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Modeling influences on winter distribution of caribou in northwestern Alaska through use of satellite telemetry

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Abstract: I hypothesize that the distribution of barren-ground caribou (*Rangifer tarandus granti*) is affected by multiple, interrelated factors. These factors include, but are not limited to, terrain and snow characteristics as well as predation pressure and habitat. To test this hypothesis, I attributed caribou locations derived from satellite telemetry over a 6 year period with terrain (elevation, slope, aspect, and ruggedness), habitat characteristics, and moose density – potentially an index of wolf predation pressure. These locations were compared to random locations, attributed using the same data layers, using logistic regression techniques to develop resource selection functions (RSFs). I found that caribou moved significantly less during mid-winter than early- or late-winter and that cows moved significantly more in April than bulls due to their earlier departure on their spring migration. Distribution was different between cows and bulls. Terrain variables were important factors but were scale-dependent. Cows avoided forested areas, highlighting the importance of tundra habitats, and selected for dwarf shrub, with relatively high lichen cover, and sedge habitat types. Bulls selected for dryas, coniferous forest and dwarf shrub habitats but against lowland sedge, upland shrub and burned tundra. Cow distribution was negatively correlated with moose density at the scale of the Seward Peninsula. My results support the hypothesis that caribou distribution during winter in northwest Alaska is affected by multiple, interrelated factors. These results may be useful for researchers to track and/or model changes in future patterns of range use over winter.

Key words: Alaska; caribou distribution; habitat; lichens; predation; *Rangifer tarandus granti*; resource selection function; satellite telemetry; terrain; Western Arctic Herd; winter range.

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Introduction

I hypothesize that the distribution of Western Arctic Herd (WAH) caribou (*Rangifer tarandus granti*) is affected by terrain and snow characteristics, as well as habitat and predation pressure. Looking across the northern landscape, caribou ecotype and disturbance (*e.g.*, wildfire and/or industrial development) are also likely to be important factors in determining distribution (Mallory & Hillis, 1998; Johnson *et al.*, 2005; Joly *et al.*, 2007a). The importance of each factor is likely to depend on the scale of the analysis (Wiens, 1989; Rettie & Messier, 2000; Johnson *et al.*, 2004; Gustine *et al.*, 2006; Mayor *et al.*, 2007). Terrain, snow conditions, habitat characteristics and predation pressure are all interrelated to some degree. High elevation, steep slopes and open habitats often have less snow due to wind scouring than do protected valleys or forested habitats. Lichen biomass is typically greater in areas that have a protective snow cover as lichens are susceptible to desiccation and wind abrasion (Holt *et al.*, 2008). Terrain is an important factor in determining winter distribution because certain conditions may be correlated with preferred habitats, as noted above, or may provide improved sightability of predators. Snow characteristics are important because movement can be impeded by deep snow, while foraging efficiency can be reduced by either deep or crusted snow (Skogland, 1978; Fancy & White, 1985; Fancy & White, 1987; Collins & Smith, 1991; Joly *et al.*, 2011). Habitat is an important factor because lichens comprise the majority of the winter diet of WAH caribou (Saperstein, 1996; Joly *et al.*, 2007b). Pregnant caribou should be the most reliant on high quality habitat during the winter months as their energetic demands are relatively higher than other classes of caribou (Cameron *et al.*, 1993; Barboza & Parker, 2008). Different habitat types may also offer varying levels of predation pressure. Similarly, different snow conditions can change the relatively vulnerability of caribou to predation (Telfer & Kelsall, 1984). Predation pressure is an important factor, as caribou not judging this risk correctly will be killed. However, if a caribou is weakened from poor nutrition and killed by a predator, the ultimate factor in its death is habitat quality - predation would be its proximate cause. Too often, this distinction is not made.

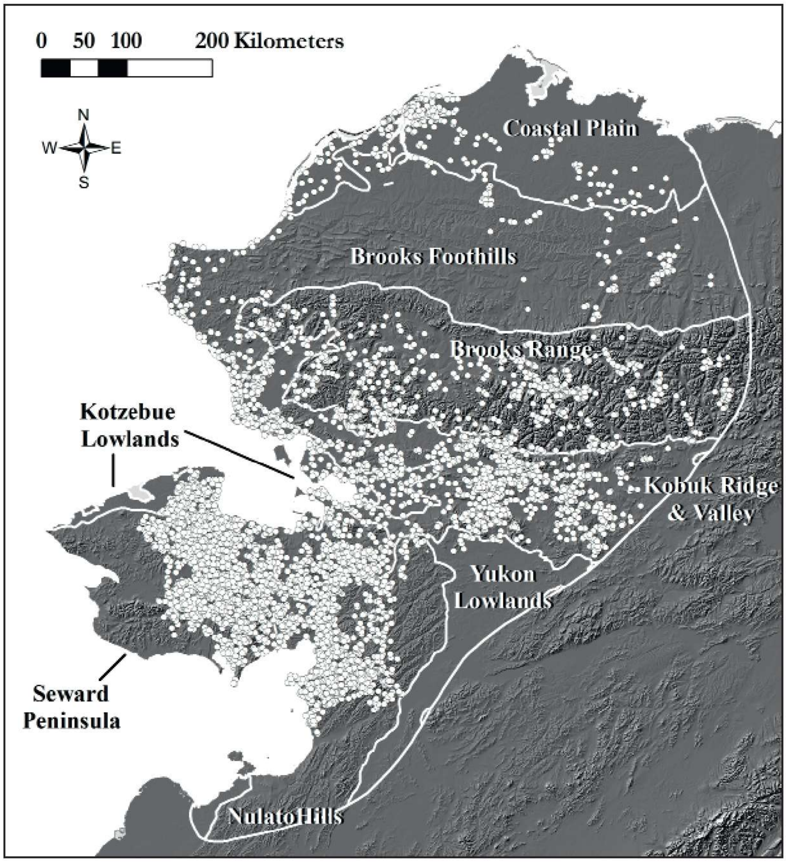

Fig. 1. Distribution of Western Arctic Herd caribou, 1999 – 2005, during winter (October through April), northwest Alaska. Caribou locations acquired by satellite telemetry from 63 cows and 7 bulls are represented by light-colored dots. The ecoregions covering the range of the herd are labeled and outlined in light gray.

The WAH experienced a population crash in the 1970s, rapidly declining from approximately 242 000 individuals in 1970 to 75 000 individuals in 1976 (Dau, 2007). The herd rebounded, reaching a population apex of approximately 490 000 individuals in 2003 (Dau, 2007). At this height, the density of caribou was 1.35/km^2, which prompted concern about overgrazing (Joly *et al.*, 2007c). The 2007 photo-estimate revealed a 23% decline to 377 000 individuals – though the cause of the decline is unknown at this time (Dau, 2007). Significant declines in lichen cover within the core winter range (Joly *et al.*, 2007c) and/or severe winter events (Dau, 2005; 2007) are potential causes. Understanding the drivers of population changes in this herd is important because it serves as a subsistence resource for scores of villages that harvest more than 10 000 caribou annually from this 1 herd (Dau, 2007).

My goals were to 1) document winter distribution of caribou during the period of peak population and 2) determine factors that help explain why caribou go where they do during winter in northwestern Alaska. This information will provide valuable insight into the factors that shape caribou distribution as a basis for predictions of potential changes in caribou distribution if the population continues to decline and to model how the suitability of winter range may change for caribou under different climate-change scenarios.

Material and methods

Study area

The study area is the range of the WAH, which covers the entire 363 000 km^2 of northwestern Alaska (63° to 71°N and from 148° to 166°W; Dau, 2007) and contains 8 major ecoregions (Fig. 1, Nowacki *et al.*, 2001). The region transitions from treeless arctic tundra in the north and west to black spruce (*Picea mariana*) stands and eventually to boreal deciduous forests in the south and east. At the northern extreme of the study area, the Coastal Plain is primarily a flat, poorly drained wetland that is underlain by continuous permafrost. The ground of the Brooks Foothills, to the south, is composed of thick continuous permafrost and supports no trees. Low shrubs, sedges, and tussock tundra dominate this region but extensive willow thickets line the many braided rivers and streams (Nowacki *et al.*, 2001). The steep angular peaks of the Brooks Range are largely barren, while alpine vegetation can be found at lower elevations (Nowacki *et al.*, 2001). Forests and woodlands dominate much of the Kobuk Ridge and Valley ecoregion on the southern flanks of the Brooks Range (Nowacki *et al.*, 2001). The Kotzebue Lowlands lie to the west of the Kobuk Ridge and Valley ecoregion and is dominated by tundra and coastal ecosystems. The Seward Peninsula ecoregion is a mosaic of extensive hills, coastal lowlands and isolated rugged mountain complexes (Nowacki *et al.*, 2001). The moist polar climate supports tundra, dryas, and shrub communities (Nowacki *et al.*, 2001). To the east is the Nulato Hills, an ecoregion dominated by low but often rugged hills. Vegetation varies widely with elevation, from well-forested areas in the river valleys to shrubs on side slopes and alpine communities on the ridges and summits (Nowacki *et al.*, 2001). The Yukon Lowlands is dominated by the confluence of the Yukon and Koyukuk Rivers which forms an expansive wetland system complex of deciduous and coniferous forests, tall shrub and muskeg communities (Nowacki *et al.*, 2001).

Caribou can be found throughout their annual range during winter, though use is more concentrated on the Nulato Hills, upper Kobuk River and eastern Seward Peninsula (Joly *et al.*, 2007a). These regions are diverse, with extensive areas of treeless tussock tundra (*Eriophorum vaginatum*, *Carex* spp.), rugged but low elevation (< 1100 m) mountains, and shrub-lined (*Salix* spp., *Alnus crispa*) riparian corridors. Lichens (*Cladina* spp., *Cetraria* spp.), mosses (*Sphagnum* spp., *Polytrichum* spp.) and shrubs (*Betula nana*, *Empetrum nigrum*, *Ledum palustre*, *Vaccinium uliginosum* and *V. vitis-idaea*) are important components in tundra habitats (Joly *et al.*, 2007c). Mean annual precipitation for the region is about 300 mm. Snow cover occurs throughout the winter (October through April), though some areas may be snow free due to wind scouring or uncommon weather events that bring above freezing temperatures and rain. Although average daily temperatures can drop to – 45 °C during winter, the average daily temperature for the winter months is -3.3 °C. Mean temperatures have risen significantly over the study period in this region, especially during the winter (Stafford *et al.*, 2000).

Data acquisition and derivation

Caribou were captured as they swam across the Kobuk River at Onion Portage, located within Kobuk Valley National Park, using motorboats. A total of 70 caribou (63 cows and 7 bulls) were instrumented with satellite telemetry collars. Caribou location data were not used for a year after deployment to ensure adequate mixing with the entire herd (Dau, 2007). A total of 7048 locations from the beginning of October through the end of April were collected from 1999-2005. A total of 20 000 random locations were developed using ArcGIS within the range of the herd. Both the satellite and random locations were attributed with the following data that had potential to affect caribou distribution. Elevation was directly obtained from a Digital Elevation Model (DEM). Slope, aspect and terrain ruggedness indices were derived from the DEM using ArcGIS (ESRI, 2006) tools. I converted aspect from degrees into a categorical variable covering the 8 cardinal directions. I created 2 terrain ruggedness coverages, 1 at a relatively fine scale (180 m cell-size) and the other at a relatively coarse scale (1 km cell-size), using a Vector Ruggedness Measure (VRM) developed by Sappington *et al.* (2007). This measure incorporates variability in both the aspect and gradient components of slope so that steep, broken terrain can be distinguished from steep, even terrain (Sappington *et al.*, 2007).

I obtained habitat classification data at 2 scales. The National Land Cover Database of 2001 (NLCD; data available from the Multi-Resolution Land Characteristics Consortium, www.mrlc.gov, accessed November 13, 2008) covers the entire study area with 30 m resolution. The development of this dataset relied heavily on remotely sensed data. The study area was covered by the following broad habitat categories; deciduous forest, coniferous forest, mixed forest, scrub, shrub, sedge, woody wetlands, herbaceous wetlands, bare ground and open water. Forested areas were defined as having > 20% vegetation cover of trees > 5 m high. If there was > 75% of 1 type (not species) of tree it was defined as that type of forest, if neither deciduous nor coniferous trees dominated, then it was defined as mixed. Scrub habitats generally had > 20% cover of low (< 20 cm high) shrubs and were "often co-associated with grasses, sedges, herbs, and non-vascular vegetation". Shrub habitats were dominated by shrubs between 20 cm and 5 m high such as *Vaccinium uliginosum*, *Betula nana*, and *Salix glauca* but could include early successional or trees stunted by environmental conditions (*e.g.*, mesic black spruce stands overlaying permafrost). Sedge habitats were dominated (> 80% cover) by sedges, grasses and forbs. This class included tussock tundra. Woody wetlands were areas of forest or shrubland whose soils were periodically saturated with water. Herbaceous wetlands were dominated by herbs (> 80% cover) and had their soils periodically saturated with water.

The second coverage was a highly detailed habitat vector map, developed by the Soil Conservation Service (SCS; Swanson *et al.*, 1985), was based on extensive ground surveys and low-level photography of the entire Seward Peninsula. This coverage was utilized only when I was performing analyses dealing solely with the Seward Peninsula and represents a fundamentally different dataset and classification system. The SCS delineated over 150 different habitat types within the region. With assistance of local vegetation experts, I aggregated these types into 12 categories; dryas (*Dryas spp.*; 35 to 65% cover), lowland sedge, lowland low shrub, tussock tundra, lichen (> 24% cover), upland low shrub, tall shrub, forest, mountain meadow, burned tundra, burned forest and miscellaneous un-vegetated areas. Mountain meadow had > 30% graminoid cover whereas upland low shrub had < 25% graminoid cover. The lowland low shrub, mountain meadow, and tussock tundra can have a strong lichen component, with up to 25% cover. These data were from the 1980s, so burned areas are > 25 years old and did not include recent burns.

Data on wolf densities were specious or nearly 20 years old in the study area and so were not analyzed. Existing data for moose density was much more comprehensive, collected annually concurrent with the study period, and may be an index of wolf density (Bergerud, 2007). I also calculated, using the Hawth's Analysis Tools (Beyer, 2006) ArcGIS extension, the distance from every satellite collar location and every random location to the nearest of the 44 villages within the study area.

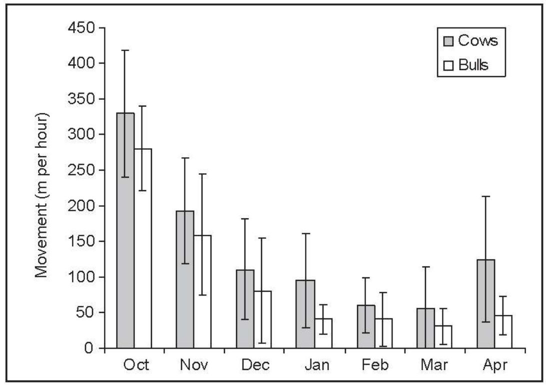

Fig. 2. Winter time movement rates of satellite collared Western Arctic Herd caribou from 1999-2005, northwest Alaska.

Statistical analysis

I used Analysis of Variance (ANOVA) to detect differences among months, between sexes in movement rates, and between satellite location and random points. I employed a logistic regression – resource selection function (RSF) approach to assess factors that influence caribou distribution during winter (Manley *et al.*, 2002). I selected Thomas and Taylor's (1990) Design II, where the locations of individually marked animals are pooled to study population level patterns. Selection or avoidance by caribou was relative to the random locations. Using an information theoretic approach, the best models were determined using Akaike's Information Criteria (AIC_c) for small sample sizes to determine the most parsimonious models (Burnham & Anderson, 2002). The full model was compared to the full model minus 1 factor using ANOVA techniques to determine significance of individual model parameters. Using the results of these analyses, I developed a resource suitability map. Significant factors were multiplied by beta coefficients derived from the best model, summed and the exponential was taken of the resultant. The final number represents the relative probability of selecting a given location as determined by the RSF (Manley *et al.*, 2002).

Results

Cows moved significantly more than bulls throughout the winter (140 m/hour versus 97 m/hr, respectively; $F_{1, 472} = 6.42$, $P = 0.01$; Fig. 2). Movement rates declined, for both cows and bulls, from October to December ($F_{1, 424} = 112.56$, $P < 0.01$, $F_{1, 42} = 21.65$, $P < 0.01$, respectively). Movement rates were lowest during mid to late winter. Cow movement rates (124 m/hr) were significantly greater than bulls (45 m/hr) during the month of April ($F_{1, 63}$ = 5.61, P = 0.02). Cows were found at lower elevations (298 m) and gentler slopes (18^0) than bulls (365 m, 23^0), but due to low sample sizes these differences were not significant ($F_{1, 68}$ = 2.06, P = 0.16, $F_{1, 68}$ = 3.33, P = 0.07, respectively). Because of these differences, I analyzed resource selection separately for bulls and cows.

The best resource selection function model for WAH cow distribution over the entire winter range incorporated slope, aspect, elevation, fine scale (180 m cell-size) terrain ruggedness, habitat and moose density (Table 1a). Cow distribution was positively correlated with slope and fine scale terrain ruggedness but negatively with elevation (Table 2a). Correlation with moose density was not significant. Aspect and habitat were significantly correlated with cow distribution as well (Table 2a). Cows significantly selected southwest to northwest aspects over others and avoided flat (no aspect) terrain (Table 2a). Scrub, shrub and sedge habitats were significantly preferred, while deciduous and mixed forests and perennial snowfields were used significantly less than expected. The resource suitability map, depicted in Fig. 3, reveals extensive areas of relatively high quality winter habitat in the western (Seward Peninsula ecoregion) and southern Nulato Hills. Areas with lower probability of use include the central Brooks Range and the Yukon Lowlands.

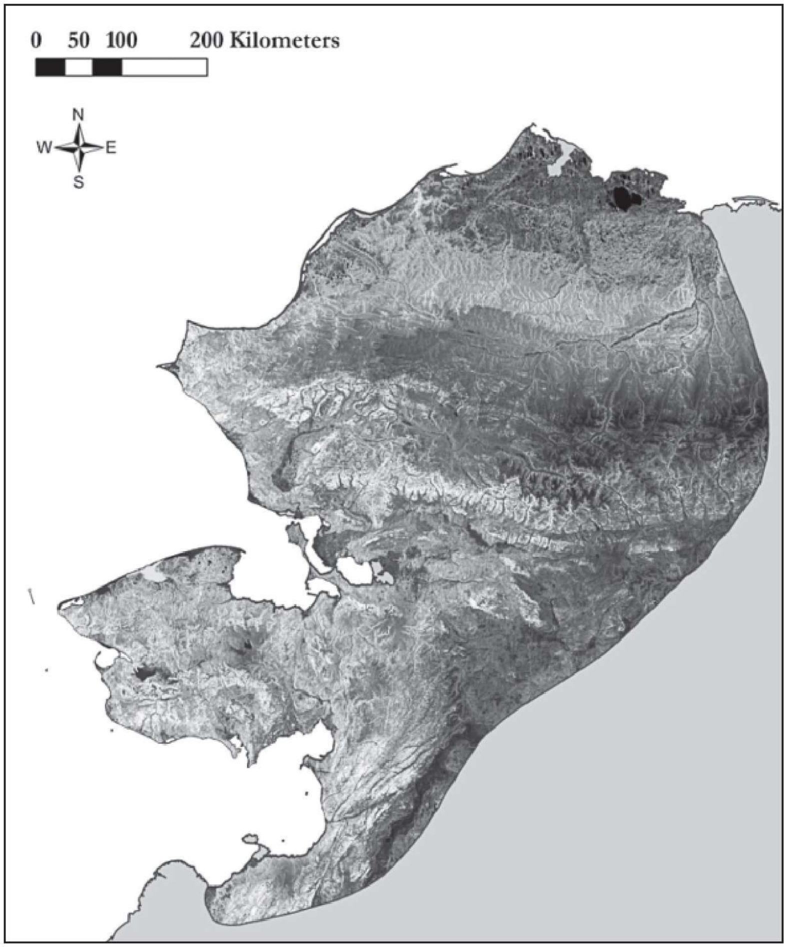

Fig. 3. Resource suitability map for Western Arctic Herd cow caribou during the winters (October through April) from 1999-2005, northwest Alaska. Lighter shades represent greater suitability (relative probability of selection).

Limiting the analysis to the Seward Peninsula, and using the more detailed SCS habitat map, the best model for cow winter distribution incorporated aspect, elevation, fine scale (180 m cell-size) terrain ruggedness, coarse scale (1 km cell-size) terrain ruggedness, habitat, and moose density (Table 1b). Cow distribution was positively associated with elevation but negatively with coarse scale terrain ruggedness and moose density (Table 2b). Aspect and habitat were significantly correlated with cow distribution (Table 2b). Cows significantly preferred northeastern aspects. Cows used lowland low shrub, tussock tundra, and mountain meadow habitats preferentially.

The differences between the analysis of the distribution of cows for the entire range and that focusing on the Seward Peninsula included: a change in the correlation with elevation from positive to negative, and negative correlations with moose density and coarse scale terrain ruggedness on the Seward Peninsula. By conducting a second analysis utilizing the range-wide (NLCD) vegetation classification, I was able to directly compare habitat selection for the entire winter and the Seward Peninsula. Selection was very similar for both regions. Cows significantly preferred dwarf scrub and sedge habitats and avoided coniferous forests in both regions. Correlations with deciduous forest (-), mixed forest (-) and dwarf shrub

Table 1. Model selection for Western Arctic Herd caribou distribution during winter (October through April) from 1999-2005, northwest Alaska. Analyses were conducted for cows and bulls for the entire winter range and just the Seward Peninsula.

A) Cows throughout the winter range

Model Parameters	df	AIC	ΔAIC
Aspect, Slope, Elevation, Ruggedness (180 m), Habitat, Moose	25	28687.83	-
Aspect, Slope, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	26	28688.09	0.26
Aspect, Slope, Elevation, Ruggedness (180 m), Habitat,	24	28688.09	0.26
Aspect, Slope, Elevation, Ruggedness (180 m and 1 km), Habitat	25	28688.31	0.48
Aspect, Slope, Elevation, Ruggedness (1 km), Habitat, Moose	25	28699.45	11.62

B) Cows on the Seward Peninsula

Model Parameters	df	AIC	ΔAIC
Aspect, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	24	8093.46	-
Aspect, Slope, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	25	8094.55	1.09
Aspect, Slope, Elevation, Ruggedness (1 km), Habitat, Moose	24	8094.69	1.23
Aspect, Slope, Elevation, Ruggedness (180 m and 1 km), Habitat	24	8096.75	3.29
Slope, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	17	8099.63	6.18

C) Bulls throughout the winter range

Model Parameters	df	AIC	ΔAIC
Slope, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	18	4329.08	-
Aspect, Slope, Elevation, Ruggedness (180 m and 1 km), Habitat	25	4330.56	1.48
Aspect, Slope, Elevation, Ruggedness (1 km), Habitat, Moose	25	4330.92	1.84
Aspect, Slope, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	26	4332.02	2.94
Aspect, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	25	4340.28	11.20

D) Bulls on the Seward Peninsula

Model Parameters	df	AIC	ΔAIC
Slope, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	17	1309.64	-
Aspect, Slope, Elevation, Ruggedness (180 m and 1 km), Habitat	24	1317.40	7.76
Aspect, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	24	1317.70	8.06
Aspect, Slope, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	25	1319.36	9.71
Aspect, Slope, Elevation, Ruggedness (1 km), Habitat, Moose	24	1319.43	9.79

Table 2. Comparison of coefficients of selection (βi) and standard errors (SE) of factors in the best models describing Western Arctic Herd caribou distribution in winter from 1999-2005, northwest Alaska. (+) indicates a positive correlation while (-) a negative one.

A) Entire winter range

	Cows (n = 63)		Bulls (n = 7)	
Factors	βi	SE	βi	SE
Aspect - SW	0.154 *	0.060		
Aspect - W	0.269 **	0.057		
Aspect - NW	0.145 *	0.058		
Aspect - Flat	-0.581 **	0.090		
Slope	0.021 **	0.001	0.016 **	0.004
Elevation	-0.001 **	0.001	-0.004 **	0.001
Ruggedness 180m	3.318 **	0.641		
Ruggedness 1km			4.044 **	0.870
Perennial snow	-2.890 **	1.010		
Deciduous forest	-0.717 **	0.220		
Coniferous forest			0.938 *	0.413
Mixed forest	-1.187 **	0.243		
Dwarf scrub	0.727 **	0.109	0.946 *	0.394
Shrub/scrub	0.436 **	0.112	0.813 *	0.400
Sedge	0.615 **	0.109		
Woody wetlands	0.269 *	0.136		

* $P < 0.05$, ** $P < 0.01$

B) Seward Peninsula

	Cows (n = 63)		Bulls (n = 7)	
Factors	βi	SE	βi	SE
Aspect - NE	0.239 *	0.109		
Elevation	0.001 **	0.001	0.001 **	0.001
Ruggedness 1km	-5.670 **	0.780	-8.169 **	2.861
Burned tundra			-1.320 *	0.560
Dryas			0.817 *	0.365
Lowland low shrub	1.016 *	0.516		
Lowland sedge			-1.327 **	0.408
Tussock tundra	1.276 *	0.507		
Upland low shrub			-1.148 *	0.481
Moose density	-0.273 *	0.134		

* $P < 0.05$, ** $P < 0.01$

(+) were not significant for the Seward Peninsula, but showed the same tendency as the correlations did for the entire winter range.

Analyses of bull distribution should be viewed with caution due to limited sample size (n = 7). The best resource selection function model for bull distribution over the entire winter range incorporated slope, elevation, fine and coarse scale (180 m and 1 km cell-size) terrain ruggedness, habitat, and moose density (Table 1c). Bull distribution was positively correlated with slope and coarse scale terrain ruggedness, but negatively correlated with elevation (Table 2a). Habitat was significantly correlated with bull distribution (Table 2a). Bulls selected scrub and coniferous forest habitats. Bull distribution differed from cows in that they were 1) positively associated with coarse scale, not fine scale, terrain ruggedness, and 2) did not show avoidance of deciduous forests and 3) associated with fewer habitat classes.

Limiting the analysis to the Seward Peninsula and the SCS habitat map, the best model for bull distribution incorporated slope, elevation, fine and coarse scale (180 m and 1 km cell-size) terrain ruggedness, habitat, and moose density (Table 1d). Bull distribution was positively correlated with elevation but negatively with coarse scale terrain ruggedness (Table 2b). Bulls showed significant preference for dryas communities, while avoiding burned tundra, lowland sedge, and upland low shrub communities (Table 2b). Similar to cows, the range-wide analysis for bulls revealed a negative correlation between distribution and elevation whereas on the Seward Peninsula the correlation was positive. Also, the correlation with coarse scale terrain ruggedness changed from positive to negative moving from the range-wide to Seward Peninsula analyses. Caribou locations (49.7 km ± 0.5 km) were significantly closer to villages than random locations (68.6 km ± 0.3 km) within the study area ($F_{1,27047}$ = 1272.25, P < 0.01).

Discussion

A complex interaction of multiple, interrelated factors drive the winter distribution of WAH caribou. My results suggest that studies that focus on a single factor as the presumed determinant of caribou population distribution or dynamics may fail to capture the full, actual situation except under rare cases. The relative importance of predators, habitat, and other factors will be very case specific (Skogland, 1991). For the WAH, all 3 general factors I analyzed (terrain, habitat and predation pressure) were correlated with caribou distribution in winter. Other factors, such as disturbance from wildfire (Joly *et al.*, 2007c; Joly *et al.*, 2010) and industrial development (Vistnes & Nellemann, 2008), which I did not analyze, might also be important for the WAH and other northern caribou herds. By analyzing multiple factors, researchers also garner insight into the cumulative effects these factors may have on caribou (see also Nellemann & Cameron, 1998; Johnson *et al.*, 2005).

The nature and relative importance of terrain features on WAH caribou distribution depended on scale – both of the landscape features themselves and of the extent of the study area. Caribou preferred relatively lower elevations across their winter range but relatively higher elevations on the Seward Peninsula. Average elevation was significantly higher on the winter range outside the Seward Peninsula than within it. Thus selection or avoidance of certain terrain features depends on the landscape available to WAH caribou. Two factors that may help explain these results are vegetation and snow, which are related to both elevation and differ between the entire range and just the Seward Peninsula. Higher terrain is common throughout the herd's range (e.g., the Brooks Range) and is associated with sparsely or non-vegetated areas; providing little forage and thus caribou would utilize relatively low terrain. Relatively high terrain is much more limited on the Seward Peninsula. Furthermore, the Seward Peninsula is a maritime climate and receives more snow on average than most of the range which experiences climate conditions more typical of continental areas. Deep snows accumulate in the lowlands of the Seward Peninsula and would explain caribou preference for relatively higher elevations there as ridges tend to be more windswept and have lower snow depths in general. Ridges with low snow accumulation tend to enhance the predictability of winter range use (Russell *et al.*, 1993). A similar, but opposite, relationship was found with coarse scale terrain ruggedness between these regions. This suggests that there may be threshold values of terrain features where caribou usage will be greatest. WAH cows showed a positive relationship with fine scale terrain ruggedness over the entire winter range. This uneven terrain may provide a diversity of habitats for foraging and softer snow conditions that allow access.

Cow distribution on the Seward Peninsula was negatively correlated with moose density. This result may seem intuitive as caribou tend to avoid habitat that has recently burned (Joly *et al.*, 2007a; Joly *et al.*, 2010), whereas moose select for it (Maier *et al.*, 2005). Furthermore, high moose densities could support high wolf densities which would reduce its suitability for caribou (Bergerud, 2007). However, moose density was not well correlated with cow distribution throughout the winter range or bull distribution at either scale, and these relationships were positive in nature. A positive correlation between caribou and wolf density could develop if wolves were successful in areas that had consistently high caribou densities during winter. Thus the lack of significant correlations among moose density and cow (entire winter range) and bull (both over the entire winter range and the Seward Peninsula) distribution may indicate that moose density may not be an adequate index of wolf density and/or the effects of predator densities on caribou distribution is more complicated than simple selection or avoidance.

WAH cows avoided forested areas across the winter range and preferred scrub, shrub and sedge habitats, highlighting the long-known importance of tundra habitats (Murie, 1935; Skoog, 1968). I found a strong agreement between the habitat associations throughout the winter range and those found on the Seward Peninsula for WAH cows. These habitat types typically have relatively high lichen cover (Swanson *et al.*, 1985). Lichens are an important component of the winter diet of WAH caribou, making up a majority of their forage (Saperstein, 1996; Joly *et al.*, 2007b). Concurrent with major declines in lichen cover within the core winter range of the WAH (Joly *et al.*, 2007c) and the percentage of lichens in their winter diet (Joly *et al.*, 2007b), the size of the WAH peaked and has declined for the first time in 30 years. Though only anecdotal, this evidence supports the theory (Klein, 1991) that lichens may be a critical component of the winter diet of large migratory herds in North America (see also Holleman *et al.*, 1979). This does not, however, refute the importance of predators on *Rangifer* population dynamics, especially at lower densities. Nor does it preclude the possibility that other factors, such as severe winter weather (Dau, 2007; Joly *et al.*, 2011), are the major driver or have had additive effects.

The distribution of bulls differed from that of cows. Preference of habitat types was muted in comparison to cows, though bulls avoided lowland sedge habitats. Bulls were found at higher elevations and steeper slopes than cows. These conditions are often associated with more open habitats, as was seen with the affinity for dryas community types on the Seward Peninsula by bulls. Also, bull distribution was not correlated with fine scale terrain ruggedness, as cow distribution was. These differences in distribution point to the use of alternative overwintering strategies between the sexes.

Though hampered by low sample sizes, my analyses suggest that bulls may be adopting an energy conservation strategy that favors reducing exposure to predation, whereas cows are sacrificing exposure to predators in return for maximizing energy intake by utilizing habitats with greater lichen forage. Higher movement rates by WAH cows, as compared to bulls, throughout the winter months supports this theory of differing overwintering strategies (Roby & Thing, 1985). Vigilance alone does not explain these differences as bulls found in higher, open habitat could identify approaching predators at a greater distance than foraging cows but the large group sizes of cow and young caribou would improve vigilance relative to the smaller bull groups. The smaller group sizes would allow bulls to utilize smaller patches and exert less grazing pressure within an area. Cows, which retain their antlers over the winter, would also have a competitive advantage in maintaining and/or usurping optimal foraging locations and feeding craters (see Holand *et al.*, 2004).

Ultimately, the trade-offs between predatory exposure and forage intake are likely due to differing energetic demands. A vast majority of cows are pregnant during the winter months; this extra energetic demand may induce cows to try to maximize energy intake through foraging rather than adopting an energy conservation strategy utilized by bulls. These strategies may be reversed in spring when cows head towards calving grounds with lower predator densities and bulls lag behind consuming emergent green vegetation high in protein content (Heard *et al.*, 1996).

The RSF map (Fig. 3) reveals higher probability of use in the Nulato Hills and Seward Peninsula. Use of the northern Brooks Foothills by WAH caribou has been limited despite moderately high probability of use as determined by the RSF (Fig. 1, Fig. 3). This lends further support to the argument that lichens are an important winter forage for WAH caribou, as forage lichen abundance is very low in this ecoregion but snow depths and wolf densities are favorable (both low) for caribou compared to other portions of the winter range. However, limitations in the RSF cannot be ruled out as an explanation for this discrepancy. Expansion of the winter range to the southeast, into the Yukon Lowlands ecoregion seems unlikely as the probability of use as determined by the RSF was quite low. Furthermore, this area already supports high wolf densities without having regular or extensive usage by the WAH, more wildfire, and lower biomass of lichens (Joly *et al.*, 2010). The western reaches of the Seward Peninsula have not been extensively used by the herd, had high probability of use and thus represent an area that has potential as an area for the herd to expand its winter range. This portion of the Seward Peninsula includes the largest towns and remaining reindeer (*Rangifer tarandus tarandus*) herds in the region, which could present problems if the herd did expand its range there (Dau, 2000).

Management implications

In order to better understand caribou distribution in winter, better information on predator densities, habitat, snow conditions, and weather should be collected. While efforts are currently underway to improve our understanding of most of these factors, it cannot be said for predator densities. To better understand caribou distribution and population dynamics in northwest Alaska, improved information is needed on predator distribution, predator abundance, predation rates and the factors that regulate them. A transition from traditional satellite collars to GPS-satellite collars will improve researchers' ability to analyze caribou movements, distribution and habitat use within the region (Joly, 2005; Joly *et al.*, 2010). Dramatic changes are taking place rapidly in the Arctic and on the winter range of the WAH specifically (ACIA, 2005; Joly *et al.*, 2007c). The analyses presented here provide a useful foundation for modeling the effects of future potential climate regimes on the abundance and quality of caribou winter range in northwest Alaska.

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