SUMMER ECOLOGY OF THE TESHEKPUK CARIBOU HERD

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A

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Abstract

The summer range of the Teshekpuk Caribou (*Rangifer tarandus granti*) Herd is currently undergoing the initial stages of petroleum exploration and development. Pre-development baseline information is necessary to interpret post-development distribution and habitat selection of caribou and to develop mitigation measures. We estimated bi-weekly distributions, diet and habitat selection by caribou during the summers, 2002-2004, based on aerial relocations of 21-49 radio-collared females. Little or no habitat selection was detected when comparing used locations to habitat available within bi-weekly utilization distributions. Habitat selection was much stronger when comparing bi-weekly utilization distributions to the remaining area of summer use. At the latter scale of analysis, there were dynamic temporal patterns in resource selection by caribou. High air temperature was strongly avoided throughout July. Tussock tundra was avoided early in the summer, but selected during August. Wet sedge was selected in June and from late-August through September. Estimates of dietary nitrogen content indicated that high nitrogen concentrations are available only for a short period in early summer, and declined well before forage biomass. Predicted dietary nitrogen concentration appeared to be much lower for the Teshekpuk Caribou Herd than for the Porcupine Caribou Herd. Successful mitigation measures for petroleum development in NPR-A will need to be spatially and temporally tailored to observed dynamic patterns in caribou resource selection. Future work should estimate the performance of caribou (e.g., survival or weight gain) in relation to habitat quality and use in order to confirm the value of selected habitats and to enhance the robustness of mitigation measures.

Table of Contents

Chapter 2

Chapter 3

List of Figures

Page

List of Tables

List of Appendices

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INTRODUCTION

The Teshekpuk Caribou Herd (TCH) is a relatively unstudied population of barren ground caribou (*Rangifer tarandus granti*) that ranges across the central portion of the North Slope of Alaska, overlapping considerably with the National Petroleum Reserve – Alaska (NPR-A). This caribou herd is an important subsistence resource. In recent years, harvest levels have been estimated at 2500-4500, with harvest taking place across the North Slope (Carroll 2005). Adding to concerns regarding the need for information about this herd's ecology is a lack of understanding regarding potential effects of climate change and oil development, both of which may play an important role in the future of this herd.

The lack of baseline data has hampered the ability to discern natural and anthropogenic changes observed in the distribution and population parameters of the adjacent Central Arctic Herd (NRC 2003). This issue was one impetus for pre-development research on the TCH. Planning for possible changes in distribution and population resulting from either climate change or a build-up of oil infrastructure within the herd's summer range will only be possible with adequate information on current distribution and habitat use.

This thesis is divided into three chapters. The first chapter addresses spatial variation in temperature and wind patterns across the summer range of the TCH. These data provide an important addition to the suite of habitat conditions that caribou can select, particularly with regard to avoiding insect harassment. Additionally, an understanding of spatial variation in the distribution of insect relief habitat is important for understanding the energetic effects of a phenological shift in the onset and duration of insect harassment that may accompany a warming climate.

The second chapter estimates bi-weekly distributions of female caribou throughout the summer period, and the influence of various habitat variables on habitat selection and distribution. Understanding how habitat selection influences distribution will allow future researchers to delve deeper into understanding how distribution influences fitness-level parameters such as weight gain and survival.

The third chapter estimates seasonal patterns in fecal estimates of dietary composition and nitrogen content, and how those estimates relate to a remotely sensed index of vegetation quantity. The relative quality of diet has important implications for reproductive success and summer weight gain of caribou. Seasonal data on diet quality will help clarify the significance of geographic areas to annual nitrogen budgets.

CHAPTER 1:

SPATIAL MODELS OF TEMPERATURE AND WIND SPEED: INDICES FOR POTENTIAL INSECT HARASSMENT OF CARIBOU[1]

Abstract: Insect harassment is an important factor in caribou habitat selection during the summer months. Air temperature and wind speed are two factors which influence insect activity. Using data from 20 weather stations, we developed spatial models for interpolating and predicting air temperature in the National Petroleum Reserve – Alaska, but were unsuccessful in developing models which could accurately predict wind speed. Temperatures were more spatially variable than wind speeds. Latitude and longitude were the most important variables in predicting air temperature. Temperatures decreased non-linearly to the north, and decreased linearly to the east. The air temperature model was most accurate during mid-summer, when insect activity was most likely to occur. The moderating effect of the Arctic Ocean on coastal temperatures likely led to model inaccuracies when air temperatures began to cool in autumn. We were unable to fit a theoretical semivariogram to residual temperature or wind data; kriging was therefore not an option. A cumulative logistic model that predicted mosquito severity from predicted temperature and wind speed confirmed the utility of our temperature and wind speed models.

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INTRODUCTION

Insect harassment, particularly by mosquitoes (*Aedes spp.)*, warble flies (*Hypoderma tarandi*) and nasal bot flies (*Cephenemyia trompe*), is an important driver of habitat selection by barren-ground caribou (e.g. Kelsall 1968, White et al. 1975, Downes et al. 1986, Walsh et al.1992). Negative energetic consequences of insect harassment are assumed to result from several sub-lethal effects that include direct energetic losses (Gulland 1995), reduction in time spent foraging (e.g. White et al. 1975, Downes et al. 1986, Dau 1986, Murphy and Curatolo 1987, Toupin et al. 1996, Mörschel and Klein 1997), selection of habitats where forage is poor in quantity or quality (Walsh et al. 1992, Russell et al. 1993, Pollard et al. 1996), and increased energy expenditure through movement (Downes et al. 1986, Fancy 1986, Murphy and Curatolo 1987, Mörschel and Klein 1997). Fitness consequences resulting from these energetic costs may include reduction in calf survival (Haukioja and Salovaara 1978, Helle and Tarvainen 1984), decreased body condition (Vincente et al. 2004), or depressed fecundity (Gulland 1995, Albon et al. 2002).

Parasitic insects form a spatially and temporally dynamic part of the landscape (Dau 1986). The potentially dynamic nature of insect-free habitats requires a spatially explicit quantification of insect activity for any study of habitat selection. Factors such as predation risk, foraging opportunities, and parasite avoidance may all influence habitat selection by caribou; knowing which factors are important at different times and at different scales is essential when designing mitigation for development activities and for understanding caribou ecology.

Because of the logistical difficulty in conducting insect abundance surveys throughout the 48,000 km^2 summer range of the Teshekpuk Caribou Herd (Chapter 2, Parrett 2007), we instead attempted to create spatial models of two weather indices commonly identified as important for predicting insect activity or occurrence: air temperature and wind speed (White et al. 1975, Downes et al. 1986, Dau 1986, Nixon 1990, Mörschel 1999). Other factors, particularly light intensity (Downes et al. 1986, Mörschel 1999) and relative humidity or saturation deficit (Dau 1986, Mörschel 1999) have been noted as important factors in determining insect activity levels, but data for those parameters were unavailable throughout much of the study area.

Most attempts to characterize the relationship between weather and insects that parasitize caribou identify weather thresholds that limit insect activity, but are often unable to consistently predict insect occurrence or severity when conditions appear suitable (Nixon 1990, Toupin et al. 1996, Mörschel 1999). Additionally, studies in various geographic areas are often in disagreement about insect activity thresholds; temperatures cold enough to limit insect activity in southern latitudes may be well within the range of temperatures suitable for cold-adapted northern species or ecotypes (White et al. 1975, Downes et al. 1986, Dau 1986, Nixon 1990, Mörschel 1999).

The purposes of this study were to 1) derive spatially and temporally accurate estimates of temperature and wind speed during the study period, and 2) create models, using consistent spatial patterns in wind speed and temperature, that could be expanded to periods when temperature and wind speeds were not as intensely measured as they were during this study. The ability to extrapolate this model outside of the study period would enable researchers to compare caribou locations collected in previous or future years to to these weather data.

Secondary goals of this study were 1) to assess the effect of Teshekpuk Lake on local temperatures, and 2) validate our wind speed and temperature models against observed levels of mosquito activity.

STUDY AREA

The study area comprised the summer range of the Teshekpuk Caribou Herd (TCH), plus areas outside that range to allow for interpolation of data throughout the summer range. The summer range of the TCH , estimated in 2002-2004, occupies the central coastal plain north of the Brooks Range in Alaska, east of Deadhorse, and west of Wainwright (Figure 1.2).

METHODS

Weather Stations

Weather across the summer range of the TCH was monitored intensively in 2004 using 20 weather stations deployed systematically throughout the study area (Figure 1.2). We placed 9 temporary weather stations in remote areas that would fill in large gaps in the spatial array of 11 permanent stations maintained by various government agencies, including the National Weather Service, Federal Aviation Administration, U.S. Department of Energy's Atmospheric Research Monitoring (ARM) program, and U.S. Geological Survey (USGS) Cryospheric Studies Project.

The 9 temporary weather stations (Onset^{TM} Bourne, MA) were equipped with sensors which recorded air temperature, relative humidity, wind speed and wind direction. Data collection rates varied from every two hours for some USGS maintained stations to every minute for a station maintained by ARM in Atqasuk. Of the 20 stations deployed in 2004, 19 collected air temperature (one sensor malfunctioned), while wind speed was only available from 16. The 9 stations deployed for this study were installed on 1.5 meter long pipes driven into the tundra. Instruments for temporary stations were approximately 1.2 meters above the ground. Permanent stations ranged from 1 to 3 meters above ground. The 9 stations installed specifically for this study were deployed on 4 or 5 July, 2004, and removed from the field on 3 or 4 September, 2004.

Weather Modeling

We modeled average daily temperature and wind speed from 7 July to 6 August, 2004. We modeled this specific time period in order to maximize the number of spatial data points, because data from temporary stations deployed specifically for this study were only available for a limited time period (6 July-2 September), and data from some other remote stations are downloaded only on an annual basis.

We first focused on individual days during that 30 day period, in order to produce the most accurate models possible for analyzing the relationship between caribou locations and temperature and wind speed. Dependent variables were average daily temperature, and average daily wind speed. Spatial explanatory variables included latitude (UTM 5N, “northing”), longitude (UTM 5N, “easting”), distance from coast (km), and elevation above sea level (m). Distance from coast was estimated using the 1:63 Alaskan coast GIS layer, while elevation was estimated using a DEM generated from 1:63 USGS maps. Non-spatial explanatory variables were day, used as a class variable, and temperature or wind speed in Barrow, used in a separate suite of models where the temperature and wind speed at Barrow had been removed as dependent variables (Figure 1.1 for schematic diagram). Using data from Barrow to adjust the intercept, rather than a variable which was temporally specific, would allow prediction of temperature and wind across the study area as long as data were available from Barrow.

In order to accommodate comparisons between models which used temperature and wind speed data from Barrow as independent variables and models which used a classification variable for each day as an intercept adjustment, data from Barrow were not included as dependent variables in data sets of comparative models. Using the same dependent data set was necessary for comparing the performance of the generalized model to day-specific models.

We used SAS PROC MIXED in order to incorporate serial autocorrelation in daily weather data, with the weather station acting as a repeated subject in the analysis (Littel et al. 1996, SAS Inst. Inc. 1999). We used maximum likelihood for comparison of fixed effects in the candidate model set, using the small sample version of Akaike's Information Criteria (AICc) for model selection (Burnham and Anderson 2002). We used restricted maximum likelihood for assessment of covariance structure (Littel et al. 1996). We used variance inflation factors, condition indices and correlation between the independent variables to assess collinearity (Belsley et al. 1980, SAS Inst. Inc. 1999). Although collinearity is less of a problem when prediction rather than explanation is the primary goal, we nevertheless attempted to avoid overparameterizing by not using models that simultaneously utilized any variables that caused condition indices greater than 5 (Belsley et al. 1980), or variance inflation factors greater than 3.

We investigated the utility of universal kriging as a method of spatial interpolation. Universal kriging allows trends in the data to be removed before modeling the residual spatial autocorrelation (Cressie 1993, Vajda and Venäläinen 2003). Methods of interpolation that are combined with trend analyses have proven effective in modeling climate data, particularly when terrain is complex (MacEachren and Davidson 1987, Collins and Bolstad 1996, Shiklomanov and Nelson 2003, Vajda and Venäläinen 2003, Rolland 2003). With sparse data, as in this study, this is akin to modeling large scale variation with polynomial linear regression, while modeling any mesoscale spatial patterns with kriging techniques.

Statistics used for assessment of accuracy and model fit included mean absolute error (MAE), R^2, Akaike weights, and deviance R^2. Akaike weight ($w_i = \exp(-1/2\ \Delta AIC_i)/\Sigma \exp(-1/2\ \Delta AIC_{i-j})$ is the weight of evidence that the model of interest ($_i$) is the best approximating model within the suite of candidate models ($_{i-j}$) (Burnham and Anderson 2002). Deviance R^2 ($R^2_{DEV} = 1-(-2\log \text{likelihood}_{(model)} / -2\log \text{likelihood}_{(null\ model)})$) can be interpreted as the proportional reduction in the -2 log-likelihood statistic (Menard 2000), unlike the coefficient of multiple determination (R^2), which measures the proportional reduction of total variation in the dependent variable (Neter et al. 1996). Following large scale spatial trend removal, we then interpolated residual values using variograms to estimate appropriate lag distance and range to use in kriging daily data sets (Cressie 1993, SAS Inst. Inc. 1999).

We used data from 1 June to 30 September, 2002 and 2003, from 5 permanent stations to validate the accuracy of the generalized model in different years, as well as outside of the 30 day period used to generate the model. Using a Tukey test, we compared residual errors associated with the period that coincided with the study dates in 2004 to residual errors from the periods preceding and following the study period.

Daily mosquito activity was classified by a single observer on the ground as none, moderate or high at a site 10 km south of Teshekpuk Lake in 2003 and 2004 (n=53 days). Data were collected sporadically in late June and throughout July. As a means of verifying the utility of the predictive temperature and wind models, we used a cumulative logistic regression model to predict a three step ordinal classification of mosquito activity using predicted daily mean temperature and wind speed at that site as independent variables (Allison 2001). We also collapsed the moderate and high categories to create a binomial classification to see if model selection was consistent between the multinomial and binomial classification systems. We used AICc for model selection (Burnham and Anderson 2002), and concordance to assess model fit (Hosmer and Lemeshow 2000).

The effect of Teshekpuk Lake on local temperatures was assessed by testing the null hypothesis that the two weather stations near Teshekpuk Lake had residual temperatures that were not significantly different from zero. One station was situated on the north shore of Teshekpuk, while the other was 15 km south of Teshekpuk. Mean residuals from the top temperature model for each station was tested with a Student's t-test.

RESULTS

Weather Modeling

Elevation and distance from the coast were both moderately correlated with latitude (r = -0.77, r = -0.75, respectively), as well as each other (r =0.73). Variance inflation factors for models that contained all 4 independent variables were all greater than 2, with the highest being 8.95. The maximum condition index for the full additive model was 6.39, with one variance decomposition proportion exceeding 0.5, and two exceeding 0.8. Although the condition index did not indicate severe collinearity problems, we did not simultaneously include latitude, elevation, or distance from the coast in any models.

Bivariate plots of temperature and the spatial variables indicated curvilinear structure between some of the spatial variables and temperature. Bivariate plots of wind speed and the spatial variables also indicated curvilinear structure for some of the variables and wind speed. As a result, we added curvilinear structure to each of the variables in the temperature and wind speed candidate model sets, as well as the logarithm of distance from coast.

Temperature Model Selection

The best temporally specific temperature model included curvilinear effects of latitude and longitude, along with an intercept adjustment for each day (Figure 1.3, Table 1.1). Temperature decreased with latitude, with temperatures decreasing more rapidly at high latitudes. The effect of longitude was nearly linear, with temperatures decreasing toward the eastern portion of the study area. The effects of latitude and longitude both interacted with day, requiring daily adjustments in the slopes of the latitude and longitude relationships. The next best model dropped the curvilinear effect of longitude in favor of a linear effect (Table 1.1). The mean absolute error for the best temperature model was 0.67° C, with an R^2 of 0.95. The Akaike weight for the top model was 0.62, with an R^2_{DEV} of 0.54. The Akaike weights for the two competing models summed to 1.00. The top model was used to predict temperatures across the study area only for the period with the complete data set.

The parameter estimates for the effect of day from a simplified model (temperature = day + latitude + longitude), which did not include Barrow in the dependent data set, were highly correlated with average daily Barrow temperature (Pearson's r = 0.91). The best generalized model which uses the temperature in Barrow as an intercept adjustment included a linear effect of longitude, a curvilinear effect of latitude, and an interaction between Barrow temperature and longitude (Table 1.2). A competing model, 0.4 AIC_C higher, dropped the interaction term. The latter model predicted a curvilinear change in temperature of -0.011 ˚C/km of northing near the southerly limit of the study area, and a -0.074 ˚C/km of northing near the coast, and a linear change in temperature of -0.01 ˚C/km of easting (Figure 1.4).

The mean absolute error for the best approximating model that utilized the Barrow temperature to make daily adjustments was 1.61° C, versus 0.91° C for the comparable model that utilized a unique model parameter to adjust the mean temperature prediction each day (Table 1.3). These errors compare to a mean daily range of 7.67 degrees in temperature values, and have respective R^2 values of 0.77 and 0.91. While the best approximating model from the complete data set supported daily adjustments in the slope of the spatial patterns through interaction terms (Table 1.1), these interactions were not well supported when using Barrow temperature as an indicator of the general temperature in the study area (Table 1.2). It is apparent through comparison of these errors that the slope adjustments conveyed through the day*latitude and day*longitude interactions are relatively important for accurate prediction.

Temperature Model Validation

Prediction errors both before and after the study period tended to be significantly larger than errors associated with the study period (Figure 1.5). The model often predicted temperatures that were warmer than those observed, but only by 2-4 degrees in most cases (Figure 1.5).

Wind Speed Model Selection

The best model for wind speed prediction included day, along with a linear response to distance from coast, and a curvilinear response to longitude (Table 1.4). There were three competing models, and the only variable common to all three was day (Table 1.4). Interactions between the day and spatial variables, which would allow the slopes of the spatial relationships to change over time, were not supported by the data, in contrast to the best approximating temperature models. The mean absolute error for the top model was 0.60 meters/second, and R^2 was 0.68. Akaike weight for this model was 0.31, with an R^2_{DEV} of 0.38.

The parameter estimates for day were only moderately correlated with the average wind speed in Barrow (Pearson's r = 0.75). The best generalized model, which replaced day with the average wind speed in Barrow, retained the same spatial variables as the top model that included Barrow in the dependent data set (Figure 1.6). Model sets with Barrow wind speed as a variable also produced multiple competing models which varied in implied spatial structure (Table 1.5). The mean absolute error for the best approximating model which used Barrow wind speed was 0.85 m/s, with an R^2 of 0.41. Compared to the average daily range in wind speeds of 3.3 m/s, the mean absolute errors for the above wind speed models are somewhat high. Comparisons of models which replace the classified day variable with average daily Barrow wind speed indicate that the loss of information resulting from the use of Barrow wind speed is not as substantial as the loss of information that results from replacing day with Barrow temperature (Table 1.6).

Wind Model Validation

Errors in wind speed prediction for the periods preceding and following the study period were not significantly different from errors associated with the time period when the study took place in 2004 (Figure 1.7). Typically, the magnitude of error was less than 1 m/s, with consistent under-prediction of wind speed.

Semivariogram Modeling

Exploratory analyses indicated that 5 lags at a distance of 50 km were adequate for semivariogram modeling. Residual variation following the removal of large scale trends in the temperature data was essentially random, with little or no spatial covariance, as indicated by experimental semivariograms created for two dates that coincided with caribou relocation surveys (Figure 1.8). Wind speed residuals did have some spatial covariance structure remaining after removal of large scale trends, but the overall spatial covariance, as indicated by the maximum gamma values, was quite small (Figure 1.8). Based on the lack of range or sill in the empirical semivariograms, we felt that no theoretical semivariograms were applicable (Cressie 1993, SAS Institute, 1999), and temperature and wind estimates were made using polynomial models alone.

Wind Speed, Temperature, and Mosquito Activity

The best model predicting three levels of mosquito activity included both wind speed and temperature, with no competing models and an Akaike weight of 0.91 (Table 1.7). This model had a concordance of 78%. When using a binary classification, the top model was still the wind speed and temperature model, but wind speed alone competed (ΔAIC = 1.08, Table 1.8). In this case the top model had an Akaike weight of only 0.55, but concordance was still relatively high at 78%. Both the modeling results and a plot of wind speed, temperature, and mosquito activity level indicate that wind speed is actually the more important variable, and appears to act as a threshold, limiting severe harassment around 4 m/s (Figure 1.10).

Teshekpuk Lake and Local Temperatures

Mean residual temperatures from a station on the north shore of Teshekpuk Lake (-0.07˚ C) and another 15 km south of Teshekpuk Lake (-0.14˚ C) were not significantly different from zero (p= 0.62 and p=0.16, respectively), indicating no substantial effect of this large lake on local temperatures.

DISCUSSION

Air temperature is an important component of summer habitat for caribou (e.g. Kelsall 1968, White et al. 1975, Downes et al. 1986, Ion and Kershaw 1989, Walsh et al.1992). In addition to changes in distribution and habitat use resulting from insect harassment there is also evidence that caribou may avoid weather conditions that are conducive to insect activity, even in the absence of actual harassment (Downes et al. 1986). This behavior may be an attempt to avoid areas that have the potential for insect activity, an attempt to behaviorally thermoregulate (Ion and Kershaw 1989), or some combination of both. For example, insect harassed caribou may suffer from excessive heat loads even at ambient temperatures within the caribou thermo-neutral zone due to the additive heat produced by insect induced movements.

The models developed in this paper allow for temperature prediction accurate to within 1˚ C on average, particularly when relatively complete spatial coverage is available. The spatially explicit nature of interpolated temperature data allows this information to be incorporated into a GIS and utilized for habitat selection analyses (Chapter 2, Parrett 2007), and may allow researchers to establish temperature thresholds that lead to behavioral responses by caribou. Knowing where and when temperatures strongly influence behavior will also allow researchers to increase understanding of when other resource attributes are only secondarily or coincidentally important in habitat selection. Additionally, researchers may be able to define geographic areas where caribou consistently seek relief from harassment.

Despite the large increase in the number of parameters that need to be estimated when using day as a classification variable, using temperature data from Barrow as a continuous intercept adjustment does not have the support in a modeling framework that Day does. In head-to-head comparisons, models that utilize a classification variable have much lower AIC_C values (Table 1.3). Although wind speed within the study area was less variable that temperature on a daily basis (CV = 0.38 versus 0.51 for temperature), it was more difficult to predict, at least with the spatial data available for this study. When comparing the wind model which allows for daily adjustments in mean wind speed throughout the study area based on a classification variable versus adjustments based on wind speed in Barrow, the relative loss of information does not appear to be substantial However, given the lack of accuracy in even the best wind speed model we built, models which used Barrow data to adjust the intercept are probably inadequate for further use. Results from semivariogram models further emphasized that there was little spatial covariance to be modeled; a given day was basically windy or not. Evidence for this idea can be seen in the large improvement in model fit through the addition of specific data associated with a given day, over the effects of spatial parameters in the model.

Results of semivariogram modeling following removal of large scale spatial trends indicated that polynomial regression alone is sufficient to model weather data at our scale of interest, particularly temperature. Although attempts to utilize kriging techniques to interpolate the remaining variance in temperature and wind speed prediction were generally unsuccessful, given a higher density of weather stations, it is likely that kriging would provide additional accuracy, and allow for local adjustment of weather estimation beyond the large scale trends that we were able to discern.

Errors associated with temporal extrapolation of the temperature models indicated that the model which used Barrow data in the independent data set was somewhat error-prone outside of the original study period, and tended to overestimate temperatures in 4 of the sites used to assess model accuracy beyond the original 2004 dataset. We speculate that the observed spatial relationship, where northern locations like Barrow tend to be cooler than other stations, may not persist in spring and fall, when temperatures are low, and the ocean has a warming or stabilizing effect, rather than the cooling effect seen in mid-summer, when the model was generated. A longer time series with spatial coverage similar to this study may allow further refinement of the temperature model outside of the original study period.

Based on residual temperatures from the predictive temperature model, Teshekpuk Lake did not appear to have a dominant influence on nearby temperatures. Consistently negative residuals would have indicated that temperatures near Teshekpuk Lake were colder than expected based on our models. The potential for no lake effect does exist; this result would concur with findings of Vajda and Vanäläinen (2003), who found that lakes in northern Finland had a minor effect on regional climate compared to geographical position and local relief. Both Haugen and Brown (1980) and Dau (1986) found that the Arctic Ocean had a strong effect on local climate only within a few kilometers of the coast, which would support the lack of any regional effect of Teshekpuk Lake on climate.

Multiple tests of the relationships between environmental parameters and insect activity have been conducted (e.g. White et al. 1975, Downes et al. 1986, Dau 1986, Nixon 1990, Mörschel 1999). Our data relating wind speed and temperature to insect harassment levels generally corroborated those previous results and give us confidence that our wind speed and temperature models are useful. Comparing model selection results when predicting presence or absence of mosquitos rather than relative activity implies that temperature is likely to have a moderating influence on mosquito activity, while wind speed is a threshold variable. This is seen most clearly in Figure 1.10, where wind speeds above 4 m/s appeared to strongly inhibit mosquito activity. In contrast, mosquito activity appeared to occur across the range of temperatures seen, with relative severity being high when temperatures were high.

MANAGEMENT IMPLICATIONS

Using data from Barrow as an independent variable eliminates the need to maintain multiple weather stations within the study area. By using the less supported, but logistically preferred temperature model when necessary, our precision decreased by an average of 0.94˚ C. Although we felt that this difference was acceptable, the fact that remote weather stations are relatively inexpensive and easily deployed using fixed-wing aircraft on the coastal plain of northern Alaska should encourage researchers in the future to add spatially explicit and accurate temperature predictions to their data sets relating to resource attributes. Accurate wind speed prediction may be a possibility as well, however, it is not clear from this data set whether increasing the number of weather stations beyond the number used in this study would allow for adequate wind speed prediction.

With a more permanent array of weather stations, a further utility of this type of weather modeling is the ability to estimate areas that consistently provide insect relief. Given accurate insect activity thresholds, researchers could, for example, estimate areas within the TCH range which are predicted to provide insect relief during the month of July, when insect activity is highest, and TCH caribou appear to be most sensitive to variation in temperature (Chapter 2, Parrett 2007).

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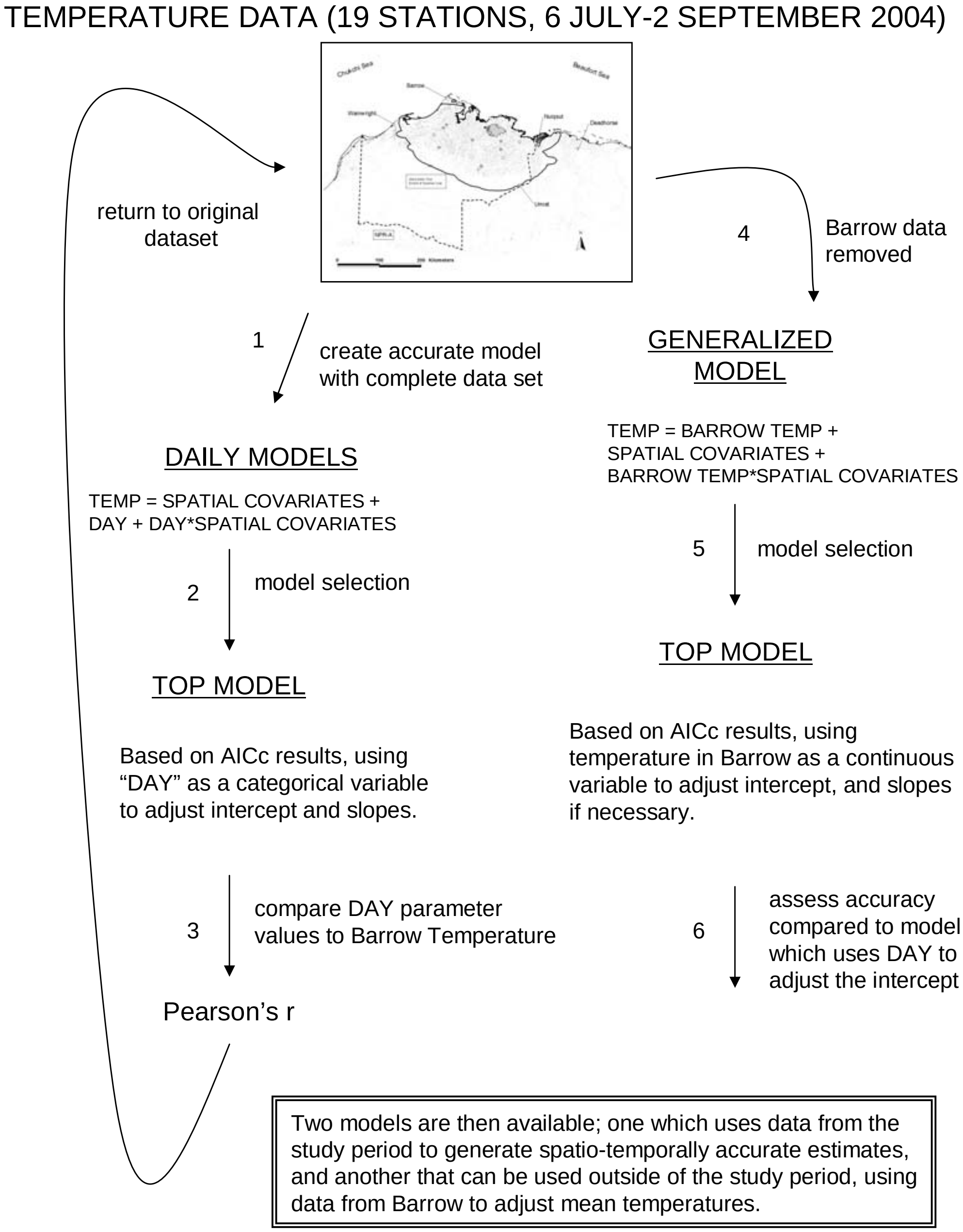


Figure 1.1 Schematic diagram of the temperature modeling process. We proceeded from original data which only spanned 30 days during the summer to a more generalized model which used the temperature in Barrow and consistent spatial relationships to predict temperatures. Modeling of wind speed followed an identical process.

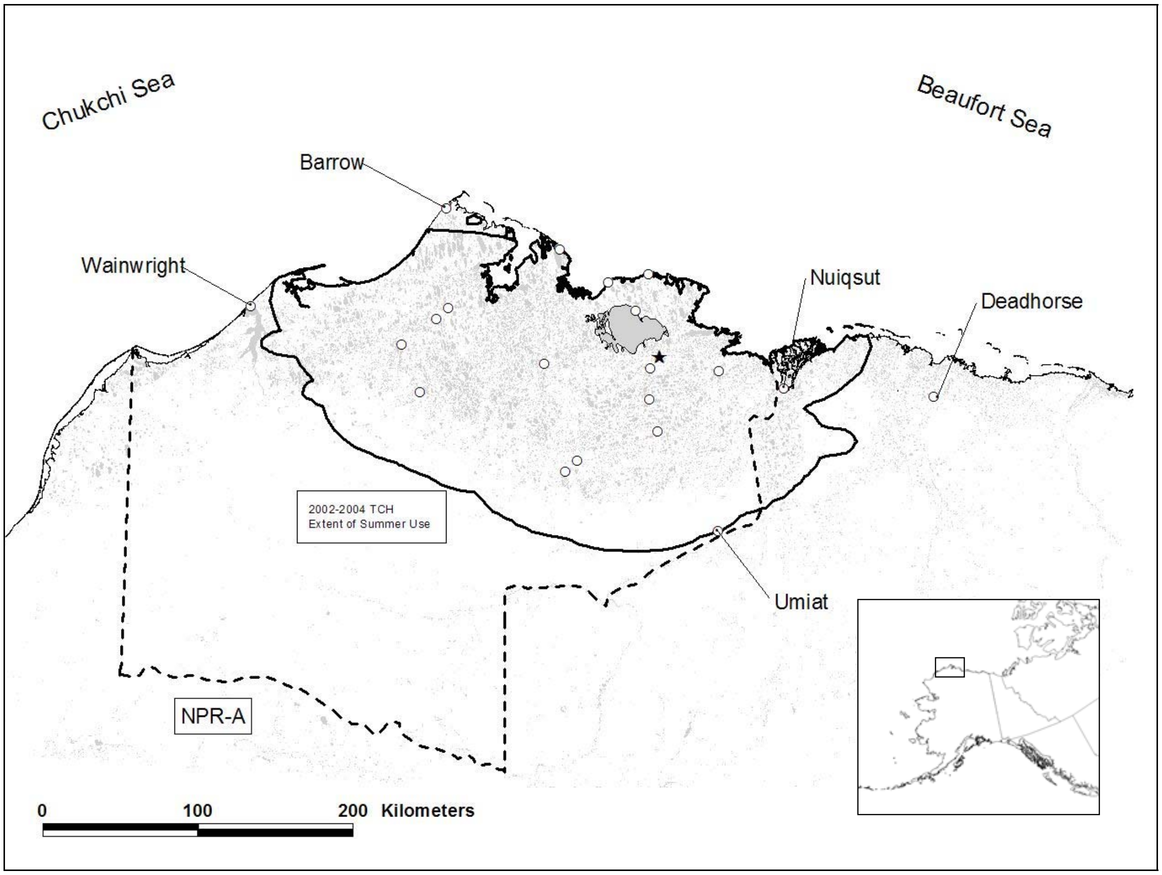
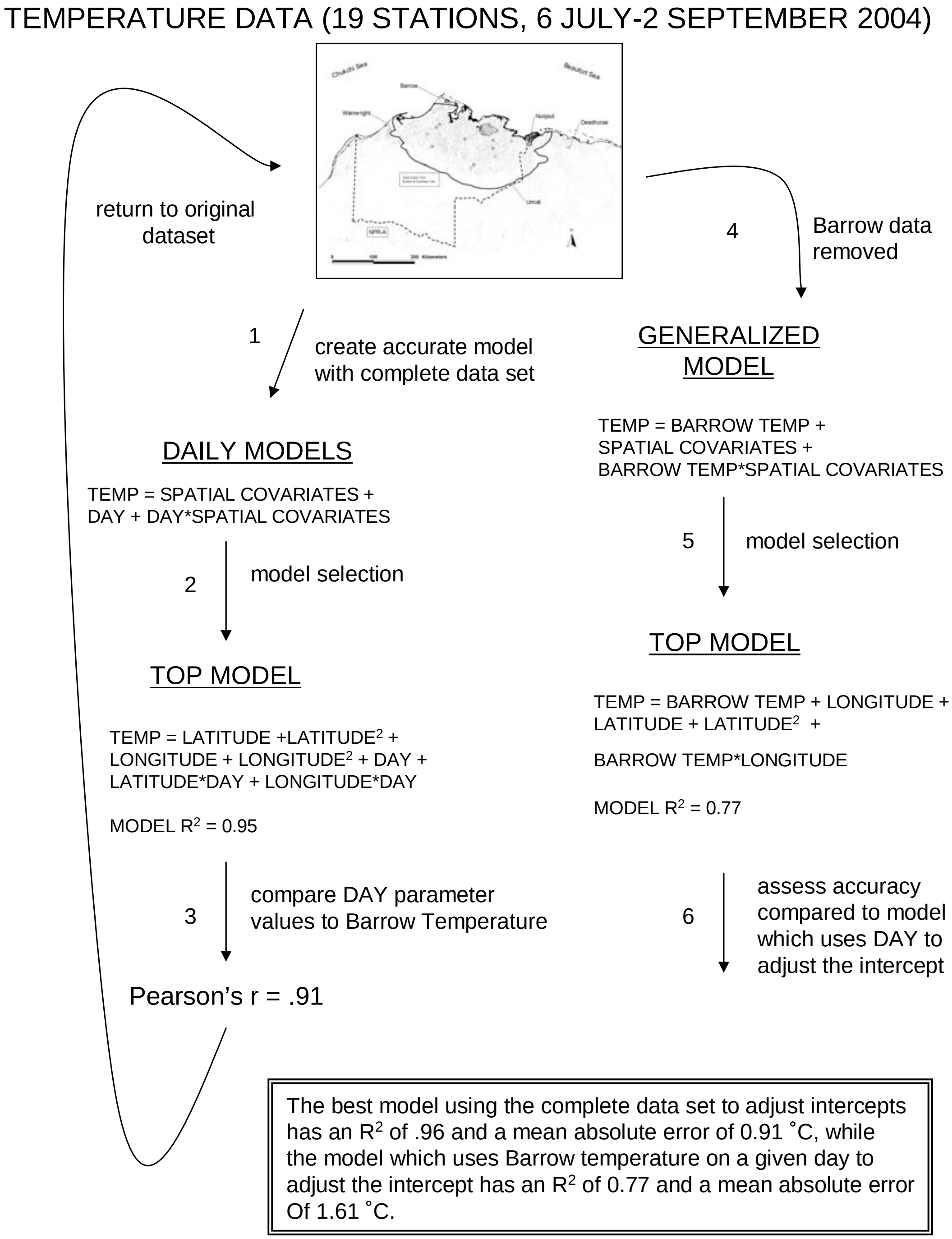


Figure 1.2 Study area with weather station locations. The Teshekpuk Caribou Herd summer range (solid line) and border of the National Petroleum Reserve-Alaska (dashed line) are indicated. Open circles indicate the locations of weather stations. The black star shows the position of Camp Olak, where mosquito activity data were collected. Inset shows position of study area within Alaska.



The best model using the complete data set to adjust intercepts has an R^2 of .96 and a mean absolute error of 0.91 ˚C, while the model which uses Barrow temperature on a given day to adjust the intercept has an R^2 of 0.77 and a mean absolute error Of 1.61 ˚C.

Figure 1.3 Schematic diagram of the temperature modeling process with results. We proceeded from original data which only spanned 30 days during the summer to a more generalized model which used the temperature in Barrow and consistent spatial relationships to predict temperatures. Modeling of wind speed followed an identical process.

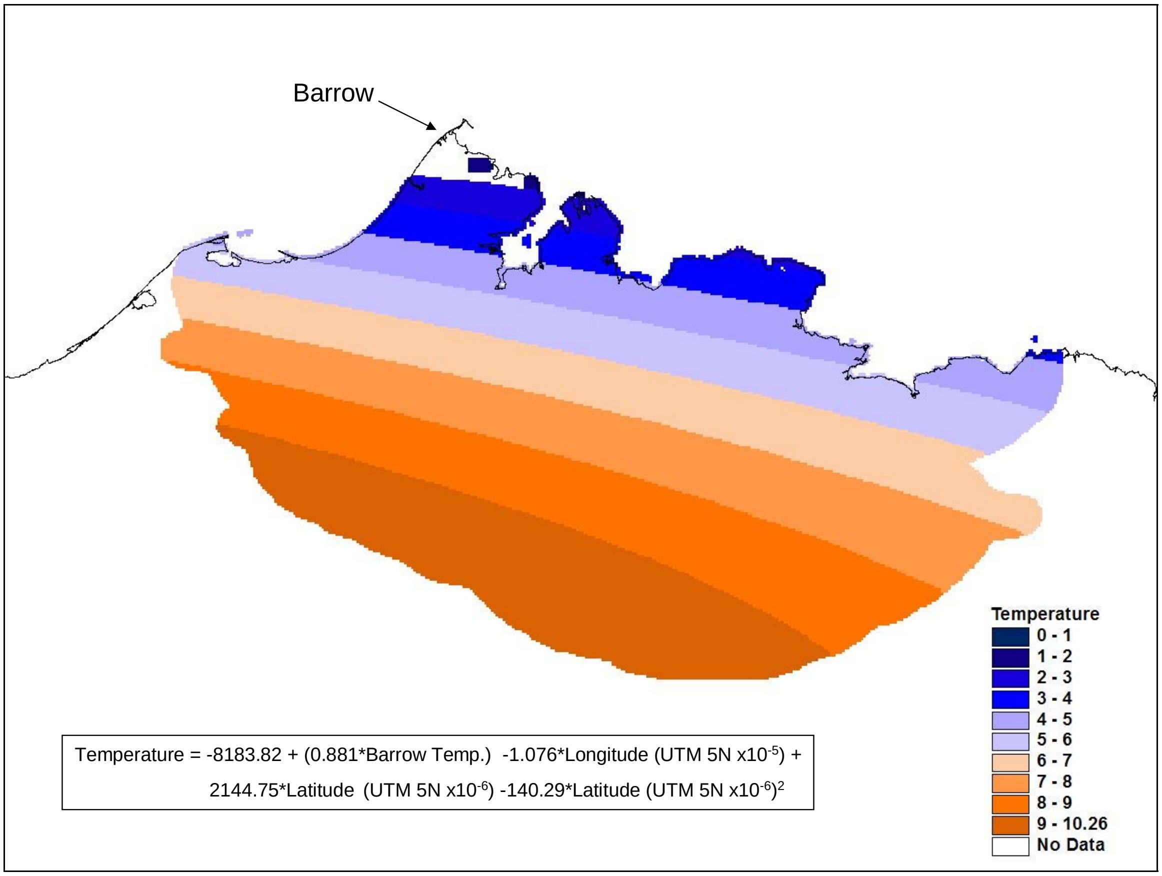


Figure 1.4 Spatial relationship among longitude, latitude, and temperature. Range of temperature within the TCH summer range are shown for the most parsimonious of the top (<2 ΔAICc) models which used the temperature in Barrow as an intercept adjustment. Temperatures displayed are those predicted for a day when the temperature in Barrow is 2˚ C (the average between 1 June and 30 September). Note that the area immediately around Barrow is not included in the summer range.

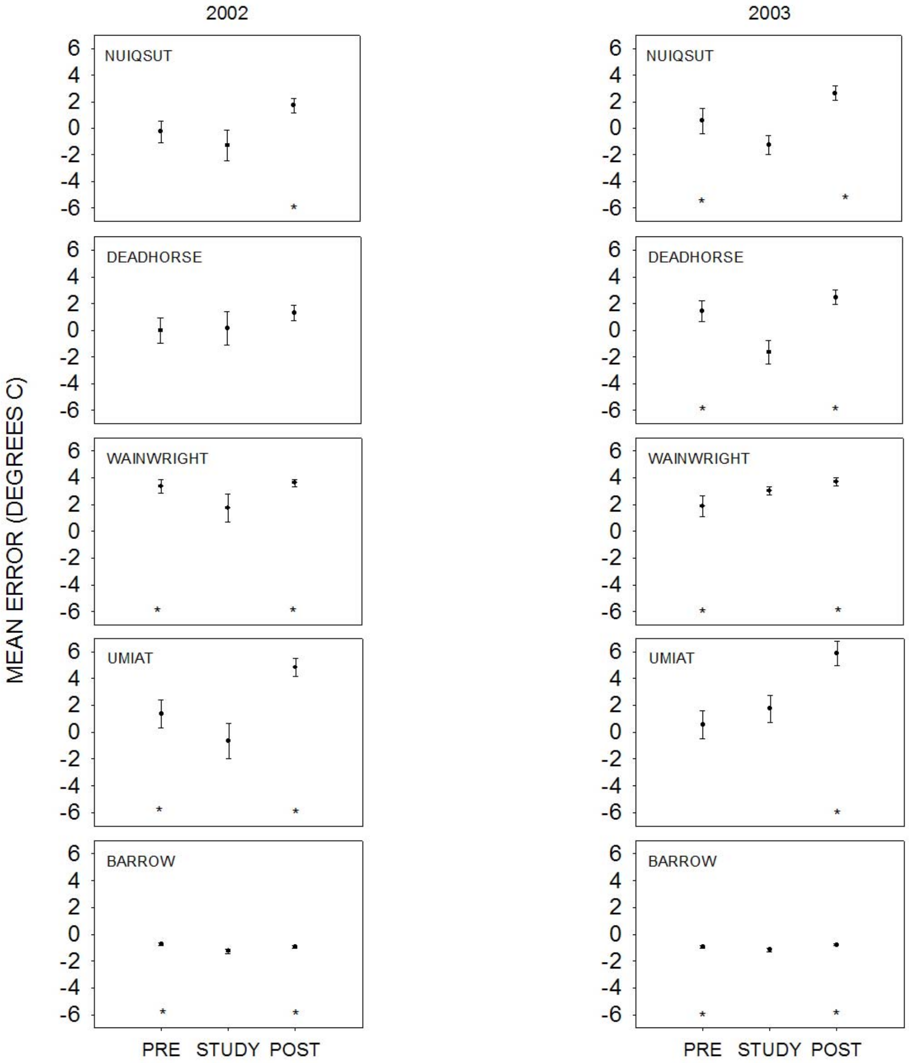


Figure 1.5 Temperature model validation. Mean errors with 95% confidence intervals for temperature predictions at 5 weather stations in or near the National Petroleum Reserve-Alaska. The model used predicted temperature based on temperature in Barrow, latitude, and longitude. The three periods correspond to the periods before (PRE =1 June–6 July), after (POST=August 7–September 30), and during (STUDY=7 July–6 August) the period of time used to generate the model in two different years before the study took place. Asterisks beneath the mean value for the PRE or POST period was significantly different from the mean error associated with the STUDY period.

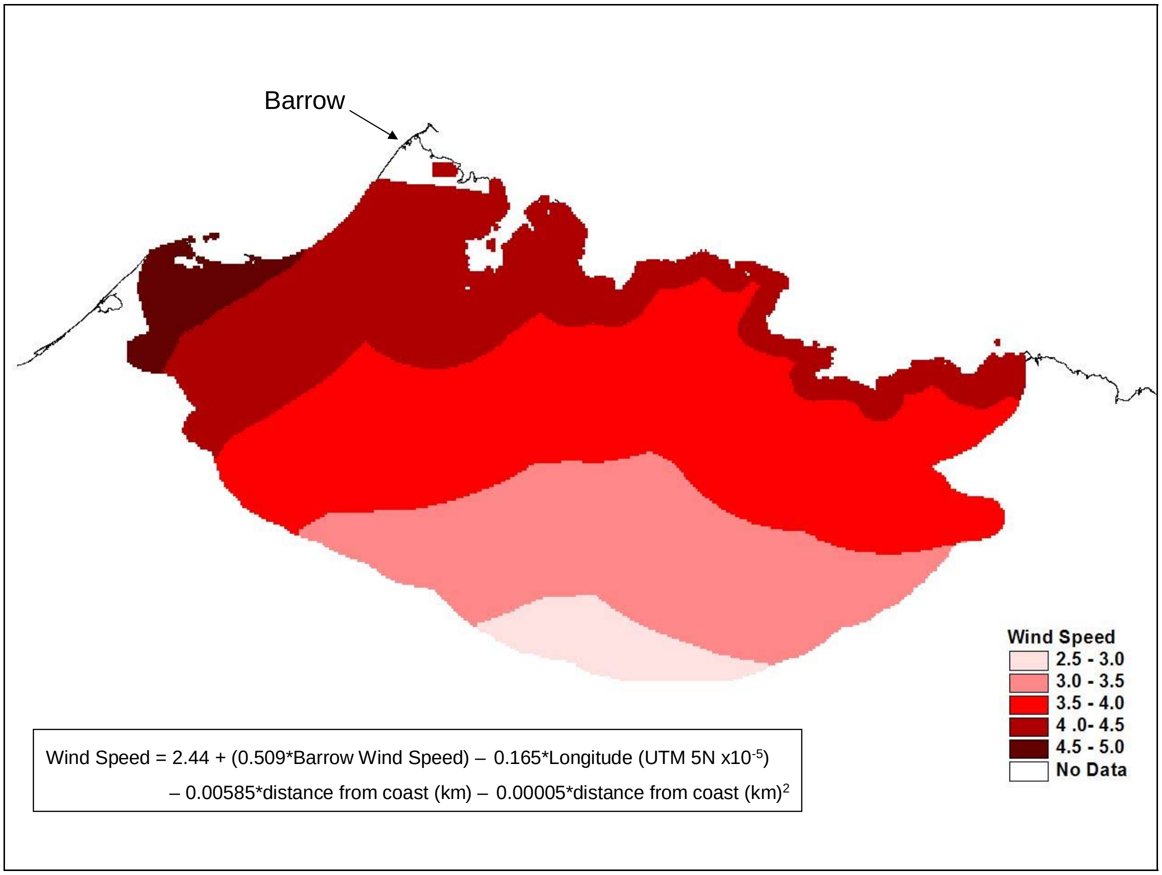


Figure 1.6 Spatial relationships among longitude, distance from coast, and wind speed. The range of wind speeds throughout the TCH summer range are shown for the top model which used Barrow wind speed to adjust the intercept. Note that the area immediately around Barrow is outside of the summer range. Predicted wind speeds shown are based on a wind speed of 5 m/s in Barrow.

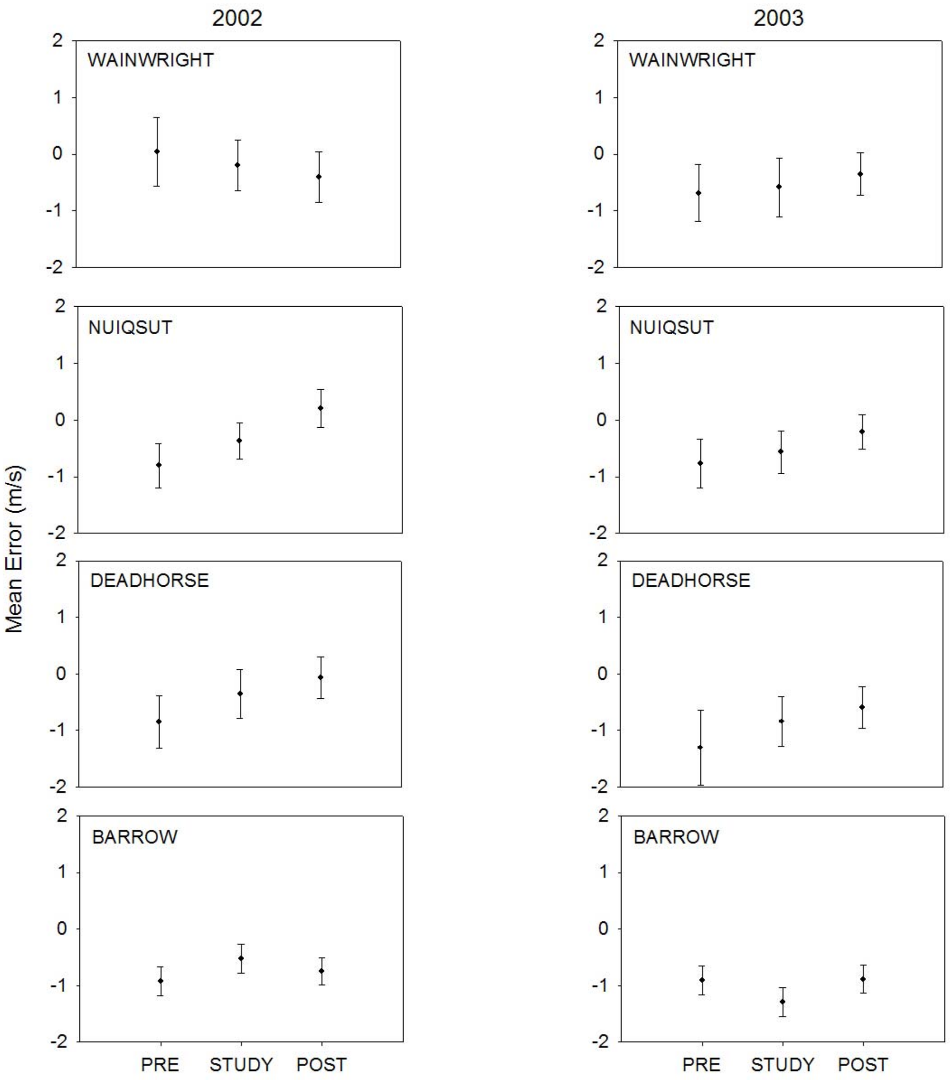


Figure 1.7 Wind speed model validation. Mean errors with 95% confidence intervals for wind speed predictions at 4 weather stations in or near the National Petroleum Reserve-Alaska. The model used predicted wind speed based on wind speed in Barrow, distance from coast, and longitude. The three periods correspond to the periods before (PRE =1 June–6 July), after (POST=August 7–September 30), and during (STUDY=7 July–6 August) the period of time used to generate the model in two different years before the study took place.

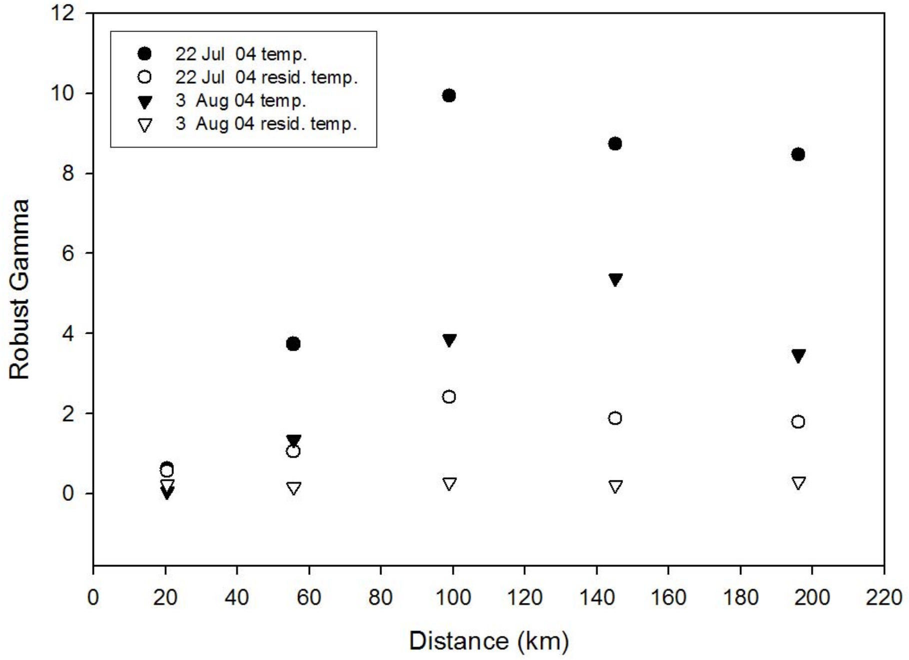


Figure 1.8 Experimental temperature semivariograms. Spatial covariance for raw temperature data, is compared to spatial covariance in residual errors remaining in the same data following removal of large scale trends related to latitude and longitude. Data from two days are displayed; 22 July and 3 August, 2004. The degree of spatial covariance is indicated by the robust gamma values. The large difference between actual and residual values indicates that much of the spatial covariation had been removed by the modeling process.

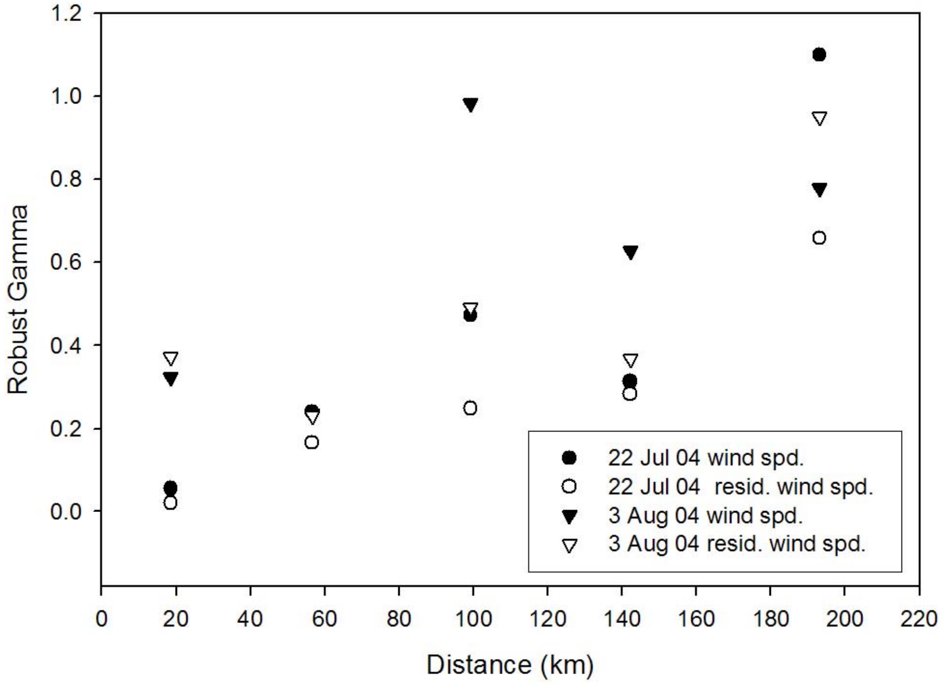


Figure 1.9 Experimental wind speed semivariograms. Spatial covariance seen in raw wind speed data is compared with spatial covariance in residual errors remaining in the same data following removal of large scale trends related to latitude and longitude. Data from two days are displayed; 22 July and 3 August, 2004. The degree of spatial covariance is indicated by the robust gamma values. The lack of a distinct difference between actual and residual wind speeds indicates that modeling did not remove a great deal of spatial variation. The relatively random scattering of points, lack of a Gaussian-like pattern in the data, and very low robust gamma values indicate that the data do not have strong spatial autocorrelation.

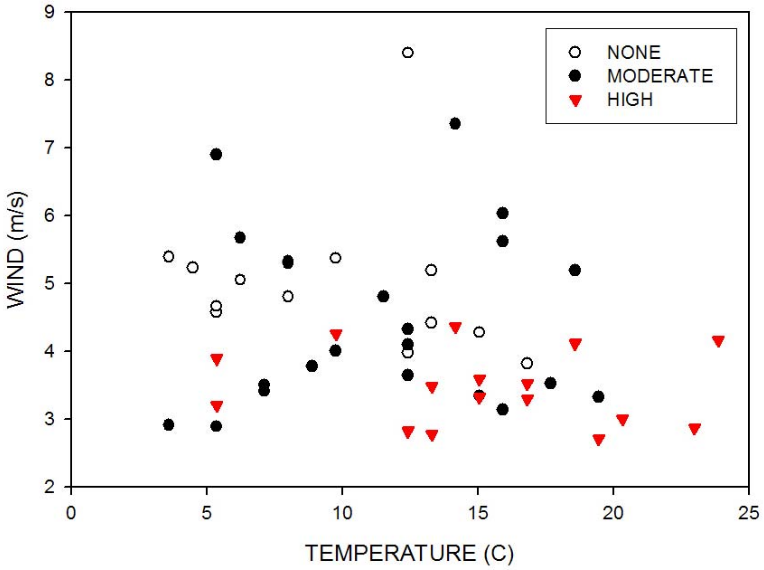


Figure 1.10 Mosquito activity, wind speed, and temperature. An ordinal assessment of daily mosquito activity was made in the field, and compared with predicted mean daily wind speed and temperature. Data are from Camp Olak, south of Teshekpuk Lake, in 2003 and 2004 (n=51).

Table 1.1 Model selection results for full temperature model. Shown are maximum likelihood AIC_C scores and Akaike weights from models used to predict temperature within the TCH summer range over a 30 day period in 2004. Data used to develop these models included temperature data from Barrow in the dependent dataset. Other than main effect models, candidate models that were more than 100 AICc from the top model are not shown.

MODEL VARIABLES[1]	AIC_C	ΔAIC_C	w_i
Day Lon Lon^2 Lat Lat^2 Day*Lon Day*Lat	1722.8	0	0.62
Day Lon Lat Lat^2 Day*Lat Day*Lon	1723.8	1	0.38
Day Lon Lat Day*Lat Day*Lon	1756.9	34.1	2.45E-08
Day	2202.4	479.6	4.5E-105
Dist	2872.8	1150.0	1.2E-250
Dist $Dist^2$	2873.0	1150.2	1.1E-250
Lat	2874.4	1151.6	5.3E-251
Lat Lat^2	2876.0	1153.2	2.4E-251
Null (with autocorrelation covariance structure)	2892.0	1169.2	8.0E-255
Lon	2896.0	1173.2	1.1E-255
Lon Lon^2	2898.0	1175.2	4.0E-256
Null (no autocorrelation)	3289.0	1566.2	0

[1] See appendix A for abbreviations.

Table 1.2 Model selection results for generalized temperature model. Shown maximum likelihood AIC_C scores and Akaike weights from models used to predict temperature within the TCH summer range over a 30 day period in 2004. The dataset used to develop these models does not include temperature data from Barrow in the dependent dataset. Data from Barrow were instead used as part of the independent data set as a replacement for the class variable "DAY." Candidate models other than univariate main effects models greater than 10 AICc from the top model are not shown.

MODEL VARIABLES[1]	AIC_c	Δ AIC_c	w_i
BrwTemp Lon Lat Lat^2 BrwTemp*Lon	2260.0	0.0	0.28
BrwTemp Lon Lat Lat^2	2260.4	0.4	0.23
BrwTemp Lon Lon^2 Lat Lat^2 BrwTemp*Lon	2261.0	1.0	0.17
BrwTemp Lon Lon^2 Lat Lat^2	2261.4	1.4	0.14
BrwTemp Lon Lat Lat^2 BrwTemp*Lat	2262.5	2.5	0.08
BrwTemp Lon Lon^2 Lat Lat^2 BrwTemp*Lon BrwTemp*Lat	2262.5	2.5	0.08
BrwTemp Lat Lon	2267.8	7.8	0.01
BrwTemp	2374.8	114.8	3.35E-26
Dist	2727.2	467.2	1E-102
Dist $Dist^2$	2728.6	468.6	1E-102
Lat	2730.5	470.5	1.9E-103
Lat Lat^2	2731.7	471.7	1.1E-103
Elev $Elev^2$	2736.2	476.2	1.3E-105
Elev	2739.3	479.3	2.6E-106
Null (with autocorrelation covariance structure)	2746.3	486.3	7.2E-107
Lon	2747.7	487.7	3.6E-107
Lon Lon^2	2749.8	489.8	1.2E-107
Null (no autocorrelation)	3108.2	848.2	1.9E-185

[1] See Appendix A for abbreviations

Table 1.3 Generalized vs. full temperature model comparison. Model fit and accuracy are compared for models which use the temperature in Barrow, Alaska on a given day, rather than a classified “DAY” variable. Both sets of models attempt to predict average daily temperatures throughout the NPR-A.

MODEL[1]	β=DAY				β=BARROW ˚C			
	AIC$_C$	m.a.e.	R^2	R^2_{DEV}	AIC$_C$	m.a.e.	R^2	R^2_{DEV}
β Lon Lon^2 Lat Lat^2 β *Lon β *Lat	1604.3	0.64˚C	0.96	0.55	2262.5	1.60˚C	0.77	0.28
β Lon Lat Lat^2 β *Lon	1823.5	0.91˚C	0.92	0.46	2260.0	1.61˚C	0.77	0.28
β Lon Lat Lat^2	1931.0	1.11˚C	0.89	0.40	2260.4	1.62˚C	0.77	0.28
β Lon Lat	2016.8	1.15˚C	0.88	0.40	2267.8	1.64˚C	0.76	0.27

AIC$_C$= Akaike’s Information Criterion, corrected for small sample size

m.a.e. = mean absolute error

R^2 = coefficient of multiple determination

R^2_{DEV} = Deviance R^2, a measure of proportionate reduction in the -2 log likelihood statistic over the null model

[1] See Appendix A for abbreviations

Table 1.4 Model selection results for full wind speed model. Shown are maximum likelihood AIC_C scores and Akaike weights from models used to predict wind speed within the TCH summer range over a 30 day period in 2004. Data used to develop these models included wind speed data from Barrow in the dependent dataset. Candidate models other than univariate models greater than 10 AICc from the top model are not shown.

MODEL VARIABLES[1]	AIC_C	ΔAIC_C	w_i
Day Dist Lon Lon^2	1265.7	0.0	0.31
Day Lat	1266.1	0.4	0.25
Day Dist Lon	1267.7	2.0	0.11
Day Dist $Dist^2$ Lon Lon^2	1267.9	2.2	0.10
Day Lat Lat^2	1268.4	2.7	0.08
Day Lon Lat	1268.4	2.7	0.08
Day Dist Lon^2	1269.7	4.0	0.04
Day LogD	1271.5	5.8	0.02
Day LogD Lon	1272.5	6.8	0.01
Day Dist	1274.9	9.2	0.00
Day	1294.5	28.8	1.7E-07
Lat	1792.2	526.5	1.4E-115
Lat Lat^2	1794.3	528.6	5.0E-116
LogD	1794.9	529.2	3.7E-116
Dist	1796.5	530.8	1.7E-116
Dist $Dist^2$	1798.5	532.8	6.2E-117
Lon Lon^2	1802.1	536.4	10E-117
Lon	1805.0	539.3	2.4E-118
Null (with autocorrelation covariance structure)	1806.0	540.3	1.4E-118
Null (no autocorrelation covariance structure)	1869.7	604.0	2.1E-132

[1] See appendix A for abbreviations

Table 1.5 Model selection result for generalized wind speed model. Shown are maximum likelihood AIC_C scores and Akaike weights from models used to predict wind speed within the TCH summer range over a 30 day period in 2004. Data used to develop these models do not include wind speed data from Barrow in the dependent dataset. The wind speed in Barrow (BrwWind) was instead used as an independent variable, replacing "Day." Candidate models other than univariate models greater than 10 AICc from the top model are not shown.

MODEL VARIABLES[1]	AIC_C	ΔAIC_C	w_i
BrwWind Dist Lon Lon^2	1442.2	0.0	0.19
BrwWind Lat BrwWind*Lat	1442.4	0.2	0.17
BrwWind LogD BrwWind*LogD	1442.8	0.6	0.14
BrwWind Lon LogD BrwWind*Lon BrwWind*LogD	1443.1	0.9	0.12
BrwWind Dist $Dist^2$ Lon Lon^2	1443.6	1.4	0.09
BrwWind Lon Dist	1443.9	1.7	0.08
BrwWind Lat	1444.4	2.2	0.06
BrwWind Lat Lat^2	1446.1	3.9	0.03
BrwWind Lon Lat BrwWind*Lon BrwWind*Lat	1446.2	4.0	0.03
BrwWind Logd	1446.2	4.0	0.03
BrwWind Lon Lat	1446.3	4.1	0.02
BrwWind Lon Dist BrwWind*Lon BrwWind*Dist	1446.7	4.5	0.02
BrwWind Dist	1447.2	5.0	0.02
BrwWind Lon LogD	1447.5	5.3	0.01
BrwWind Dist BrwWind*Dist	1449.2	7.0	0.01
BrwWind	1457.9	15.7	7.3E-05
Lat	1666.4	224.2	3.9E-50
LogD	1667.6	225.4	2.1E-50
Lat Lat^2	1668.2	226.0	1.6E-50
Dist	1668.2	226.0	1.6E-50
Dist $Dist^2$	1670.1	227.9	6.1E-51
Lon Lon^2	1671.3	229.1	3.3E-51
Null (with autocorrelation covariance structure)	1674.9	232.7	5.5E-52
Lon	1675.0	232.8	5.2E-52
Null (no autocorrelation covariance structure)	1730.5	288.3	4.6E-64

[1] See Appendix A for abbreviations

Table 1.6 Generalized vs. full wind speed model comparison. Model fit and accuracy are compared for models which use the wind speed in Barrow, Alaska on a given day, rather than a classified “day” variable. Both sets of models attempt to predict average daily wind speed throughout the NPR-A.

MODEL	β=DAY				β=BARROW WIND SPEED (m/s)			
	AIC_C	m.a.e.	R^2	R^2_{DEV}	AIC_C	m.a.e.	R^2	R^2_{DEV}
β DIST LON LON^2	1157.0	.60	.68	0.38	1442.2	.85	.41	0.17
β LAT β *LAT	1183.6	.60	.69	0.40	1442.4	.86	.39	0.17
β LOGD β *LOGD	1202.2	.62	.68	0.39	1442.8	.86	.40	0.17
β LON LOGD β *LON β *LOGD	1248.3	.58	.70	0.42	1443.1	.86	.40	0.17
β DIST DIST^2 LON LON^2	1158.4	.60	.69	0.38	1443.6	.85	.41	0.17
β LON DIST	1160.5	.61	.68	0.37	1443.9	.86	.40	0.17

AIC_C= Akaike’s Information Criterion, corrected for small sample size
m.a.e. = mean absolute error
R^2 = coefficient of multiple determination
R^2_{DEV} = Deviance R^2, a measure of proportionate reduction in the -2 log likelihood statistic over the null model

Table 1.7 Model selection results for cumulative logistic regression predicting mosquito activity. Maximum likelihood AIC_C scores and Akaike weights are shown. Models predicted ordinal insect activity (none, moderate, high) at a single location, Camp Olak, within the TCH summer range. Temperature and wind speed were generated by generalized models for the Camp Olak location. Percent concordance (C) is also reported.

Model	AIC_C	ΔAIC_C	w_i	C
WINDSPEED TEMPERATURE	98.56	0.00	0.91	77.9
WINDSPEED	103.55	4.99	0.08	76.3
TEMPERATURE	107.50	8.94	0.01	66.7
NULL	114.81	16.25	0.00	

Table 1.8 Model selection results for binomial logistic regression predicting mosquito activity. Maximum likelihood AIC_C scores and Akaike weights are shown. The models predicted binary insect activity (none, active) at a single location, Camp Olak, within the TCH summer range. Temperature and wind speed were estimated using generalized models for the Camp Olak location. Percent concordance (C) is also reported.

Model	AIC_C	ΔAIC_C	w_i	C
WINDSPEED TEMPERATURE	55.87	0.00	0.55	78.4
WINDSPEED	56.95	1.08	0.32	79.0
TEMPERATURE	59.20	3.33	0.10	66.6
NULL	62.03	6.16	0.03	

CHAPTER 2:

DYNAMIC HABITAT SELECTION BY CARIBOU IN THE NATIONAL PETROLEUM RESERVE-ALASKA[1]

Abstract: The summer range of the Teshekpuk Caribou (*Rangifer tarandus*) Herd is almost entirely contained within the National Petroleum Reserve – Alaska (NPR-A), where petroleum development is just beginning. Pre-development baseline information is necessary to interpret post-development distribution and habitat use of caribou and to develop mitigation measures, should development occur. We estimated bi-weekly distributions and habitat selection by caribou in the NPR-A during summer, 2002–2004, based on aerial relocations of 21–49 radio-collared females. Little or no habitat selection was detected when comparing used locations to habitat available within bi-weekly utilization distributions. Habitat selection was much stronger when comparing bi-weekly utilization distributions to the remaining extent of summer use. At the larger scale of analysis, there were dynamic temporal patterns in resource selection by caribou. Areas of highest air temperature were strongly avoided only during mid- to late- July. Tussock tundra was avoided early in the summer, but selected during August. Wet sedge was selected from August through September. Successful mitigation measures for petroleum development in NPR-A will need to be spatially and temporally tailored to observed dynamic patterns in caribou resource selection. Future work should estimate the performance of caribou (e.g., survival or weight gain) in relation to habitat use in order to

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[1] Prepared for submission to the Journal of Wildlife Management as Parrett, L.S, B. Griffith and G.M. Carroll. Dynamic habitat selection by caribou in the National Petroleum Reserve – Alaska.

confirm the value of selected habitats and to enhance the robustness of mitigation measures.

INTRODUCTION

Barren ground caribou (*Rangifer tarandus granti*) are the most mobile terrestrial mammals (Fancy et al. 1989). Most herds have extensive seasonal migrations, but even during non-migratory periods, caribou exhibit high movement rates relative to other ungulates (Fancy et al. 1989). During the snow-free season, movement rates have commonly exceeded 15 km/day (Fancy et al. 1989, Philo et al. 1993, Prichard et al. 2001, Griffith et al. 2002), and travel rates as high as 90 km/day have been recorded (Griffith et al. 2002). As a result of their ability to travel great distances in relatively short periods of time, caribou are able to select habitats from a large geographic extent. The potentially high cost of long-range travel is reduced by highly efficient locomotion (Fancy and White 1987), and may be further offset by energetic benefits accrued through an ability to locate and track changes in habitat suitability from an expansive suite of available habitats (e.g. Klein 1970, Fancy and Whitten 1991, Wolfe 2000, Barten et al. 2001, Kelleyhouse 2001, Griffith et al. 2002, Jones 2005). At smaller scales, the ability to select plants and plant parts that are the most nutritious both affords and encourages a highly mobile lifestyle (White et al. 1975, White and Trudell 1980, Boertje 1981, White et al. 1981, Kuropat 1984, Boertje 1990).

Resources available to caribou during the short arctic summer are in a constant flux. Availability of insect relief can change on an hourly basis, (Dau 1986, Walsh et al.

1992, Mörschel and Klein 1997), snow cover can change markedly over the course of several days (Stone et al. 2002), as can plant phenology (Whitten and Cameron 1980, Griffith et al. 2002, Jorgenson et al. 2002). Changes can also occur on larger temporal scales, such as the accumulation of vegetative biomass over the summer range (Griffith et al. 2002). In addition, shifts in patterns of habitat selection may occur independent of changes in resources. For example, physiological demands on the animals themselves, such as rapid increases in the energetic demands of lactation, increases in the ability of calves to forage independently (Parker et al. 1990, Knott et al. 2004, Knott et al. 2005), and the decreasing vulnerability of calves (with age) to predation may induce shifts in patterns of habitat selection.

In this paper, we address the problem of dynamic resource availability during summer. We use models of habitat selection with temporally adjusted availabilities to describe the changing influence of a combination of resource attributes (land cover type, vegetation quantity and quality, terrain ruggedness, and the potential for harassment by parasitic insects) that have been shown in previous research to be important factors in the distribution of barren-ground caribou (Walsh et al. 1992, Nelleman and Cameron 1996, Wolfe 2000, Kelleyhouse 2001, Griffith et al. 2002). At very small scales, the highly mobile nature of caribou means that use of a given area is typically brief. Additionally, the expense required to accurately measure habitat use at high resolution requires an approach that characterizes habitat use at large scales. We used low resolution, remotely sensed habitat data, comparing two extents of available habitat to describe large scale habitat use and patterns of resource selection.

Our objectives were to characterize the geographic distribution of females in the Teshekpuk Caribou Herd (TCH) throughout the snow-free period, examine annual fidelity to seasonal ranges, and describe habitat selection patterns throughout the snow-free period for this relatively unstudied population of barren-ground caribou. This herd was chosen for study, in part, to gain information about distribution and habitat selection to aid in management and mitigation of future petroleum exploration and development activities. Lack of knowledge about distribution and habitat use prior to development has compromised attempts to detect changes in distribution or habitat following development on the summer range of the adjacent Central Arctic Herd (National Research Council 2003). Very little is known about habitat use by the TCH outside of the calving period (Kelleyhouse 2001, Carroll et al. 2005). Most calves are born late in the first week of June, within 20 km of Teshekpuk Lake (Kelleyhouse 2001, Carroll et al. 2005).

STUDY AREA and HERD

The study area was defined as the area utilized by collared females from the Teshekpuk Caribou Herd (TCH) during the snow-free period (June-September), 2002–2004. An exception occurred in 2004, when 5 of 16 TCH females failed to return to the TCH calving grounds after wintering over 200 km east of previously described wintering grounds. They subsequently spent the summer with the adjacent Central Arctic Herd (Carroll 2005). We did not utilize locations from 2004 of these 5 animals for any analyses. The area utilized by the remainder of the collared caribou in 3 sequential summers covered the coastal plain north of the Brooks Range in Alaska between the Kuk

River in the west and the Kuparuk River in the east (Figure 2.1). This area overlaps considerably with the National Petroleum Reserve – Alaska (NPR-A), an area set aside in 1923 for petroleum exploration and development.

In addition to spanning the snow free period within the study area, the timing of animal relocations was also delimited by two important biological events; calving and the initiation of rutting activities. Estimated median calving dates from 2002-2004 were 2, 8, and 7 June respectively. Rutting behavior is typically initiated in mid-September (pers. obs.).

The physiography of the area is characterized by low relief (<300m elevation), and is covered with thousands of thaw lakes ranging in size from less than 1 km^2 to over 800 km^2. A dominant feature of the landscape is the 815 km^2 Teshekpuk Lake, which is often ice-covered until late July or early August, and is thought to have a cooling effect on the surrounding landscape (Donovan Price, National Weather Service, Barrow, pers. comm., but see Chapter 1, Parrett 2007). The average temperature in Barrow, just north of the study area, was 2.9° C during the 2002–2004 study period (June –September).

The relatively low density of predators is a significant feature of the study area. Reynolds (1989) estimated 0.5–2 grizzly bears (*Ursus arctos*) per 1000 km^2 in the study area, compared to 10-30 bears per 1000 km^2 in adjacent areas to the south higher than 300m in elevation. Wolf (*Canis lupus*) density in an area encompassing the TCH summer range was last estimated in 1996 at 1.8–2.9 wolves per 1000 km^2 (Carroll 1997), compared to 6.6 wolves per 1000 km^2 in the adjacent Gates of the Arctic National Park (Layne Adams, pers comm.). Wolves are likely to be less abundant in the caribou summer range due to the lack of denning habitat, potential for rabies outbreaks related to high arctic fox (*Alopex lagopus*) densities, and the vulnerability of wolves to hunters in the open country (Carroll 2000). During 15 years of caribou radio-tracking surveys (1990-2004), no wolves have been seen on the TCH range during the snow-free period. Golden eagles (*Aquila chrysaetos*), an important predator of newborn caribou in some areas (Whitten et al. 1992), are occasionally seen in the study area during the calving period (Wright 2000, Ritchie et al. 2003), but their numbers have not been quantified over the entire summer range of the TCH. The majority of the summer range appears to be used primarily by immature eagles (Ritchie et al. 2003, McIntyre 2004), which may be more important predators of young caribou than are nesting eagles (Young et al. 1995).

Four villages are within or near the borders of this study area, and residents of those villages heavily utilize the TCH as a subsistence resource, harvesting an estimated 2500-4500 caribou per year (Carroll 2001, Carroll 2003, Carroll 2005). Using modified aerial photo direct count methodology (Davis et al. 1979), the TCH population was last estimated at 45,166 in 2002 (Carroll 2003).

METHODS

Caribou Locations

A sample of 31-50 radio-collared females was maintained in the TCH during the 2002-2004. Caribou were captured and equipped with either a very high frequency (VHF) collar alone, or VHF transmitter combined with a platform terminal transmitter (PTT) collar, or global positioning system (GPS) collar (Telonics, Mesa AZ). Animals were captured within 50 km of Teshekpuk Lake (Figure 2.1) using a hand-held net gun fired from a Robinson-44 helicopter. Capture work was conducted in late June or early July, except for 2002, when caribou were captured in early September. All capture and subsequent monitoring complied with animal care and use guidelines set forth by the Institute of Arctic Biology and the Alaska Department of Fish and Game (IACUC permit 02-61, ADFG permit 03-0008, respectively).

Collared animals were located at approximate 2-week intervals, beginning in mid-June and continuing until snow covered the ground in September each year. Relocations were obtained from a Bellanca Scout or Piper PA-18 Supercub equipped with wing-mounted directional antennae. Aircraft were flown directly over the marked caribou at an altitude less than 300m above ground level, and the position was recorded to one decimal minute with a hand held Garmin 12XL global positioning system, recording in WGS 84 map datum. Re-location data were converted from WGS84 to NAD 27 for analysis using the NADCON program provided by the National Geodetic Survey (Silver Spring, MD). During some VHF telemetry flights, animals that were equipped with PTT collars were not located in the interest of time, and locations reported by ARGOS were used if the locations had an accuracy estimate of <300m and were taken within a day of the radio-tracking surveys. When animals were widely distributed, radio-tracking would take 2 days to complete in order to locate all of the marked animals.

Caribou Distribution

Bi-weekly distributions were estimated as the 99% fixed kernel utilization distribution (UD) of all female caribou located during a survey (Silverman 1986, Worton 1989) in program Kernel HR v. 4.27 (Seaman et al. 1998). The smoothing parameter was selected using least squares cross validation (Seaman and Powell 1996, Seaman et al. 1998), with automatic cell size selection (Seaman et al. 1998). A minimum of 20 locations was required for the estimation of a bi-weekly distribution (Silverman 1986, Seaman et al. 1999). We estimated the summer extent of use as that area which was contained within the extent of the aggregate of all independently generated bi-weekly estimates. This methodology parallels those used to estimate the extent of calving habitat available to the arctic Alaskan herds (e.g., Wolfe 2000, Kelleyhouse 2001, Griffith et al. 2002).

Seasonal Fidelity

We used non-parametric multiple response permutation procedures (MRPP) to test for significant differences in herd distribution between years, as well as between sequential surveys in the same year (Mielke and Berry 2001, Cade and Richards 2001). The program BLOSSOM (Mielke and Berry 2001) sequentially removes and replaces a given location from one distribution with a location from the second distribution, using Euclidean distance measurements to assess the probability that two sets of locations are from the same distribution. Because we were unable to conduct surveys on the same dates each year, we limited comparisons of between-year distributions to those that were separated at most by 3 calendar days (e.g., 24 June 2002 vs. 27 June 2003).

Habitat Selection – Study Design, Extent and Grain

We used a Type II study design (Thomas and Taylor 1990, Thomas and Taylor 2006), pooling locations of individually marked animals in order to study population-wide selection patterns and their variation through time. This approach has been used in previous studies, where dynamic patterns in habitat selection and availability were considered an issue (Arthur et al. 1996, Jones 2005). The assumption that a given extent of habitat is available to all animals in a Type II analysis is occasionally questioned (Johnson 1980, Thomas and Taylor 1990), but high rates of daily movement (4-18 km/d, Prichard et al. 2001) and the ~2 week relocation interval suggest that all habitats in our study area were potentially available to all individuals. Our 2 week relocation interval also minimized or eliminated temporal autocorrelation among successive locations of individual animals (McNay et al. 1994).

We conducted habitat selection analyses at two scales (Figure 2.2). Large Scale analyses compared randomly selected points within the bi-weekly 99% UD's (used) to randomly selected points that were within the extent of summer use but outside the bi-weekly 99% UD, 2002-2004 (available but unlikely to have been used). This was roughly equivalent to Johnson's (1980) 2nd order selection and minimized contamination of available points with points that were actually used (Lancaster and Imbens 1996, Keating and Cherry 2004). The resolution (grain, Wiens 1989) of estimated habitat attributes at this scale was 9 km^2.

Small Scale analyses compared the bi-weekly locations of collared animals (used) to randomly selected locations within the bi-weekly 99% UD's (available). This was roughly equivalent to Johnson's (1980) 3rd order selection, and available points were more likely to have been contaminated (Lancaster and Imbens 1996, Keating and Cherry 2004) by use than in the large scale analyses. The resolution (grain) of estimated habitat attributes at this scale was 1 km^2.

Unavailable Habitats

All portions of the bi-weekly 99% utilization distribution that extended into the Arctic Ocean were declared to be functionally unavailable. We also declared on-shore areas with a high percentage of surface water to be functionally unavailable (c.f. , Zielinski 2004, Rolstad 2000, Sergio and Bogliani 2000). In addition to eliminating areas that were basically deep aquatic habitats, we also hoped to reduce the potential for areas with low biomass estimates to be avoided in the habitat selection analyses simply because the biomass estimates of aquatic habitats are extremely low (Holben 1986, Wolfe 2000, Lawhead et al. 2004, Macander 2005).

We used a land cover map with 100 m^2 pixel size (Muller et al. 1999), and an independent data set from 16 female Teshekpuk Herd caribou equipped with PTT collars to establish thresholds of surface water coverage that inhibited or eliminated caribou use. The caribou data set was taken from a larger sample of 51 PTT equipped caribou active between 1990 and 2002. The data set was sub-sampled to include only 1) locations between June 1 and September 15, 2) locations with estimated accuracy $\leq$ 300 meters (Service Argos, Landover, Maryland), and 3) 60 randomly selected relocations per animal. Using these screening criteria, locations from 16 animals were available for further analyses.

For each caribou location, we estimated the percentage of water, including the ocean, as the number of 100 m^2 pixels in the surrounding 100 (1 km^2) and 900 (9 km^2) cells that were classified as water. These dimensions corresponded to the grain of our small and large scale habitat selection analyses, respectively. All 1 km^2 or 9 km^2 cells which exceeded the upper 5% of the distribution of percent water were declared unavailable for small scale and large scale habitat selection analyses.

Random Locations

Random locations were generated within the two extents of interest using the program Animal Movement (Hooge and Eichenlaub 1997) at appropriate scales. Eight-hundred random locations were generated for each bi-weekly survey; 300 were generated within the 99% UD, and 500 were generated within the summer extent, with some random points later excluded for excessive water coverage at both scales, and some random points within the summer extent excluded because they fell within the 99% UD.

Habitat Layers

Vegetation biomass.--

Relative vegetative biomass was estimated using the Normalized Difference Vegetation Index (NDVI) (Tarpley et al. 1984, Tucker and Sellers 1986). NDVI has been successfully used to estimate relative vegetation biomass in grassland ecosystems with little canopy structure (e.g. Kennedy 1989, Hansen 1991, Prince 1991). NDVI has also been correlated with animal density and habitat selection in multiple studies (Oesterheld et al. 1998, Wolfe 2000, Kelleyhouse 2001, Leimgruber 2001, Griffith et al. 2002, Jones 2005).

NDVI data used in this study was produced by the sensor onboard the Systeme pour l'Observation de La Terre (SPOT) satellite. NDVI was estimated at 1 km^2 resolution, with a geographic accuracy of <800 meters and a multi-temporal relative accuracy of < 500 meters. NDVI data composites were generated at approximately 10 day intervals, with values retained in the data set corresponding to the highest value recorded for a given pixel during the compositing period, and the date upon which that maximum occurred. This method allows an estimate of NDVI to be generated over a large area despite problems with cloud cover that prevent complete coverage on a daily basis.

In order to estimate NDVI for dates other than those observed, the per-pixel rate of change for a given pixel was estimated. We accomplished this by subtracting the pixel value of an immediately preceding composite image from the pixel value of the subsequent composite image, and dividing by the number of days that elapsed between pixel observations. These rates were used to interpolate NDVI between pixel observations, assuming a linear rate of change within nominal 10 day composite periods (Appendix B 1–3).

Vegetation growth rate.--

Vegetation growth and senescence rates have been estimated using the rate of change in NDVI estimates from sequential images (Reed et al. 1994), and correlated to animal use in multiple studies (Wolfe 2000, Kelleyhouse 2001, Griffith et al. 2002, Jones 2005). Since our NDVI estimates were obtained from composite images, we attempted to standardize the interval of estimation by creating interpolated estimates of NDVI both 5 days before the survey day(s), and 5 days afterwards, and estimating the rate of change between those dates (Appendix C 1–3). The 10-day interval was used rather than the simple, interpolated rate estimate in order to avoid situations where rates were being estimated from drastically different periods, for example from the day before the survey to 15 days later, versus 15 days before the survey to the day after the survey.

Land cover class.—

Analyzed land cover classes included 1) moist graminoid, 2) wet graminoid, 3) tussock tundra, and 4) non-vegetated land cover classes. The latter two classes were collapsed from multiple classes to simplify the analyses and increase statistical power. Tussock tundra was collapsed from a) acidic and b) typical dwarf-shrub tussock-graminoid tundra, and c) low-shrub tundra. The non-vegetated class was collapsed from a) water and b) barren ground land cover classes.

Original plant community composition was estimated using land cover classes described by Muller et al. (1999). Seven vegetation classes were delineated using Landsat Multispectral Scanner imagery for the Kuparuk River basin (Muller et al. 1998), and then extrapolated across the North Slope (Muller et al. 1999). Accuracy for the Kuparuk Basin was estimated at 85% (Muller et al. 1998), and assumed to be similar in our study area.

The original land cover map was produced with 100m^2 resolution. For this study, we reclassified the map in two ways, such that each 100m^2 pixel represented the most common vegetation class in the surrounding 100 pixels (1km^2), or in the second case, the surrounding 900 pixels (9km^2). In cases where there was no simple majority, the pixel classification would revert to the classification of the 100m^2 pixel that the point was in. Note that this reclassification scheme is different from that used to estimate the percentage of water used to delineate functionally unavailable habitats.

Terrain ruggedness.--

We estimated terrain ruggedness using the program TERRAIN and a digital elevation map with 60m resolution (based on Nelleman and Cameron (1996); program written by Jim Greslin, and first implemented by Wolfe (2000)). TERRAIN calculates a digital terrain ruggedness index (DTRI) based on the total elevation change as well as number of slope changes, where DTRI = (SEC *SDC) / (SEC+SDC), where SEC = the sum of absolute elevation changes, and SDC = the number of slope direction changes. Estimates are calculated at 2 kilometer intervals from 2 km to 10 km, extending half the distance in opposite directions parallel to the slope of the pixel of the origin.

Weather and Parasitic Insects.--

Insect harassment, particularly by mosquitoes (*Aedes spp.)*, warble flies (*Hypoderma tarandi*) and nasal bots (*Cephenemyia trompe*), is considered an important driver of habitat selection by barren-ground caribou (Kelsall 1968, White et al. 1975, Downes et al. 1986, Nixon 1990, Walsh et al. 1992). Because of the difficulty in conducting range-wide insect abundance surveys, we instead used spatially interpolated temperature estimates as an index to potential insect harassment. This model relied on the temperature in Barrow as well as latitude and longitude to estimate temperatures across the study area (Chapter 1, Parrett 2007). We also attempted to model wind speed, another important factor in determining suitable conditions for parasitic insect activity, but were unsuccessful in developing a satisfactory model (Chapter 1, Parrett 2007). While factors in addition to temperature and wind speed, particularly light intensity (Downes et al. 1986, Mörschel 1999) and humidity or saturation deficit (Dau 1986, Mörschel 1999) can be important factors in determining suitable conditions for insect harassment, data relating to these parameters were unavailable across the study area.

Habitat Trends – Study Period in Context

Because the arctic is warming (Chapman and Walsh 1993, Jones et al. 1999, Comiso 2003) and observations of increasing trends in satellite derived estimates of biomass (Myneni et al. 1997) imply changes in forage availability, we tested for trends in NDVI in the study area. We obtained 8 km^2 resolution NASA AVHRR Pathfinder NDVI imagery (James and Kalluri 1993), calculated the median value within the summer extent of use for a fixed date of 21 July, and tested for significant linear trends between 1982 and 2001.

Habitat Selection – Statistical Analyses

All of the continuous habitat variables were converted to z-scores (observed value – mean value / standard deviation) in order to facilitate comparisons between the effect sizes of respective resources on habitat selection.

In order to avoid difficulties in model interpretation arising from the presence of collinearity, we used several techniques to detect significant and potentially deleterious correlation between the potential explanatory variables. Pearson correlation coefficients, variance inflation factors, and condition indices were all used to examine the relative correlation and effect of simultaneous inclusion of explanatory variables on model inference (Belsley et al. 1980, SAS Institute 1999). Variance inflation factors greater than 10 were considered high enough to warrant exclusion. Condition indices greater than 10, combined with variance decomposition proportions greater than 0.5, were also grounds for removing explanatory variables (Belsley et al. 1980).

We modeled habitat selection using logistic regression (Manly et al. 2002, but see Keating and Cherry 2004 for issues with interpreting use-availability data), using Akaike's Information Criteria (AIC) for model selection, with the lowest scoring model from a suite of suitable models indicating the best approximating model for each survey at each scale of analysis, with models scoring within 2 AIC of the top model interpreted as competing models (Burnham and Anderson 2002). Single scale-specific models that spanned the study period were considered, but preliminary analyses indicated that time-β_i interactions appeared too complex to be adequately described using a single model, so we modeled each survey independently. Parameter estimates were calculated using maximum likelihood (SAS Inst. 1999). Best approximating models were tested for goodness-of-fit to the logistic curve with the Hosmer-Lemeshow test (Hosmer and Lemeshow 2000), and deviance R^2 ($R^2_{DEV} = 1-(-2\log \text{likelihood}_{(\text{model of interest})} / -2\log \text{likelihood}_{(\text{null model})})$ was used to assess model fit.

Because of the potential for cows with calves to behave differently from cows without calves, we tested for differences in habitat use between those two groups during the calving period using MANOVA for continuous variables, and a likelihood ratio chi-square test for the nominal land cover class variable. An interaction between presence of a calf and year on habitat use was also considered. Since confirmation of calf presence became increasingly difficult as the season progressed, we tested for a calf effect only in the mid-June surveys.

RESULTS

Radio Tracking

During the 3 year study, we were able to fly 16 radio-tracking surveys that had produced at least 20 relocations (Table 2.1). Scheduled surveys were missed or delayed due to poor weather and logistical difficulties in each year. Estimated caribou densities during surveys, calculated by dividing the last population estimate by the size of the 99% UD, varied widely from 1–374 / km^2. The extent of summer use, 2002–2004, was a 48,865 km^2 area centered at 70 degrees, 15.0 minutes north, 154 degrees, 37.8 minutes west (Figure 2.1). The 99% utilization distribution for each survey is shown in Appendix D.

Fidelity

MRPP comparisons between years were complicated due to the occasional inability to fly surveys at similar times between years. Because of the temporal limitations we imposed for inter-annual comparisons of distribution, only 5 comparisons were possible, of which 3 were statistically non-significant, indicating that caribou were similarly distributed at approximately the same time in different years (Table 2.2). In contrast, only 4 of 13 within-year comparisons were non-significant (Table 2.3).

Influence of Water on Habitat Availability

Over 95% of the 960 satellite relocations used to assess the influence of water on habitat availability had < 72% water in the surrounding 1 km^2, but areas with 100% water in the surrounding 1 km^2 were also utilized > 1% of the time (Figure 2.3). At the 9 km^2 grain of use, 95% of the locations had less than 57% water in the surrounding 9 km^2, but there were locations with as much as 91% water (Figure 2.3). Based on this information, we eliminated habitats that contained more than 72% water in the surrounding 1 km^2 as unavailable to caribou. This eliminated 6% of the total summer extent from consideration, presumably only the central portions of bodies of water greater than 1 km^2. In comparison, over 19% of the 100 m^2 pixels covered by the summer extent were classified as water.

Historical Trends in Habitat

Median NDVI value on the 21st of July within the TCH summer extent of use increased at a rate of 0.004 per year between 1982 and 2001 ($p=0.02$, $R^2 = 0.26$). NDVI values range from 0 to 1, and the average median value during the study period was 0.44.

Dynamic Habitat Selection

Very little selection or avoidance was indicated throughout the course of the snow-free period at the small scale (Figure 2.4). Model fit was quite poor at this scale of analysis. The average R^2_{DEV} for the 16 small scale models was only 0.05. In two cases, the null model was indicated as the best approximating model (Table 2.4). In three cases, quasi-complete separation of data points was detected; models with this problem are noted (Table 2.4). In two cases, tussock tundra was an available habitat which was not used, and in one, unvegetated was an available class which was not used. Parameter estimates reported are those from models that included the variable with quasi-complete separation, as exclusion of the problem variables did not substantially change the parameter estimates for unaffected variables (Webb et al. 2004).

At the larger scale, selection and avoidance was apparent, and in many cases dynamic. The average R^2_{DEV} for the 16 models was 0.39, ranging from 0.07 to 0.85 (Table 2.5). Models from data in August and early September had relatively poor fit, while consistently strong negative responses to high temperature produced well-fit models for data from July. Two dynamic patterns in resource selection included changes in the selection of high biomass, which was avoided early in the season, gradually changing to selection or neutral effect late in the summer, and a response to high temperature which was generally neutral except for July, when it was strongly avoided (Figure 2.5).

The average estimated temperature at used locations on dates when the 4 strongest responses to temperature were observed ranged from 4.5 to 10.9˚ C, and the maximum estimated temperature at a used location on any of those dates was 12.3˚ C. On the date with the highest average estimated temperature across the study area (15.3 degrees; 15 August, 2004) avoidance of high temperatures was weak, based on both the confidence interval for the effect of temperature on use for that specific survey, as well as the fact that temperature was not included in the best approximating habitat selection model for that survey (Table 2.5).

Other distinct patterns included increasing selection for tussock tundra starting in mid-June followed by a neutral response occurring by mid-August, with a similar response to water, and a pattern of increasing selection for wet sedge throughout the summer period (Figure 2.5, Table 2.5).

There were no differences in habitat use by cow caribou with calves and cows without calves at either the 1 km^2 grain of use, or the 9 km^2 grain of use (Figure 2.6), and interactions with year were non-significant for all of the continuous habitat variables. A likelihood ratio chi-square test indicated that use of land cover types was not significantly different between cows with calves (n=54) and cows without calves (n=36) at the 1 km^2 or 9 km^2 grain of use (p=0.98, p=0.60).

DISCUSSION

Conclusions in this study are limited in scope to those scales which were available and appropriate for analyses. An additional quantitative limitation is imposed by the overlap of used and available points, particularly at the smaller scale, which limits the ability to predict probability of use, and constrains interpretation to simple ranking of habitats (Keating and Cherry 2004). We also acknowledge two sources of autocorrelation in the data; the first is spatial, and arises from strong latitudinal gradients in the NPR-A, where different attributes of the landscape tend to be spatially autocorrelated with one another. For example, an area with large lakes will tend to have wet sedge land cover types, flat terrain, low biomass, and low vegetation growth rates. Through assessing collinearity in the independent variables, we eliminated the possibility that strong autocorrelation was influencing parameter estimation. However, even weak effects of spatial autocorrelation are likely to cause underestimates of variance (Legendre 1993), and should be addressed in future studies (Nielsen et al. 2002). A further complication is that caribou, by their very nature, are nearly always found near other caribou. Movements and selection of habitats by individuals are not likely to be independent of other caribou, although the likelihood that a marked caribou is affecting other marked caribou in the study may be low during periods when densities are low. Methods do exist for assessing individual patterns of selection within a framework that also estimates population-based parameters (Thomas et al. 2006, Thomas and Taylor 2006).

Patterns in Resource Selection

Despite minor problems associated with analytical methods, several conclusions can be drawn about resource selection by caribou in the NPR-A. We found that despite high movement rates and dynamic patterns in habitat selection, use of geographic areas was remarkably consistent. Herd distribution between years was statistically similar 60% of the time, while distributions separated by as little as two weeks were only similar 30% of the time. Resources available to caribou in the NPR-A are in a constant state of flux during the summer, which could explain why distributions vary so much within a year, despite inter-annual consistency. Movements that occur at a very large scale provide an opportunity to repeatedly select foraging patches and habitats at a small scale. Caribou can choose foraging habitats that vary in vegetation biomass, vegetation quality, and the abundance of preferred plant species, with potential compromises occuring to avoid predators and parasitic insects. The dynamic nature of the landscape in the NPR-A, combined with caribou movement rates as high as 90 km/day, implies that caribou are active habitat selectors, responding to changes in the environment.

In order to document the dynamic nature of the caribou-resource relationship, we assessed habitat selection at bi-weekly intervals. Analytical methods which ignore the potentially important interaction between habitat selection and time may be confused by inconsistent or contradictory results; for example if an organism strongly avoided a particular resource early in a study period, gradually moving toward strong selection of that resource late in a study period, an analysis which pools those data may produce results which indicate a lack of selection or avoidance, accompanied by large standard errors. By analyzing each survey separately or adding a temporal covariate that interacts with the effects of habitat selection, the chance of identifying potentially important periods in the life cycle of the organism is increased.

We found little evidence for selection at the small scale. Although there may be no selection occurring at this scale, we believe this result arises due to a high degree of contamination, where many available points were actually used by unmarked caribou, particularly when the utilization distribution is relatively small, and caribou density is expected to be high. Opportunities for habitat selection by individual caribou are probably limited at this scale, and may be influenced by a lack of habitat heterogeneity within the bi-weekly distribution and the potential for competition with conspecifics. The lack of strong selection at this scale is in many ways simply an affirmation that the 99% utilization distribution is an accurate representation of habitat use by the caribou herd.

Large Scale Responses

Land Cover Classes.--

At the larger scale, evidence for selection was strong, and temporally dynamic. Resource attributes that are fixed features of the landscape, such as terrain ruggedness, land cover class, and percentage of water, also elicited the most consistent responses by caribou. While the moist sedge land cover class was typically avoided, the wet sedge land cover class showed the opposite response, with consistent selection. Caribou responded to both the tussock tundra land cover class and water with avoidance or lack of selection in June, followed by selection in mid to late summer. This similarity in the patterns of selection for tussock tundra and water is notable, as these two resources appear to be spatially segregated; the southern portion of the study area, where tussock tundra was most common, was not the area with the largest or most abundant lakes. Personal observations (L.S. Parrett) during surveys indicated that when caribou were distributed in areas with an abundance of tussock tundra, they were nevertheless near large bodies of water; this may be a response to oestrid harassment. The sandy banks of large lakes and the opportunity to stand in shallow water may provide some relief from oestrid flies, allowing caribou to occupy foraging areas in close proximity to insect relief. Oestrids were observed to be active during ground surveys when these aerial observations were noted.

The selection of certain land cover types may indicate selection of certain forage plants. For example, selection of tussock tundra land cover classes, areas with an abundance of *Eriophorum vaginatum,* has been noted for both the Western Arctic and Porcupine Caribou herds during calving (Kelleyhouse 2001, Griffith et al. 2002). In this study, wet sedge, dominated by *Carex aquatilus* and *Eriophorum angustifolium*, tended to be the selected land cover type for the Teshekpuk Herd during calving. While *Eriophorum spp*. did appear in calving diet of the TCH (Chapter 3, Parrett 2007), they did not dominate the calving period diet as they do for the Western Arctic and Porcupine Herds (Kuropat 1980, Thompson and McCourt 1981, Russell et al. 1993, Griffith et al. 2002). Selection for the tussock tundra did occur in our analysis, but not until early August, when *Salix* began to displace *Eriophorum* in the composition of fecal samples (Chapter 3, Parrett 2007). Diet selection was generally consistent with expectations based on large scale habitat selection, with the exception of early in the summer, when lichens and mosses dominated the diet (Chapter 3, Parrett 2007), despite large scale selection of wet and moist sedge habitats.

Temperature.--

The most dynamic patterns in habitat selection were to resource attributes that tend to vary most in space and time, such as temperature and biomass rate of change. While high temperatures were never selected at the large scale, they were strongly avoided throughout July. Avoidance of high temperatures was also indicated in late September and October, but this may be an artifact; the temperature model was known to perform poorly late in the study period, possibly due a reversal in the spatial trends in temperature resulting from the warming effect of the ocean in autumn (Chapter 1, Parrett 2007).

Data did not indicate a threshold that induced avoidance of high temperature; avoidance occurred when available temperatures were as low as 7° C (27 June, 2003), and did not occur with temperatures as high as 15° C (August 3, 2004). Both temperatures fall within typically reported thresholds for insect activity on the Arctic coast of Alaska and Canada (White et al. 1975, Dau 1986, Nixon, 1990); however, wind may have been an alleviating factor when there was no indicated response to temperatures that reached 15˚ C. Data available for wind speed on that day from 16 stations in or near the summer range of the TCH indicated speeds ranging from 3.7 –7.3 m/s, which are near threshold wind speeds thought to be strong enough to inhibit mosquito or oestrid fly activity (White et al. 1975, Dau 1986, Nixon 1990).

During the course of this study, mosquito activity has been observed at temperatures near 0˚ C within the range of the Teshekpuk Herd, and we have also observed that the presence of mosquitoes does not always elicit a large scale spatial response from caribou. The occasional lack of large scale response to temperature may be the result of smaller scale variation in insect activity that cannot be explained by temperature alone, or perhaps due to the different behavioral response of caribou that can occur when oestrid flies are present (Espmark 1968, Dau 1986). Periods with high temperatures but no apparent spatial response were in mid-August, when oestrid flies were known to be active, but mosquito activity on the North Slope had dropped off considerably. Although we did not identify a specific temperature threshold that produced a spatial response, caribou responded with remarkable consistency by avoiding higher temperatures throughout July.

NDVI and NDVI rate.--

The response to NDVI at the larger scale was a consistent avoidance of high NDVI values through June and early July, followed by inconsistent responses later in the summer. The lack of selection for biomass may be mediated by other factors in habitat selection, including insect avoidance and selection for forage quality rather than quantity.

Kelleyhouse (2001) found evidence for selection for high NDVI rate on the TCH calving grounds. Although we measured habitat use and availability at different scales than Kelleyhouse, we did not see similar results. Lack of selection for NDVI rate, particularly in mid-June, when high NDVI was avoided, was not consistent with selection of high forage quality. A complicating factor with respect to the use of NDVI rate as a proxy for forage quality is that NDVI rate can be strongly influenced by factors other than vegetation growth, such as a change from snow or ice to water, or water clarity (Macander 2005). Given the likelihood that forage quality is an important factor in both large and small scale habitat selection, we do not consider the lack of selection of NDVI rate to be a repudiation of this potentially important mechanism.

Terrain Ruggedness.--

During most surveys, at both scales there was little or no preference or selection of terrain ruggedness, although it was avoided during July. We believe this response is simply due to the fact that insect relief habitat along the coast tends to be uniformly flat. In theory, terrain ruggedness should appeal in particular to relatively immobile parturient cows and their neonates by allowing for a range of phenology to occur within small areas (Nellemann and Cameron 1996). Although this mechanism is improbable a few weeks after calving, when calves are highly mobile, the lack of response to this habitat feature at any time may be in part due to the scale at which elevation changes were measured (60 m), along with the resolution at which use was measured.

Other factors in habitat selection.--

We believe predation was not an important factor in determining where TCH caribou were located within the summer range. However, given the low densities of predators seen throughout the summer range, this entire area provides relatively predator-free habitat compared to the foothills and mountains, and may be an important factor in the seasonal selection of habitats within the annual range.

We failed to detect any significant differences in habitat preferences between cows with and without calves. This result may have arisen in part because many of the cows without calves were parturient animals that had already lost calves, and at the time of the surveys, were still using the same areas as cows that still had calves. A more definitive analysis would require a mid-June comparison between cows with calves, and cows with velvet-covered antlers, which are the only females which can be confidently described as non-parturient from the air (Whitten 1995). The number of marked cows with velvet covered antlers ranged from 0–8 of 29-32 individuals from 2002–2004; sample sizes too small for effective analyses, and a small proportion of the population in any year.

MANAGEMENT IMPLICATIONS

Estimating temporal patterns in habitat selection can facilitate the mitigation of development, particularly by allowing managers to make time-specific adjustments to activity schedules, and thereby avoid disturbing selected habitats. In addition, the identification of habitats which are not always used, but may be energetically important, can be gained through temporally specific analysis of habitat selection. For example, caribou move from calving areas to coastal insect relief habitats in early July through narrow corridors east and northwest of Teshekpuk Lake (Figure 2.1). Although use of these areas may be brief, ensuring passage to, and perhaps more importantly from, insect relief habitats during the month of July may be an important aspect of mitigating future development in the TCH range. The mitigation of industrial activities during the behaviorally sensitive calving period is often an important component of management plans; if the calving period is defined through consistency in habitat selection, mitigation efforts focused on the calving grounds may need to extend to the end of June. A second life-history period, where response to temperature and insect harassment dominate habitat selection, could be defined as the entire month of July. A third period defined by consistent patterns in habitat selection would then extend from the beginning of August through the remainder of the snow-free period. Future studies of summer habitat selection and movement pattern would help to confirm the utility of these three periods from a management perspective.

Resource selection studies rely on the assumption that selection of a habitat disproportionate to its availability means that habitat is important to fitness and survival of the organism, and worth preferential treatment in management plans. We have found that when we define availability as the area described by the bi-weekly 99% utilization distribution, there is either no evidence for selection, or more likely, that all of the habitat was selected. In either case, management on the basis of habitat selection within the 99% utilization distribution is not possible. In contrast, repeated use of the same areas between years may provide a management tool. For example, the combined 99% utilization distributions for the three periods defined in the previous paragraph (Calving, July, and Late Summer) could form the boundaries of temporally specified caribou conservation areas. Given the apparent lack of evidence for selective behavior at small scales, which may be in part due to the difficulty involved in determining which habitats are unused, we suggest that measures of animal performance such as survival or growth of calves may provide a better measure of habitat quality than preferential use.

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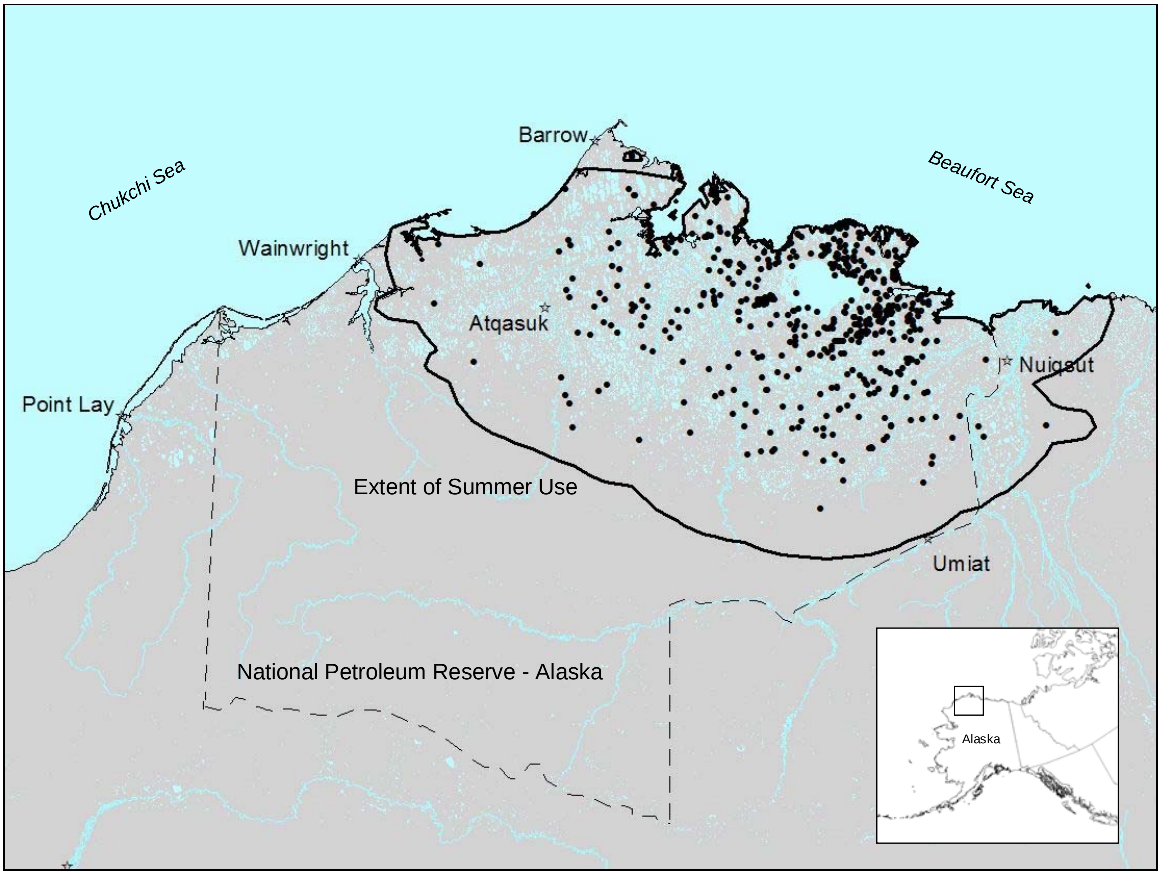

Figure 2.1 Study area with caribou locations. The Teshekpuk Caribou Herd extent of summer use is indicated by the solid line with 527 aerial survey re-locations (mid-June–early October, 2002–2004) of radio-marked female caribou depicted (solid circles). Not depicted are the locations of 5 female caribou which did not return to the calving grounds in 2004, and spent the remainder of that summer with the adjacent Central Arctic Herd. Also depicted is the border of the National Petroleum Reserve-Alaska (dashed line). The entire study area is located in the central portion of the coastal plain north of the Brooks Range in Alaska.

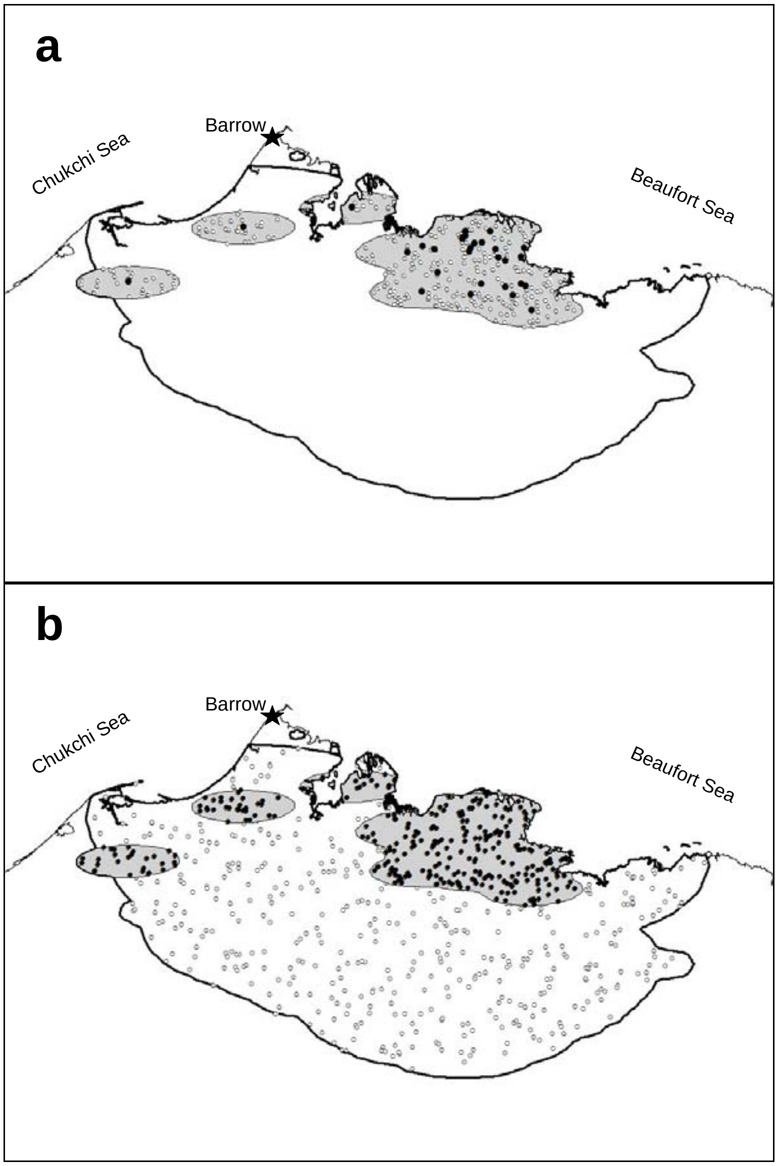

Figure 2.2 Scales of interest for habitat selection analyses. The summer extent of use is the thick line, and the 99% utilization distribution is shaded. Figure 2-a, the smallest extent of interest, compares used points (dark, n=30) versus random points (open, n=300) within the 99% utilization distribution. The larger extent of interest, figure 2-b, compares random points with the 99% utilization distribution (dark, n=300) to random points in the remaining summer extent of use (open, n=500). The smaller scale is intended to compare use to availability, while the larger is intended to compare used points to unused points. The measured grain of use differs for each scale, with use measured at 1 km^2 at the smaller extent of interest, and use measured at 9 km^2 at the larger extent of interest. The study area is located on the central coast of the North Slope of Alaska. Actual locations from a June 11, 2002 relocation survey are depicted.

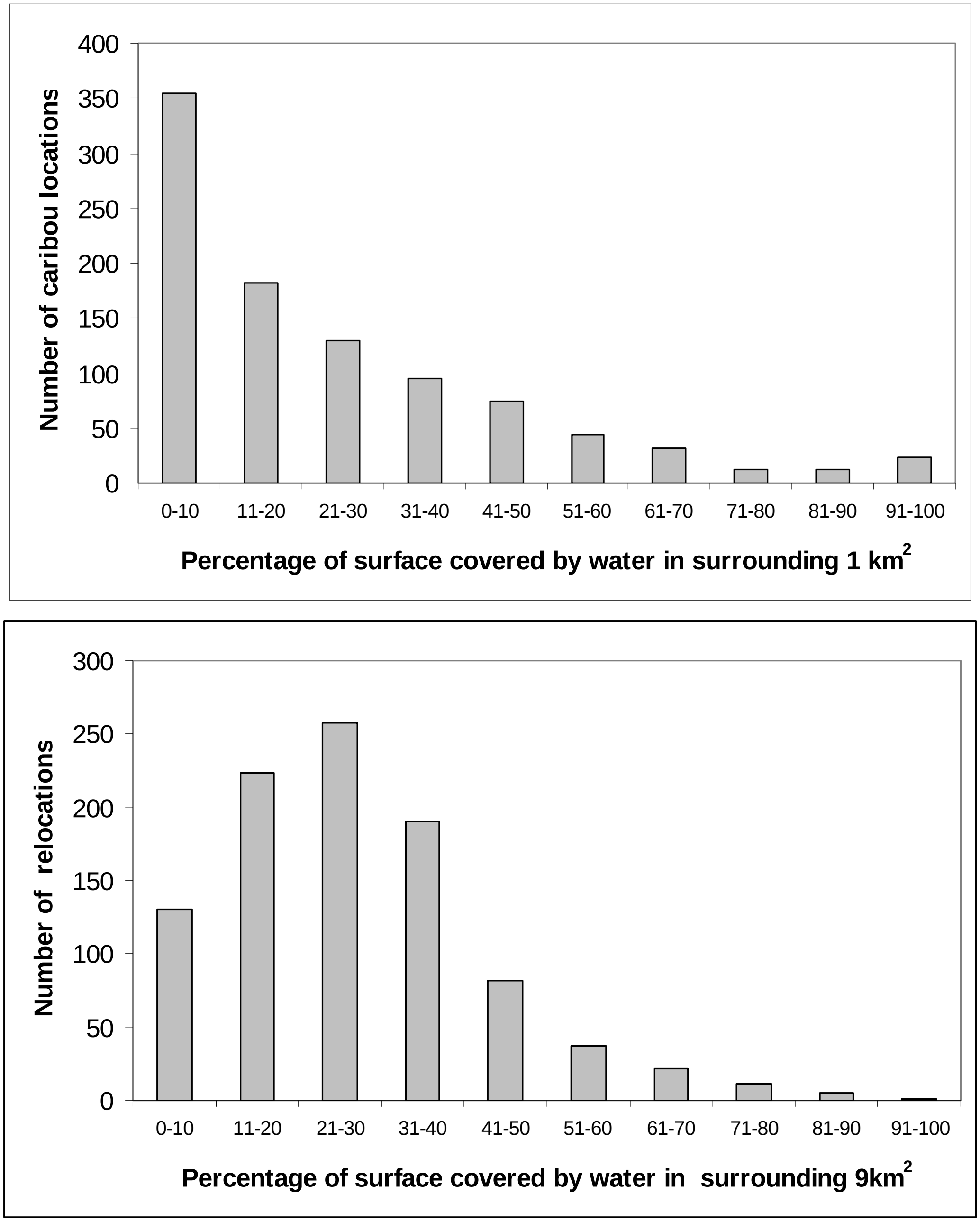

Figure 2.3 Caribou locations in relation to water. The percentages of water in the surrounding 1 km^2 and 9 km^2 are indicated for 960 female caribou locations drawn from a larger sample of satellite relocations taken from 1990-2002. Over 95% of the 1 km^2 pixels contain < 72% water, while 95% of the 9 km^2 pixels contain <57% water.

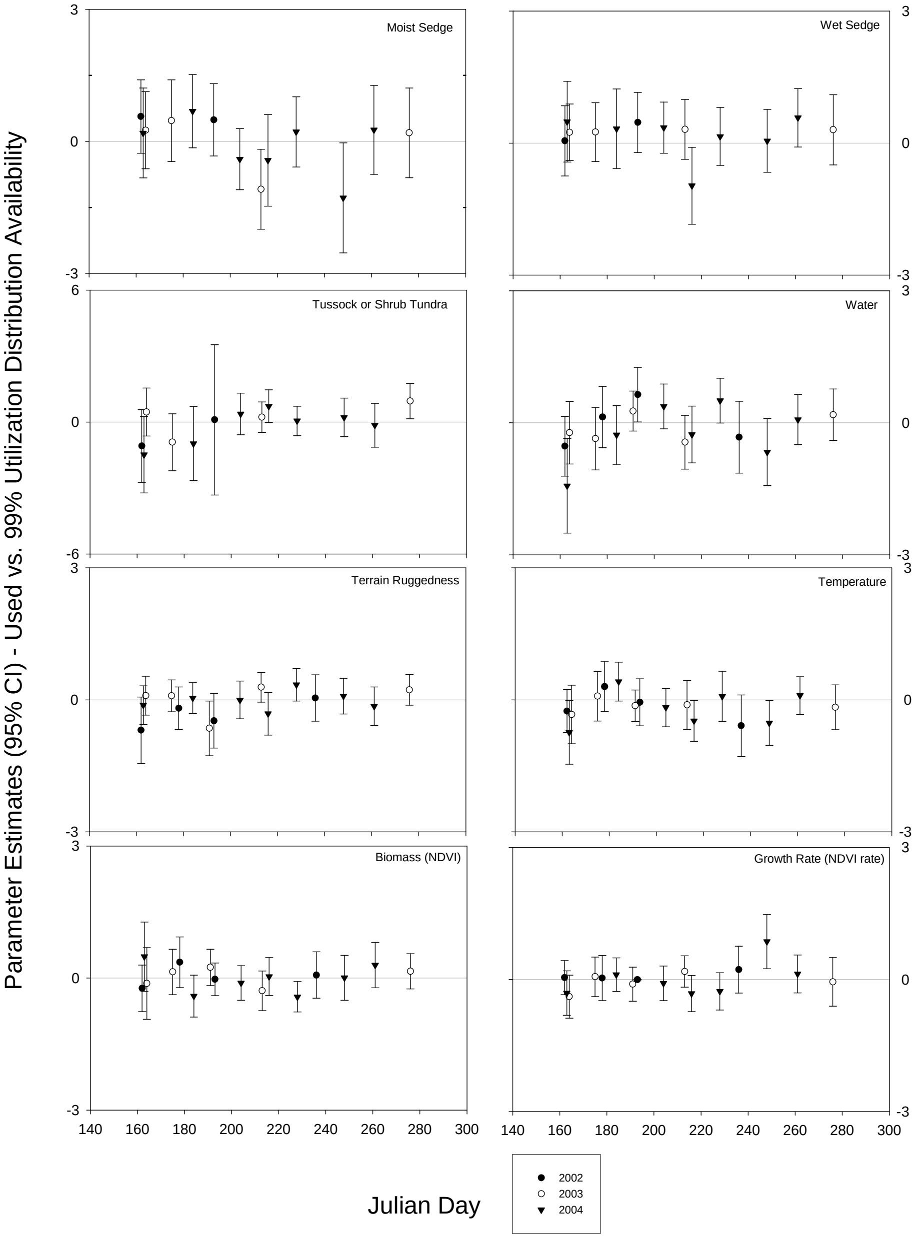

Figure 2.4 Habitat selection coefficients for small scale analyses. The analysis compared used locations to random locations drawn from the 99% utilization distribution for each survey date. Estimates above zero indicate selection of a resource, while estimates below zero indicate avoidance. Estimates from differing resources are comparable due to the utilization of z-scores in the analysis, rather than raw values. Note the differing Y-axis values for the tussock tundra land cover class. Missing values occur for the moist sedge, wet sedge and tussock land cover types due to quasi-complete separation errors in the analysis. Parameter estimates are from global models.

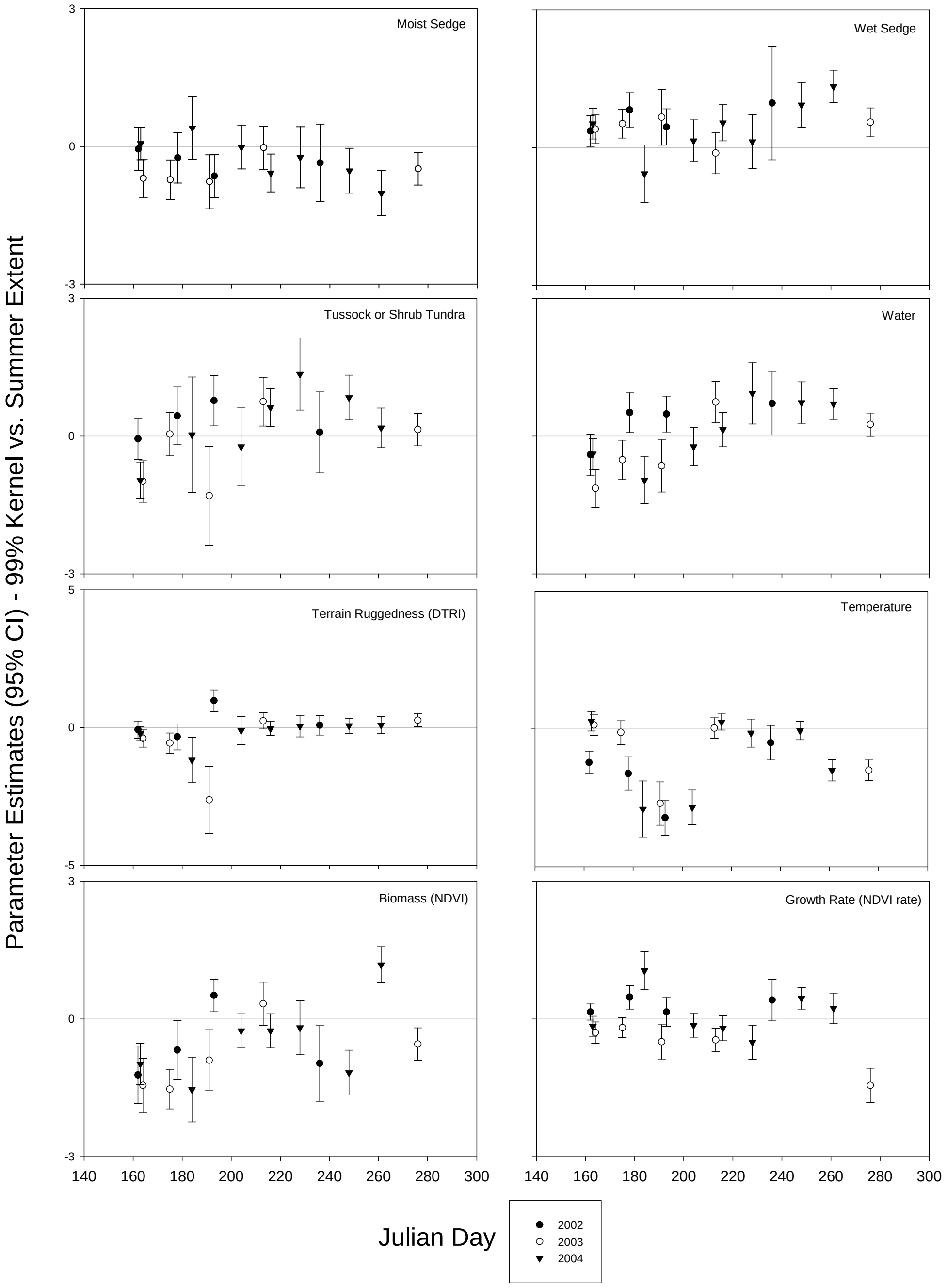

Figure 2.5 Habitat selection coefficients for large scale analyses. The analysis compared random locations from the 99% kernel to random locations drawn from the remaining extent of summer use for each survey date. Estimates above zero indicate selection of a resource, while estimates below zero indicate avoidance. Estimates from differing resources are comparable due to the utilization of z-scores in the analysis, rather than raw values. Parameter estimates are from global models.

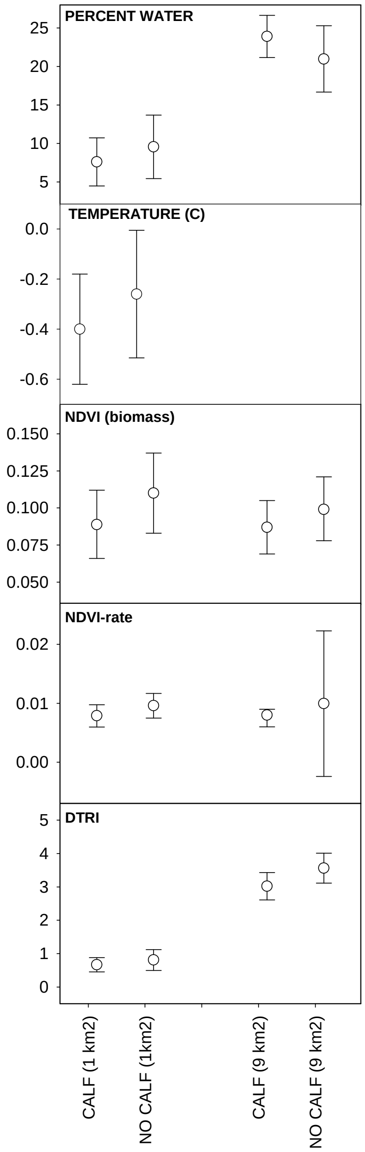

Figure 2.6 Habitat use by cows with and without calves. Manova results (mean ±95% CI) compare habitat characteristics in mid-June for cows seen with calves versus cows that did not have a calf. Habitat characteristics were measured at approximately 1 km^2 and 9km^2 resolution. The deterministic model used to estimate temperature is actually calculated for the actual location, and has no inherent scale.

Table 2.1 Timing and results of summer radio tracking surveys, 2002-2004. Fixed kernels were estimated using least squares cross validation and automatic cell size selection. Estimated densities are calculated from the most recent population estimates, and do not consider the possibility that males and females may have distinct distributions at any or all of these times.

Survey Date	Season	99% kernel (km^2)	n	estimated caribou/km2
11 Jun 02	Calving	7611	30	5.3
27 Jun 02	Post Calving	6592	28	6.1
12 Jul 02	Mosquito	2462	28	16.3
24 Aug 02	Late Summer	39899	21	1.00
13 Jun 03	Calving	6841	32	5.9
24 Jun 03	Post Calving	4513	33	8.9
10 Jul 03	Mosquito	107	49	373.8
1 Aug 03	Insect	32810	44	1.2
2 Oct 03	Late Summer	6229	40	6.4
11 Jun 04	Calving	10984	31	3.6
2 Jul 04	Mosquito	1246	29	32.1
22 Jul 04	Insect	546	38	73.3
3 Aug 04	Insect	28166	34	1.4
15 Aug 04	Late Summer	36733	37	1.1
4 Sep 04	Late Summer	25444	30	1.6
17 Sep 04	Late Summer	10364	33	3.9

Table 2.2 Comparisons of herd distribution on similar dates between years. Distributions are compared using the multiple response permutation procedure. A high probability indicates that the distributions are statistically similar.

Period 1		Period 2		
Date	No. relocations	Date	No. relocations	Probability
11 Jun 02	30	13 Jun 03	32	p=0.111
13 Jun 03	32	11 Jun 04	31	p=0.251
27 Jun 02	28	24 Jun 03	33	p=0.002
12 Jul 02	27	10 Jul 03	49	p<0.001
1 Aug 03	44	3 Aug 04	34	p=0.562

Table 2.3 Within-year comparisons of herd distribution in sequential surveys. Distributions were compared using the multiple response permutation procedure. A high probability indicates that the two distributions are similar.

Period 1		Period 2		
Date	No. relocations	Date	No. relocations	Probability
11 Jun 02	30	27 Jun 02	28	p<0.001
27 Jun 02	27	12 Jul 02	28	p=0.049
12 Jul 02	27	24 Aug 02	21	p<0.001
13 Jun 03	32	24 Jun 03	33	p=0.692
24 Jun 03	33	10 Jul 03	49	p<0.001
10 Jul 03	49	1 Aug 03	44	p<0.001
1 Aug 03	44	2 Oct 03	40	p=0.003
11 Jun 04	31	2 Jul 04	29	p<0.001
2 Jul 04	29	22 Jul 04	38	p=0.010
22 Jul 04	38	3 Aug 04	34	p<0.001
3 Aug 04	34	15 Aug 04	37	p=0.804
15 Aug 04	37	4 Sep 04	30	p=0.165
4 Sep 04	30	17 Sep 04	33	p=0.629

Table 2.4 Small scale habitat selection model selection results. Shown are parameter estimates (SE) from selected and competing models comparing used locations within the 99% utilization distribution to random points within the 99% utilization distribution. Estimates in **bold** indicate that a variable was in the best approximating model; estimates in **bold*** with an asterisk indicate that the variable was dropped in one or more competing models. Parameter estimates in standard font indicate that the variable was included only in competing models (<2 AIC from the top model), and an empty cell indicates that the variable was not in any of the competing models. A Q indicates that quasi-complete separation was encountered during analysis, and a valid parameter estimate was generated. Models are arranged according to Julian day.

Date	Year	Intercept	Tussock/ Shrub	Moist Sedge	Wet Sedge	Water	NDVI	NDVI-rate	DTRI	Temperature	R^2_{DEV}	C^1
11-Jun	2002	**-2.54 (.27)**				**-0.36* (.22)**	-0.16 (.25)		**-0.73 (.36)**	**-.43 (.21)**	0.09	71.3
11-Jun	2004	**-2.72 (.30)**	-1.41 (.87)	0.15 (.52)	0.43 (.46)	**-1.16 (.36)**	0.27 (.35)	-0.16 (.23)	-0.14 (.22)	**-0.50 (.22)**	0.10	73.2
13-Jun	2003	**-2.23 (.21)**				**-0.51 (.25)**	-0.18 (.40)	**-0.44 (.21)**		**-0.34 (.21)**	0.05	67.4
24-Jun	2003	**-2.10 (.20)**				**-0.37* (.21)**	0.09 (.21)				0.02	58.0
27-Jun	2002	**-5.54 (72.5)**	**-8.96 (Q)**	**3.90 (Q)**	**3.35 (Q)**	0.21 (.34)	**0.43* (0.26)**		-0.22 (.24)	0.38 (.25)	0.08	70.0
2-Jul	2004	**-2.28 (.20)**								**0.35* (.21)**	0.02	60.0
10-Jul	2003	**-5.03 (64.5)**	**-9.24* (Q)**	**3.17* (Q)**	**3.33* (Q)**		0.07 (.16)		**-0.58 (.30)**		0.05	47.4
12-Jul	2002	**-1.11 (.54)**					-0.09 (.17)	**-0.006* (.004**)	**-0.58 (.29)**		0.04	65.4
22-Jul	2004	**-2.26 (.20)**	0.50 (.45)	-0.38(.35)	0.36 (.29)	**-0.26* (.18)**	**-0.25* (.17)**	-0.09 (.20)	-0.09 (.20)	-0.14 (.20)	0.03	61.6
1-Aug	2003	**-1.87 (.16)**									0.00	
3-Aug	2004	**-2.47 (.25)**	**0.85 (.31)**	**-0.21 (.44)**	**-0.87 (.43)**		0.07 (.21)	-0.25 (.19)	-0.31 (.24)	**-0.54 (.20)**	0.07	71.2
15-Aug	2004	**-2.20 (.20)**				**0.31 (.17)**	**-0.39 (.15)**	-0.27 (.20)	**0.39* (.17)**		0.06	68.0
24-Aug	2002	**-6.08 (118.7)**	**3.81 (Q)**	**2.36 (Q)**	**3.63 (Q)**	-0.32 (.40)		-0.18 (.27)	0.03 (.27)	**-0.57* (.30)**	0.08	71.0
4-Sep	2004	**-2.45 (.23)**	0.24 (.44)	-1.31 (.63)	0.03 (.36)	-0.29 (.23)	0.15 (.24)	**-0.72 (.27)**		**-0.29* (.19)**	0.05	67.0
17-Sep	2004	**-2.08 (.18)**									0.00	
2-Oct	2003	**-2.38 (.30)**	**0.92* (.35)**	**0.06* (.48)**	**0.19* (.36)**	0.22 (.29)	0.17 (.16)		0.23 (.17)		0.04	46.7

[1] C stands for concordance, the percentage of binary comparisons (used versus available) where the model predicted a higher probability of use for the point that was actually used. The value shown is from the best approximating model, as is the value indicated for R^2_{DEV}.

Table 2.5 Large scale habitat selection model selection results. Shown are parameter estimates (SE) from selected and competing models comparing random points within the 99% utilization distribution to random points within the remaining summer extent of use. Estimates in **bold** indicate that a variable was in the best approximating model; estimates in **bold*** with an asterisk indicate that the variable was dropped in one or more competing models. Parameter estimates in standard font indicate that the variable was included only in competing models (<2 AIC from the top model), and an empty cell indicates that the variable was not in any of the competing models. Models are arranged according to Julian day.

Date	Year	Intercept	Tussock/ Shrub	Moist Sedge	Wet Sedge	Water	NDVI	NDVI-rate	DTRI	Temperature	R^2_{DEV}	C^1
11-Jun	2002	**-1.39 (.15)**	-0.07 (.23)	-0.06 (.24)	0.38 (.17)	**-0.52 (.19)**	**-1.38 (.31)**	**0.18 (.09)**	-0.16 (.16)	**-1.23 (.20)**	0.36	87.6
11-Jun	2004	**-0.31 (.12)**	**-0.96 (.02)**	**0.06 (.18)**	**0.52 (.16)**	**-0.39* (.17)**	**-0.98 (.23)**	**-0.16* (.11)**	**-0.22* (.13)**	**0.28* (.18)**	0.85	75.2
13-Jun	2003	**-0.72 (.14)**	**-0.97 (.22)**	**-0.73 (.20)**	**0.41 (.16)**	**-1.10 (.20)**	**-1.29 (.21)**	**-0.28 (.12)**	**-0.38 (.15)**	0.14 (.19)	0.23	80.8
24-Jun	2003	**-1.48 (.17)**	**-0.002 (.23)**	**-0.69 (.21)**	**0.52 (.16)**	**-0.57 (.20)**	**-1.65 (.23)**	**-0.21* (.11)**	**-0.58 (.19)**	-0.13 (.22)	0.31	84.9
27-Jun	2002	**-2.87 (.29)**	**0.44 (.32)**	**-0.25 (.28)**	**0.82 (.19)**	**0.51 (.21)**	**-0.68 (.33)**	**0.47 (.13)**	**-0.34* (.24)**	**-1.62 (.31)**	0.49	91.7
2-Jul	2004	**-7.03 (.81)**	0.03 (.04)	0.4 (.34)	-0.57 (.32)	**-0.93 (.22)**	**-1.43 (.34)**	**1.03 (.20)**	**-1.15 (.42)**	**-3.26 (.49)**	0.74	97.3
10-Jul	2003	**-7.55 (.85)**	**-1.30 (.55)**	**0.77 (.3)**	**0.66 (.31)**	**-0.64 (.29)**	**-0.90 (.34)**	**-0.5 (.19)**	**-2.63 (.62)**	**-2.71 (.40)**	0.73	97.3
12-Jul	2002	**-3.15 (.28)**	**0.76 (.28)**	**-0.63 (.24)**	**0.43 (.19)**	**0.55 (.19)**	**0.58 (.16)**	0.15 (.16)	**0.94 (.2)**	**-3.38 (.28)**	0.53	93.5
22-Jul	2004	**-3.86 (.34)**					-0.17 (.12)	**-0.2* (.11)**		**-3.11 (.25)**	0.57	94.4
1-Aug	2003	**1.02 (.16)**	**0.76 (.27)**	**-0.04 (.24)**	**-0.13 (.23)**	**0.74 (.23)**	**0.36* (.19)**	**-0.46 (.13)**	**0.24* (.15)**	.20 (.15)	0.09	71.2
3-Aug	2004	**0.4 (.12)**	**0.7 (.20)**	**-0.63 (.20)**	**0.51 (.18)**	**0.22* (.15)**	-0.18 (.13)	-0.19 (.13)		0.25 (.15)	0.07	68.2
15-Aug	2004	**-1.36 (.19)**	**1.26 (.39)**	**-0.16 (.32)**	**0.2 (.29)**	**1.07 (.3)**	-0.27 (.26)	**-0.47 (.17)**		-0.21 (.21)	0.12	75.1
24-Aug	2002	**2.20 (.23)**	0.09 (.45)	-0.36 (.43)	0.95 (.63)	**0.74 (.31)**	**-0.88 (.37)**	**0.44 (.21)**	0.08 (.18)	**-0.52 (.28)**	0.36	88.5
4-Sep	2004	**0.29 (.15)**	**0.83 (.25)**	**-0.53 (.24)**	**0.93 (.23)**	**0.72 (.22)**	**-1.19 (.24)**	**0.45 (.12)**	0.04 (.13)	-0.04 (.16)	0.30	86.2
17-Sep	2004	**-1.08 (.15)**	**0.19 (.22)**	**-1.03 (.25)**	**1.31 (.18)**	**0.68 (.16)**	**1.19 (.20)**	**0.24 (.17)**	0.09 (.16)	**-1.47 (.19)**	0.34	87.0
2-Oct	2003	**-0.75 (.12)**	**0.14 (.18)**	**-0.49 (.18)**	**0.55 (.16)**	**0.25 (.13)**	**-0.55 (.18)**	**-1.45 (.19)**	**0.26 (.12)**	**-1.50 (.19)**	0.17	76.8

[1] C stands for concordance, the percentage of binary comparisons (used versus unused) where the model predicted a higher probability of use for the point that was actually used. The value shown is from the best approximating model, as is the value indicated for R^2_{DEV}.

CHAPTER 3:

SEASONAL PATTERNS IN FECAL ESTIMATES OF CARIBOU DIET NITROGEN CONTENT AND REMOTELY SENSED FORAGE BIOMASS[1]

Abstract: Protein accumulation and conservation is essential for caribou reproduction and fitness. Winter diets of caribou tend to be low in nitrogen (N), so protein accumulation must occur during the short arctic summer. We used two methods to estimate dietary N content for the Teshekpuk Caribou Herd (TCH). One method estimated N content based on estimated diet composition and phenologically adjusted N content of forage species. A second method used nitrogen associated with the neutral detergent fiber fraction (NDF–N) of fecal material to index nitrogen content. NDF–N indexes plant nitrogen alone, without the influence of nitrogen binding compounds and nitrogen endogenous to the caribou. NDF–N was correlated with both nitrogen content predicted from diet composition ($R^2 = 0.69$) and NDVI, a remotely sensed index of vegetation greenness ($R^2 = 0.72$). NDF–N and total fecal nitrogen were highly correlated in this study ($R^2 = 0.96$), implying that fecal nitrogen alone may provide an adequate index for caribou. Diet composition methods of estimating N content implied that inter-herd differences in N content of forage can be substantial. Both methods of estimating N content indicated that high dietary N content was limited to a short period in summer, and N diet quality diminished well before landscape levels of forage biomass.

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[1] Prepared for submission to the Journal of Wildlife Management as Parrett, L.S., P.S. Barboza and B. Griffith. Seasonal patterns in caribou diet nitrogen content and remotely sensed forage biomass.

INTRODUCTION

The flush of highly digestible, high nitrogen forage available to calving caribou (Whitten and Cameron 1980, Russell et al. 1993, Jorgenson et al. 2002) may be one of the reasons that large populations of barren-ground caribou (*Rangifer tarandus granti*) in North America migrate into northern coastal habitats (e.g., Kelsall 1968, Klein 1970, Kuropat and Bryant 1980, Russell et al. 1993, Griffith et al. 2002b). Only during the short season when green forage is available, typically from early June through August, can caribou accumulate protein at high rates (Allaye-Chan 1991, Chan-Mcleod et al. 1999). In contrast, caribou can deposit fat all year (Allaye-Chan 1991, Chan-Mcleod et al. 1999).

Although likelihood of conception is well predicted by body mass and fat reserves (Cameron et al. 1993, Cameron and Ver Hoef 1994, Gerhart et al. 1997), Allaye-Chan (1991) found that fetal and neonatal weights were better predicted by maternal protein stores in late pregnancy. Newborn *Rangifer* calves are over 90% lean mass, of which protein constitutes almost 20% (Ringberg et al. 1981, Barboza and Parker 2006). Over 80% of this fetal mass is deposited during the last trimester of gestation (Robbins and Robbins 1979, Oftedal 1985).

Recent studies have demonstrated that caribou and reindeer utilize dietary rather than endogenous nitrogen (N) for maintenance in late winter (Barboza and Parker 2006). Minimizing body protein loss conceivably conserves protein reserves for fetal growth (Parker et al. 2005). Although caribou can tolerate very low dietary N in late gestation and still deliver viable calves (Parker et al. 2005), sufficient protein reserves must be accumulated at some point in the year in order for the female to ensure adequate fetal growth.

For reindeer and high arctic populations of caribou where nitrogen-poor lichens and mosses constitute a large part of the late winter diet, nitrogen intake is typically low during peak fetal development (e.g., Person et al. 1980, Boertje 1990, Russell et al. 1993, Sakkinen et al. 2001, Storeheier et al. 2002). As a result, protein allocated toward fetal growth must be primarily derived from reserves accumulated during the short Arctic growing season.

Although the significance of nitrogen in the annual cycle of caribou is well documented, direct estimates of intake are difficult to obtain in a natural setting. Indirect estimates of intake through fecal indices are logistically possible, but can be difficult to interpret, primarily due to an inability to discern dietary and endogenous sources of N (Hobbs 1987, Van Soest 1994).

Fecal N (FN) is composed of metabolic N and undigested dietary N (Robbins 1983). Metabolic fecal N (MFN) is primarily composed of microbial and digestive tissue, while the dietary fraction is composed of indigestible residues associated with plant cell walls (Van Soest 1994). As a result, N associated with fecal neutral detergent fiber (NDF–N) should better indicate current N intake than total FN. Because increasing dry matter intake (DMI) levels correspond with increased demands on digestive tissue, MFN reflects DMI (Van Soest 1994). When MFN is estimated through subtraction as the remaining portion of FN after accounting for NDF–N, small amounts of neutral detergent soluble dietary nitrogen contained in the feces may be included in the estimate of MFN as secondary metabolite-bound nitrogen. This inclusion is significant because it biases the estimate of endogenous N, and therefore FN, upwards by an amount equivalent to tannin or phenol bound nitrogen.

Fecal indices of diet quality, especially FN, have been evaluated in both experimental situations (e.g. Mould and Robbins 1981, Howery and Pfister 1990, Brown et al. 1995, Hodgman et al. 1996, Osborn and Ginnet 2001, Page and Underwood 2006) and natural situations (Holochek et al. 1982, Leslie and Starkey 1985, Leslie at al. 1989, Kucera 1997, Osborn and Jenks 1998, Blanchard et al. 2003). In one study with direct comparisons, estimates of nitrogen content on an NDF basis rather than whole feces resulted in more precise estimates of diet quality (Hodgman et al. 1996).

Nitrogen intake estimates, regardless of method, can be logistically prohibitive to obtain. If we assume that caribou feces are an accurate representation of the foraging landscape, a positive relationship between fecal NDF–N and the normalized difference vegetation index (NDVI, Tarpley et al. 1984), a landscape scale remotely sensed index of vegetation quantity, could provide a useful tool for long-term monitoring of forage nitrogen availability. NDVI is a satellite based measurement of relative greenness (Tarpley et al. 1984, Tucker and Sellers 1986). Although primarily intended as an index of vegetation quantity (Tarpley et al. 1984, Tucker and Sellers 1986), the rapid rise and decline of vegetative biomass during the arctic summer means that the overall level of biomass is likely to mirror changes in quality that are associated with the rapid growth and subsequent senescence of vegetation (Whitten and Cameron 1980, Russell et al. 1993, Jorgenson et al. 2002).

The three primary objectives of our research on caribou were 1) to estimate seasonal patterns in population level dietary nitrogen content, 2) to estimate seasonal changes in population level diet composition, and 3) to evaluate the relationship between estimates of nitrogen content and a landscape scale estimate of vegetation quality (NDVI).

STUDY AREA

The study area was defined as the area utilized by collared females from the Teshekpuk Caribou Herd during the snow-free period (June-September), 2002–2004 (Chapter 2, Parrett 2007). This area covered the coastal plain north of the Brooks Range in Alaska between the Kuk River in the west and the Kuparuk River in the east (Figure 3.1). Dominant vegetation types in the study area were wet and moist sedge communities (Muller et al. 1999).

METHODS

During the snow-free season, 2002-2004, we relocated 21-49 radio collared female caribou every two weeks, weather permitting. Fecal sampling took place concurrent with or immediately following aerial surveys, and search efforts were concentrated on areas where caribou had recently been observed. Two additional samples were collected from geographically distinct portions of the winter range in April, 2004. During each sampling bout, we collected 20 or more fresh fecal groups over the course of 1 to 3 days. Pellet temperature and the presence of mucous layers were used to verify freshness. In addition to samples obtained through ground surveys, we collected feces directly from immobilized animals during associated capture work. All captures complied with animal care and use guidelines set forth by the Institute of Arctic Biology and the Alaska Department of Fish and Game (IACUC permit 02-61, ADFG permit 03-0008). We haphazardly selected single pellets from each pellet group to create composite samples for subsequent analyses. Samples were air dried in paper bags at room temperature prior to analyses.

Micro-histological analyses of fecal samples (Sparks and Malechek 1968) were conducted at the Washington State University Wildlife Habitat Nutrition Laboratory. Relative density of epidermal plant fragments was estimated based on 25 views of 4 prepared slides per sample. Although several correction factors that attempt to account for differential digestion and fragmentation are available in the literature (e.g. Duquette 1984, Russell et al. 1993, Ihl and Klein 2001), we used correction factors provided by Russell et al. (1993) for further analyses, primarily because those correction factors were derived from known intakes of mixed diets in *Rangifer*, rather than single forages or *in vitro* digestibilities (Appendix E).

Estimates of dietary N content were made using two methods. One method indexed N intake using direct estimates of NDF–N in the feces. A second estimate was made by weighting phenologically appropriate estimates of N content of forage plants by the corrected relative abundance of those plants in the feces, inferred from micro-histology. Forage N values were taken from various studies where seasonal forage quality analyses were conducted. In particular, moss N content was obtained from Boertje (1981), lichen N from Chapin et al. (1980), evergreen shrub and forb N from Russell et al. (1993), and deciduous shrub and sedge N from Whitten and Cameron

(1980). Some forages appeared to have constant seasonal N values (moss, lichen, evergreen shrub), while others had strong seasonal patterns in N content (willow, sedges). We modeled the seasonal N dynamics of sedges and willows in order to estimate seasonal N content commensurate with our fecal sampling dates (Appendix F). As an inter-herd comparison of dietary N content, we used published diet data for the Porcupine Caribou Herd (PCH, Russell et al. 1993), weighting the diet composition estimates for the PCH by the same phenologically adjusted plant N content estimates used for the TCH to estimate dietary N content. We pooled both PCH and TCH data by seasons in the annual cycle of barren ground caribou described by Russell et al. (1993).

While the phenological patterns in N content in caribou forages are well documented, the date-specific estimates of plant N concentrations we used to predict dietary N content levels from estimated diet composition are well over 20 years old (Whitten and Cameron 1980). Parmesan and Yohe (2003) have documented a 2.3 day/decade advance in global phenology. If this pattern also occurred in our study region, phenologically specific estimates of N content could be off by as much as 6 days. To address this potential error, we assessed changes in estimated N content values and resultant changes in the statistical relationship between NDF–N and estimated N content levels after advancing our phenological estimates of N content by 6 days. Differences in estimated forage N were tested with a paired t-test. We also investigated the effect of using raw plant fragment counts, rather than diet estimates corrected for digestibility, on dietary N content estimates, using a paired t-test to test for significance.

Fecal samples for fiber and N analyses were ground to pass through a 20 mesh wire filter and dried at 60˚C to constant weight. Fiber fractions were extracted using an Ankom Fiber analyzer with Na_2SO_3 extraction (Van Soest et al. 1991, Ankom Technology 1998). N and NDF–N were estimated using a LECO elemental analyzer (CNS2000, LECO, St. Joseph, MI). Samples contained varying amounts of soil, so fiber and nitrogen contents were corrected for ash content, and reported on an organic matter (OM) basis. Ash content was determined directly from remnants of LECO analyses. Endogenous nitrogen was estimated as the non-fiber fraction of FN (gN/100gOM – gNDF–N /100gOM). All fiber and nitrogen analyses were performed at the Institute of Arctic Biology, University of Alaska Fairbanks.

We estimated the average NDVI within the summer distribution of the herd from 10-day maximum-value composite images from the sensor onboard the Systeme pour l'Observation de La Terre (SPOT) satellite (Chapter 2, Parrett 2007). SPOT Vegetation data has a 1 km^2 resolution. Images are composited on the 1st, 11th, and 21st day of each month, and we interpolated to the fecal sampling date using data from the bracketing composite images (Chapter 2, Parrett 2007). All statistical analyses were conducted on data corresponding to the fecal sampling date. For the purposes of display, we pooled fecal data by NDVI composite date to produce a simplified figure that showed seasonal trends in our two estimates of dietary N content, as well as the three year mean NDVI value by composite date. NDVI composite dates were chosen as the pooling interval because of the relative regularity with which NDVI was estimated in comparison to the irregularity with which fecal samples were collected. The raw data from fecal samples, including nitrogen, fiber, and plant fragment counts, are presented in Appendix G.

RESULTS

Twenty-one composite fecal samples were collected during 2002-2004. Micro-histological analysis of fecal material showed seasonal changes in the abundance of different plant groups (Figure 3.2, Appendix E). Moss and lichen formed up to 80% of the estimated diet in April and early June. Throughout June, sedges, typically a mixture of *Carex* and *Eriphorum* spp., gradually became more important, and were dominant throughout July. Willows were an important constituent in the diet in early July, and throughout August. By mid-August the estimated diet was largely similar to late winter and early-June diets, with over 70% moss and lichen combined, indicating a return to typical winter forages.

Fecal NDF–N increased from late winter lows of 0.78 g/100g OM to seasonal highs in late July of 2.57g/100g OM (Figure 3.3, Appendix G). Estimated dietary N concentrations increased from late winter lows of 0.70 g /100g DM to a peak in early July of 2.06 g/100g DM (Figure 3.3, Appendix E). Dietary N concentrations for the PCH far exceeded estimates for the TCH between mid-June and late-August, peaking at 2.97 g/100g DM in late June, but appeared to be marginally lower throughout the winter (Figure 3.4).

NDF–N tracked patterns in both N content predicted from diet composition (R^2 = 0.69, $P < 0.0001$), and seasonal changes in NDVI (R^2 = 0.72, $P < 0.0001$; pooled data in Figure 3.3) moderately well. Predicted dietary N content and NDF–N diverged from

NDVI in early August (Figure 3.3). The mean change in dietary N content after advancing phenology forward by 6 days was -1.53% ($P = 0.016$), with a maximum of -7.18% in late July, and the R^2 between estimated forage N and NDF–N went down to 0.67. The mean change in dietary N content when using raw plant fragment counts rather than diet estimates corrected for digestibility was + 29.5% ($P = 0.0008$), with a maximum of +237% in early September.

Fecal N and NDF–N were highly correlated ($R^2 = 0.96$). On average, 66% of the total fecal N was NDF–N. While NDF–N varied seasonally (Figure 3.3), the seasonal pattern in the endogenous portion of the nitrogen was not striking, although the highest values, indicating high levels of dry matter intake, did occur in August (Figure 3.5) and were loosely correlated with the abundance of shrubs in the diet ($R^2 = 0.39$, $P = 0.0024$).

DISCUSSION

Diet Composition

Barren ground herds with data on calving ground diets include the Porcupine Caribou Herd (PCH), Western Arctic Herd (WAH), and Bathurst (Thompson and McCourt 1981, Kuropat 1984, Griffith et al. 2002a, Griffith et al. 2002b). The PCH and WAH herds tended to have diets during calving dominated by sedges, particularly *Eriphorum vaginatum* (Thompson and McCourt 1981, Kuropat 1984, Russell et al. 1993, Griffith et al. 2002b), while the diet on the Bathurst calving ground was dominated by lichens (Griffith et al. 2002a). Similar to the Bathurst caribou herd, TCH diets consistently appeared to lag behind many other herds in both the timing and degree of willow utilization (Kelleyhouse 2001, Figure 3.2).

Available correction factors are based on very limited data in studies that did not use seasonally appropriate or geographically relevant mixed forages, so we also reported raw uncorrected (Appendix G). The importance of accurate correction factors is particularly apparent when looking at how estimates of dietary N content are altered by correction factors. Although counts of raw plant fragments are undoubtedly incorrect estimates of diet composition, any inaccuracies propagated by faulty correction factors have large consequences for interpretation of both dietary content and quality.

Dietary N Content

We assessed how advances in phenology related to climate change might affect our estimates of forage N with data collected by Whitten and Cameron (1980). Our intent was to ensure that our results were not somehow biased by using phenologically inappropriate estimates of forage N. It should be noted however, that interannual differences in phenology are often similar in magnitude to the 6 day advance we assessed (Dutton and Endres 1991). While a 6 day advance in phenology would not change our conclusions in this paper, the fact that our estimates of forage N content dropped by an average 1.53% with a maximum drop in July of 7.2% is noteworthy, and may imply that if caribou are unable to adjust their foraging behavior accordingly, a climate induced advance in phenology may have net consequences that negatively influence N intake.

Dietary N concentrations appeared to differ widely between the PCH and TCH, particularly in mid-summer. The observed difference in dietary N content between herds is likely to be further magnified by seasonal variation in DMI (McEwan and Whitehead 1970). Griffith et al. (2002b) noted that relative to other herds, the PCH accumulated a high percentage of their annual N intake on the calving grounds. Our data on comparative dietary N content corroborate that statement (Figure 3.4). It should be noted that a thorough test of this hypothesis would require propagation of error associated with correction factors, plant N content estimates, and sampling variation, as well as a thorough understanding of N intake and assimilation, as opposed to content.

The TCH grew at approximately 3 times the maximum rate ever observed for the PCH between 1978 and 2002 (Griffith et al. 2002b), yet N content of the diet on the summer range was substantially lower for the TCH than for the PCH. Because N accumulation and conservation play such an important role in reproductive success, the PCH must either take in more N than is minimally required, while the TCH N requirements are at least adequate, or the TCH intake requirements are substantially less than those of the PCH. The latter situation is possible, if body sizes are also smaller than the PCH. Limited evidence does suggest that mean newborn mass of TCH calves is lower than other arctic Alaskan herds (Griffith et al. 2002b, Arthur and Del Vecchio 2007, Parrett and Carroll unpublished data).

Fecal NDF–N

Major criticisms of fecal nitrogen indices include the potential bias introduced by protein binding tannins (Mould and Robbins 1981, Hobbs 1987) and the inability to relate fecal N to measures of fitness and productivity (Brown et al. 1995, Kucera 1997). By utilizing fecal N associated with NDF, we attempted to eliminate the potential for tannin-bound nitrogen to influence our fecal N index. Our use of NDF–N assumes that highly digestible N in cell contents increases proportionately with N in plant cell walls when plants are consumed in the vegetative phase.

We found that NDF–N tracked estimated dietary N content and remotely sensed estimates of vegetation growth, particularly during the increase phase of biomass curve. The sharp decline in both observed fecal N content and predicted dietary nitrogen content appear to be related to large scale patterns in vegetation senescence, where landscape scale forage quality apparently declined well before vegetation quantity declined. Late summer declines in N content are well documented in caribou forages (Chapin et al. 1980, Whitten and Cameron 1980, Russell et al 1993, Lenart et al. 2002). Total non-structural carbohydrates (TNC) and *in-vitro* dry matter digestibility (IVDMD) tend to be constant or drop less precipitously during the summer than does nitrogen content (Whitten and Cameron 1980, Chapin et al. 1986, Lenart et al. 2002). This difference in decline rates may result in caribou shifting from a diet with high nitrogen content in the early summer to a diet with high digestible energy in late summer. The fact that estimated N content levels decline well before NDVI declines (Figure 3.3) is further evidence of the decoupling of the NDVI-forage N quality relationship even before vegetation begins to senesce.

FN was highly correlated with NDF–N, and largely driven by NDF–N. Use of Na_2SO_3 in neutral detergent extraction removes phenolic compounds from fecal material (Holochek et al. 1982, Howery and Pfister 1990, Van Soest et al. 1991). As a result, we would expect to see peaks in our estimate of endogenous nitrogen associated with tannin-rich forages. In fact, although there were no seasonal patterns in endogenous N during the summer (Figure 3.4), the 3 fecal samples with the greatest estimated combined evergreen and deciduous shrub content were the 3 fecal samples with the highest estimated endogenous nitrogen content. This result may suggest that using NDF–N rather than FN does reduce or eliminate the upward bias in FN caused by protein binding compounds on estimates of relative nitrogen intake, as suggested by Holochek et al. (1982) and Howery and Pfister (1990). Peaks in endogenous N are also expected with high DM intake, however, and availability of willow may promote high DM intake rates. Nevertheless, the fact that NDF–N and FN were so highly correlated may mean that the extra step required to eliminate the influence of endogenous and tannin-bound nitrogen is unnecessary for caribou on arctic ranges.

An additional concern with the interpretation of fecal N indices is related to variable DM intakes associated with seasonal forage availabilities. When forages are high in both quality and quantity, intake levels will also be high (McEwan and Whitehead 1970, Trudell and White 1981, White 1983). At high intake levels, output levels of both dry matter and fecal N will be high, but fecal N will be disproportionately higher from both increases in MFN losses and inefficiently digested plant residues (Barboza, Parker and Hume, in press). In our case, the use of NDF–N rather than FN eliminates the issue of an upward bias related to increases in MFN concentration (Van Soest 1994). However, if the proportion of digestible to indigestible N plant material is not constant, this increase in fecal N content, irrespective of dietary N concentration, may be the cause of the gap observed between dietary N content estimates and fecal NDF–N after early July (Figure 3.3).

Fecal Nitrogen and NDVI

NDVI is widely used to estimate relative vegetative biomass in wildlife studies (e.g. Leimgruber 2001, Griffith et al. 2002b, Hurlbert and Haskell 2003, Boone et al. 2006, Thomas et al. 2006, van Bommel et al. 2006). NDVI is collected globally and currently has a historical record extending nearly 30 years for some sensor systems (Brown et al. 2006), and may provide an inexpensive method to index habitat quality over large areas. NDVI and other remotely sensed habitat attributes are attractive tools from a theoretical and logistical perspective. It is therefore encouraging to see a remotely sensed metric of habitat quality positively correlated with an animal based metric of habitat quality, although caution is warranted. Minimally, any nitrogen index, fecal or otherwise, should reflect dietary nitrogen content. The fact that both of our estimates of N content were most closely related to NDVI only during the early portion of the growing season suggests that NDVI would only be appropriate as an index of available dietary nitrogen concentration during a short period well before peak biomass occurs. During the course of the entire summer, seasonally integrated NDVI may be more useful as an index of available digestible energy.

Rangifer populations vary in their dependence upon spring forages for calf development (Barboza and Parker 2006). For some populations, changes in early spring phenology could affect newborn calf weights. For other populations that rely less on spring forages for calf development, changes in spring phenology would more likely affect lactational output. If lactational demands fail to coincide with availability of high N forages, indicated by the initiation of the NDVI growth phase, negative consequences for calf growth and survival are likely (Griffith et al. 2002b).

The seasonal curve in NDVI can change in multiple ways. Advances in phenology will drive the curve left, while delays will drive the curve to the right (Figure 3.3). A change in the slope or length of the increase phase of growth, representing a change in the time available for forages high in digestible N, could also have consequences for both calf survival and the ability of the cow to regain condition over the course of the summer.

MANAGEMENT IMPLICATIONS

Monitoring diet quality, either through fecal indices or remotely sensed measures of diet quality, will provide data that could be compared to measures of animal performance. Annual monitoring of fecal indices may also provide a method to assess inter-annual changes in diet quality, particularly if changes in distribution or habitat use occur. Supplementing information gained through fecal indices with the remotely sensed NDVI shows promise, particularly if the seasonal relationships between NDVI, forage biomass, forage nitrogen content, and digestible energy can be more thoroughly understood.

The observed difference in dietary N content estimates between the PCH and TCH asks a compelling question: is the TCH diet inadequate from an N perspective? To begin with, the TCH population size was last estimated in 2002 (Carroll 2005). A population decline in the past 5 years would put this question into a more current context.

Additionally, more data on N content and DMI, as well as an estimate of daily-seasonal N intake requirements would help to answer this question. Data on body sizes for both young and adult caribou are necessary to estimate N requirements.

Because of the brevity of the arctic growing season, an inability to access sufficient protein resources during lactation could affect milk production in the current year (Allaye-Chan 1991), and newborn calf weight in the following year (Allaye-Chan 1991), with pursuant implications for survival of calves (Haukioja and Salovaara 1978, Helle and Tarvainen 1984, Skogland 1984, Clutton-Brock et al. 1987, Pietsch et al. 1999, Norberg and Nieminen 2004). Inability to access high quality resources may exist if warming tends increase insect induced movements away from preferred foraging sites (Kruse et al. 2004), or if displacement resulting from industrial development occurs (Wolfe 2000, Griffith et al. 2002b, Lawhead et al. 2004, Johnson et al. 2005). The TCH summer range is almost entirely contained with the National Petroleum Reserve – Alaska (NPR-A), where petroleum development is in initial stages.

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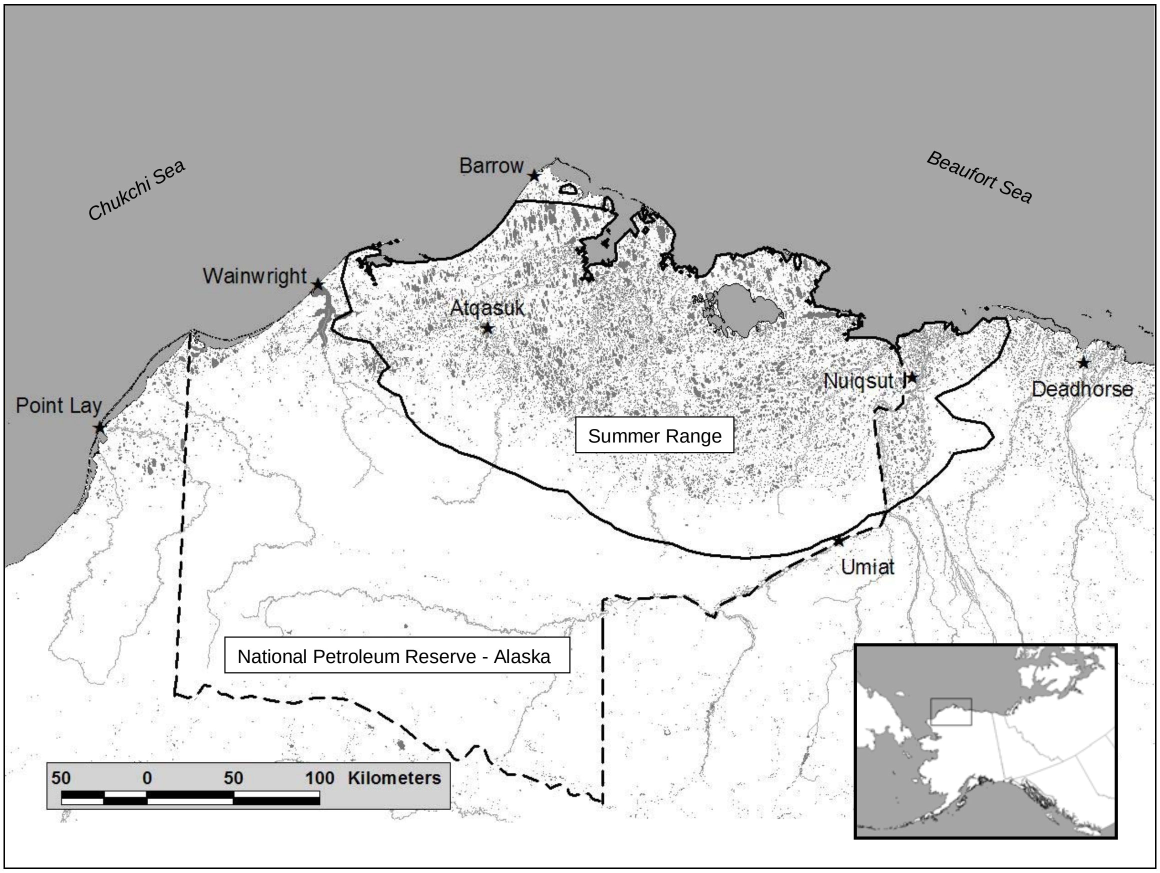

Figure 3.1 Study area. The Teshekpuk Caribou Herd summer range (dark line) is indicated within the National Petroleum Reserve-Alaska (dashed line). The entire study area is located in the central portion of the coastal plain north of the Brooks Range in Alaska.

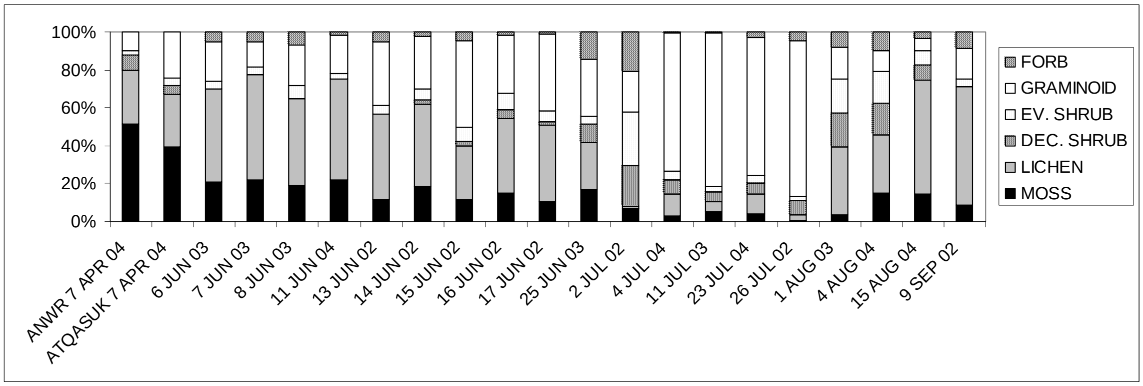

Figure 3.2 Seasonal diet composition of the Teshekpuk Caribou Herd. Diet composition was estimated using fecal micro-histology. Data are corrected for differential digestibility or fragmentation using seasonal correction factors(Russell et al. 1993, Appendix F). The x-axis is arranged by Julian day, with multiple years combined.

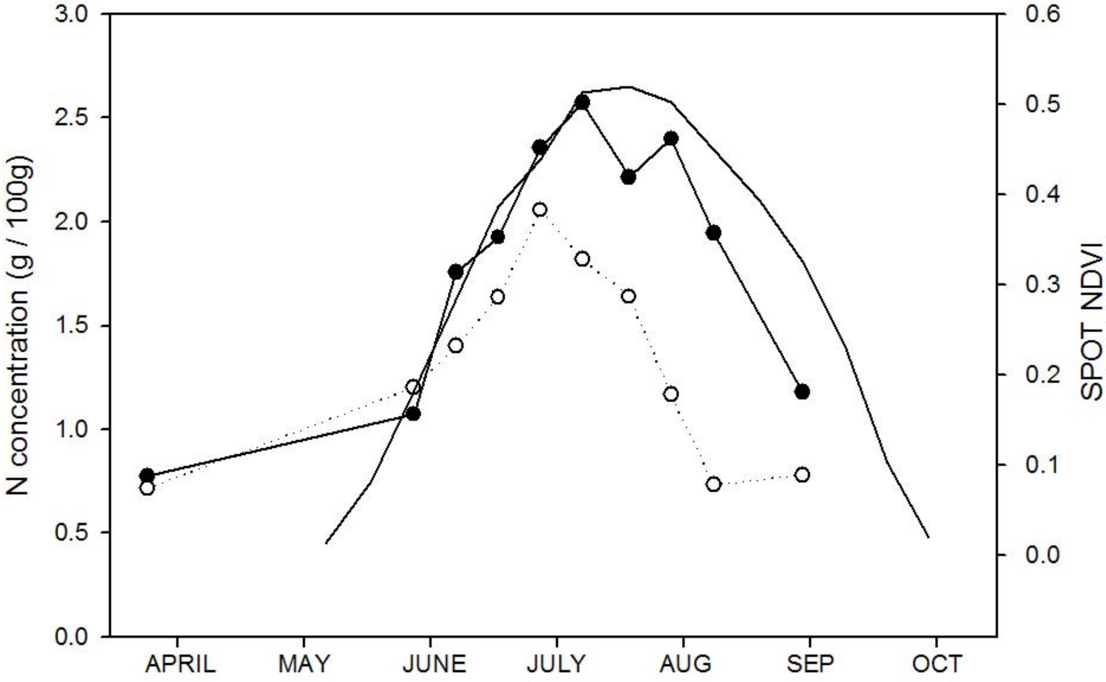

Figure 3.3 Seasonal patterns in NDF-N, estimated dietary N content, and NDVI. The smoothed line is the 3 year average (2002-2004) of bi-weekly NDVI values. Nitrogen related data (n=21) are pooled by NDVI composite date for display purposes. Closed circles represent average grams of NDF-N per 100g fecal organic matter, while open circles indicate the grams of N predicted per 100g forage dry matter.

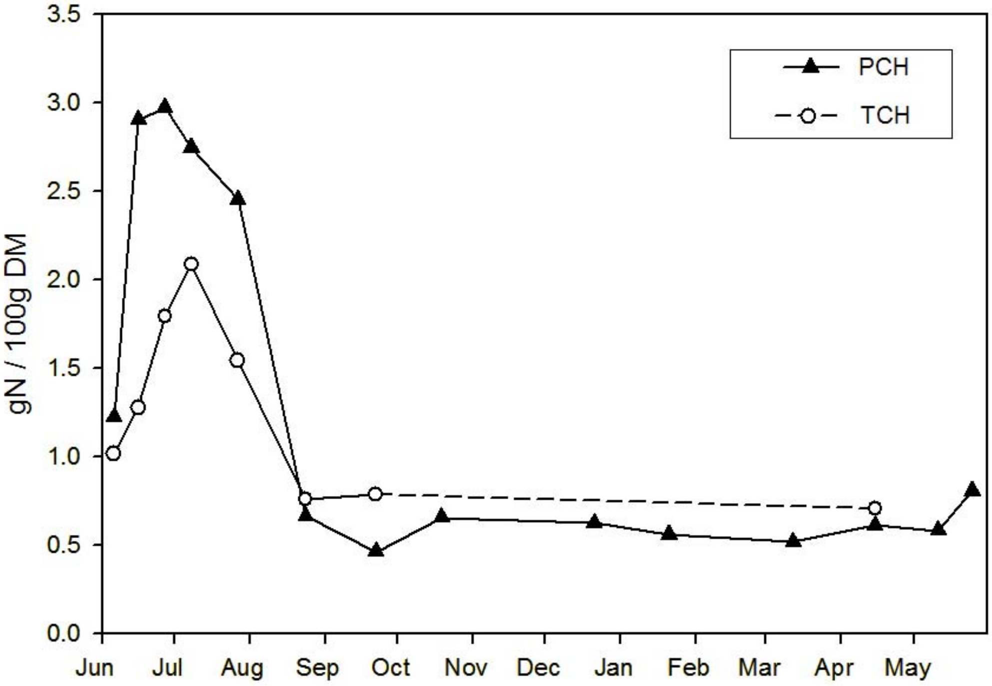

Figure 3.4 Estimated dietary nitrogen concentration for the TCH versus PCH. Data are grouped by seasons in the annual cycle of barren ground caribou described by Russell et al. (1993). Estimates were calculated by weighting dietary composition by phenologically adjusted forage N estimates. Dietary composition was estimated using micro-histology of fecal samples, correcting the percentage of observed plant fragments for differential digestibility by plant group (Russell et al. 1993).

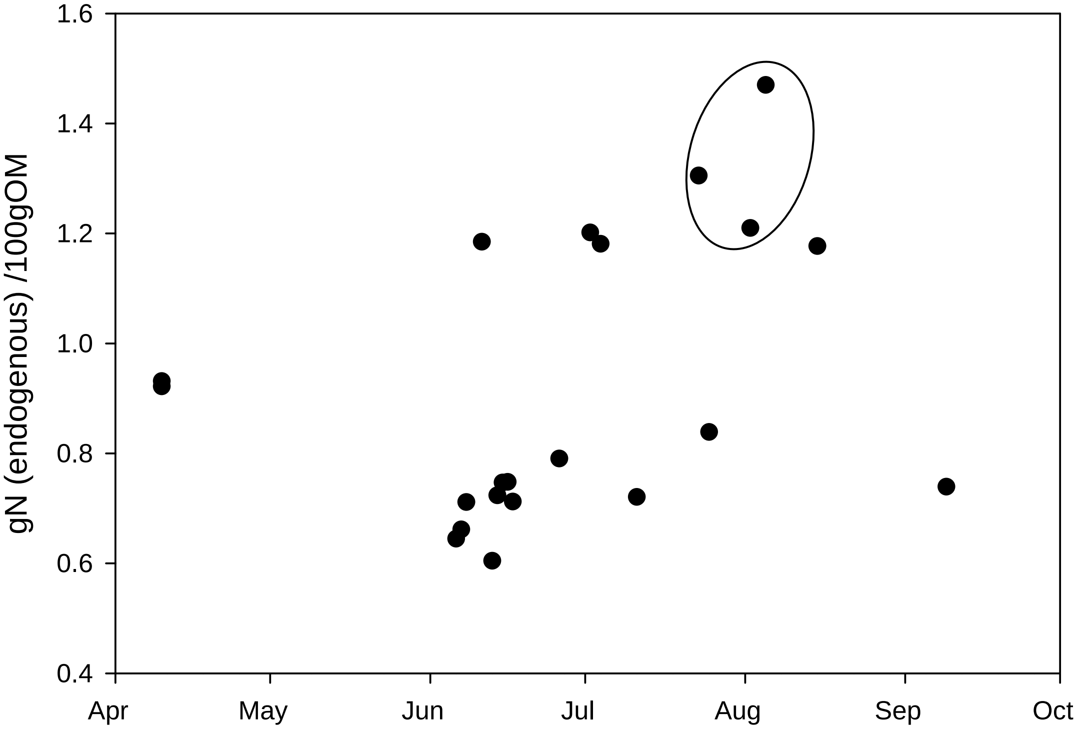

Figure 3.5 Seasonal pattern in endogenous fecal nitrogen (EN = FN - NDF–N). The 3 highest values (circled) were also the samples with the highest shrub content. This may reflect an increase in the non-fiber fraction of nitrogen in the feces due to nitrogen binding phenols.

CONCLUSIONS

The Teshekpuk Caribou (*Rangifer tarandus granti*) Herd (TCH) is a relatively unstudied herd. In addition to ongoing survey and inventory studies (e.g., Carroll 2005, Carroll 2003) previous studies have focused primarily on distribution (Philo 1993, Prichard et al. 2001, Kelleyhouse 2001, Carroll et al. 2005). A secondary focus of research has been on habitat selection during calving (Kelleyhouse 2001, Carroll et al. 2005). This study extends the body of knowledge regarding distribution, habitat selection, and diet throughout the summer period. Lack of knowledge about distribution and habitat use prior to development has compromised attempts to detect changes in distribution or habitat following development on the summer range of the adjacent Central Arctic Herd (National Research Council 2003). The TCH spends the majority of the summer in the National Petroleum Reserve – Alaska, where petroleum exploration and development is just beginning.

Mosquitoes (*Aedes spp.)*, warble flies (*Hypoderma tarandi*) and nasal bot flies (*Cephenemyia trompe*), are important drivers of habitat selection by barren-ground caribou (e.g. Kelsall 1968, White et al. 1975, Downes et al. 1986, Walsh et al.1992). Attempting to monitor and inventory insect activity at temporal and spatial resolutions adequate for habitat selection studies would be financially and logistically prohibitive. Air temperature and wind speed are commonly identified as important factors in determining the occurrence and intensity of insect harassment (White et al. 1975, Downes et al. 1986, Dau 1986, Nixon 1990, Mörschel 1999). As a result, we developed spatial models of air temperature and wind speed in order to index the potential for insect harassment across the TCH summer range. We were particularly successful in modeling air temperature, which proved to be a significant influence on habitat selection in July.

Distribution of female caribou during the course of the study generally agreed with previous findings (Philo 1993, Prichard et al. 2001, Kelleyhouse 2001, Carroll et al. 2005). Summer distribution is likely to stay consistent in the near future, given the inter-annual fidelity that the TCH displayed during the course of this study. Habitat selection during the summer tended to be dynamic, with the influence of various resources shifting in both direction and magnitude of importance. At large scales, caribou selected wet sedge tundra in June, avoided higher temperatures in July, and selected tussock tundra in August. At small scales, habitats used by marked caribou were not different from random locations within the 99% utilization distribution. We believe that the lack of difference in used and available habitats is validation that the 99% utilization distribution is an accurate representation of the distribution of the entire herd. A contrary result would have implied that certain habitats within the 99% utilization distribution were more likely to be used, and therefore that those habitats were perhaps more important. The contrasting results of large and small scale habitat selection analyses reinforce the use of the 99% as the geographically relevant unit of management. Despite high rates of movement observed for the TCH during the summer (Prichard et al. 2001) and the dynamic nature of habitat selection, the consistency with which areas are used between years reinforces the utility of temporally tailored management.

The TCH diet appears to be dominated by lichens and mosses during winter and late spring, and by sedges during the summer. This result is generally in concordance with larger scale patterns in habitat selection. The estimated diet contrasts with the heavily studied Porcupine Caribou Herd, whose diet is dominated in late spring by sedges, and in mid-summer by forbs and willows (Russell et al. 1993, Griffith et al. 2002). The consequence of this difference in diet composition appears to be a major difference in the nitrogen concentration of the diet. Possible implications of an annual inadequacy in nitrogen intake are low birth weights (Parker et al. 2005) and low quality milk production (Chan-McCleod et al. 1999), the fitness consequences of both of which are in conflict with population level patterns of rapid growth which have been observed since 1978 (Griffith et al. 2002, Carroll 2003). Further research on both TCH diet quality and the nitrogen intake requirements of wild caribou are necessary to interpret our preliminary data on TCH diet composition.

Patterns in large scale distribution and habitat selection are becoming well established for the TCH. In contrast, vital rates such as calf survival, adult survival, immigration, and emigration have not been estimated with confidence. Should development occur on a large scale within the TCH summer range in the future, mitigation efforts may suffer from our lack of understanding regarding the primary influences on the population trajectory of the TCH. Future research should focus the influence of habitat on fitness level parameters such as survival and weight gain.

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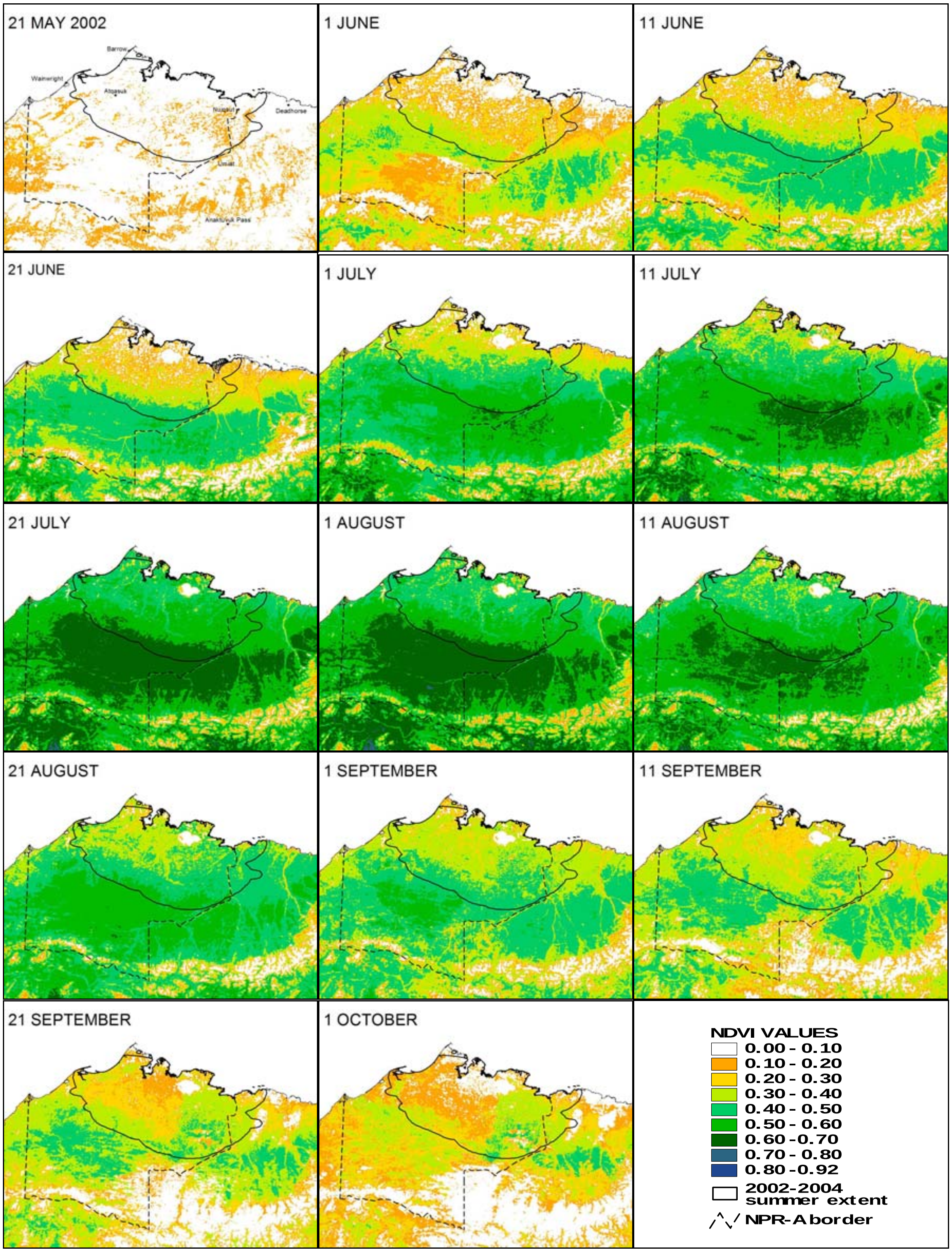
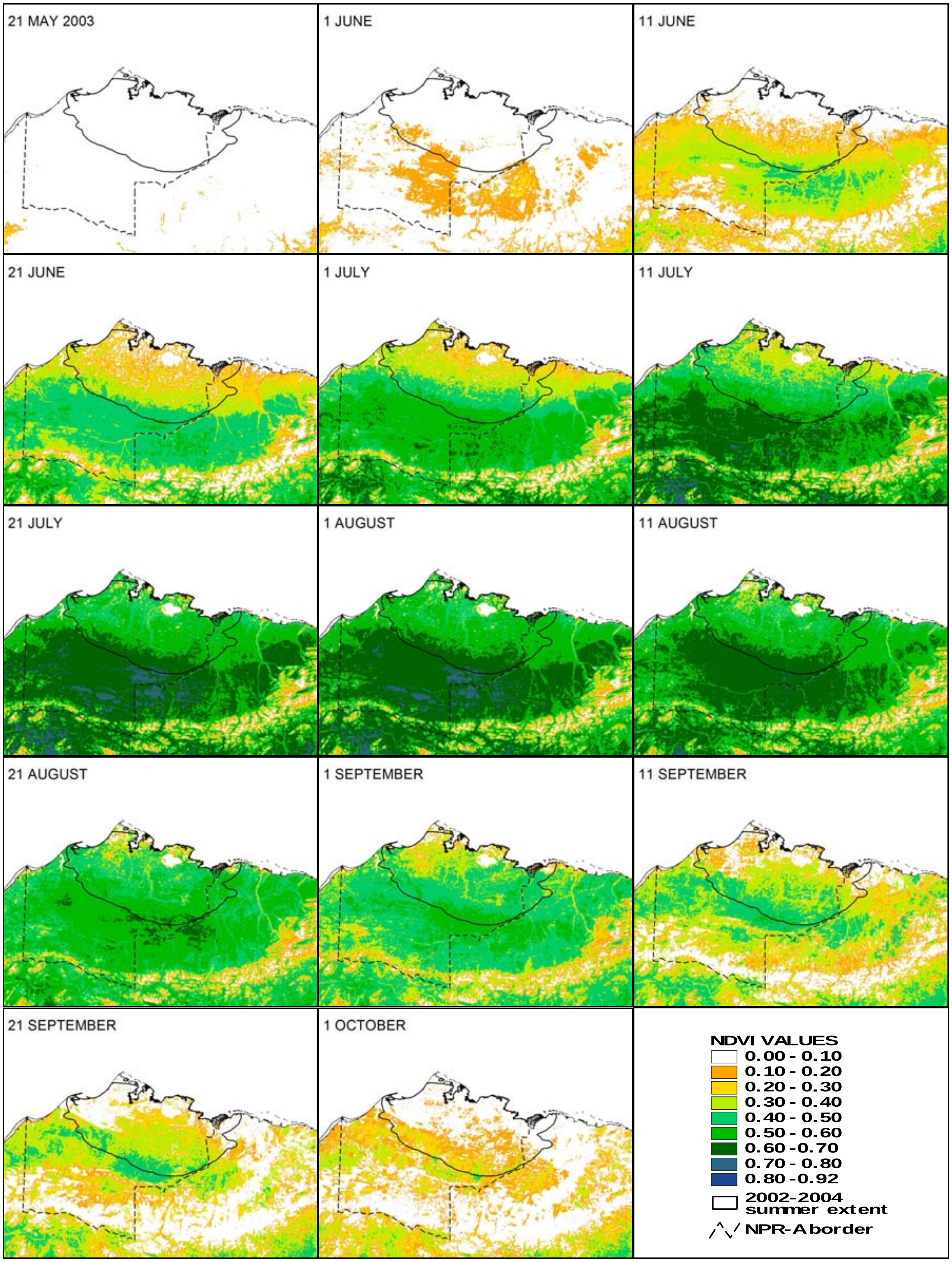
Appendix A. Weather Modeling Abbreviations.

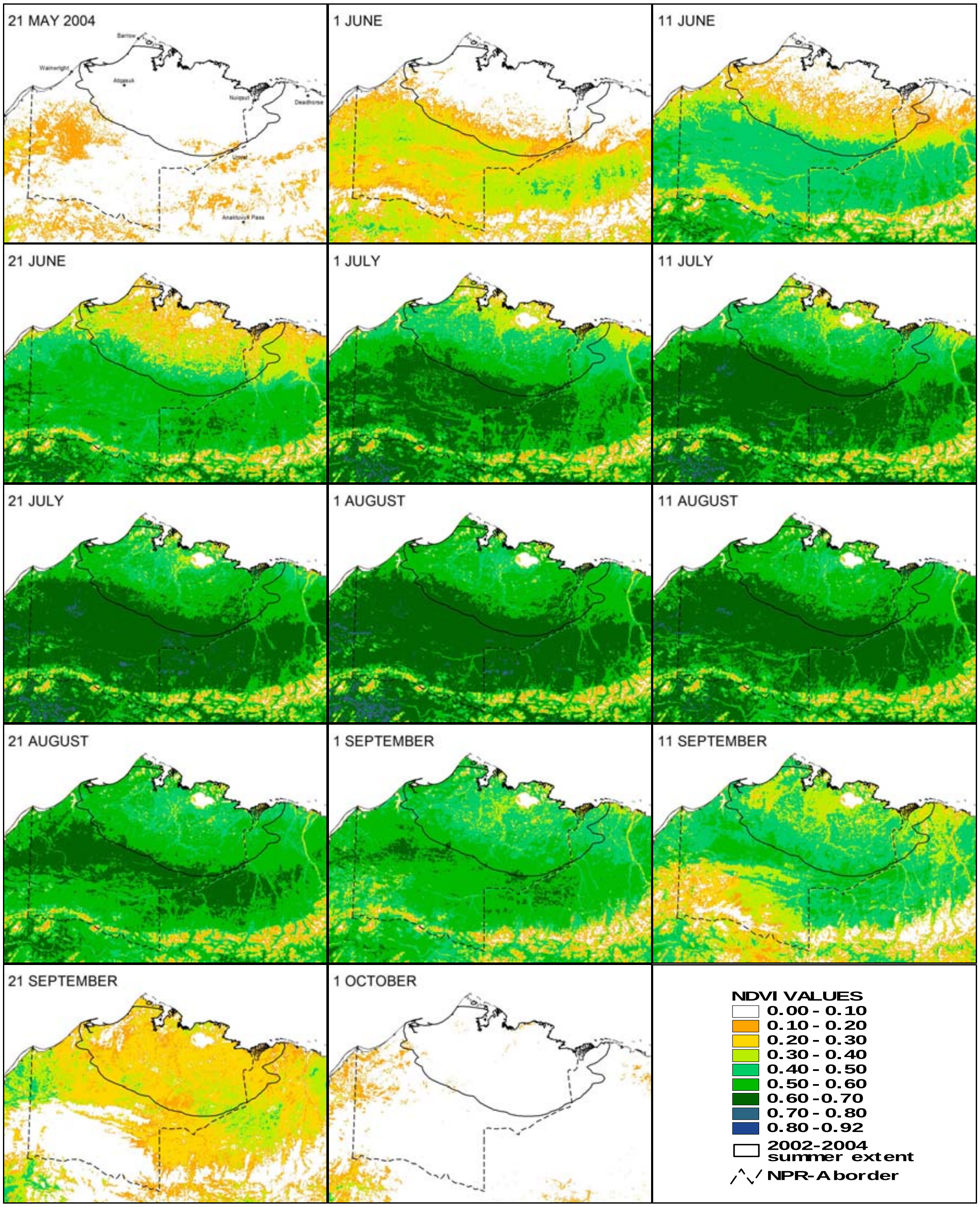
Abbreviation	Definition
BrwTemp	Temperature in Barrow on a given day
BrwWind	Wind speed in Barrow on a given day
Day	Categorical variable for a given day
Dist	Distance from coast (km)
Elev	Elevation (m)
Lat	Latitude, in UTM 5N (m/1000000)
Lat^2	Latitude squared
LogD	Logarithm (base 10) of distance from coast
Lon	Longitude, in UTM 5N (m/100000)
Lon^2	Longitude squared
Null	Model with no spatiotemporal covariates



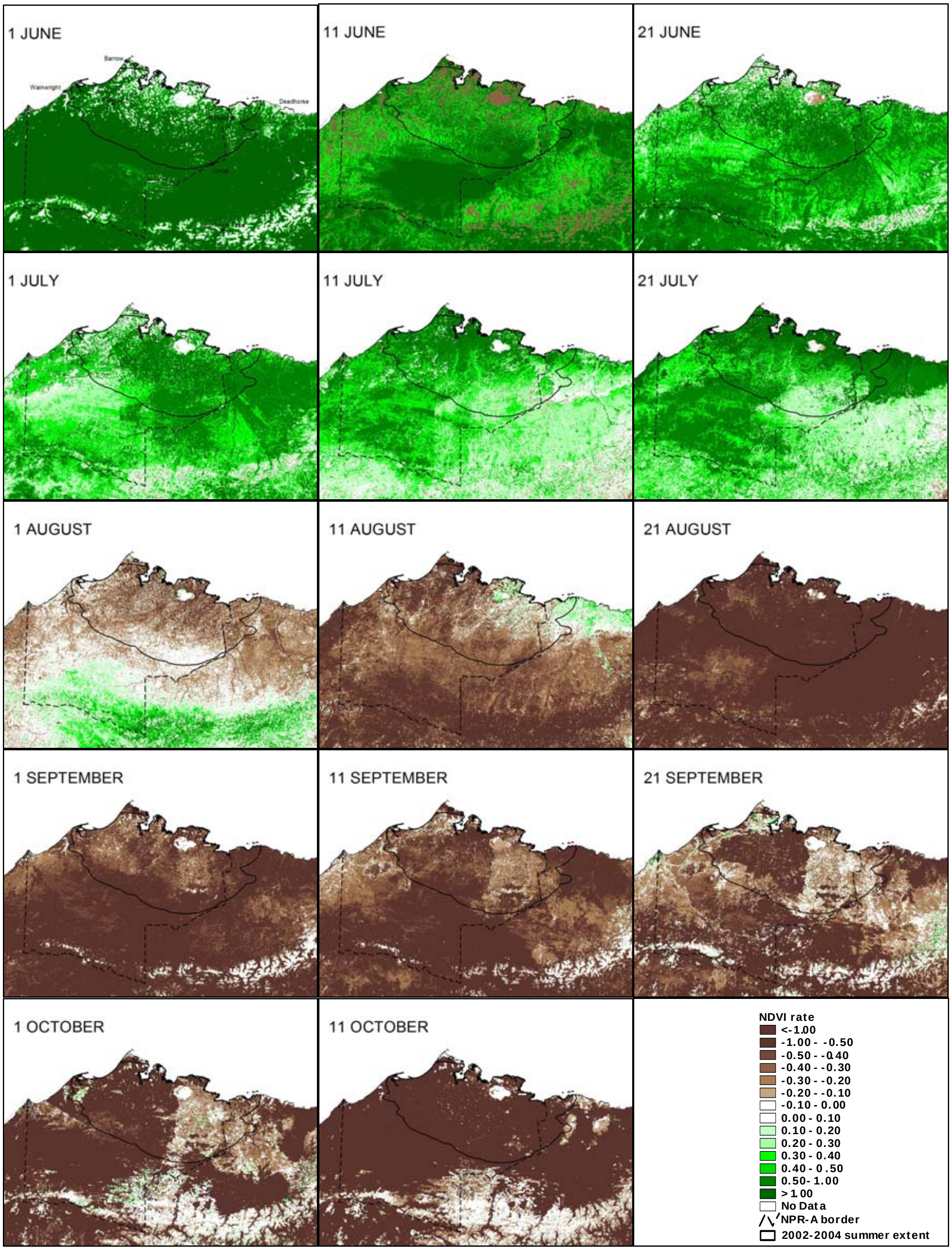
APPENDIX B-1. 2002 NDVI. Estimated values were interpolated from images made up from multiple SPOT satellite passes composited at 10 day intervals.



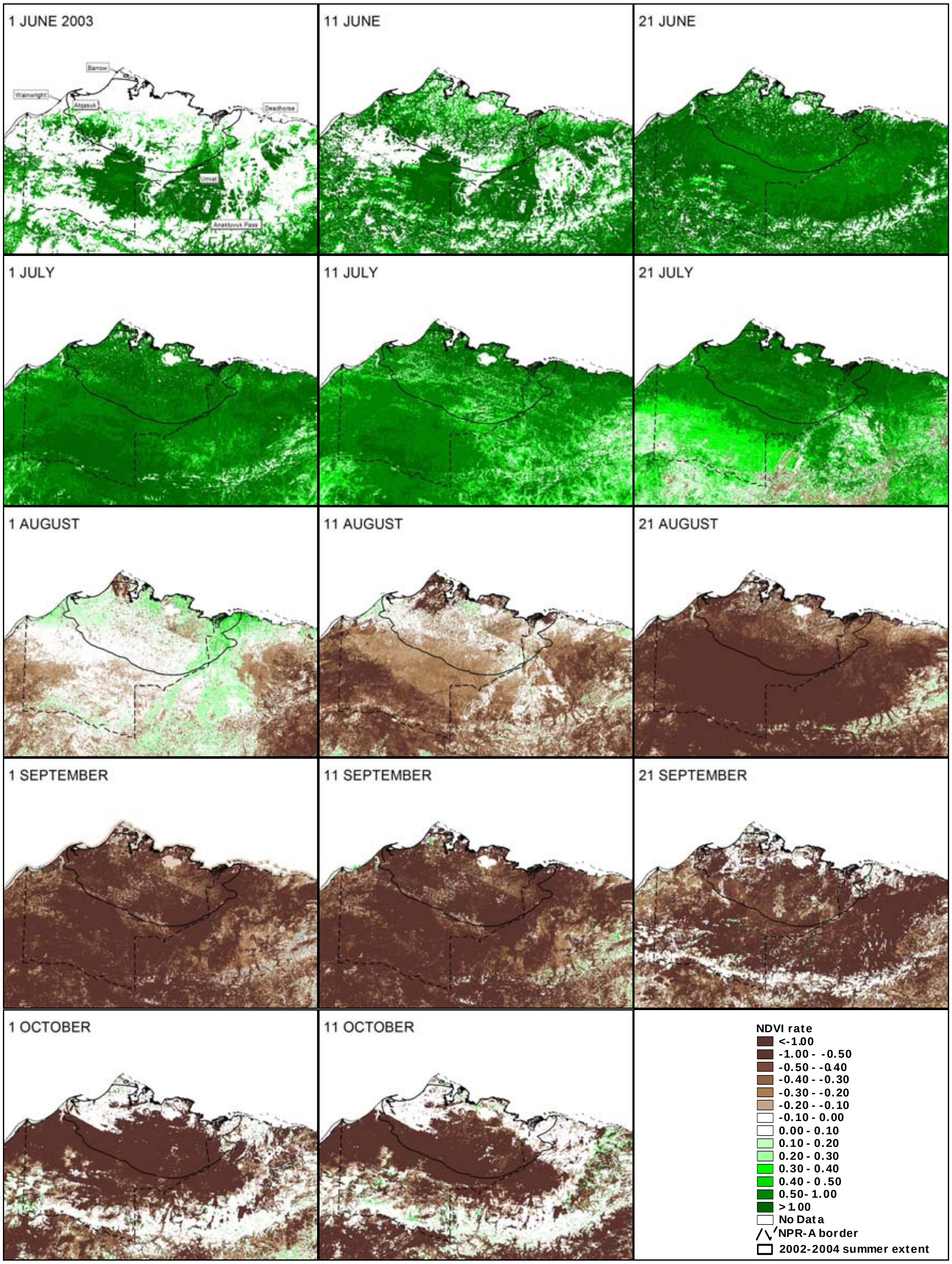
APPENDIX B-2. 2003 NDVI. Estimated values were interpolated from images made up from multiple SPOT satellite passes composited at 10 day intervals.



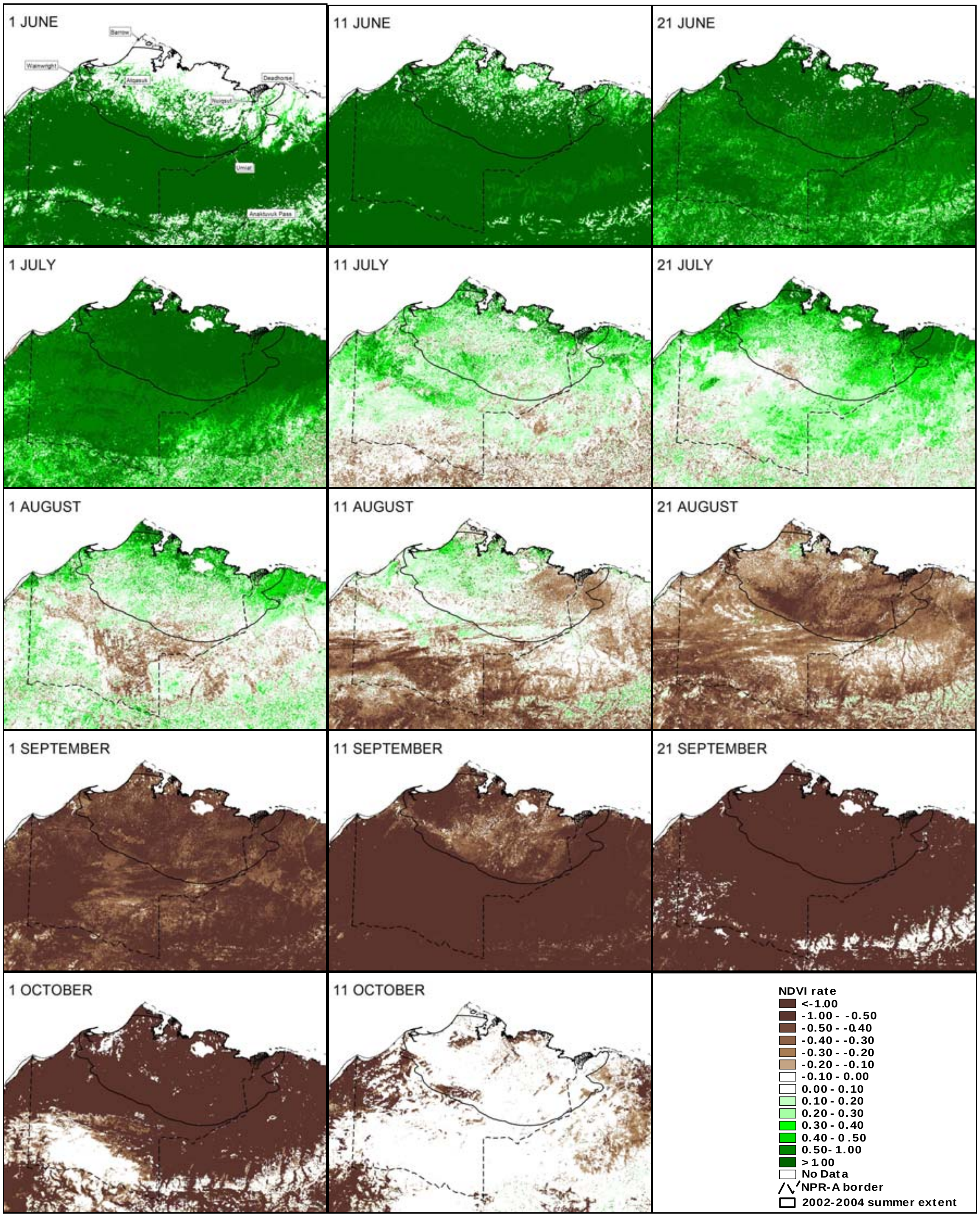
APPENDIX B-3. 2004 NDVI. Estimated values were interpolated from images made up from multiple SPOT satellite passes composited at 10 day intervals.



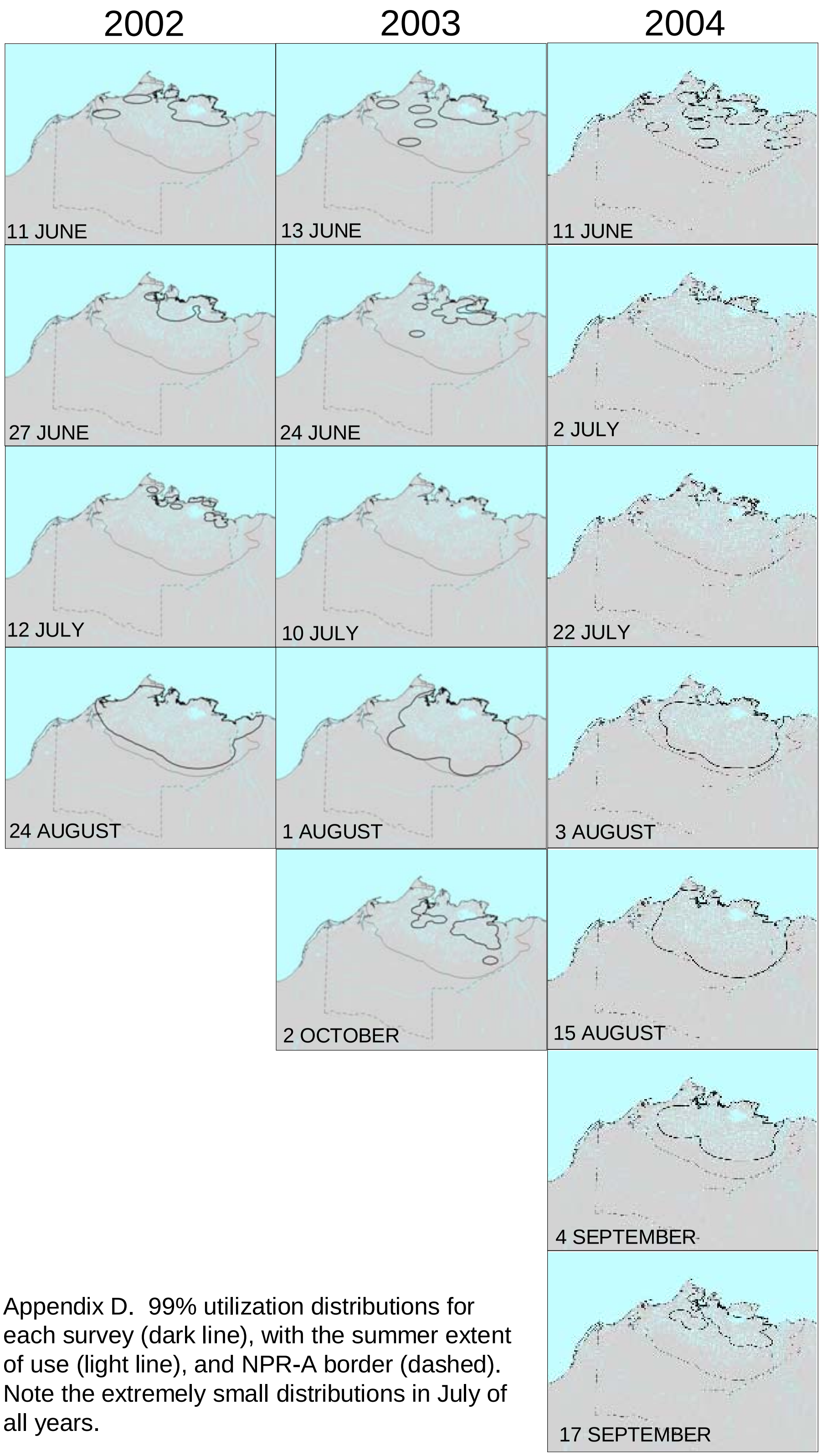
APPENDIX C-1. 2002 NDVI Rate. Estimated values were interpolated from images made up from multiple satellite passes composited at 10 day intervals, and represent the estimated daily change in NDVI since the previous image. Note that the colors on the legend do not represent equal intervals.



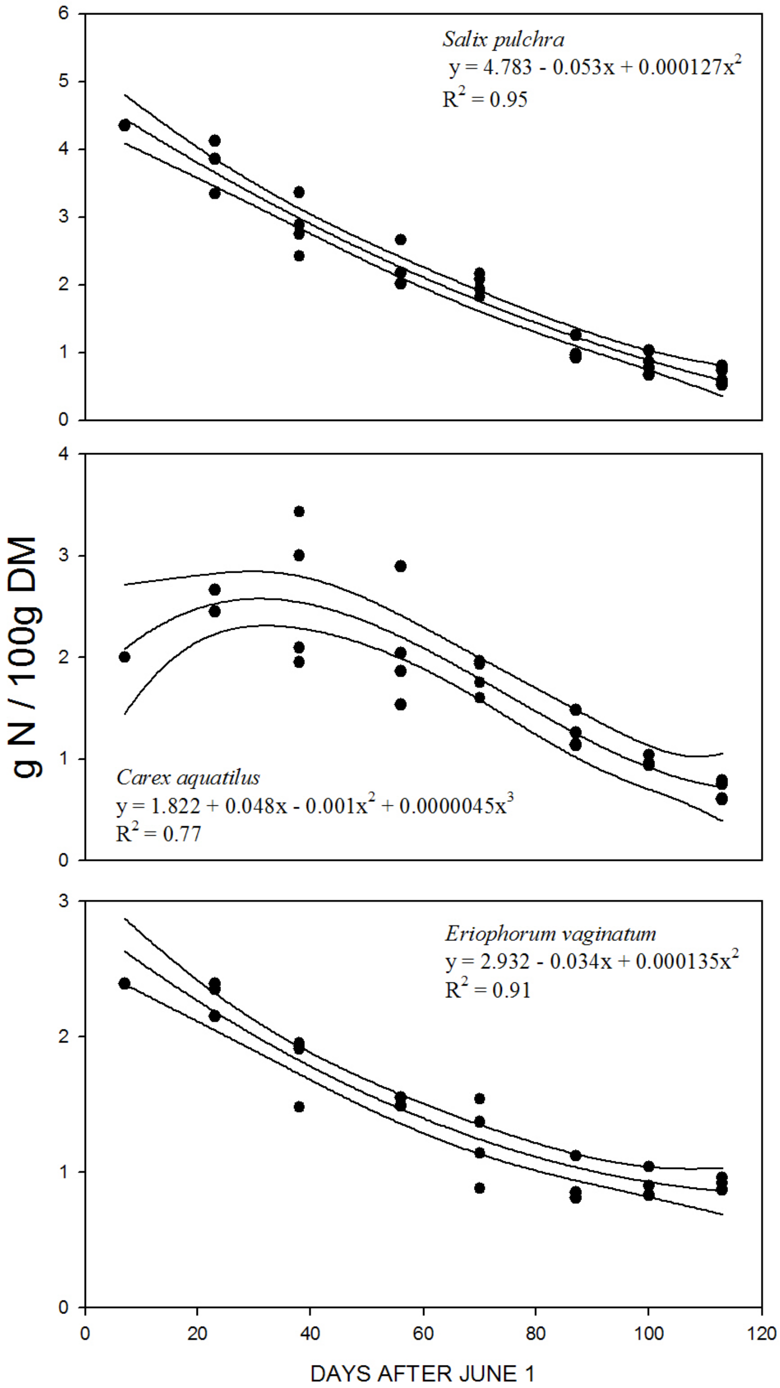
APPENDIX C-2. 2003 NDVI Rate. Estimated values were interpolated from images made up from multiple satellite passes composited at 10 day intervals, and represent the estimated daily change in NDVI since the previous image. Note that the colors on the legend do not represent equal intervals.



APPENDIX C-3. 2004 NDVI Rate. Estimated values were interpolated from images made up from multiple satellite passes composited at 10 day intervals, and represent the estimated daily change in NDVI since the previous image. Note that the colors on the legend do not represent equal intervals.



Appendix D. 99% utilization distributions for each survey (dark line), with the summer extent of use (light line), and NPR-A border (dashed). Note the extremely small distributions in July of all years.



Appendix E. Seasonal patterns in nitrogen content in selected caribou forages; 95% confidence intervals indicated. Original data from Whitten and Cameron (1980). These patterns, along with stable nitrogen contents estimates from other literature sources, were used to estimate dietary nitrogen content from mixed diets estimated through fecal microhistology.

Appendix F. Diet composition, corrected for digestibility (Appendix F, Table 2), and estimates of dietary nitrogen per 100g dry matter for samples collected on the summer range of the Teshekpuk Caribou Herd. Estimates of dietary nitrogen are calculated by weighting the dietary abundance of a plant group by its phenologically appropriate nitrogen content (Appendix F, Table 3).

Table 1. Corrected diet composition and estimated dietary nitrogen concentration.

Sampling Date	Pooling Period[1]	Moss %	Lichen %	Evergreen Shrub %	Deciduous Shrub %	Graminoid %	Forb %	gN / 100g DM
10 Apr 2004 (Atqasuk)	Spring	51.4	28.6	8.0	2.0	10.1	0.0	0.70
10 Apr 2004 (ANWR)[2]	Spring	39.3	27.9	4.5	4.2	24.2	0.0	0.71
6 Jun 2003	Calving	20.6	49.1	0.0	4.6	20.5	5.3	1.03
7 Jun 2003	Calving	22.1	55.2	0.0	4.3	13.3	5.1	0.91
8 Jun 2003	Calving	19.1	45.9	0.0	6.9	21.5	6.7	1.10
11 Jun 2004	Post Calving	21.9	53.1	0.0	2.9	20.4	1.8	0.95
13 Jun 2002	Post Calving	11.7	44.8	0.0	4.8	33.7	5.0	1.26
14 Jun 2002	Post Calving	18.7	43.3	2.3	5.5	27.9	2.3	1.19
15 Jun 2002	Post Calving	11.6	28.5	2.0	7.5	46.0	4.4	1.57
16 Jun 2002	Post Calving	14.8	39.6	4.5	8.5	30.6	2.0	1.32
17 Jun 2002	Post Calving	10.4	40.2	2.1	5.9	40.0	1.4	1.37
26 Jun 2003	Movement	17.0	24.9	9.4	4.4	30.0	14.3	1.79
2 Jul 2002	Early Summer	6.8	1.1	21.3	28.7	21.4	20.6	2.19
4 Jul 2004	Early Summer	3.2	11.2	7.5	4.4	73.3	0.4	2.04
11 Jul 2003	Early Summer	5.0	5.5	4.8	2.9	81.3	0.4	2.03
23 Jul 2004	Mid-Summer	3.8	10.5	6.0	4.1	72.9	2.7	1.77
25 Jul 2002	Mid-Summer	0.5	3.1	7.2	2.2	82.1	4.9	1.91
2 Aug 2003	Mid-Summer	3.5	36.1	17.7	17.6	17.2	8.0	1.26
5 Aug 2004	Mid-Summer	15.2	30.5	16.5	17.3	10.5	10.1	1.23

Appendix F (Continued). Diet composition, corrected for digestibility (Appendix F, Table 2), and estimates of dietary nitrogen per 100g dry matter for samples collected on the summer range of the Teshekpuk Caribou Herd. Estimates of dietary nitrogen are calculated by weighting the dietary abundance of a plant group by its phenologically appropriate nitrogen content (Appendix F, Table 3).

Table 1 (Continued). Corrected diet composition and estimated dietary nitrogen concentration.

15Aug 2004	Late Summer	14.2	60.4	8.1	7.8	6.1	3.4	0.76
9 Sep 2002	Fall Migration	8.6	62.6	0.2	3.7	16.3	8.6	0.79

Table 2. Digestibility and Fragmentation Correction Factors (Russell et al. 1993)

Plant Group	Winter	Spring	Summer
Moss =	1.17x	1.00x	1.00x
Lichen =	1.66x	12.44 +(1.33x)	3.8x
Evergreen Shrub =	0.38x	1.91 + (0.34x)	2.03x
Deciduous Shrub =	1.00x	-1.20 + (0.49x)	0.48x
Graminoid =	1.05x	1.00x	1.60x
Forb =	100- Sum Other Groups	100- Sum Other Groups	100- Sum Other Groups

Table 3. Nitrogen content of various plant groups. Some plant groups have relatively constant nitrogen contents, while other have strong phenological patterns.

Plant Group	Nitrogen Content
Moss	0.85gN/100gDM(constant)
Lichen	0.40gN/100gDM(constant)
Evergreen Shrub	0.9gN/100gDM(constant)
Deciduous Shrub	Formula(Appendix E)
Graminoid	Formula (Appendix E)
Forb	3.25gN/100gDM (constant)

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[1] Pooling periods from Russell et al. (1993), used for comparison with Porcupine Caribou Herd data.

[2] Outside of the described summer range; we collected samples from a group of TCH caribou wintering in the northern portion of the Arctic National Wildlife Refuge.

Appendix G. Fecal nitrogen (N), neutral detergent fiber nitrogen (NDF–N), endogenous nitrogen (EN), fiber proportions and diet constituents of 21 fecal samples collect on the Teshekpuk Caribou Herd summer range. Nitrogen data is reported on an organic matter (OM) basis due to the varying influence of soil adhered to fecal material. Diet data is reported as a percentage of the total number of identifiable fragments observed during microhistological analysis.

Sampling Date	Pooling Date	gFN /100gOM	gNDF–N /100gOM	gEN /100gOM	NDF %	ADF %	moss %	lichen %	evergreen shrub %	deciduous shrub %	graminoid %	forb %
10 Apr 2004 (Atqasuk)	11 Apr	1.65	0.72	0.93	65.4	39.5	37.8	18.9	12.3	5.1	25.9	0.0
10 Apr 2004 (ANWR)[1]	11Apr	1.76	0.83	0.92	64.7	38.7	52.3	20.5	6.3	9.5	11.4	0.0
6 Jun 2003	11 Jun	1.87	1.22	0.64	72.3	42.1	24.2	34.1	10.2	1.2	24.1	6.2
7 Jun 2003	11 Jun	1.86	1.20	0.66	71.4	39.5	26.6	40.7	9.5	0.9	16.1	6.2
8 Jun 2003	11 Jun	1.92	1.21	0.71	69.2	38.1	21.2	29.0	16.8	1.6	23.9	7.5
11 Jun 2004	11 Jun	1.84	0.66	1.18	63.1	29.3	27.0	39.9	4.8	0.9	25.2	2.2
13 Jun 2002	21 Jun	2.24	1.63	0.60	74.5	43.0	13.6	29.7	10.9	0.9	39.1	5.8
14 Jun 2002	21 Jun	2.27	1.55	0.72	73.1	43.6	20.6	26.4	12.3	7.5	30.7	2.5
15 Jun 2002	21 Jun	2.49	1.75	0.75	72.3	47.5	11.9	12.7	17.0	6.6	47.3	4.5
16 Jun 2002	21 Jun	2.55	1.80	0.75	72.8	47.4	15.0	20.7	19.6	11.8	30.9	2.0
17 Jun 2002	21 Jun	2.77	2.05	0.71	76.7	51.7	11.3	23.5	13.1	7.2	43.4	1.5
26 Jun 2003	1 Jul	2.72	1.93	0.79	71.2	50.4	17.0	9.4	7.5	21.7	30.1	14.3

[1] Fecal samples were collected in two geographically distinct areas of the winter range, near Atqasuk and on the north side of the Arctic National Wildlife Refuge (ANWR)

Appendix G (Continued). Fecal nitrogen (N), neutral detergent fiber nitrogen (NDF-N), endogenous nitrogen (EN), fiber proportions and diet constituents of 21 fecal samples collect on the Teshekpuk Caribou Herd summer range. Nitrogen data is reported on an organic matter (OM) basis due to the varying influence of soil adhered to fecal material. Diet data is reported as a percentage of the total number of identifiable fragments observed during microhistological analysis.

Sampling Date	Pooling Date	gFN /100gOM	gNDF–N /100gOM	gEN /100gOM	NDF %	ADF %	moss %	lichen %	evergreen shrub %	deciduous shrub %	graminoid %	forb %
2 Jul 2002	11 Jul	3.55	2.34	1.20	64.4	50.8	6.8	0.3	14.2	44.6	13.4	20.7
4 Jul 2004	11 Jul	3.55	2.37	1.18	70.8	54.9	4.5	4.2	3.1	22.4	65.3	0.5
11 Jul 2003	11 Jul	3.29	2.57	0.72	78.7	58.9	7.3	2.1	2.1	14.4	73.5	0.6
23 Jul 2004	1 Aug	3.17	1.86	1.31	63.5	47.2	5.5	4.0	2.9	18.0	65.7	3.9
25 Jul 2002	1 Aug	3.41	2.57	0.84	77.0	57.4	0.7	1.1	1.5	20.4	69.7	6.6
2 Aug 2003	11 Aug	3.74	2.53	1.21	68.4	52.7	4.5	12.3	11.2	47.8	13.9	10.3
5 Aug 2004	11 Aug	3.74	2.27	1.47	64.1	51.7	18.4	9.7	10.3	41.5	7.9	12.2
15Aug 2004	21 Aug	3.12	1.95	1.18	64.2	46.3	24.5	27.4	6.6	29.0	6.6	5.9
9 Sep 2002	11 Sep	1.91	1.18	0.74	65.9	34.1	18.6	35.8	4.0	0.7	22.2	18.7