregnant females ascended to higher elevations with less forage but better escape terrain to avoid common predators including wolf (*Canis lupus*) and grizzly bear (*Ursus arctos*). Therefore, we predicted that female bands would use habitat closer to escape terrain more than males.

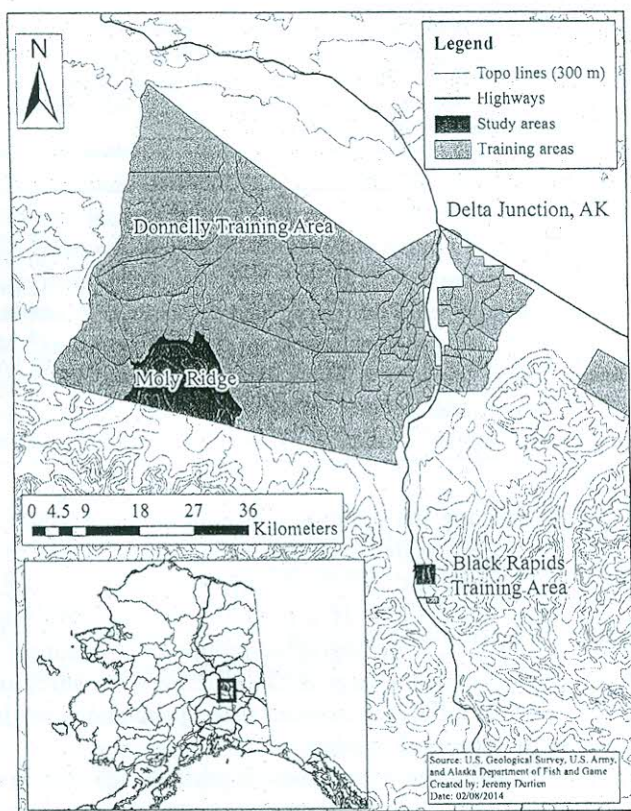
Conventional sampling techniques for mountain ungulates typically consist of aerial or on-foot surveys (Sumner 1948, Udevitz et al. 2006, Liu et al. 2008, Schmidt et al. 2011). However, remotely activated cameras or camera traps are an increasingly used tool in the evaluation of wildlife presence and habitat use (Nichols et al. 2011) and may be advantageous in situations where conventional techniques are restricted or too expensive. Although knowledge on the use of camera traps in ecological research is increasing (Jackson et al. 2006, Bhattacharya et al. 2012, Massara et al. 2015), mountain sheep research has seen limited application. Camera traps have effectively captured the diel use of water sources by Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) in northern Utah (Whiting et al. 2009), and have been used to obtain population size estimates for desert bighorn sheep (*O. c. mexicana*) in New Mexico. These estimates were equally accurate to those derived from aerial and ground surveys (Perry et al. 2010).

The low use of camera traps in relation to mountain sheep is likely a combined result of the difficult terrain that mountain sheep inhabit and, until recently, the lack of technology capable of operating in extreme climatic conditions. With the advent of technology capable of operating for multiple months in sub-freezing temperatures without servicing, researchers no longer must access camera traps on a weekly or monthly basis (Tobler et al. 2009, Pesenti and Zimmermann 2013). Freedom from constant maintenance allows researchers to avoid wasting resources accessing remote areas, decreases safety concerns, and allows for data collection when access is not feasible.

Our objectives were to model the occupancy of Dall's sheep across multiple seasons using detection-non-detection data from an array of camera traps operating for 15 months (Aug 2013–Oct 2014). With these data, we used occupancy models to determine important abiotic and biotic habitat covariates for, and seasonal variations of, sheep occupancy. In addition, we evaluated camera traps as an effective method for the study of mountain sheep. We predicted that camera traps would effectively capture the diel habitat use of Dall's sheep and that the incorporation of time lapse images would increase detections of animals.

## STUDY AREA

We investigated Dall's sheep occupancy probabilities on 2 study areas: Molybdenum Ridge (Moly Ridge) within Donnelly Training Area (DTA) and Black Rapids Training Area (BRTA) of Fort Wainwright, Alaska (Fig. 1). The Moly Ridge study area (~190 km<sup>2</sup>) was located on the northern edge of the Alaska Range, approximately 50 km southwest of Delta Junction, Alaska (Fig. 1). The entire Moly Ridge study area included an approximately 10-km long isolated granite ridgeline and a large flat plain to the south that isolated most of the optimal sheep habitat within the ridgeline from the greater Alaska Range. Black Rapids Training Area (~11 km<sup>2</sup>) was adjacent to the Richardson Highway in the Delta River valley approximately 70 km south of Delta Junction, Alaska. Black Rapids Training Area was in the center of the Alaska Range, was more dynamic topographically with large contiguous patches of escape terrain, and was bordered by a braided river valley. The ridgeline of the Moly Ridge study area and BRTA were alpine areas with prevalent graminoids (e.g., fescue grass [*Festuca* spp.]), low growing forbs (e.g., narcissus anemone [*Anemone narcissiflora*] and lousewort [*Pedicularis* spp.]), dwarf shrubs (e.g., white arctic mountain heather [*Cassiope tetragona*] and eightpetal mountain-avens [*Dryas octopetala*]), and unconsolidated rocky slopes. The expansive plain within the Moly Ridge study area was treeless and consisted mostly of taller shrubs (e.g., willow [*Salix* spp.]) and graminoids. Elevations at Moly Ridge and BRTA ranged from 1,000 to 1,900 m and from 1,050 to 1,525 m, respectively, and slope percentages ranged from 0 to 272% (i.e., 0–70°). Both study areas were exposed to high wind conditions, especially during winter ( $\bar{x}$  = 19.3 km/hr; National Oceanic and Atmospheric Administration 2015), leading to large windswept slopes ideal for sheep winter habitat. Light snow was common



**Figure 1.** Location of the Molybdenum (Moly) Ridge and Black Rapids Training Area Dall's sheep study sites in interior Alaska, 2013–2014. Black Rapids Training Area is within a contiguous portion of the Alaska Range and Molybdenum Ridge is located on the northern periphery of the range.

throughout the winter with some severe snow events; light rain was common through the summer. Temperatures for both areas ranged from approximately 30°C to –40°C and daily sunlight from approximately 20.5 hours/day to 4 hours/day in the summer and winter, respectively. The cold winter season stretches from early-November to early-April and the warm season lasts from mid-May to early-September. Arctic ground squirrel (*Urocitellus parryii*), caribou (*Rangifer tarandus*), red fox (*Vulpes vulpes*), and grizzly bear are other common species of both study areas.

## METHODS

We installed cameras on Moly Ridge ( $n = 45$ ) and BRTA ( $n = 9$ ) during July and August 2013. We stratified the study areas by 3 classes of slope percentage: flat ( $\leq 15\%$ ), inclined ( $15\% < \text{slope} \leq 45\%$ ), and steep (slopes  $> 45\%$ ), which constituted 46.9%, 41.2%, and 11.0% of Moly Ridge and 7.8%, 61.1%, 38.2%, of BRTA, respectively. We divided the study areas into slope strata to allow sampling across a wide range of habitat quality, but also so we did not deploy most of our effort in likely sub-optimal habitat (e.g., flat). We wanted much of our effort in the narrow band of likely optimal sheep habitat (i.e.,  $> 45\%$  slope and  $< 500$  m from escape terrain). We used a sample size calculation in MacKenzie and Royle (2005) to proportionally allocate sampling effort for each stratum, using expected estimates of occupancy and detection and desired levels of precision. For the study design, we assumed occupancy estimates of 0.1, 0.5, and 0.8 and

detection estimates of 0.2, 0.4, and 0.4, respectively, for the flat, inclined, and steep strata (Gionfriddo and Krausman 1986, Rachlow and Bowyer 1998). This resulted in the allocation of effort as 5, 23, and 17 cameras for the flat, inclined, and steep strata, respectively, for the Moly Ridge study area and 0, 5, and 4 for the flat, inclined, and steep strata, respectively, for the BRTA study area.

We determined camera locations through a spatially balanced design. A spatially balanced survey is a probability-based survey generated via the reversed randomized quadrant-recursive raster (RRQRR) algorithm (Stevens and Olsen 2004, Theobald et al. 2007); we calculated the RRQRR using ArcGIS (ArcGIS v10.0; Environmental Systems Research Institute, Redland, CA, USA). The RRQRR algorithm allows for varying numbers of sample site locations per strata by assigning relative inclusion probabilities to each stratum (Theobald et al. 2007). Using our sampling effort calculations, we developed inclusion probabilities that would adequately distribute the correct number of camera locations per strata.

We chose camera sites within 100 m of the identified coordinates that would provide the best opportunity to capture an image of sheep using the area. If we could not safely access the area of the chosen camera location ( $n = 4$ ) then we chose a location that would capture an image of the predetermined camera coordinates. We used Reconyx PC800 and PC900 Professional Hyperfire Infrared cameras (Reconyx, Holmen, WI, USA). We installed cameras upon Reconyx t-post mounts, thunderbolt mounts, or within security boxes affixed to rock faces.

Moly Ridge and BRTA are active training areas of the United States Army; thus, researcher access of the Moly Ridge study area was when DTA was conducting range cleanup, a 3-week period during late-July and early-August 2013 and 2014, in which no live fire training occurs. This period was long enough to conduct camera installation and vegetation sampling. Additionally, we conducted a shorter maintenance trip in October 2014 during a gap in training operations. All field and sampling procedures were approved by the Colorado State University Institutional Animal Care and Use Committee (IACUC #13-4114A).

We programmed cameras to trigger by a combination of movement and infrared signature and to record a time lapse image every hour. Once a trigger occurred, the camera captured 3 images in succession, with 1 second between images. The camera would then take no pictures for a 15-second quiet period to conserve digital memory. Following the first camera maintenance, and noting the amount of space still available on the memory cards, we removed the quiet period and decreased the time lapse from 1 hour to 30 minutes for the last 3 months of the study.

We sampled vegetation during the summer 2014 field season at each camera location. We established 30, 0.5-m<sup>2</sup> quadrats every 5 m along a 50-m transect perpendicular to the camera face and at varying distances from the transect at each 5-m point (Dertien 2016). We estimated aerial and ground coverage of 12 different abiotic and biotic coverage classes at each quadrat (Table 1). We identified all vascular

**Table 1.** Summary of abiotic and biotic coverage classes measured in quadrats within 50 m of all camera locations during summer 2014 on study areas of Molybdenum Ridge and Black Rapids Training Area, Alaska, USA.

Coverage class	Description
Bare ground	Soil devoid of any other cover
Gravel	Small bare rock <2 cm diameter
Rock	Bare rock >2 cm diameter
Litter	Dead vegetative matter fully detached from a plant
Lichen	All lichen genera including on rock
Moss	All moss genera including on rock
Graminoid	Grass, sedge, and rush species
Forb	Herbaceous non-graminoid species
Dwarf shrub	Woody species <20 cm in height
Shrub	Woody species >20 cm in height
Tree	Tree species of all heights
Water	Standing and flowing water

plants in a quadrat to species; because of logistical reasons, we identified species in quadrats each 10 m from the camera, out to 50 m (e.g., 10 m, 20 m).

#### Data Processing and Analysis

Because of the quantity of photos captured, we placed all photos taken from a camera in order of capture into Windows Movie Maker (Microsoft, Redmond, WA, USA) and created 2-frame/second videos. This served 2 purposes: videos provided a quick and seamless method of viewing thousands of photos and researchers could detect wildlife in the back and middle ground of a photo that would likely be overlooked without the rapid succession of images.

We uploaded all photos into a Windows Access photo viewer interface (Ivan and Newkirk 2016) and recorded sheep detections along with specific demographic (i.e., female or young male, male, or unknown) and behavioral details (i.e., moving or traveling, grazing, resting, vigilant, or unknown). Finally, we truncated sheep detections at approximately 500 m from the camera for analysis because of decreased detection beyond this distance and changing habitat conditions. We binned these data into 1-week occasions across the 15 months (64 weeks) of continuous sampling.

We analyzed our data using the single season occupancy model in Program MARK (White and Burnham 1999), but given the relatively large-scale movements of sheep throughout a season, the assumption of intra-seasonal closure was violated. Thus we interpreted occupancy estimates as habitat use (MacKenzie 2006). We defined 2 demographic groups: female groups (females and young males) and male groups (adult males). We defined 10 biologically hypothesized seasons taking into consideration rutting, lambing, and potential differences in the movement patterns of male and female groups (Table 2). We censored 2 weeks between each season to allow for independence and animal movement between occasions and censored days when researchers were camped near cameras during July 2014. We treated each season as a separate group in our analysis rather than using a multi-season robust design model because of low sample size, the increased number of parameters needed for the multi-season model, and difficulty

**Table 2.** Dates for the 10 habitat use seasons of Dall's sheep across 15 months of continuous sampling on study areas of Molybdenum Ridge and Black Rapids Training Area, interior Alaska, USA, 2013–2014. We censored 2 weeks between each season and when researchers were camped on Molybdenum Ridge in July 2014.

Season classification	Start date	End date
Late-summer 2013	11 Aug 2013	7 Sep 2013
Pre-rut 2013	22 Sep 2013	19 Oct 2013
Rut 2013	03 Nov 2013	30 Nov 2013
Post-rut 2013	15 Dec 2013	11 Jan 2014
Winter 2014	26 Jan 2014	08 Mar 2014
Late-winter 2014	23 Mar 2014	19 Apr 2014
Lambing 2014	04 May 2014	07 Jun 2014
Summer 2014	22 Jun 2014	12 Jul 2014
Late-summer 2014	27 Jul 2014	30 Aug 2014
Pre-rut 2014	14 Sep 2014	18 Oct 2014

interpreting immigration and emigration parameters when closure is violated (Kendall et al. 1995, MacKenzie et al. 2009, Falke et al. 2012). Finally, we treated study area (Moly Ridge vs. BRTA) as a grouping variable resulting in 40 groups (i.e., 2 demographic groups  $\times$  10 seasons  $\times$  2 study areas). Given the large distance between the study areas and probable difference between sheep populations, we included study area in all models.

We estimated weekly snow depths for each camera location classifying the snow depth in sequential images into 1 of 6 categories (no snow or trace, 10 cm, 20 cm, 30 cm, 40 cm, 50 cm). We installed snow posts with 20-cm sections of contrasting black and white paint in front of 4 cameras, which aided in estimating snow depth at all camera locations. In addition, we assigned cameras as on or off trail, dependent on if the camera was capturing an image of an apparent wildlife trail. Wildlife trails appeared as an increase of barren ground and lower growing vegetation compared to the surrounding landscape.

We determined abiotic covariates from remote sensing data (U.S. Geological Survey, National Elevation Dataset [USGS NED]) using ArcGIS and included camera site elevation (m), mean slope (%), a camera's viewshed area (ha), surface distance of camera site to escape terrain (m), and surface distance of camera site to static military firing points (m). Distance from escape terrain was the surface distance from the camera site to a contiguous area of >1 ha of barren or rocky slopes >60% grade (Wakelyn 1987, McKinney et al. 2003). Camera viewshed was the land area (ha) that the camera captured within 500 m of the camera location, which we determined using the ArcGIS Viewshed tool. Finally, we used information of scheduled on-ground military training that occurred within the boundaries of the study areas. We calculated training days as the number of military training days per season per study area. We tested for correlation between all covariates (abiotic and vegetation); we censored 1 covariate from any covariate pair with a correlation coefficient  $|r| > 0.7$ .

We hypothesized individual covariate relationships and temporal structures that would best model sheep habitat use ( $\psi$ ) and detection ( $p$ ). We used a 2-step modeling approach using corrected Akaike's Information Criterion (AIC<sub>c</sub>)

cumulative weights to reduce unsupported covariates and determine the best model structures that explained  $\psi$  and  $p$  (Lebreton et al. 1992, Doherty et al. 2012, Bromaghin et al. 2013). First, holding  $p$  constant, we constructed a balanced set of all possible additive  $\psi$  models, with the addition of 2 hypothesized interactions between season and study area and between demographic group and distance to escape terrain. We retained all group effects, covariates, and interactions with cumulative weights  $>0.50$  for a second round of analysis. We repeated this procedure for  $p$  by maintaining  $\psi$  constant and varying  $p$  across variables of interest. We combined all variables for  $\psi$  and  $p$  retained for the second round of analysis into a global model. We calculated final cumulative weights from a balanced model set of all additive combinations of these variables with and without the interaction terms. We then chose a predicting model that contained all variables with a cumulative weight  $>0.50$  from this model set (Barbieri and Berger 2004). This procedure allowed us to handle a large number of variables efficiently but also avoided possible spurious results (Doherty et al. 2012, Bromaghin et al. 2013).

#### Habitat Use Maps

We used remote sensing, vegetation, and snow depth data in conjunction with our chosen prediction model to create habitat use maps for the Moly Ridge study area. We created raster layers of slope percentage, distance from escape terrain (m), and elevation (m) in ArcGIS using USGS NED digital elevation model layers. Then we created interpolative cokriging or ordinary kriging raster layers of mean seasonal snow depth and all vegetation covariates supported in our occupancy prediction model with significant ( $P \leq 0.05$ ) spatial autocorrelation.

Cokriging, as with ordinary kriging, uses point estimates and the spatial autocorrelation of a variable to interpolate values of that variable across a surface. However, cokriging can include other spatial variables (e.g., elevation, slope) to increase predictive abilities of the model (Xu et al. 2015). To examine spatial cross-correlation, we calculated Mantel's test in R (R Core Development Team 2015) between supported ground coverage covariates and remotely sensed abiotic data. Then, we created cokriging layers of ground coverages and any significantly ( $P \leq 0.05$ ) cross-correlated abiotic variable.

Finally, we created habitat use maps using the ArcGIS version 10.0 raster calculator using our occupancy prediction model, including important temporal and demographic effects and spatial covariates.

## RESULTS

During the 15 months of sampling, camera traps captured approximately 825,000 photos, over 19,202 camera trap days. We captured 7,837 images of sheep. Of these, 1,952 images were between seasons and censored, resulting in 2,652 and 3,233 images from Moly Ridge and BRTA, respectively, for habitat use analysis. Both triggered and time lapse programming captured images of sheep. Time lapse images successfully captured animals close to the camera and up to approximately 1,200 m from the camera location. Approximately 1,000 time lapse images recorded sheep. This technique was the sole form of sheep detection for 17% of the camera locations that captured sheep images. We captured nocturnal instances of sheep moving ( $n=46$ ), foraging ( $n=6$ ), and resting ( $n=5$ ) outside the hours of civil twilight (i.e., when the sun is not visible but less than  $6^\circ$  below the horizon) at both study areas. The majority of nocturnal detections (82.4%) were between 1 November 2013 and 1 March 2014 when daylight hours were the fewest of the sampling period.

#### Model Results

The first step in our modeling approach culled 5 variables (i.e., elevation, dwarf shrub coverage, vegetation species richness, viewshed, military training days) for  $\psi$  and study area for  $p$ . Retained  $\psi$  covariates included an interaction between demographic group and distance to escape terrain, slope percentage, snow depth, and graminoid coverage. In addition, habitat use varied seasonally and by study area. Distance from firing point was retained but exhibited unexpected positive correlation results, possibly indicating biases between covariate values and the study design. Finally, trail and viewshed were retained for modeling  $p$  (Dertien 2016).

Our second round of modeling focused on a final model set consisting of all possible additive combinations of the variables retained from the first round. Our prediction model

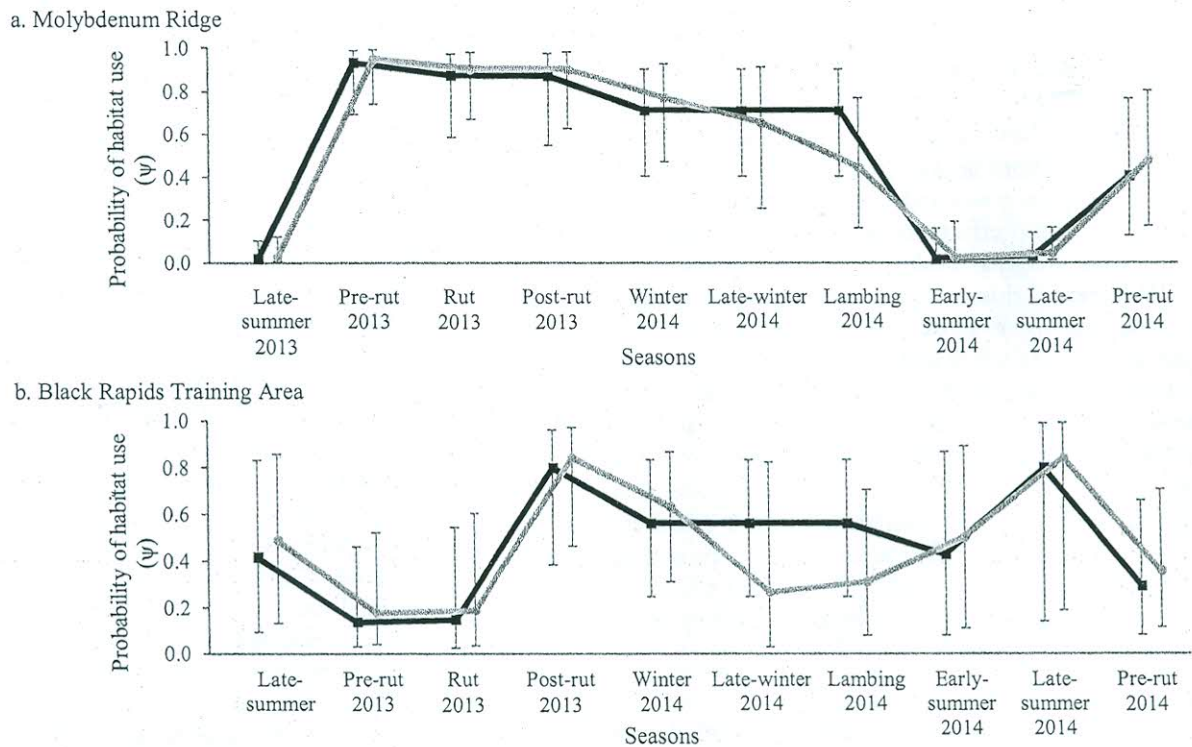
**Table 3.** Top 5 occupancy models from analysis of Dall's sheep on study areas in interior Alaska, USA, 2013–2014. Habitat use ( $\psi$ ) varied temporally between all seasons except when held constant for individuals in female groups (F and young M) during winter 2014 to lambing 2014 (seasons), this varied by study area (area). An interaction between distance to escape terrain (escape) and demographic group (sex), slope percentage (slope), snow depth (snow), and graminoid cover (gram) were supported in the top 2 occupancy models. Detection probability ( $p$ ) was correlated to a camera taking an image of a wildlife trail (trail) and area of a camera's viewshed (view).

Model	$\Delta AIC_c$	$AIC_c w_i^a$	ML <sup>b</sup>	$K^c$
$\psi$ (seasons $\times$ area + escape $\times$ sex + slope + snow + gram) $p$ (trail + view)	0.000	0.399	1.000	29
$\psi$ (seasons $\times$ area + escape $\times$ sex + slope + snow + gram) $p$ (trail)	1.066	0.234	0.587	28
$\psi$ (seasons $\times$ area + escape $\times$ sex + slope + snow) $p$ (trail+view)	1.258	0.213	0.533	28
$\psi$ (seasons $\times$ area + escape $\times$ sex + slope + snow) $p$ (trail)	2.044	0.144	0.360	27
$\psi$ (seasons $\times$ area + escape $\times$ sex + snow) $p$ (trail + view)	9.816	0.003	0.007	27

<sup>a</sup> Akaike's Information Criterion with correction for small sample size model weight.

<sup>b</sup> Model likelihood.

<sup>c</sup> Number of parameter in each model.



**Figure 2.** Dall sheep grouped as female (black lines; F and young M) and male (gray lines; adult M) habitat use across 10 seasons of sampling on Molybdenum Ridge (a) and Black Rapids Training Area (b), interior Alaska, 2013–2014. To create these graphs, we set covariate values to slope = 50%, distance to escape terrain = 500 m, snow = 10 cm, graminoid = 6.5%. Error bars are 95% confidence intervals.

included seasonal, study area, and demographic differences for sheep habitat use (Table 3). The prediction model included differences between the 10 seasons, except for constant habitat use of individuals in female groups during the winter, late-winter, and lambing seasons. Although sheep habitat use of Moly Ridge was highest during the pre-rut to winter seasons (Fig. 2a), BRTA had very low use during the pre-rut and rut season, and the highest use in the post-rut and late-summer season (Fig. 2b). Habitat use was

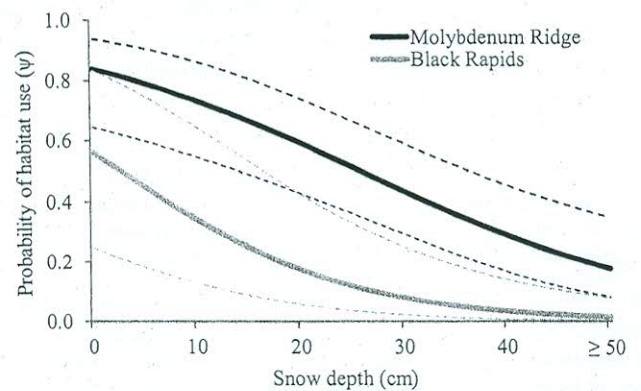
positively correlated with slope percentage and graminoid cover, and negatively correlated with distance to escape terrain and snow depth. Detection was constant temporally and was higher if the camera was on wildlife trail and negatively correlated with viewshed size.

Temporal use estimates of sampling units on Moly Ridge were higher during the rut, winter, and lambing seasons for female and male groups (Fig. 2a). However, male groups showed a steady decline in habitat use following the rut

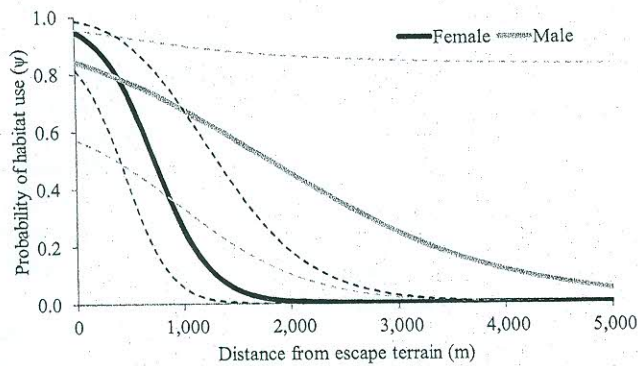
**Table 4.** Cumulative corrected Akaike's Information Criterion weights ( $\sum w_i$ ) for factors in the final balanced model set of habitat use ( $\psi$ ) and detection probability ( $p$ ) for Dall's sheep in interior Alaska, USA. We included variables with  $\sum w_i$  values >0.5 in the prediction model.

Variables	$\sum w_i$
$\psi$ study area	1.000
$\psi$ seasons <sup>a</sup>	1.000
$\psi$ seasons $\times$ area	1.000
$\psi$ distance to escape terrain	1.000
$\psi$ snow depth	1.000
$\psi$ sex	0.998
$\psi$ distance to escape terrain $\times$ sex	0.995
$\psi$ slope	0.995
$\psi$ graminoid cover	0.631
$\psi$ distance to firing point	0.315
$\psi$ forb cover	0.302
$p$ trail	1.000
$p$ viewshed	0.619

<sup>a</sup> Habitat use varied temporally among all seasons, except female group (F and young M) habitat use, which was constant during the winter 2014 to lambing 2014 seasons.



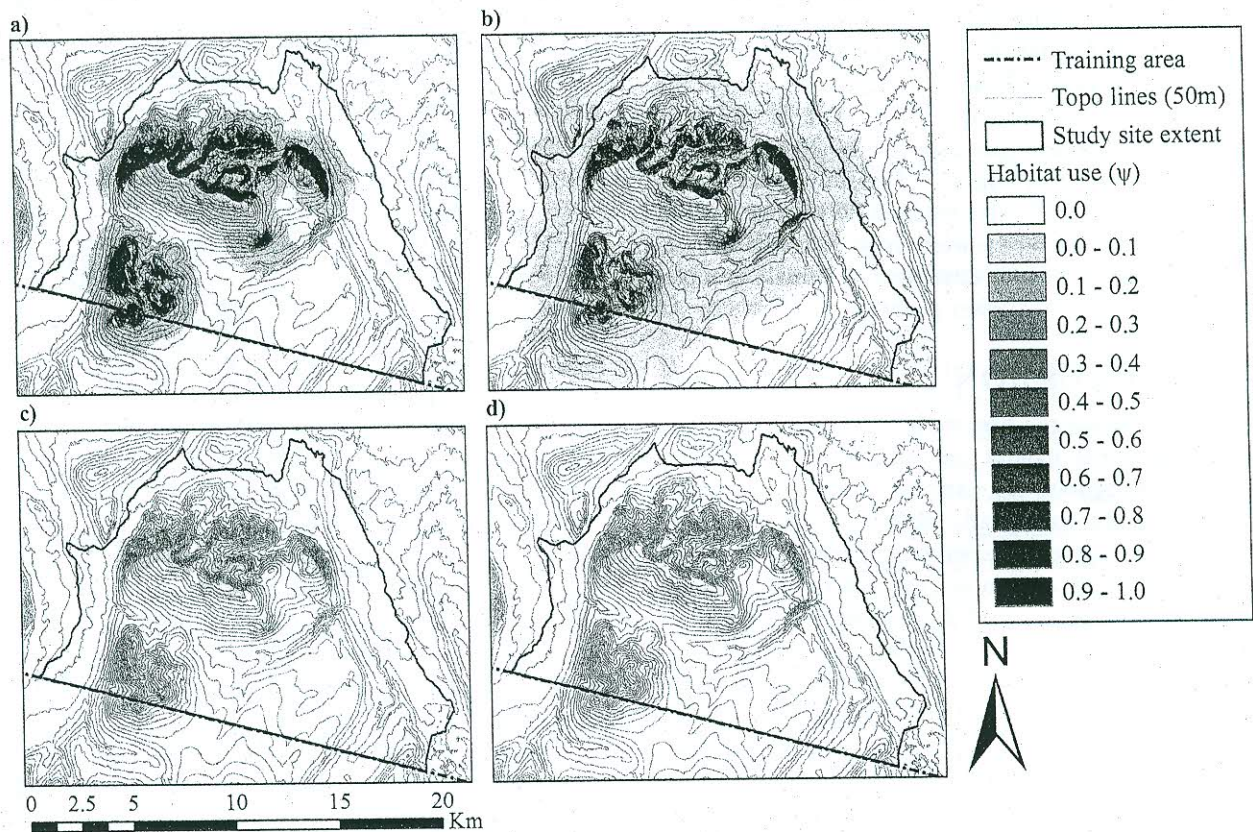
**Figure 3.** The probability of Dall's sheep habitat use decreased steadily with increasing snow depth on the interior Alaska study sites of Molybdenum Ridge and Black Rapids Training Area (BRTA), 2013–2014. Sheep use of BRTA appears especially sensitive to snow accumulation; use approaches 0.1 at approximately 30 cm. To produce these graphs, we held slope, distance to escape terrain, and graminoid cover to 50%, 500 m, and 4.6%, respectively. Dashed lines are 95% confidence intervals.



**Figure 4.** Habitat use by Dall's sheep was negatively correlated with the distance from escape terrain for female (F and young M) and male (adult M) groups on study sites of interior Alaska, 2013–2014. Female groups appeared to concentrate habitat use closer to escape terrain, whereas male use included areas farther from escape terrain but with lower precision. We calculated estimates for graphs by fixing slope, snow depth, and graminoid cover to 50%, 10 cm, and 4.6%, respectively. Dashed lines are 95% confidence intervals.

season; this differed from female group use, which was best supported by constant use through the winter and lambing seasons (Fig. 2a). Seasonal habitat use estimates of BRTA found support for higher use in post-rut and early winter 2013 and within the summer 2014 seasons (Fig. 2b); however, precision was low in part because of the relatively small sample size of camera locations.

Model results indicated support for abiotic factors including slope percentage, snow depth, and distance to escape terrain as the most important covariates predicting sheep habitat use (Tables 3 and 4). Slope percentage ( $\hat{\beta} = 0.08 \pm 0.02$  [SE]) showed a positive relationship with sheep use for both study areas. Moly Ridge summer habitat use was minimal and thus only the steepest slopes were predicted to have any habitat use. Winter habitat use for both study areas and summer habitat use for BRTA was  $\geq 0.50$  for sites with slopes  $\geq 60\%$  when within 500 m of escape terrain. Snow depth showed a negative relationship ( $\hat{\beta} = -0.90 \pm 0.19$ ) with sheep habitat use on both study areas. Results indicated that probability of habitat use for a sampling location on Moly Ridge dropped below 0.50 with 10–20 cm of snow, and habitat use approached zero once snow depths were  $\geq 50$  cm (Fig. 3). Sheep use of BRTA followed a stronger negative relationship; use dropped below 0.1 with  $>30$  cm snow depth (Fig. 3). In addition, results indicated an interaction between demographic group and escape terrain ( $\hat{\beta} = -0.003 \pm 0.001$ ), indicating support for female group habitat use concentrated closer to escape terrain versus male group use (Fig. 4). Finally, our prediction model had some support for the cover of graminoids ( $\hat{\beta} = 0.12 \pm 0.06$ ) predicting sheep habitat use (Table 4). Female and male winter habitat use was  $>0.50$  in areas of  $>9\%$  graminoid cover contingent on being  $>45\%$  slope and within 500 m of escape terrain.



**Figure 5.** Habitat use probability map examples depict the habitat use ( $\psi$ ) of Dall's sheep in the pre-rut season of 2013 for individuals grouped as female (a; F and young M) or male (b; adult M) versus the late-summer season of 2014 for individuals grouped as female (c) or male (d) on the Molybdenum Ridge study site, interior Alaska. The probability of habitat use was higher for both demographic groups in the pre-rut 2013 season, compared to low habitat use estimates during the late-summer season 2014 (i.e.,  $\psi \leq 0.30$ ).

Whether or not a camera was positioned on a wildlife trail best predicted detection probability ( $p=0.43 \pm 0.03$  [on trail];  $p=0.15 \pm 0.02$  [off trail]; Table 4). We found evidence that detection decreased with the increasing camera viewshed area ( $\beta = -0.07 \pm 0.04$ ); however, the confidence interval of the beta included zero and the negative relationship is suspect.

### Habitat Use Maps

Mantel's test results found significant correlation between graminoid cover and slope percentage ( $P < 0.001$ ) but not between graminoid cover and elevation ( $P = 0.757$ ). We did not find significant cross-correlation between seasonal snow depths and slope ( $P = 0.882$  [pre-rut 2013]) or elevation ( $P = 0.267$  [pre-rut 2013]). Therefore, we created a cokriging map of graminoid with slope percentage data and an ordinary kriging map of snow depth (Gong et al. 2014, Xu et al. 2015). Habitat use maps then included graminoid and seasonal snow depth layers and varied between seasonal and demographic differences.

Habitat use maps of Moly Ridge during the pre-rut 2013 season show the highest concentration of habitat use for female and male groups in areas surrounding the northwestern face, westernmost bowl, and northernmost arm of the ridgeline (Fig. 5a and b). In addition, there was high probability of habitat use for the easternmost peak of Moly Ridge for female and male groups (Fig. 5a). We detected several male groups in this area throughout the study period, but no female groups.

The habitat use of Moly Ridge during the late-summer 2014 season is a sharp contrast to habitat use of the pre-rut season (Fig. 5c and d). Habitat use is still concentrated in the northwestern portions of Moly Ridge but is generally estimated for female and male groups as  $< 0.30$  for even the most optimal sheep habitat. We detected only males during this season on the westernmost slopes of Moly Ridge and the areas around the easternmost peak of Moly Ridge. However, males show a lower probability of use than female groups.

## DISCUSSION

This was the first study to use camera traps to examine the seasonal habitat use of Dall's sheep. Cameras operated throughout the sampling seasons and captured the diel, seasonal, and yearly patterns of the Dall's sheep population. Through the incorporation of occupancy models with camera data and camera site estimates of vegetation coverages, we estimated the probability of habitat use considering different abiotic and biotic covariates.

Probability of habitat use varied between our 2 study areas and between our 10 different seasons. Sheep occupied Moly Ridge from the onset of the rut to post-lambing, when sheep likely migrated off the military installation to higher elevations of the Alaska Range for better foraging and mineral lick opportunities (Spiers and Heimer 1990). In contrast, estimates of BRTA habitat use were more variable and less precise with notable increases during the post-rut and late-summer seasons and decreases during the 2013 pre-rut and rutting seasons (Fig. 2a). Black Rapids Training

Area, unlike Moly Ridge, is within a contiguous range of optimal sheep habitat, presumably allowing for greater movement of sheep groups in and out of the training area and likely constitutes only a portion of female and male group seasonal ranges. Therefore, an important consideration for future camera trap studies of mountain sheep habitat use is to select study areas that attempt to capture the entire extent of a sheep population's yearly range or is spatially segregated from other seasonal ranges.

We did not find support for ground-based military activities or fixed firing points affecting sheep habitat use. There was only a 2-day ground training operation on Moly Ridge during the sampling period so inference of military activity effects is limited to this short period for the vast majority of the sampling points. Ground-based training at BRTA was non-fire operations and was rather consistent for the first 8 seasons, then more than doubled during the late-summer 2014 season. Sheep images during this season more than tripled compared to the same season the previous year, adding to the conclusion that minor on-ground military training had no discernable effect on sheep habitat use during this study.

Female and male habitat use of both study areas overlapped seasonally and by site covariates. The presence of adult males with female bands extended beyond the pre-rut and rut seasons and into the winter season on Moly Ridge and the late-summer season on BRTA. Male habitat use declined on Moly Ridge during the late-winter season, whereas female group use remained constant throughout the winter and lambing seasons. Female bands may occupy winter ranges for up to 9 months of the year (Hoefs and Bayer 1983), which would be consistent with our results of presence from mid-September 2013 to early-June 2014. Across all seasons, we found that female bands were more likely to concentrate closer to escape terrain, whereas adult males were less predictable and had a relatively higher probability of habitat use farther from escape terrain. Male bands spatially segregate from female bands prior to lambing, potentially moving into less optimal habitat (Geist 1971, Corti and Shackleton 2002). During lambing, female use is highly associated with steep escape terrain and predator avoidance (Rachlow and Bowyer 1994, 1998). In addition, Geist (1971) notes that young males in western Canada are frequently observed traveling longer distances into more novel territories (wandering) than female groups, which could provide insight into the estimated male habitat use farther from escape terrain. However, we caution about making broader inferences given the imprecise estimates of male habitat use beyond approximately 500 m from escape terrain (Fig. 4).

As we predicted, in addition to proximity to escape terrain, slope percentage, snow depth, and graminoid cover were important site covariates correlated with sheep habitat use. The overarching paradigm of mountain sheep habitat is that it lies at an optimum between the ability to escape predators and available forage. Although our estimated sheep habitat use was positively correlated with increasing slope and graminoid cover, habitat use was negatively correlated with

increasing snow depths and distance from escape terrain. Dall's sheep are presumed to stay close to escape terrain to evade predators and avoid areas with deep snow because of increased energy loss from movement through the snow, digging to find forage, and being slowed down when pursued by a predator (Burles and Hoefs 1984, Hoefs et al. 1986). Dall's and Stone's sheep (*O. d. stonei*) have been observed avoiding areas with snow depth >30 cm (Seip and Bunnell 1985, Nichols 1988), a finding further supported by our model results. Increased accumulation of snow at camera locations could further explain the decrease in habitat use for both study areas from the post-rut to the winter seasons.

We found moderate support for graminoid coverage positively influencing habitat use and no support for vegetation species richness or forb coverage affecting habitat use. Sheep habitat use has been documented to be predominately restricted to areas near escape terrain and windswept slopes; thus, finding a lack of support for biotic factors predicting use was expected. Habitat use as a factor of plant biota could potentially be more decipherable with a larger sample size and much shorter occasion durations.

Positioning a camera on an obvious wildlife trail greatly improved the chances of detecting a sheep; however, this came with the trade-off that sheep were typically detected traveling through the area rather than behaving otherwise. Time lapse photos of non-trail areas had lower detection probabilities but allowed for sampling of larger habitat areas and captured more images of sheep grazing or resting. The size of a camera's viewshed was negatively related to detection probability, opposite of our prediction. A possible explanation is that the human observer missed more detections in images of larger viewsheds compared to smaller viewsheds. A double-observer approach during photo processing could calculate if the probability of detecting a sheep, given that a sheep appeared in an image, was negatively correlated with viewshed size.

The cameras were a novel item at the treeless sampling sites, possibly prompting sheep to interact and investigate the cameras and camera mounts. Time lapse images captured sheep grazing near cameras immediately before triggered images of sheep investigating the camera, indicating that sheep may not have been attracted to an area because of the camera. Detection probabilities were possibly biased slightly high by conspicuous cameras, but this is difficult to assess without further research.

Mountain sheep are considered diurnal animals and little direct evidence is available recording nocturnal activities (Geist 1971, Hoefs 1976). We have provided evidence that Dall's sheep move and graze during the night and that these events appear concentrated during seasons with the lowest daylight hours. Observations of domestic hill sheep have reported nocturnal activity is common during winter months when daylight is limited and then ceases soon after the spring equinox (Wallace 1884). A study of desert bighorn sheep assessed differences in radio-collar signal strengths and determined that nocturnal activity was common across the entire year (Alderman et al. 1989). Dall's sheep appear active during nocturnal periods, increasing foraging time, especially

during long periods of darkness. The vast majority of our nocturnal detections were skewed towards motion-triggered images rather than time lapse images because the illumination from the camera flash reaches only 10–20 m beyond the camera. Future research with camera traps, in conjunction with other methods, is needed to better quantify Dall's sheep nocturnal behaviors.

## MANAGEMENT IMPLICATIONS

Dall's sheep use Moly Ridge and BRTA at different intensities throughout the majority of the year. Our results show migration from higher elevations to Moly Ridge occurred at least one month earlier than previously found and that both training areas are used by females during the lambing season. This indicates that both training areas are important lower elevation conservation areas for this sheep population. Military training on Moly Ridge appears to be appropriately timed after lambing and before pre-rut seasons, when sheep habitat use is minimal. Training in these areas should be avoided during the rut, winter, and lambing seasons to reduce overlap of training and these important seasons for sheep reproduction and survival.

Data collection on large military installations and in mountain sheep habitat can be challenging given difficulties sampling in isolated study areas. Camera traps successfully operated in mountain sheep habitat, which allowed for the seasonal estimation of sheep habitat use. The incorporation of time lapse images greatly increased the quantity of photo data but markedly increased our detections of sheep. With this sampling tool, which provides a continuous record of climatic and wildlife data, more accurate management decisions can be made for wildlife in challenging environments.

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