

DISTRIBUTION, ABUNDANCE, AND QUALITY OF FORAGE WITHIN THE  
SUMMER RANGE OF THE CENTRAL ARCTIC CARIBOU HERD

A

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By

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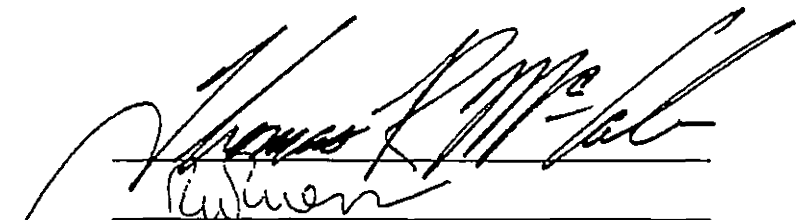
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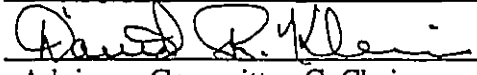
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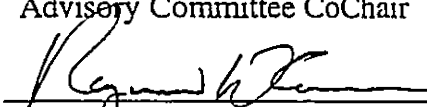
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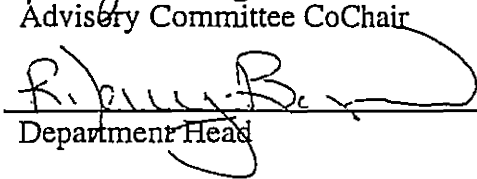
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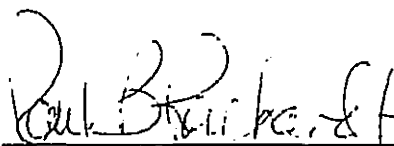
  
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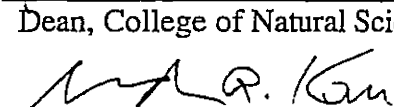
  
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## ABSTRACT

Distribution, abundance, and quality of summer forage available to caribou (*Rangifer tarandus granti*) of the Central Arctic Herd were determined in July and August, 1989 - 1990. Plant cover, an index of available biomass, was measured at three sites within 50 km of the arctic coast. In general, plant cover increased with distance from the coast. Cover of forbs and evergreen shrubs was higher at inland sites ( $P < 0.001$ ), whereas cover of willows (*Salix* spp.) was highest at the coastal site ( $P < 0.001$ ). Higher plant cover inland is largely attributable to a greater proportion of drier habitats. Differences in forage quality among sites, however, were small and inconsistent. I conclude that by feeding inland during insect-free periods, caribou realize a net energy benefit, because of higher plant biomass, higher proportion of drier habitat, and greater species diversity than coastal areas.

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## INTRODUCTION

During July and early August, caribou (*Rangifer tarandus granti*) of the Central Arctic Herd (CAH), move primarily in response to changes in insect activity. During warm, calm periods, insect activity increases, and caribou move toward the arctic coast (White *et al.*, 1975; Roby, 1978; Smith and Cameron, 1985a; Dau, 1986; Cameron *et al.*, 1995). If insect activity remains high, caribou may continue moving along the coast into the prevailing northeasterly winds. Under extreme harassment, they wade into the Beaufort Sea for relief (White *et al.*, 1975; Cameron, pers. comm.). With lower temperatures and/or higher wind velocities, insect activity declines, and caribou disperse inland (White *et al.*, 1975; Roby, 1978; Dau, 1986; Cameron *et al.*, 1995).

Responses of caribou to insect harassment differ with the insect species present. In early summer (late June through mid-July), movements are predominately mosquito-induced (Culicidae: *Aedes nigripes*, *A. impiger*, and *A. cataphylla*). In late summer, (late July through early August), oestrid flies (Oestridae: warble flies *Oedemagena tarandi* and nasal bot flies *Cephenemyia trompe*) become increasing influential. There is, however, considerable temporal overlap, as mosquitoes are active until late in the season (Roby, 1978; Dau, 1986).

Typically, caribou respond to harassment by mosquitoes by decreasing time spent feeding and increasing time spent moving (Curatolo, 1975; White *et al.*, 1975; Roby, 1978; Dau, 1986). Aggregations form in which "predator swamping" reduces individual



exposure to mosquitoes (Helle and Aspi, 1983; Dau, 1986); these groups seek areas of lower insect activity, such as cooler coastal areas and unvegetated river deltas, sand dunes, and gravel pads (Child, 1974; Roby, 1978; Fancy, 1983; Murphy and Curatolo, 1987).

Caribou tend not to aggregate when harassed only by oestrid flies (Roby, 1978). Instead, groups may fragment into individuals and pairs and move to coastal or other unvegetated areas (Dau, 1986). Typically, caribou react by standing motionless, head down, occasionally shaking or snorting (Roby, 1978; Dau, 1986). Under extreme harassment, they may run aberrantly for long periods (Curatolo, 1975).

Coastal areas provide some relief from this harassment because of lower activity of insects there (White *et al.*, 1975; Roby, 1978; Dau, 1986; Nixon 1991). The cooler, windier conditions within 3 km of the coast are generally unfavorable for mosquitoes (Dau, 1986) Occupying coastal areas, therefore, allows caribou to reduce the frequency of energetically costly behavior, such as running, and to minimize the loss of feeding time (White *et al.*, 1975; Dau, 1986; Fancy, 1986).

When insect activity declines caribou move inland, although the process usually is more gradual and less directed than movements to the coast (Dau, 1986). Nonetheless, movements can be rapid, especially after caribou have remained in coastal areas for an extended period (i.e., >3 days) (Dau, 1986).

Ostensibly, caribou move inland for better foraging opportunities (White *et al.*, 1975, Whitten and Cameron, 1980; Cameron, 1983; Smith and Cameron, 1985; Dau, 1986; Fancy, 1986; Walsh *et al.*, 1992). In so doing, they presumably maximize energy intake during periods of low insect activity, a benefit that outweighs the energetic cost of moving between coastal and inland areas. To examine the validity of this assumption, I tested the following hypothesis:

(H<sub>0</sub>): The abundance and quality of forage species does not differ between coastal and inland areas.

I compared the cover of plant lifeforms and species, and the nutrient quality of 7 key forage species, in coastal and inland areas. Using some of these data, I then modeled the energetic costs and benefits of moving to, and foraging in inland areas versus remaining in coastal areas. Finally, I discuss the potential consequences of future oilfield development along the arctic coast on the CAH.

## METHODS

### STUDY AREA

The study area was located on the Arctic Coastal Plain of Alaska and included the Kuparuk Development Area (KDA), which is approximately 50 km west of Prudhoe Bay (148° W; 70° 15' N). The KDA comprises all or part of 3 producing oil fields that together form an extensive system of roads, well pads, pipelines, and processing and support facilities (Figure 1). The area is poorly drained coastal tundra with oriented thaw-lakes (Webber and Walker, 1975). Coastal fog is common in summer. Mean July temperature at the coast is ~ 5°C, whereas 40-50 km inland it is ~ 8°C (Walker, 1980).

### VEGETATION SAMPLING

#### *Plant Cover*

Three study sites were sampled, one at the coast (CST), a second 45 km inland (INL), and a third approximately midway between (MID). Each site was 6.4 km (4 mi) long (E-W) and 3.2 km (2 mi) wide (N-S), ~ 20.5 km<sup>2</sup> (8 mi<sup>2</sup>) in total area, composing eight 2.6-km<sup>2</sup> sections (USGS 1:63,000 topographic map). The INL site marked the approximate southernmost extent of coastal and inland movements of the CAH during summer (Cameron, pers. comm.) (Figure 2).

Sites were sampled three times in 1989 and 1990: 1-6 July, 13-18 July, and 25-30 July. For each period, vegetation cover was sampled on 4 east-west line transects, each

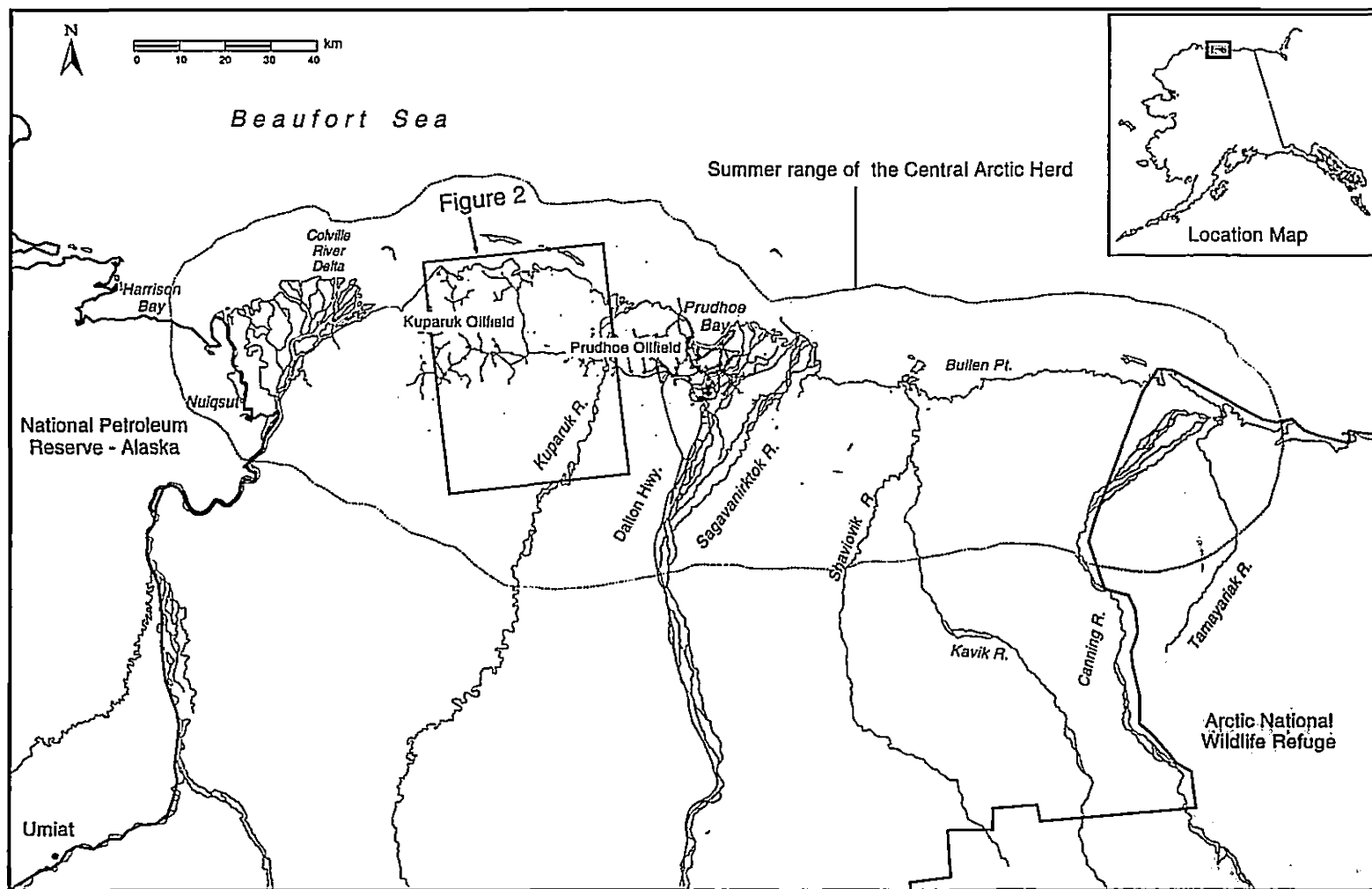


Figure 1. Location of the study area and approximate summer range of the Central Arctic caribou herd (95% adaptive kernel contour based on locations of radio-collared females, 1988-93; Cameron, unpublished data).

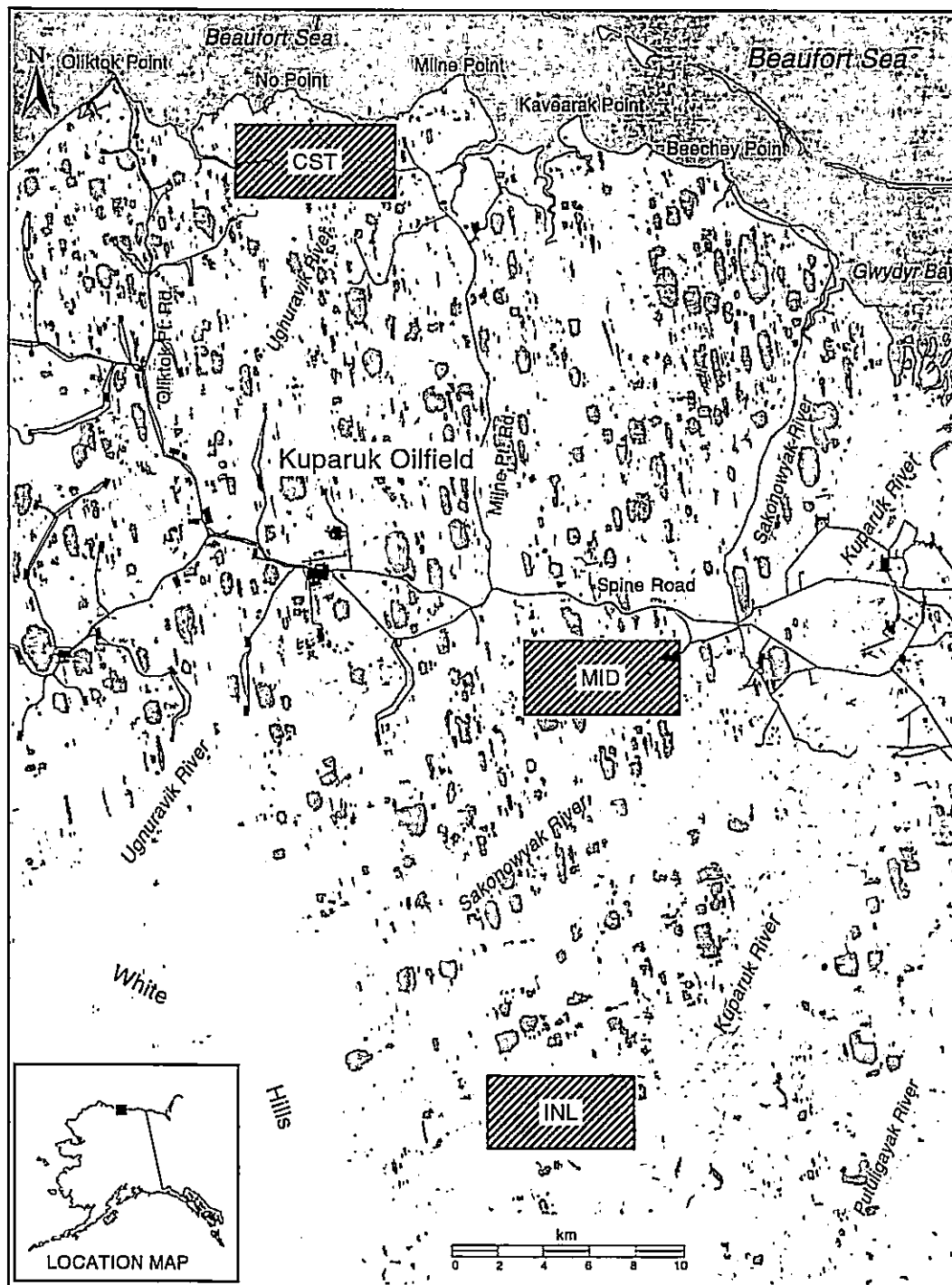


Figure 2. Vegetation sampling sites in the Kuparuk region, Alaska, 1989-90.

with a randomly chosen starting point. For a particular site, two transects were sampled per day for 2 consecutive days. Sampling began at the CST site and ended with the INL site (e.g., 1-2 July at CST, 3-4 July at MID, 5-6 July at INL). The starting point for each transect was estimated using 1:18,000 true-color aerial photographs. Sampling was at 100-m intervals, measured by counting paces, beginning at the end of the first 100-m interval. Navigation along the transect lines was by compass heading and reference to ground features on the aerial photographs.

At each 100-m interval, the prevailing community type was recorded after Walker's (1983) Hierarchical Tundra Vegetation Classification (Appendix A). Plant cover was estimated with a 1-m long, 10-pin, point-frame (Mueller-Dombois and Ellenberg, 1974). Sharpened metal pins were lowered, and all plant species intercepted was recorded. More than one hit per pin was possible if multiple layers of vegetation were present. Species were assigned to classes based on lifeform (Appendix B). Percent cover was calculated by dividing the total number of hits of each species or lifeform by the total number of possible pins for each transect.

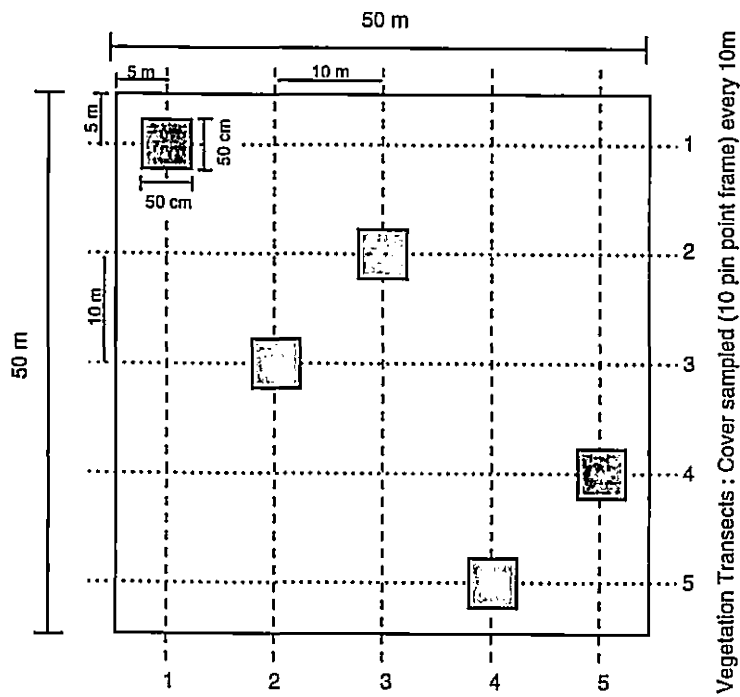
#### *Biomass-to-cover Relationships*

A double-sampling approach was used to relate biomass to cover. Sampling was done during 1-9 August, 1989-90, for 6 key species only: sedges *Carex Bigelowii*, *C. aquatilis*, *Eriophorum angustifolium*, and *E. vaginatum*, and the willows *Salix arctica* and *S.*

*pulchra*. At each site, 16-18 plots were sampled. These plots were placed subjectively in many habitats to sample a wide range of cover for each key forage species. Plots were 50 by 50-m, in which 5, 50-m transects were placed starting at 5, 15, 25, 35, and 45 m along one side (Figure 3). Cover was estimated every 10 m along each transect as described previously. A 50 by 50-cm area, at one randomly selected point-frame sampling location along each transect, was clipped at root level for sedges; for willows, only leaves and floral parts were removed (Figure 4). Samples were dried at 60°C to a constant weight (generally ~ 48 h) and weighed to the nearest 0.1 g. Percent cover of each species was calculated as already noted and paired with the biomass sample for that transect.

#### *Forage Quality*

Samples for nutrient analysis were collected on the second day of cover sampling at each site for each time period. Sample (enough for ~2-3 g dry weight) of each of the 6 key species and the forb *Pedicularis* spp. were collected at various points along each transect, in an attempt to characterize the entire site. Again, sedge and forb species were cut at root level, and willow leaves and floral parts removed (Figure 4). All samples were sealed in plastic bags and frozen until analyzed. Two subsamples of each species were oven-dried at 60°C to a constant weight (generally ~ 48 h) and ground in a Wiley mill with a 20 mm mesh screen.



Clip Plot Locations ( 1 per veg transect; random order)

Figure 3. Design and layout of biomass-to-cover double sampling plots at study sites.

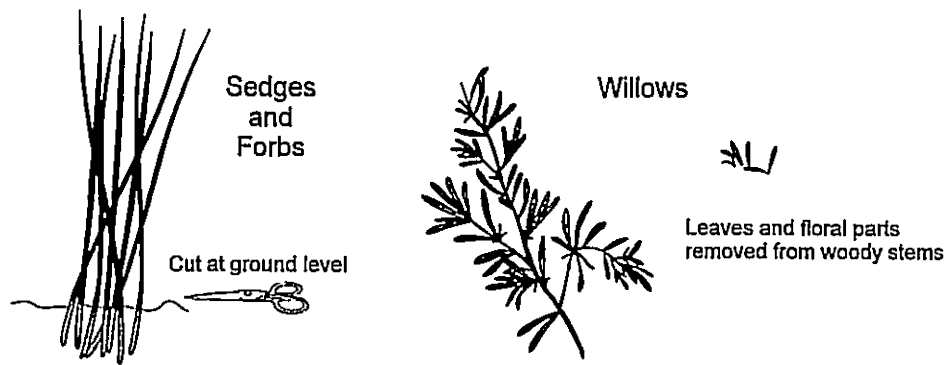


Figure 4. Protocol for collecting biomass samples in a biomass-to-cover double sampling plot and for forage quality analyses.



One set of subsamples was sent to Palmer Research Center, University of Alaska, and analyzed for nitrogen (N), acid detergent fiber (ADF), and neutral detergent fiber (NDF). *In vitro* dry matter digestibility (IVDMD) was determined on the second set of subsamples using fistulated caribou (Person *et al.*, 1980) at the Large Animal Research Station, University of Alaska Fairbanks.

## STATISTICAL ANALYSES

### *Plant Cover*

SAS statistical software (SAS Institute, 1989) was used for all analyses. Data on cover, expressed as percentages, were square root-arcsine transformed to stabilize variances. Reported means are based on nontransformed data, but F and P-values are based on transformed data. Bartlett-Box tests ( $\alpha = 0.05$ ) were used to verify homoscedasticity of variances.

A Multivariate Analysis of Variance (MANOVA; Johnson and Wichern, 1982) was used to determine differences in percent cover for all plant lifeforms by location (CST, MID, INL) and time period (1-6 July, 12-18 July, and 24-30 July) and to determine differences in percent cover for individual species by location and time period. Analysis of variance (ANOVA) was then used for each lifeform species. Tukey's Honestly Significant Different (HSD) pairwise comparison test was used to determine differences between treatments ( $\alpha=0.05$ ).

### *Site Comparisons by Habitat Type*

Plant cover recorded at each 100-m interval was classified by habitat type (after Walker, 1983) and grouped to produce 7 habitat types: water; wet tundra; moist tundra; moist tussock sedge-low shrub tundra; shrubland; partially vegetated; and barrens (Appendix A). Percent cover was recalculated by habitat type for each transect. The habitats designated water and barrens were not analyzed, because they both composed one recorded type (water and bare soil, respectively). Additionally, the habitats shrubland and partially vegetated were regrouped with moist tussock sedge-low shrub tundra, because the sample size was too small for analysis. ANOVA's were used to test for differences in each lifeform and individual species, and Tukey's HSD tests were used to determine differences among sites.

### *Biomass-to-cover Relationships*

For the paired cover (%) and biomass values ( $\text{g/m}^2$ ), simple linear regressions were calculated and tested for significance. An analysis of covariance (ANCOVA) by species was performed to examine among-site (covariate) differences in the slopes of the regression lines.

### *Forage Quality*

ANOVA was used to compare variables reflecting forage quality: crude protein ( $\text{N} \times 6.25$ ), ADF, cell solubles ( $1 - \text{NDF}$ ), hemicellulose ( $\text{NDF} - \text{ADF}$ ), and IVDMD for each key species. Tukey's HSD was used to determine differences by site.

## RESULTS

### PLANT COVER

The overall MANOVA for lifeform and species was significant for location ( $P = 0.023$ ; Pillias F), but not for time period ( $P = 0.132$ ; Pillias F). Accordingly, time periods were pooled, which increased sample size from 8 to 24 transects per site.

#### *Overall Site Comparisons*

In general, plant cover increased with distance from the coast (i.e.,  $CST < MID < INL$ ) (Table 1). Percent cover of evergreen shrubs, forbs, fruticose lichens, sedges, and mosses was higher at the inland sites (MID and INL). Although the  $P$ -value ( $P = 0.066$ ) for fruticose lichens and sedges was  $> 0.05$ , according to the Tukey's test differences were significant. In contrast, willow cover was highest at the CST site, as was crustose lichen cover and abiotic cover (i.e., water, litter, sand).

Cover of individual plant species by site (Appendix B) was usually similar to the assigned lifeform. Patterns for some species, however, were quite different. For example, cover values for *Carex aquatilis*, *Vaccinium vitis-idaea*, and *Dactylina arctica* were highest at the CST site.

Table 1. Mean (SE) percent cover categorized by lifeform by site, Kuparuk region, Alaska, 1989-90.

Lifeform	CST (n=24)	MID (n=24)	INL (n=24)	F	P-value
	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>		
<b>Forage</b>					
Shrubs	1.99 (0.24) <sup>A</sup>	4.04 (0.32) <sup>B</sup>	3.25 (0.33) <sup>B</sup>	13.4	<0.01
Fruticose Lichens	1.56 (0.19) <sup>A</sup>	2.16 (0.19) <sup>B</sup>	2.17 (0.26) <sup>B</sup>	2.9	0.06
Forbs	0.29 (0.07) <sup>A</sup>	0.51 (0.07) <sup>B</sup>	0.79 (0.10) <sup>B</sup>	12.4	<0.01
Grasses-Sedges	6.07 (0.35) <sup>A</sup>	6.73 (0.39) <sup>B</sup>	7.35 (0.43) <sup>B</sup>	2.8	0.07
Willows	4.07 (1.29) <sup>A</sup>	2.01 (0.85) <sup>B</sup>	2.72 (0.93) <sup>C</sup>	25.0	<0.01
<b>Nonforage</b>					
Abiotic-Litter	71.17 (2.00) <sup>A</sup>	66.60 (1.72) <sup>A</sup>	60.16 (1.69) <sup>B</sup>	10.0	<0.01
Crustose Lichens	0.59 (0.08) <sup>A</sup>	0.32 (0.08) <sup>B</sup>	0.17 (0.05) <sup>B</sup>	11.3	<0.01
Mosses	14.29 (1.45) <sup>A</sup>	17.73 (1.75) <sup>A,B</sup>	23.58 (1.91) <sup>B</sup>	7.7	<0.01

<sup>1</sup> Means with the same letter (Tukey HSD at  $P \leq 0.05$ ) are not significantly different by site.

For willows, cover differed by growth form. Prostrate willows occurred at the coast, whereas upright willows were more common inland. Percent cover of prostrate willows, *Salix phlebophylla*, *S. reticulata*, *S. rotundifolia*, and *S. pulchra*, was highest at the CST site. Cover of upright willows, *S. arctica* and *S. lanata*, was highest at the MID and INL sites, respectively (Appendix B).

#### *Site Comparisons by Habitat Type*

Differences in plant lifeform by site were greatly reduced when partitioned by habitat type. Even so, some differences among sites remained, with higher cover at the MID and INL sites. Habitat distribution was also different by site. The MID and INL sites contained a greater proportion of moist tundra and moist tussock sedge-low shrub tundra, and a slightly greater proportion of wet tundra habitat types. The CST site had a greater proportion of barrens habitat (Table 2).

There were no differences in percent cover of any of the lifeforms by site for wet tundra (Table 3a). Percent cover of two species of sedges was higher at the MID and INL sites; one species of lichen was higher at the CST and MID sites (Appendix C).

Table 2. Percentages of grouped<sup>1</sup> habitat types by site, Kuparuk region, Alaska, 1989-90.

Habitat Type	CST	MID	INL	All Sites
Water	6.9%	9.5%	8.8%	8.2%
Wet tundra	13.8%	19.0%	17.5%	16.4%
Moist tundra	20.7%	28.4%	26.3%	24.6%
Moist tussock sedge-low shrub tundra	30.5%	40.1%	42.3%	36.9%
Barrens	28.2%	3.0%	5.1%	13.9%

<sup>1</sup> Habitats groupings are shown in Appendix A.

Table 3a. Mean (SE) percent cover of plant lifeform by site in habitats classified as wet tundra, Kuparuk region, Alaska, 1989-90.

Lifeform	CST (n=24)	MID (n=24)	INL (n=24)	F	P-value
	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>		
<b>Forage</b>					
Evergreen Shrubs	0.56 (0.11)	0.58 (0.26)	0.53 (0.19)	0.8	0.51
Foliose Lichens	0.57 (0.15)	0.30 (0.15)	0.26 (0.14)	2.9	0.06
Forbs	0.27 (0.09)	0.21 (0.09)	0.42 (0.13)	1.0	0.47
Grasses-Sedges	6.90 (0.67)	7.43 (0.99)	7.28 (0.76)	0.1	0.95
Willows	0.53 (0.13)	0.56 (0.14)	0.42 (0.17)	2.8	0.36
<b>Nonforage</b>					
Abiotic-Litter	73.90 (2.67)	74.18 (2.85)	79.24 (2.78)	1.8	0.17
Crustose Lichens	0.10 (0.05)	0.00 (0.00)	0.08 (0.06)	1.5	0.24
Mosses	16.08 (2.33)	11.32 (2.44)	15.65 (2.87)	2.2	0.12

Table 3b. Mean (SE) percent cover of plant lifeform by site in habitats classified as moist tundra, Kuparuk region, Alaska, 1989-90.

Lifeform	CST (n=24)	MID (n=24)	INL (n=24)	F	P-value
	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>		
<b>Forage</b>					
Evergreen Shrubs	3.76 (0.39) <sup>A</sup>	6.47 (0.72) <sup>B</sup>	3.93 (0.43) <sup>A</sup>	7.6	<0.01
Fruticose Lichens	2.95 (0.37)	3.68 (0.48)	2.98 (0.46)	1.1	0.35
Forbs	0.42 (0.09)	0.90 (0.16)	0.99 (0.22)	3.0	0.06
Grasses-Sedges	9.06 (0.56)	9.57 (0.61)	8.10 (0.49)	1.7	0.19
Willows	3.70 (0.45) <sup>A</sup>	1.42 (0.18) <sup>B</sup>	2.49 (0.24) <sup>C</sup>	15.3	<0.01
<b>Nonforage</b>					
Abiotic-Litter	53.43 (2.51)	49.29 (2.59)	51.62 (2.64)	0.7	0.52
Crustose Lichens	1.03 (0.16) <sup>A</sup>	0.60 (0.22) <sup>B</sup>	0.18 (0.07) <sup>B</sup>	12.1	<0.01
Mosses	22.26 (1.89)	26.69 (2.59)	28.75 (2.64)	1.8	0.18

Table 3c. Mean (SE) percent cover of plant lifeform by site in habitats classified as moist tussock sedge-low shrub tundra, Kuparuk region, Alaska, 1989-90.

Lifeform	CST (n=24)	MID (n=24)	INL (n=24)	F	P-value
	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>		
<b>Forage</b>					
Evergreen Shrubs	2.97 (1.05) <sup>A</sup>	11.47 (1.63) <sup>B</sup>	7.86 (0.95) <sup>B</sup>	19.4	<0.01
Fruticose Lichens	3.05 (0.88)	5.22 (0.96)	4.67 (0.79)	2.6	0.08
Forbs	0.18 (0.18) <sup>A</sup>	0.58 (0.17) <sup>A,B</sup>	1.44 (0.32) <sup>B</sup>	9.5	<0.01
Grasses-Sedges	11.33 (1.61)	12.14 (1.15)	9.53 (0.96)	1.1	0.34
Willows	7.08 (1.40) <sup>A</sup>	2.23 (0.55) <sup>B</sup>	2.51 (0.58) <sup>B</sup>	5.0	<0.01
<b>Nonforage</b>					
Abiotic-Litter	37.89 (3.38)	37.27 (2.57)	35.22 (1.79)	0.1	0.87
Crustose Lichens	2.39 (0.77) <sup>A</sup>	0.45 (0.15) <sup>B</sup>	0.49 (0.21) <sup>B</sup>	4.5	0.02
Mosses	30.90 (3.87)	29.17 (2.49)	37.40 (2.42)	2.2	0.12

<sup>1</sup> Means with the same letter (Tukey HSD at  $P \leq 0.05$ ) are not significantly different by site.

Differences in cover of plant lifeforms by site were detected for moist tundra (Table 3b). Again, higher cover generally occurred at the MID or INL sites. Cover of evergreen shrubs was higher at the MID site than at the CST or INL sites. In contrast, cover of willows was highest at the CST site. Again, prostrate willows contributed to the higher cover values at the CST site (Appendix D). Cover of fruticose lichens was similar in all locations; however, cover of crustose lichens was highest at the CST site.

Differences by site were most pronounced in moist tussock sedge-low shrub tundra (Table 3c), for which cover, again, was generally higher at the MID and INL sites. Cover of forbs was much higher at the INL site than at the CST site. Additionally, species diversity of forbs was highest at the INL site (Appendix E). Cover of evergreen shrubs also was higher at the INL and MID sites than at the CST site. Crustose lichen cover was higher at the CST site. Percent cover of willows was also higher at the CST site than at the MID or INL sites, owing to the abundance of *Salix pulchra* encountered along several transects at the CST site.

#### **BIOMASS-TO-COVER RELATIONSHIPS**

Coefficient of variation ( $r^2$ ) values of the regressions of biomass-to-cover varied from a high of 0.83 for *C. aquatilis* at the CST site to a low of 0.03 for *E. vaginatum* at the MID site. All biomass-to-cover regressions were significant except for *E. vaginatum* at the MID site and *S. arctica* at the CST site (Figure 5-7)



Slopes of the regression lines for *C. aquatilis*, *E. angustifolium*, and *S. arctica* were significantly different among study sites (Table 4). The slope of the 3 regressions at the MID site was greater than at the CST or INL sites, indicating higher biomass for a particular percent cover. The slopes were not significantly different among sites for *C. Bigelowii*, *E. vaginatum*, and *S. pulchra*.

#### FORAGE QUALITY

Forage quality did not differ significantly by time period, so these data were pooled accordingly and reanalyzed by site only. Where significant differences did occur, no consistent trends were noted, although crude protein content of forage was generally highest at the CST site (Table 5).

Only *S. arctica* and *S. pulchra* differed in cell solubles. Values for *S. arctica* were higher at the INL site than at the MID site; the CST site was intermediate. Cell solubles of *S. pulchra* were higher at the CST site than at the MID site; and intermediate at the INL site. No significant differences were detected in ADF, hemicellulose, or *in vitro* digestibility among sites.

Crude protein levels were highest at the CST site for every species except *Salix arctica*. However, they were significantly higher only for *C. Bigelowii*, *Eriophorum vaginatum*, and *Pedicularis* spp. Phenology of species, although not recorded, was earlier at the CST sites than at the MID and INL sites and the higher protein levels may be due to this difference in phenological progression.

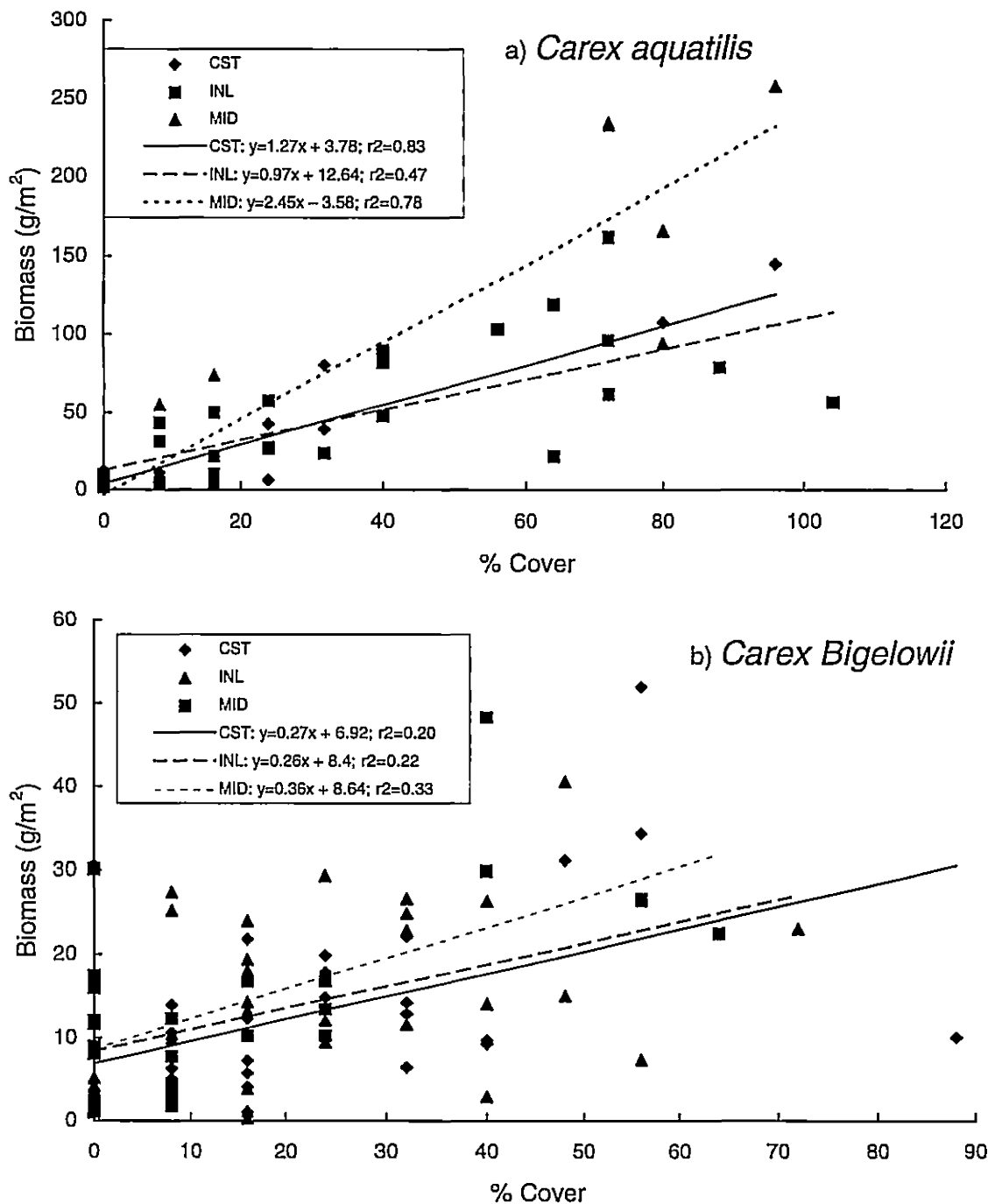


Figure 5. Biomass-to-cover regressions for a) *Carex aquatilis* and b) *C. Bigelowii*, Kuparuk region, Alaska, 1989-90.

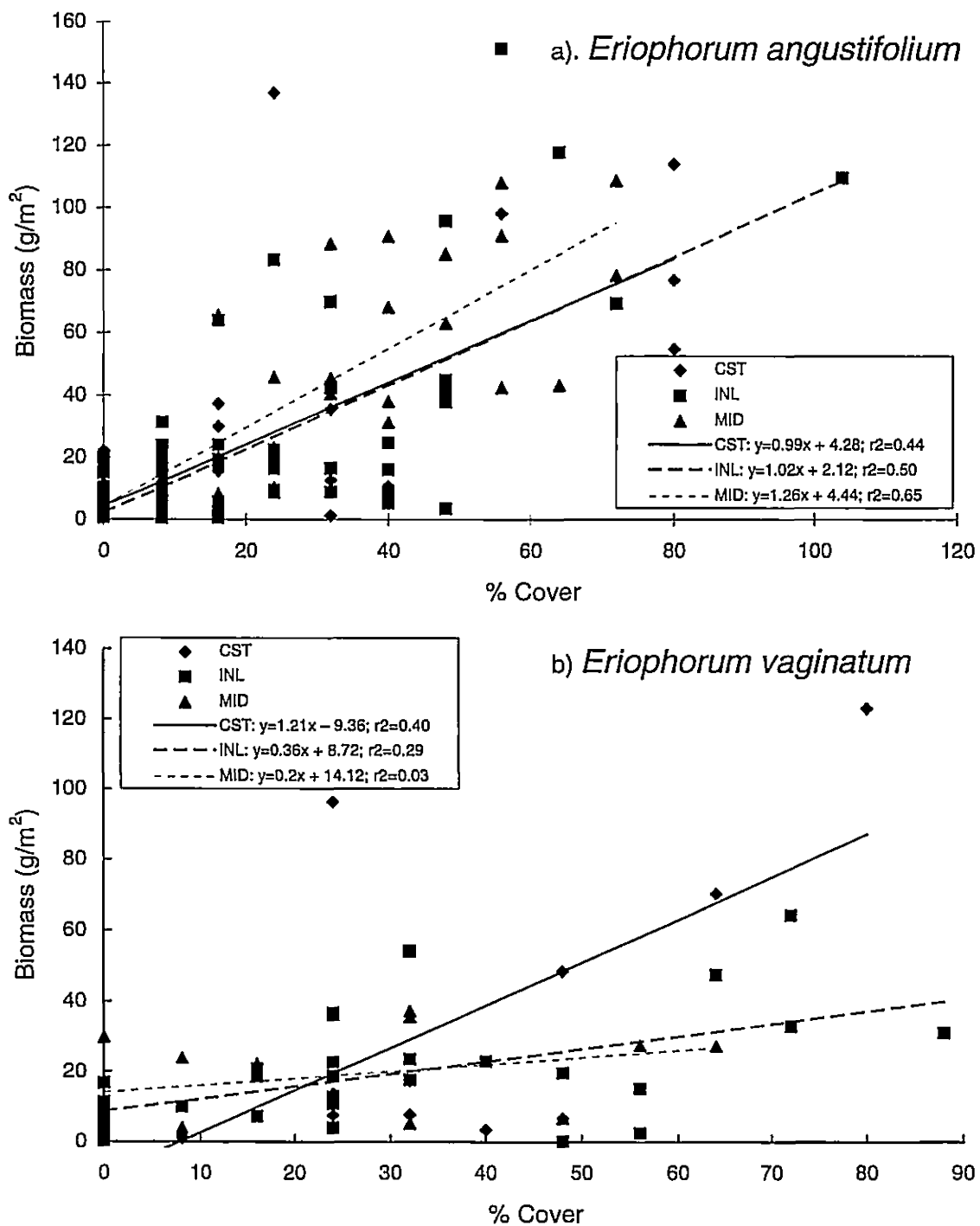


Figure 6. Biomass-to-cover regressions for a) *Eriophorum angustifolium* and b) *E. vaginatum*, Kuparuk region, Alaska, 1989-90.

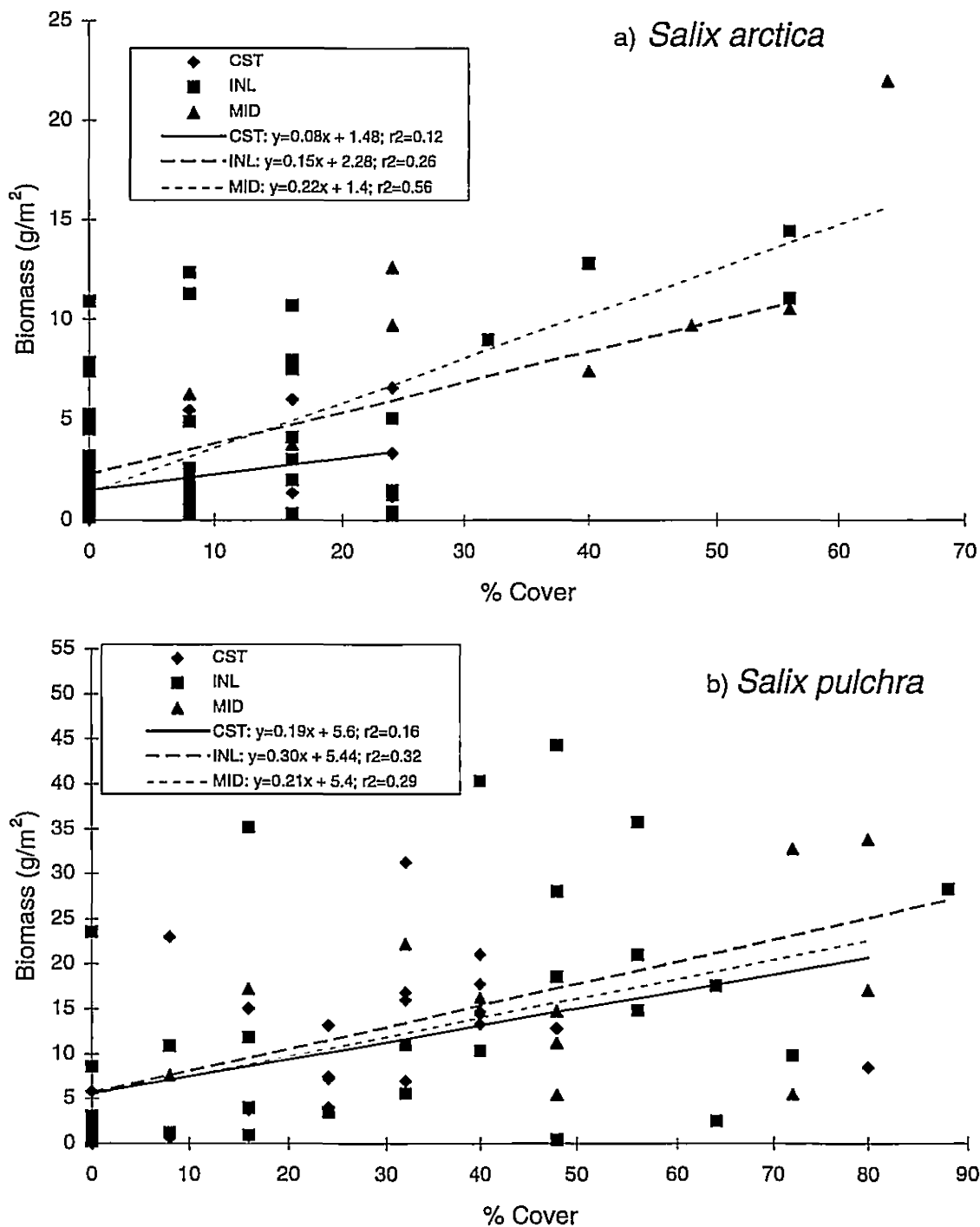


Figure 7. Biomass-to-cover regressions for a) *Salix arctica* and b) *S. pulchra*, Kuparuk region, Alaska, 1989-90.

Table 4. Biomass-to-cover regression parameters and ANCOVA comparing slopes among sites for key forage species, Kuparuk region, Alaska, 1989-90.

Lifeform / Species	CST (n=16)					MID (n=18)					INL (n=18)					ANCOVA	
	Slope	Int	r <sup>2</sup>	F	P-value	Slope	Int	r <sup>2</sup>	F	P-value	Slope	Int	r <sup>2</sup>	F	P-value	F	P-value
<b>Grasses-Sedges</b>																	
<i>Carex aquatilis</i>	1.27	3.78 <sup>A</sup>	0.83	59.8	0.00	2.46	-3.58 <sup>B</sup>	0.78	46.6	0.00	0.97	12.64 <sup>A</sup>	0.47	23.8	0.00	6.0	<0.01
<i>Carex Bigelowii</i>	0.27	6.92	0.20	9.2	0.00	0.36	8.64	0.33	12.5	0.00	0.26	8.40	0.22	11.6	0.00	0.1	0.87
<i>Eriophorum angustifolium</i>	0.99	4.28 <sup>A</sup>	0.44	27.9	0.00	1.26	4.44 <sup>B</sup>	0.65	57.2	0.00	1.03	2.12 <sup>A</sup>	0.50	76.0	0.00	8.3	<0.01
<i>Eriophorum vaginatum</i>	1.20	-9.36	0.40	9.0	0.01	0.20	14.12	0.03	1.4	0.27	0.36	8.72	0.29	14.4	0.00	1.9	0.16
<b>Willows</b>																	
<i>Salix arctica</i>	0.08	1.48 <sup>A</sup>	0.12	3.8	0.07	0.22	1.40 <sup>B</sup>	0.56	16.2	0.00	0.15	2.28 <sup>A</sup>	0.26	20.4	0.00	10.0	<0.01
<i>Salix pulchra</i>	0.19	5.60	0.16	5.8	0.02	0.21	5.40	0.29	6.0	0.03	0.30	5.44	0.32	14.9	0.00	1.2	0.32

<sup>A</sup> Means with the same letter (Tukey HSD at  $P \leq 0.05$ ) are not significantly different by site.

Table 5. Mean (SE) nutrient quality for key forage species among sites, Kuparuk region, Alaska, 1989-90.

Variable / Lifeform / Species	CST (n=24)	MID (n=24)	INL (n=24)	F	P-value
	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>		
<b>Crude Protein</b>					
Grasses-Sedges					
<i>Carex aquatilis</i>	12.84 (0.40) <sup>A</sup>	12.83 (0.23) <sup>A</sup>	11.76 (0.33) <sup>A</sup>	3.4	0.05
<i>Carex Bigelowii</i>	14.66 (0.37) <sup>A</sup>	12.42 (0.25) <sup>B</sup>	10.73 (0.28) <sup>C</sup>	35.7	<0.01
<i>Eriophorum angustifolium</i>	12.00 (0.62)	11.77 (0.74)	11.28 (0.36)	0.3	0.76
<i>Eriophorum vaginatum</i>	13.27 (0.55) <sup>A</sup>	10.73 (0.32) <sup>B</sup>	10.56 (0.38) <sup>B</sup>	11.6	<0.01
Forbs					
<i>Pedicularis</i> spp.	16.57 (0.13) <sup>A</sup>	14.61 (0.45) <sup>B</sup>	13.58 (0.51) <sup>B</sup>	9.8	<0.01
Willows					
<i>Salix arctica</i>	15.09 (0.85)	16.28 (0.90)	15.05 (0.55)	0.7	0.53
<i>Salix pulchra</i>	16.54 (0.83) <sup>A</sup>	15.67 (0.43) <sup>A,B</sup>	14.15 (0.69) <sup>B</sup>	3.3	0.05
<b>Hemicellulose</b>					
Grasses-Sedges					
<i>Carex aquatilis</i>	35.63 (0.78)	35.19 (0.67)	33.73 (0.88)	1.6	0.21
<i>Carex Bigelowii</i>	36.04 (0.74)	35.96 (0.56)	34.53 (1.28)	0.9	0.44
<i>Eriophorum angustifolium</i>	36.04 (0.96)	35.42 (0.70)	38.37 (1.29)	2.4	0.11
<i>Eriophorum vaginatum</i>	35.00 (0.64)	35.91 (1.34)	34.04 (0.65)	1.0	0.39
Forbs					
<i>Pedicularis</i> spp.	12.58 (0.68)	19.62 (4.14)	14.97 (1.03)	2.1	0.14
Willows					
<i>Salix arctica</i>	9.93 (0.73)	15.09 (4.54)	10.40 (0.31)	0.7	0.50
<i>Salix pulchra</i>	10.21 (0.91)	15.31 (4.75)	5.31 (0.93)	3.1	0.06
<b>Cell Solubles</b>					
Grasses-Sedges					
<i>Carex aquatilis</i>	30.96 (0.77)	30.17 (1.21)	30.60 (0.88)	0.2	0.83
<i>Carex Bigelowii</i>	31.65 (1.17)	29.53 (1.06)	31.89 (1.96)	0.8	0.46
<i>Eriophorum angustifolium</i>	27.70 (1.19)	27.57 (1.47)	26.69 (0.60)	0.2	0.82
<i>Eriophorum vaginatum</i>	25.88 (1.22)	24.66 (0.95)	23.88 (0.68)	1.0	0.38
Forbs					
<i>Pedicularis</i> spp.	45.62 (1.68)	43.83 (1.61)	39.89 (1.86)	3.0	0.07
Willows					
<i>Salix arctica</i>	53.82 (2.09) <sup>A,B</sup>	51.01 (3.73) <sup>A</sup>	62.37 (1.59) <sup>B</sup>	4.2	0.02
<i>Salix pulchra</i>	61.73 (2.69) <sup>A</sup>	48.88 (3.89) <sup>B</sup>	58.90 (2.15) <sup>A,B</sup>	5.0	0.01
<b>Acid Detergent Fiber</b>					
Grasses-Sedges					
<i>Carex aquatilis</i>	33.41 (1.12)	34.64 (0.65)	35.67 (0.86)	1.6	0.21
<i>Carex Bigelowii</i>	32.31 (0.98)	34.52 (1.04)	33.59 (0.82)	1.3	0.28
<i>Eriophorum angustifolium</i>	36.27 (1.08)	37.01 (1.51)	34.94 (1.43)	0.6	0.56
<i>Eriophorum vaginatum</i>	39.12 (1.72)	39.43 (1.15)	42.08 (1.16)	1.4	0.25
Forbs					
<i>Pedicularis</i> spp.	41.80 (1.19)	43.86 (1.27)	45.14 (1.09)	2.0	0.15
Willows					
<i>Salix arctica</i>	36.24 (2.62)	33.90 (2.90)	27.23 (1.54)	3.0	0.06
<i>Salix pulchra</i>	28.07 (2.27)	35.81 (2.79)	35.79 (2.92)	2.9	0.07
<b>in vitro Dry Matter Digestibility</b>					
Grasses-Sedges					
<i>Carex aquatilis</i>	43.02 (1.42)	40.65 (2.25)	35.36 (2.43)	1.7	0.22
<i>Carex Bigelowii</i>	35.92 (1.83)	43.40 (1.09)	40.88 (1.62)	3.0	0.08
<i>Eriophorum angustifolium</i>	38.03 (2.21)	30.60 (1.54)	31.75 (1.42)	2.5	0.11
<i>Eriophorum vaginatum</i>	38.80 (1.29)	40.13 (3.26)	37.15 (3.99)	0.2	0.86
Forbs					
<i>Pedicularis</i> spp.	63.65 (1.57)	55.40 (1.67)	55.82 (2.45)	2.9	0.09
Willows					
<i>Salix arctica</i>	54.74 (1.05)	54.12 (1.65)	55.03 (1.37)	0.1	0.95
<i>Salix pulchra</i>	29.08 (1.46)	21.37 (1.15)	23.88 (2.31)	2.5	0.12

<sup>1</sup> Means with the same letter (Tukey HSD at  $P \leq 0.05$ ) are not significantly different by site.

## DISCUSSION

Overall, sites differed primarily in the amounts of forage present: cover of plant species increased with distance from the coast. In large part, this was a reflection of differing proportions of habitat types among sites. Although wet tundra was present in similar proportions at all sites, the INL and MID sites included more moist tundra and more moist tussock sedge-low shrub tundra than the CST site. Plant cover was higher in these latter habitats than in wet tundra. Additionally, within these drier habitats, plant cover was higher at the MID and INL sites. Also, a greater number of species were present at the MID and INL sites. Because replicate sampling occurred within specific sites, legitimately, these conclusions can apply only to those sites. Nonetheless, if these sites are indeed representative of the area in general, these conclusions can be generalized for the summer range of the CAH.

Cover of forbs was highest at the INL site. Many species, such as *Cerastium* spp., *Hedysarum* spp., and *Papaver macounii*, occurred only at the MID and INL sites. Forbs were rare at the CST site. Sedges, especially species such as *Carex Bigelowii* and *Eriophorum vaginatum*, were more abundant at the MID and INL sites. Percent cover of fruticose lichens, especially *Cetraria nivalis* and *C. cucullata*, also was higher at the MID and INL sites. Conversely, there was a greater proportion of crustose lichen species at the CST site.

Cover of most willows was consistently highest at the CST site; only cover of *Salix arctica* and *S. lanata* was higher at the MID and INL sites. In large part, higher willow cover at the CST site was due to the prevalence of *S. pulchra*, especially in moist tussock sedge-low shrub tundra. There were major differences in the growth form of *S. pulchra* among sites. It was a vine-like prostrate willow at the CST site, whereas it was usually a vertical shrub, sometimes up to 1 m high, at the INL site.

Whether the higher cover of *S. pulchra* is a sampling peculiarity of the sites chosen or, alternatively, indicative of generally higher willow cover along the arctic coast in the Kuparuk region is difficult to determine. At the CST site, most willow cover was encountered along the banks of the Ugnuravik River. Selection of the MID site with the Sakonowyak River and the INL site with the Kuparuk River was intended to allow representative sampling of riparian willows at those locations. There were, however, only small stands of riparian willow along the Sakonowyak River, and, while there were large stands of tall riparian willows along the Kuparuk River, the INL site was situated too far west to encounter them.

If sampling sites were representative of the CAH summer range, these data indicate that inland areas are better foraging habitat than coastal areas. Especially important is the higher cover of forbs, which are high in nitrogen and soluble carbohydrates (Klein, 1990). Forbs also are highly digestible, even in late summer, and are highly preferred by caribou (Kelsall, 1968; Kuropat and Bryant, 1980; Trudell and White, 1981; Boertje, 1981;



Moore, 1982). Additionally, intake of forbs can be high even when cover (and biomass) is low (Trudell and White, 1981), as nearly all of their above-ground portions are eaten (e.g. *Pedicularis* spp.). More importantly, effective availability is increased by frequent walking during the grazing bout (White and Trudell, 1980b), as caribou and reindeer opportunistically select forbs while grazing (Wright, 1979). Overall digestibility of caribou diets would be higher by increasing the proportion of forbs and small increases in digestibility can result in large increases in net energy gain (White, 1983).

Because forbs are a preferred forage, their local biomass declines quickly with grazing (White and Trudell, 1980a). High densities of caribou at the coast during insect harassment, combined with lower forb availability, may quickly eliminate forbs as a diet component. If this occurred, my sampling may have underestimated the absolute abundance of forbs at the coast; however, it would still reflect the relative availability of forbs to caribou following grazing.

Trudell and White (1981) documented higher eating rates by caribou for upright willows than for prostrate willows and these increases in grazing rates can result in substantially higher energy balance for caribou. At the MID and INL sites, several preferred willow species, *Salix arctica*, which is prostrate, and *S. lanata*, which is upright (White *et al.*, 1975), were more abundant. Although *S. pulchra*, a highly preferred species (White *et al.*, 1975; White and Trudell, 1980a; Boertje, 1981; Moore, 1982), was more abundant at the CST site, the prostrate form of *S. pulchra* prevailed at the CST site, whereas the upright form was more common at the INL site.

Although selected only relative to availability, the higher sedge and grass cover at the MID and INL sites is important because grasses and sedges constitute 15-20% of summer diets of caribou (Moore, 1982), due to their high abundance on the coastal plain. Plant secondary compounds are poorly developed in grasses and sedges (Chapin, 1980; Bryant and Kuropat, 1980), so the retention of dead leaves may be the primary defense from grazers (White and Trudell, 1980a). Biomass-to-cover ratios of *C. aquatilis* and *E. angustifolium* were highest at the MID site. Higher live:dead ratios of tissue of these sedges, should decrease handling time for caribou (White and Trudell, 1980a), resulting in a diet with higher digestibility.

Fruticose lichens are not a major constituent of summer diets of the CAH (White *et al.*, 1975), yet they may play an important role in summer nutrition. Preferred species of lichen, especially *Cetraria cucullata* and *C. nivalis*, both of which were more abundant at the MID and INL sites, are highly digestible and may help dilute plant defensive compounds (Moore, 1982). Fruticose lichens also may become a larger component of the diet as other species become depleted with grazing and trampling. Tethered reindeer increased the proportion of fruticose lichens in their diets as availability of willows and forbs declined from grazing (White and Trudell, 1980a). In contrast, cover of nonpreferred crustose lichens (White and Trudell, 1980a; Moore, 1982; Saperstein, 1993) was higher at the CST site.

The distribution of habitat types among sites lead to most of the observed differences in plant abundance. Wet tundra was present in similar proportions at all sites, and cover

of plant species by site in this habitat was similar. In contrast, the INL and MID sites included more moist tundra and more moist tussock sedge-low shrub tundra. Additionally, within the moist tussock sedge-low shrub tundra habitat, percent cover of forbs was higher at the MID and INL sites.

Overall, differences in the quality of key forage species selected for analysis among sites were not significant. Due to subtle differences in the phenological progression between years, however, some differences in forage quality may have been masked. Crude protein levels at the CST site were higher, which may allow caribou, in part, to compensate for lower plant cover (and therefore biomass) when foraging at the coast during periods of insect harassment. Nonetheless, there were no differences in digestibility of species among sites. The higher variability in forage quality among species, rather than among sites, suggests that selection by species and plant lifeform was more important than selection by region in maximizing the plane of nutrition during mid-summer (Klein, 1970; Klein 1990). In this case, the greater abundance of plants and greater species and habitat diversity in inland areas would provide more opportunity for selecting higher quality forage than in coastal areas (White and Trudell, 1980a).

#### **NUTRITIONAL IMPLICATIONS**

To assess the possible energetic advantages of foraging inland, I constructed a model comparing the net energy difference of a caribou foraging in coastal areas only versus moving to, and foraging in inland areas during insect-free conditions. Grazing rates in different habitat types were from White *et al.* (1975) and Trudell and White (1980b). The

energy cost of movement and daily time spent feeding under different levels of insect harassment were from Fancy (1986). I multiplied the grazing rate for each habitat by the percent occurrence of that habitat at the CST and INL sites, yielding an average grazing rate for each site. Lacking data on proportionate habitat use, conservatively, this model assumes that a caribou spent equal time feeding in each habitat.

From this model, I calculated that a caribou would realize a net energy gain of 63 KJ/day (Table 6) by moving to the insect-free INL site to feed, even after including the energy cost of moving between sites and the associated loss of foraging time. Moreover, as demonstrated in White (1983), any accompanying increase in forage digestibility can result in disproportionately large gains in net energy retention. For example, a 5% increase in overall digestibility of the diet from selective foraging increases the net energy gain over 6-fold (398 KJ/day). This is a realistic scenario given the higher digestibility of forbs and the increased abundance of forbs at the INL site.

Once at the INL site, it is energetically advantageous to remain inland until insect harassment reoccurs. For example, the net energy gain of remaining inland exceeds that of the CST site during insect-free periods by 818 KJ/day, or, assuming a 5% higher digestibility inland, 1,117 KJ/day. Under mild harassment, the difference decreases to 73 KJ/day (334 KJ/day at +5% digestibility inland). Nevertheless, as harassment becomes severe, a caribou would realize a net energy loss (-559 KJ/day; +5% digestibility, -378 KJ/day) by remaining at the INL site. Although this model ignores much of the

Table 6. Input parameters and calculation steps of a model illustrating the energetic costs/benefits of caribou foraging at the coast vs. inland sites.

Input Parameters	CST	INL
<b>Percent Habitat Type<sup>1</sup></b>		
Wet tundra	14%	18%
Moist tundra	21%	26%
Moist tussock sedge-low shrub tundra	31%	42%
Barrens	28%	5%
<b>Grazing Rates (g dry wt/min)<sup>2</sup></b>		
Wet tundra	2.5	2.5
Moist tundra	3.3	3.3
Moist tussock sedge-low shrub tundra	3.5	3.5
Barrens	1.0	1.0
<b>Grazing Rates * Percent Habitat</b>		
Wet Tundra	0.34	0.44
Moist Tundra	0.68	0.87
Moist Tussock Sedge Tundra	1.07	1.48
Barrens	0.28	0.05
<b>Average Grazing Rate (g dry wt. / min.)</b>	<b>2.38</b>	<b>2.84</b>
Daily time eating [90 kg caribou] (min/day)	760	700
Daily dry matter intake [DMI] (g dry wt./day)	1806	1986
Diet digestibility	40%	40%
Daily digestible dry matter intake [DDMI]	723	794
Energy (KJ/g dry wt.)	4	4
Daily digestible energy intake [DEI] (KJ/day)	2890	3177
conversion factor	0.82	0.82
<b>Daily Metabolizable Energy Intake [MEI] (KJ/day)</b>	<b>2370</b>	<b>2605</b>
<b>Energetic cost of movement between CST and INL</b>		
Extra distance traveled (km/day)	0	30
Energetic cost (KJ) / km (90kg caribou) <sup>3</sup>	6	6
Total energetic costs (KJ/day for C/I movements)	0	172
<b>Daily Metabolizable Energy Balance (KJ/day)</b>	<b>2370</b>	<b>2,433</b>
<b>Energy gain from moving to, and feeding, at INL from the CST site</b>	<b>KJ/day</b>	<b>% FMR<sup>3</sup></b>
Assume equal digestibility (40%)	63	9%
Assume +5% digestibility at INL site (45%)	389	58%
<b>Energy gain/loss from remaining at INL vs. moving to CST site</b>		
Assume equal digestibility (40%)	818	121%
Assume +5% digestibility at INL site (45%)	1117	165%
Assume mild insect harassment at INL site (560 min. eating/day) <sup>3</sup>	73	11%
Assume mild harassment (560 min. eating/day) and 45% digestibility	334	49%
Assume severe insect harassment at INL site (390 min. eating/day) <sup>3</sup>	-559	-83%
Assume severe harassment (390 min. eating/day) and 45 % digestibility	-565	-84%

<sup>1</sup> from this study

<sup>2</sup> from White *et al.*, 1975; Trudell and White, 1980b

<sup>3</sup> from Fancy, 1986; FMR=Fasting Metabolic Rate (675 KJ/day)

complexity involved in caribou summer foraging, it does illustrate the benefits of moving to coastal areas during periods of increasing insect harassment and returning to inland feeding areas when insect activity declines.

#### MANAGEMENT IMPLICATIONS

The characteristics of inland areas (higher forb cover, greater abundance of moist and moist tussock sedge-low shrub tundra, more upright vs. prostrate willows, and higher sedge and fruticose lichen cover) indicate better foraging opportunities for caribou. More important, in view of the probable influence of insect harassment on energy balance, is free access to both coastal and inland areas. Maximizing forage intake in inland habitats when conditions permit and moving to coastal relief habitats during periods of high insect activity provides a net energy advantage over remaining at and foraging in either coastal or inland areas. The net energy gain from these coastal and inland movements would lead to greater weight gain during summer and should facilitate lactation and growth of young.

Recently, overall fecundity of CAH caribou west of the Sagavanirktok River (i.e., those in contact with the Kuparuk and Prudhoe Bay oilfields) was reported to be lower than for those under disturbance-free conditions east of the Sagavanirktok River (Cameron, 1995). Clearly, the presence of elevated pipelines, roads, and other oilfield facilities can impede movements of caribou (Child, 1974; Fancy, 1983; Smith and Cameron, 1983; Smith and Cameron 1985b; Curatolo and Murphy, 1986; Murphy and Curatolo, 1987). My model (Table 6) indicates that restrictions on coastal-inland movements can result in a net energy loss and, therefore, lower rates of summer weight

gain. In turn, the probability of parturition decreases logistically with body weight in the previous autumn (Cameron *et al.*, 1993; Cameron and Ver Hoef, 1995).

Future expansion of oilfield-related activities along the arctic coast could result in additional restrictions on caribou movements between coastal insect relief habitat and inland foraging habitat resulting in continued low parturition rates currently being observed. Thus, further development that does not -- or cannot --- provide for unimpeded coastal/inland movements of caribou could further depress body condition and reproductive success of the CAH.

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Appendix A. Tundra Vegetation Classification (in part from Walker [1983], Hierarchical Tundra Vegetation Classification)

Final Grouping	Walker and Acevedo (1987) Landsat Units (Initial Grouping)	Walker Level B and C Units
Water	Water	I. Water
Wet Tundra	Wet Tundra	II. Very Wet Tundra
		III. Wet Tundra
Moist Tundra	Moist Tundra	IV. Moist/Wet Tundra Complex
		Va. Moist Sedge, Dwarf Shrub Tundra
Moist Tussock Sedge-Low Shrub Tundra	Moist Tussock Sedge-Low Shrub Tundra	Vb. Moist Tussock Sedge, Dwarf Shrub Tundra
		Vc. Dry Dwarf Shrub, Crustose Lichen Tundra
		Vd. Dry Dwarf Shrub, Fruticose Lichen Tundra
		VI. Moist Tussock Sedge, Low Shrub Tundra
		VII. Moist Shrub-rich Tundra
	Shrubland	VIII. Shrubland or Shrub Tundra
	Partially Vegetated	IX. Partially Vegetated
Barrens	Barrens	X. Light Colored Barrens
		XI. Dark Colored Barrens

Appendix B. Mean (SE) percent cover of species by site, Kuparuk region, Alaska, 1989-90.

Lifeform / Species	CST (n=24)	MID (n=24)	INL (n=24)	F	P-value
	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>		
<b>Forage</b>					
<b>Evergreen Shrubs</b>					
<i>Arctostaphylos rubra</i>	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	1.0	0.39
<i>Cassiope tetragona</i>	0.32 (0.09) <sup>A</sup>	0.69 (0.11) <sup>B</sup>	0.55 (0.08) <sup>B</sup>	6.3	<0.01
<i>Dryas integrefolia</i>	1.55 (0.18) <sup>A</sup>	3.34 (0.27) <sup>B</sup>	2.69 (0.30) <sup>B</sup>	14.1	<0.01
<i>Vaccinium vitis-idaea</i>	0.11 (0.04) <sup>A</sup>	0.00 (0.00) <sup>B</sup>	0.00 (0.00) <sup>B</sup>	11.8	<0.01
<b>Fruticose Lichens</b>					
<i>Alectoria nigricans</i>	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.0	1.00
<i>Cetraria cucullata</i>	0.09 (0.03) <sup>A</sup>	0.73 (0.11) <sup>B</sup>	1.02 (0.15) <sup>B</sup>	30.4	<0.01
<i>Cetraria islandica</i>	0.05 (0.02)	0.09 (0.04)	0.11 (0.04)	0.7	0.49
<i>Cetraria nivalis</i>	0.05 (0.02) <sup>A</sup>	0.28 (0.07) <sup>B</sup>	0.39 (0.08) <sup>B</sup>	11.2	<0.01
<i>Cladina</i> spp.	0.06 (0.02)	0.11 (0.09)	0.03 (0.03)	0.6	0.53
<i>Dactylina arctica</i>	0.36 (0.07) <sup>A</sup>	0.18 (0.05) <sup>B</sup>	0.11 (0.03) <sup>B</sup>	6.2	<0.01
<i>Hypogymnea subobscura</i>	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	1.0	0.39
<i>Masonhalea richardsonii</i>	0.01 (0.01) <sup>A,B</sup>	0.07 (0.03) <sup>A</sup>	0.01 (0.01) <sup>B</sup>	3.7	0.03
<i>Ochrolechia</i> spp.	0.35 (0.10) <sup>A</sup>	0.07 (0.03) <sup>B</sup>	0.11 (0.04) <sup>A,B</sup>	4.9	0.01
<i>Peltigera apthosa</i>	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	2.0	0.14
<i>Stereocaulon</i> spp.	0.07 (0.03)	0.01 (0.01)	0.01 (0.01)	2.4	0.10
<i>Thamnolia</i> spp.	0.49 (0.06) <sup>A,B</sup>	0.58 (0.07) <sup>A</sup>	0.36 (0.08) <sup>B</sup>	3.6	0.03
<b>Forbs</b>					
<i>Astragalus umbellatus</i>	0.00 (0.00) <sup>A</sup>	0.10 (0.04) <sup>B</sup>	0.08 (0.03) <sup>B</sup>	4.6	0.01
<i>Cerastium</i> spp.	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	2.0	0.14
<i>Hedysarum</i> spp.	0.00 (0.00)	0.01 (0.01)	0.01 (0.01)	0.5	0.59
<i>Ledum palustre</i>	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	1.1	0.34
<i>Lupinus arcticus</i>	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	2.3	0.11
<i>Oxytropis</i> spp.	0.00 (0.00)	0.02 (0.02)	0.03 (0.02)	1.4	0.25
<i>Papaver macounii</i>	0.00 (0.00)	0.01 (0.01)	0.01 (0.01)	0.8	0.45
<i>Pedicularis</i> spp.	0.07 (0.02) <sup>A</sup>	0.08 (0.02) <sup>A</sup>	0.20 (0.04) <sup>B</sup>	5.5	<0.01
<i>Polygonum bistorta</i>	0.00 (0.00)	0.02 (0.02)	0.03 (0.02)	2.0	0.14
<i>Polygonum viviparum</i>	0.03 (0.01)	0.06 (0.03)	0.03 (0.02)	0.4	0.67
<i>Pyrola grandiflora</i>	0.00 (0.00) <sup>A</sup>	0.04 (0.02) <sup>A,B</sup>	0.08 (0.02) <sup>B</sup>	6.1	<0.01
<i>Ranunculus nivalis</i>	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	1.0	0.39
<i>Saussurea angustifolia</i>	0.02 (0.01)	0.07 (0.03)	0.15 (0.05)	2.8	0.07
<i>Saxaifraga oppositifolia</i>	0.05 (0.04)	0.00 (0.00)	0.00 (0.00)	2.0	0.15
<i>Saxifraga</i> sp.	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	1.1	0.34
<i>Saxifraga cernua</i>	0.01 (0.01)	0.02 (0.02)	0.00 (0.00)	1.3	0.29
<i>Saxifraga hirculus</i>	0.02 (0.01)	0.01 (0.01)	0.03 (0.02)	0.5	0.61
<i>Senecia atropurpureus</i>	0.00 (0.00)	0.00 (0.00)	0.01 (0.01)	1.0	0.39
<i>Silene acaulis</i>	0.03 (0.01)	0.01 (0.01)	0.01 (0.01)	1.5	0.23
<i>Silene gracilis</i>	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	1.0	0.39

<sup>1</sup> Means with the same letter (Tukey HSD at  $P \leq 0.05$ ) are not significantly different by site.

Appendix B (cont). Mean (SE) percent cover of species by site, Kuparuk region, Alaska, 1989-90.

Lifeform / Species	CST (n=24)	MID (n=24)	INL (n=24)	F	P-value
	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>		
<b>Grasses-Sedges</b>					
<i>Hierochloe alpina</i>	0.01 (0.01)	0.00 (0.00)	0.00 (0.00)	1.0	0.39
<i>Arctagrostis latifolia</i>	0.05 (0.03)	0.01 (0.01)	0.02 (0.01)	0.7	0.51
<i>Carex aquatilis</i>	1.47 (0.15) <sup>A</sup>	0.81 (0.14) <sup>B</sup>	0.65 (0.07) <sup>B</sup>	11.3	<0.01
<i>Carex Bigelowii</i>	0.90 (0.11) <sup>A</sup>	1.49 (0.18) <sup>B</sup>	1.45 (0.16) <sup>B</sup>	5.0	<0.01
<i>Carex chordorrhiza</i>	0.00 (0.00) <sup>A</sup>	0.04 (0.02) <sup>A,B</sup>	0.10 (0.04) <sup>B</sup>	3.2	0.05
<i>Carex maritima</i>	0.02 (0.02)	0.00 (0.00)	0.00 (0.00)	1.0	0.39
<i>Carex membranacea</i>	0.00 (0.00) <sup>A</sup>	0.07 (0.03) <sup>B</sup>	0.04 (0.02) <sup>A,B</sup>	4.4	0.02
<i>Carex misandra</i>	0.39 (0.08)	0.40 (0.08)	0.24 (0.05)	2.1	0.13
<i>Carex rariflora</i>	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	1.1	0.34
<i>Carex rotundata</i>	0.01 (0.01) <sup>A</sup>	0.09 (0.03) <sup>A,B</sup>	0.16 (0.05) <sup>B</sup>	6.2	<0.01
<i>Carex rupestris</i>	0.01 (0.01)	0.00 (0.00)	0.02 (0.02)	1.1	0.35
<i>Carex saxatilis</i>	0.02 (0.01) <sup>A</sup>	0.09 (0.03) <sup>A,B</sup>	0.21 (0.08) <sup>B</sup>	4.7	0.01
<i>Carex scirpoidea</i>	0.01 (0.01)	0.07 (0.03)	0.05 (0.03)	3.0	0.06
<i>Carex vaginata</i>	0.01 (0.01)	0.00 (0.00)	0.04 (0.03)	1.6	0.20
<i>Dupontia fisheri</i>	0.05 (0.03)	0.01 (0.01)	0.01 (0.01)	2.0	0.15
<i>Equisetum variagatum</i>	0.03 (0.02)	0.07 (0.03)	0.07 (0.02)	1.2	0.32
<i>Eriophorum angustifolium</i>	2.80 (0.21)	2.79 (0.23)	3.33 (0.19)	2.5	0.09
<i>Eriophorum scheuchzeri</i>	0.07 (0.03)	0.04 (0.02)	0.02 (0.01)	1.0	0.36
<i>Eriophorum vaginatum</i>	0.32 (0.13) <sup>A</sup>	0.60 (0.09) <sup>B</sup>	0.76 (0.11) <sup>B</sup>	9.4	<0.01
<b>Willows</b>					
<i>Salix arctica</i>	0.36 (0.06) <sup>A</sup>	0.75 (0.09) <sup>B</sup>	0.44 (0.06) <sup>A</sup>	8.4	<0.01
<i>Salix lanata</i>	0.00 (0.00) <sup>A</sup>	0.13 (0.04) <sup>B</sup>	0.39 (0.07) <sup>C</sup>	27.1	<0.01
<i>Salix ovalifolia</i>	0.04 (0.02)	0.01 (0.01)	0.00 (0.00)	3.0	0.06
<i>Salix phlebophylla</i>	0.21 (0.07) <sup>A</sup>	0.05 (0.02) <sup>A,B</sup>	0.01 (0.01) <sup>B</sup>	5.7	<0.01
<i>Salix pulchra</i>	1.70 (0.19) <sup>A</sup>	0.11 (0.04) <sup>B</sup>	1.00 (0.16) <sup>C</sup>	50.3	<0.01
<i>Salix reticulata</i>	1.28 (0.13) <sup>A</sup>	0.98 (0.12) <sup>A,B</sup>	0.89 (0.08) <sup>B</sup>	3.6	0.03
<i>Salix rotundifolia</i>	0.49 (0.10) <sup>A</sup>	0.01 (0.01) <sup>B</sup>	0.00 (0.00) <sup>B</sup>	37.1	<0.01
<b>Nonforage</b>					
<b>Abiotic-Litter</b>					
Soil	17.9 (1.84) <sup>A</sup>	12.7 (2.35) <sup>A</sup>	12.4 (2.31) <sup>A</sup>	3.3	0.04
Water	29.1 (1.94) <sup>A</sup>	32.7 (2.65) <sup>A</sup>	19.2 (2.65) <sup>B</sup>	9.6	<0.01
Litter	21.5 (1.01) <sup>A</sup>	21.0 (0.84) <sup>A</sup>	28.6 (1.65) <sup>B</sup>	11.3	<0.01
<b>Crustose Lichens</b>					
Unidentified	0.57 (0.07) <sup>A</sup>	0.32 (0.08) <sup>B</sup>	0.17 (0.05) <sup>B</sup>	11.0	<0.01
<b>Mosses</b>					
Unidentified	14.3 (1.45) <sup>A</sup>	17.7 (1.75) <sup>A,B</sup>	23.6 (1.91) <sup>B</sup>	7.7	<0.01

<sup>1</sup> Means with the same letter (Tukey HSD at  $P \leq 0.05$ ) are not significantly different by site.

Appendix C. Mean (SE) percent cover of species by site in habitats classified as wet tundra, Kuparuk region, Alaska, 1989-90.

Lifeform / Species	CST (n=24)	MID (n=24)	INL (n=24)	F	P-value
	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>		
<b>Forage</b>					
<b>Evergreen Shrubs</b>					
<i>Arctostaphylos rubra</i>	0.00 (0.00)	0.02 (0.02)	0.00 (0.00)	1.0	0.39
<i>Cassiope tetragona</i>	0.05 (0.05)	0.12 (0.09)	0.18 (0.13)	0.4	0.68
<i>Dryas integrifolia</i>	0.51 (0.10)	0.39 (0.18)	0.40 (0.17)	1.4	0.26
<b>Fruiting Lichens</b>					
<i>Cetraria cucullata</i>	0.07 (0.07)	0.15 (0.09)	0.06 (0.06)	0.6	0.56
<i>Cetraria islandica</i>	0.02 (0.02)	0.02 (0.02)	0.00 (0.00)	0.5	0.63
<i>Cetraria nivalis</i>	0.00 (0.00)	0.00 (0.00)	0.05 (0.05)	1.1	0.34
<i>Cladina</i> spp.	0.07 (0.07)	0.00 (0.00)	0.00 (0.00)	1.0	0.39
<i>Dactylina arctica</i>	0.09 (0.05)	0.02 (0.02)	0.03 (0.03)	0.9	0.40
<i>Ochrolechia</i> spp.	0.02 (0.02)	0.03 (0.03)	0.00 (0.00)	0.5	0.63
<i>Thamnia</i> spp.	0.28 (0.11) <sup>A</sup>	0.11 (0.11) <sup>AB</sup>	0.02 (0.02) <sup>B</sup>	3.6	0.03
<b>Forbs</b>					
<i>Lupinus arcticus</i>	0.00 (0.00)	0.00 (0.00)	0.03 (0.03)	1.1	0.34
<i>Pedicularis</i> spp.	0.07 (0.05)	0.29 (0.12)	0.13 (0.08)	1.9	0.15
<i>Polygonum viviparum</i>	0.10 (0.06)	0.00 (0.00)	0.00 (0.00)	3.0	0.05
<i>Pyrola grandiflora</i>	0.00 (0.00)	0.00 (0.00)	0.04 (0.04)	1.1	0.34
<i>Saxifraga hirculus</i>	0.04 (0.04)	0.04 (0.03)	0.00 (0.00)	0.8	0.47
<b>Grasses-Sedges</b>					
<i>Arctagrostis latifolia</i>	0.15 (0.12)	0.03 (0.03)	0.00 (0.00)	1.1	0.35
<i>Carex aquatilis</i>	3.41 (0.45) <sup>A</sup>	1.94 (0.43) <sup>A</sup>	2.42 (0.61) <sup>A</sup>	3.5	0.04
<i>Carex atrofusca</i>	0.03 (0.03) <sup>A</sup>	0.67 (0.31) <sup>AB</sup>	0.28 (0.12) <sup>B</sup>	3.1	0.05
<i>Carex Bigelowii</i>	0.30 (0.09)	0.37 (0.17)	0.26 (0.10)	0.1	0.91
<i>Carex chordorrhiza</i>	0.00 (0.00)	0.12 (0.07)	0.07 (0.07)	1.5	0.23
<i>Carex membranacea</i>	0.00 (0.00)	0.04 (0.04)	0.05 (0.05)	0.5	0.59
<i>Carex misandra</i>	0.45 (0.19) <sup>A</sup>	0.06 (0.05) <sup>A</sup>	0.47 (0.15) <sup>A</sup>	3.6	0.03
<i>Carex rotundata</i>	0.00 (0.00) <sup>A</sup>	0.26 (0.14) <sup>AB</sup>	0.04 (0.04) <sup>B</sup>	3.6	0.03
<i>Carex saxatilis</i>	0.04 (0.03)	0.48 (0.21)	0.18 (0.14)	2.8	0.07
<i>Carex scirpoidea</i>	0.00 (0.00)	0.04 (0.04)	0.06 (0.06)	0.5	0.58
<i>Dupontia fisheri</i>	0.14 (0.08)	0.00 (0.00)	0.00 (0.00)	3.0	0.06
<i>Equisetum variegatum</i>	0.02 (0.02)	0.04 (0.03)	0.00 (0.00)	1.0	0.39
<i>Eriophorum angustifolium</i>	2.38 (0.43)	3.30 (0.41)	3.24 (0.52)	0.8	0.45
<i>Eriophorum scheuchzeri</i>	0.21 (0.09)	0.08 (0.04)	0.16 (0.08)	0.6	0.56
<i>Eriophorum vaginatum</i>	0.07 (0.07)	0.02 (0.02)	0.05 (0.05)	0.1	0.92
<b>Willows</b>					
<i>Salix arctica</i>	0.27 (0.09)	0.20 (0.09)	0.33 (0.13)	0.3	0.75
<i>Salix lanata</i>	0.00 (0.00)	0.22 (0.16)	0.05 (0.05)	1.3	0.29
<i>Salix ovalifolia</i>	0.02 (0.02)	0.00 (0.00)	0.00 (0.00)	1.0	0.39
<i>Salix phlebophylla</i>	0.11 (0.09)	0.00 (0.00)	0.00 (0.00)	1.7	0.19
<i>Salix planifolia</i>	0.27 (0.12)	0.00 (0.00)	0.17 (0.10)	2.6	0.08
<i>Salix reticulata</i>	0.53 (0.22)	0.22 (0.09)	0.36 (0.13)	0.8	0.46
<i>Salix rotundifolia</i>	0.12 (0.09)	0.00 (0.00)	0.00 (0.00)	2.7	0.07
<b>Nonforage</b>					
<b>Abiotic-Litter</b>					
Litter	13.80 (1.16)	15.04 (2.05)	12.07 (1.39)	0.7	0.49
Soil	48.21 (3.93)	37.51 (7.49)	37.15 (6.10)	1.6	0.21
Water	11.90 (2.34)	24.95 (4.51)	26.69 (5.27)	1.7	0.18
<b>Crustose Lichens</b>					
Unidentified	0.10 (0.05)	0.00 (0.00)	0.08 (0.06)	1.5	0.24
<b>Mosses</b>					
Unidentified	16.08 (2.33)	11.32 (2.44)	15.65 (2.87)	2.2	0.12

<sup>1</sup> Means with the same letter (Tukey HSD at  $P \leq 0.05$ ) are not significantly different by site.



Appendix D. Mean (SE) percent cover of species by site in habitats classified as moist tundra, Kuparuk region, Alaska, 1989-90.

Lifeform / Species	CST (n=24)	MID (n=24)	INL (n=24)	F	P-value
	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>		
<b>Forage</b>					
<b>Evergreen Shrubs</b>					
<i>Cassiope tetragona</i>	0.51 (0.13)	0.95 (0.20)	0.52 (0.10)	2.6	0.08
<i>Dryas integrifolia</i>	2.97 (0.36) <sup>A</sup>	5.52 (0.58) <sup>B</sup>	3.41 (0.39) <sup>A</sup>	8.6	<0.01
<i>Vaccinium vitis-idaea</i>	0.24 (0.09) <sup>A</sup>	0.00 (0.00) <sup>B</sup>	0.00 (0.00) <sup>B</sup>	11.0	<0.01
<b>Fruitlese Lichens</b>					
<i>Cetraria cucullata</i>	0.14 (0.06) <sup>A</sup>	1.37 (0.28) <sup>B</sup>	1.32 (0.23) <sup>B</sup>	22.0	<0.01
<i>Cetraria islandica</i>	0.10 (0.06)	0.23 (0.10)	0.15 (0.07)	0.6	0.56
<i>Cetraria nivalis</i>	0.10 (0.05) <sup>A</sup>	0.54 (0.13) <sup>B</sup>	0.70 (0.16) <sup>B</sup>	8.6	<0.01
<i>Cladina</i> spp.	0.07 (0.04)	0.07 (0.06)	0.03 (0.02)	0.2	0.82
<i>Dactylina arctica</i>	0.68 (0.13) <sup>A</sup>	0.32 (0.10) <sup>B</sup>	0.13 (0.04) <sup>B</sup>	8.2	<0.01
<i>Masonhalea richardsonii</i>	0.03 (0.02) <sup>A,B</sup>	0.14 (0.05) <sup>A</sup>	0.00 (0.00) <sup>B</sup>	5.0	<0.01
<i>Ochrolechia</i> spp.	0.68 (0.18) <sup>A</sup>	0.12 (0.05) <sup>B</sup>	0.19 (0.09) <sup>B</sup>	5.3	<0.01
<i>Stereocaulon</i> spp.	0.17 (0.07) <sup>A</sup>	0.03 (0.02) <sup>A,B</sup>	0.00 (0.00) <sup>B</sup>	4.6	0.01
<i>Thamnolia</i> spp.	0.91 (0.14) <sup>A</sup>	0.81 (0.14) <sup>A</sup>	0.45 (0.15) <sup>B</sup>	6.2	<0.01
<b>Forbs</b>					
<i>Astragalus umbellatus</i>	0.00 (0.00) <sup>A</sup>	0.22 (0.11) <sup>B</sup>	0.13 (0.04) <sup>A,B</sup>	3.9	0.03
<i>Oxytropis</i> spp.	0.00 (0.00)	0.05 (0.03)	0.04 (0.02)	1.4	0.27
<i>Papaver macounii</i>	0.00 (0.00)	0.08 (0.08)	0.01 (0.01)	0.7	0.50
<i>Pedicularis</i> spp.	0.12 (0.05)	0.12 (0.05)	0.21 (0.06)	1.5	0.23
<i>Polygonum bistorta</i>	0.00 (0.00)	0.02 (0.02)	0.09 (0.05)	2.7	0.07
<i>Polygonum viviparum</i>	0.02 (0.02)	0.14 (0.06)	0.04 (0.02)	2.6	0.08
<i>Pyrola grandiflora</i>	0.00 (0.00)	0.06 (0.03)	0.04 (0.02)	2.0	0.14
<i>Saussurea angustifolia</i>	0.05 (0.03)	0.06 (0.04)	0.16 (0.06)	1.6	0.21
<b>Grasses-Sedges</b>					
<i>Arctagrostis latifolia</i>	0.01 (0.01)	0.00 (0.00)	0.03 (0.03)	0.5	0.62
<i>Carex aquatilis</i>	1.68 (0.26) <sup>A</sup>	0.79 (0.19) <sup>B</sup>	0.42 (0.12) <sup>B</sup>	10.8	<0.01
<i>Carex atrofusca</i>	0.02 (0.02) <sup>A</sup>	0.31 (0.10) <sup>B</sup>	0.28 (0.07) <sup>B</sup>	7.5	<0.01
<i>Carex Bigelowii</i>	1.71 (0.29) <sup>A</sup>	2.56 (0.32) <sup>B</sup>	1.75 (0.16) <sup>A,B</sup>	3.3	0.04
<i>Carex chondrorhiza</i>	0.00 (0.00)	0.05 (0.03)	0.15 (0.07)	2.5	0.09
<i>Carex misandra</i>	0.68 (0.12)	0.81 (0.24)	0.40 (0.08)	1.5	0.23
<i>Carex rotundata</i>	0.02 (0.02) <sup>A</sup>	0.18 (0.07) <sup>A,B</sup>	0.21 (0.08) <sup>B</sup>	4.0	0.02
<i>Carex saxatilis</i>	0.02 (0.02) <sup>A</sup>	0.18 (0.06) <sup>B</sup>	0.22 (0.09) <sup>B</sup>	4.0	0.02
<i>Carex scirpoidea</i>	0.01 (0.01) <sup>A</sup>	0.22 (0.08) <sup>B</sup>	0.10 (0.05) <sup>A,B</sup>	3.7	0.03
<i>Eriophorum angustifolium</i>	4.62 (0.33)	4.13 (0.33)	4.22 (0.27)	0.6	0.56
<i>Eriophorum vaginatum</i>	0.17 (0.10)	0.11 (0.06)	0.10 (0.04)	0.1	0.94
<b>Willows</b>					
<i>Salix arctica</i>	0.64 (0.11)	1.07 (0.20)	0.56 (0.11)	1.8	0.17
<i>Salix lanata</i>	0.00 (0.00) <sup>A</sup>	0.21 (0.09) <sup>B</sup>	0.59 (0.10) <sup>C</sup>	21.5	<0.01
<i>Salix phlebophylla</i>	0.30 (0.12) <sup>A</sup>	0.09 (0.05) <sup>A,B</sup>	0.01 (0.01) <sup>B</sup>	4.4	0.02
<i>Salix pulchra</i>	3.07 (0.43) <sup>A</sup>	0.15 (0.08) <sup>B</sup>	1.35 (0.21) <sup>C</sup>	50.6	<0.01
<i>Salix reticulata</i>	2.29 (0.20) <sup>A</sup>	1.80 (0.28) <sup>A</sup>	1.13 (0.12) <sup>B</sup>	10.6	<0.01
<i>Salix rotundifolia</i>	1.01 (0.20) <sup>A</sup>	0.02 (0.02) <sup>B</sup>	0.00 (0.00) <sup>B</sup>	37.4	<0.01
<b>Nonforage</b>					
<b>Abiotic-Litter</b>					
Litter	37.29 (1.39)	35.05 (0.99)	38.69 (1.94)	1.3	0.29
Soil	15.56 (2.46)	13.85 (2.81)	11.96 (2.38)	1.3	0.27
Water	0.10 (0.05)	0.31 (0.14)	0.96 (0.35)	3.0	0.06
<b>Crustose Lichens</b>					
Unidentified	1.00 (0.16) <sup>A</sup>	0.60 (0.22) <sup>B</sup>	0.18 (0.07) <sup>B</sup>	11.8	<0.01
<b>Mosses</b>					
Unidentified	22.26 (1.89)	26.69 (2.59)	28.75 (2.64)	1.8	0.18

<sup>1</sup> Means with the same letter (Tukey HSD at  $P \leq 0.05$ ) are not significantly different by site.

Appendix E. Mean (SE) percent cover of species by site in habitats classified as moist tussock sedge-low shrub tundra, Kuparuk region, Alaska, 1989-90.

Lifeform / Species	CST (n=24)	MID (n=24)	INL (n=24)	F	P-value
	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>	Mean (SE) <sup>1</sup>		
<b>Forage</b>					
<b>Evergreen Shrubs</b>					
<i>Cassiope tetragona</i>	1.16 (0.62)	3.46 (1.77)	2.15 (0.56)	3.1	0.05
<i>Dryas integrifolia</i>	1.66 (0.66) <sup>A</sup>	7.97 (0.97) <sup>B</sup>	5.71 (0.83) <sup>B</sup>	18.8	<0.01
<i>Ledum palustre</i>	0.00 (0.00)	0.04 (0.04)	0.00 (0.00)	1.0	0.38
<i>Vaccinium vitis-idaea</i>	0.15 (0.11)	0.00 (0.00)	0.00 (0.00)	2.6	0.09
<b>Frustricose Lichens</b>					
<i>Cetraria cucullata</i>	0.09 (0.09) <sup>A</sup>	1.54 (0.41) <sup>B</sup>	2.43 (0.41) <sup>B</sup>	14.1	<0.01
<i>Cetraria islandica</i>	0.00 (0.00)	0.10 (0.07)	0.18 (0.11)	1.2	0.30
<i>Cetraria nivalis</i>	0.00 (0.00) <sup>A</sup>	0.47 (0.20) <sup>A</sup>	0.47 (0.17) <sup>A</sup>	3.3	0.04
<i>Cladonia</i> spp.	0.35 (0.19)	0.26 (0.19)	0.07 (0.07)	0.9	0.41
<i>Dactylina arctica</i>	0.94 (0.55)	0.26 (0.10)	0.15 (0.08)	1.1	0.35
<i>Masonhalea richardsonii</i>	0.00 (0.00)	0.05 (0.05)	0.08 (0.08)	0.4	0.66
<i>Ochrolechia</i> spp.	0.41 (0.23)	0.20 (0.11)	0.09 (0.07)	0.7	0.49
<i>Thamnolia</i> spp.	1.09 (0.55)	2.33 (0.74)	1.13 (0.31)	2.0	0.14
<b>Forbs</b>					
<i>Astragalus umbellatus</i>	0.00 (0.00)	0.04 (0.04)	0.09 (0.06)	0.9	0.42
<i>Hedysarum</i> spp.	0.00 (0.00)	0.02 (0.02)	0.00 (0.00)	1.0	0.38
<i>Lupinus arcticus</i>	0.00 (0.00)	0.05 (0.05)	0.00 (0.00)	1.0	0.38
<i>Papaver macounii</i>	0.00 (0.00)	0.00 (0.00)	0.10 (0.10)	0.9	0.43
<i>Pedicularis</i> spp.	0.18 (0.18)	0.06 (0.06)	0.05 (0.05)	0.2	0.85
<i>Polygonum bistorta</i>	0.00 (0.00)	0.11 (0.11)	0.00 (0.00)	1.0	0.38
<i>Polygonum viviparum</i>	0.00 (0.00)	0.00 (0.00)	0.09 (0.06)	1.8	0.18
<i>Pyrola grandiflora</i>	0.00 (0.00) <sup>A</sup>	0.06 (0.06) <sup>AB</sup>	0.34 (0.14) <sup>B</sup>	4.3	0.02
<i>Saussurea angustifolia</i>	0.00 (0.00)	0.24 (0.12)	0.65 (0.29)	2.9	0.06
<b>Grasses-Sedges</b>					
<i>Arctagrostis latifolia</i>	0.00 (0.00)	0.04 (0.04)	0.02 (0.02)	0.4	0.65
<i>Carex aquatilis</i>	0.00 (0.00)	0.10 (0.07)	0.00 (0.00)	2.0	0.14
<i>Carex atrofusca</i>	0.00 (0.00)	0.00 (0.00)	0.02 (0.02)	0.9	0.43
<i>Carex Bigelowii</i>	3.12 (0.92)	2.76 (0.57)	2.44 (0.48)	0.1	0.89
<i>Carex membranacea</i>	0.00 (0.00)	0.22 (0.10)	0.05 (0.05)	2.8	0.07
<i>Carex misandra</i>	0.00 (0.00)	0.02 (0.02)	0.09 (0.05)	1.7	0.19
<i>Carex rotundata</i>	0.00 (0.00)	0.08 (0.08)	0.09 (0.06)	0.7	0.51
<i>Carex vaginata</i>	0.09 (0.09)	0.00 (0.00)	0.00 (0.00)	1.2	0.30
<i>Eriophorum angustifolium</i>	2.81 (0.81) <sup>A</sup>	4.20 (0.70) <sup>A</sup>	1.99 (0.38) <sup>A</sup>	3.5	0.04
<i>Eriophorum vaginatum</i>	5.31 (1.35)	4.76 (0.97)	4.82 (0.62)	0.4	0.68
<b>Willows</b>					
<i>Salix arctica</i>	0.09 (0.09) <sup>A</sup>	1.41 (0.31) <sup>B</sup>	0.76 (0.17) <sup>B</sup>	9.8	<0.01
<i>Salix lanata</i>	0.00 (0.00)	0.58 (0.46)	0.00 (0.00)	2.5	0.09
<i>Salix phlebophylla</i>	0.66 (0.46)	0.23 (0.23)	0.00 (0.00)	1.4	0.25
<i>Salix pulchra</i>	6.99 (1.40) <sup>A</sup>	0.24 (0.18) <sup>B</sup>	1.76 (0.54) <sup>C</sup>	19.5	<0.01
<i>Salix reticulata</i>	3.54 (0.84)	1.56 (0.52)	1.61 (0.28)	2.1	0.13
<i>Salix rotundifolia</i>	1.05 (0.55) <sup>A</sup>	0.00 (0.00) <sup>B</sup>	0.00 (0.00) <sup>B</sup>	6.7	<0.01
<b>Nonforage</b>					
<b>Abiotic-Litter</b>					
Litter	33.23 (3.28)	35.39 (2.69)	33.35 (1.80)	0.4	0.67
Soil	4.67 (1.52)	1.83 (0.77)	1.88 (0.40)	1.9	0.16
Water	0.00 (0.00)	0.05 (0.05)	0.00 (0.00)	2.6	0.09
<b>Crustose Lichens</b>					
Unidentified	2.39 (0.77) <sup>A</sup>	0.45 (0.15) <sup>B</sup>	0.49 (0.21) <sup>B</sup>	4.5	0.02
<b>Mosses</b>					
Unidentified	30.80 (3.88)	29.17 (2.49)	37.40 (2.42)	2.3	0.11

<sup>1</sup> Means with the same letter (Tukey HSD at  $P \leq 0.05$ ) are not significantly different by site.