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AGAINST THE SPRING WAVE:
UNGULATE MIGRATION PHENOLOGY IN A CHANGING ARCTIC

A Thesis in
Ecology
by
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Abstract

Migration is a widespread adaptation to seasonal variability in resource distribution and availability. Through effects on resource phenology, composition, and abundance, climate change may disrupt the predictability of seasonal patterns of resource availability, with consequences for migratory timing and resource tracking by consumers. These impacts may be especially pronounced in the Arctic, where recent climatic warming is in excess of twice the global average. For long-distance migrants, the Green Wave Hypothesis has served as a broadly applicable framework for understanding the role of spatially propagating resource phenology in spring migration departure from wintering grounds, migratory rate, and timing of arrival at summer breeding grounds. While avian migrants and subarctic ungulates have been the focus of previous research on this topic, little focus has been placed to date on the impacts of climate change on ungulate migration phenology in the Arctic. Here, I use a framework based on the predictions of the Green Wave Hypothesis to investigate climatic effects on caribou (*Rangifer tarandus*) migration in a low-Arctic system. I begin in Chapter 2 by quantifying the spring wave in vegetation green-up phenology, finding that an unexpected trend in its direction of propagation is related to a suite of abiotic conditions including temperature, precipitation, and sea ice extent. Chapter 3 is an examination of caribou migration phenology, and the results presented therein suggest that the timing of arrival on the calving grounds is entrained by photoperiod, but is influenced secondarily by population density and timing of green-up.

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LIST OF ABBREVIATIONS

DMI – Danish Meteorological Institute

EVI – Enhanced Vegetation Index

FMH – Forage Maturation Hypothesis

GWI – Green Wave Index

IRG – Instantaneous Rate of Green-up

NDVI – Normalized Difference Vegetation Index

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“Where am I?” said Billy Pilgrim.

“Trapped in another blob of amber, Mr. Pilgrim. We are where we have to be just now – three hundred million miles from Earth, bound for a time warp which will get us to Tralfamadore in hours rather than centuries.”

“How – how did I get here?”

“It would take another Earthling to explain it to you. Earthlings are the great explainers, explaining why this event is structured as it is, telling how other events may be achieved or avoided. I am a Tralfamadorian, seeing all time as you might see a stretch of the Rocky Mountains. All time is all time. It does not change. It does not lend itself to warnings or explanations. It simply is. Take it moment by moment, and you will find that we are all, as I’ve said before, bugs in amber.”

Kurt Vonnegut, *Slaughterhouse Five*

Chapter 1 – Ecological Foundations of Climate Change and Migration Phenology

Background

Migration arises from a seasonal repositioning of a population's distribution, and is found in a diversity of taxa and environments (Milner-Gulland et al., 2011). Because the inherent value of migration arises from the ability of organisms to track seasonal changes in their environment (Cresswell et al., 2011), it is a trait potentially subject to the far reaching effects of climate change (Bowlin et al., 2010; Seebacher and Post, 2015). By altering patterns of both resource availability and quality in time and space, climate change may consequently reduce the efficacy of migration as a resource tracking strategy. The benefits of migration lie in a spatiotemporal synchrony between migrant populations and resource availability, which can be an important driver of reproductive capacity and population size (Both et al., 2009). Overwhelmingly, the focus of studies of potential consequences of climate change for migratory dynamics in time and space have focused on birds (Both et al., 2009; Butler, 2003; Cotton, 2003; Gordo, 2007), while comparatively little is known about the implications of climate change for migration in large herbivores, a taxon represented by many long-distance migrants.

Resource availability influences the spatial distribution of herbivores (Hebblewhite et al., 2008), leading to differential use of forage sites based on, and potentially migration between, areas of differing resource quality. Ideally, herbivores track resource phenology in such a way that their population distribution is synchronous with optimal resources in multiple spatial and temporal scales. However, photoperiod as a cue for migratory onset in many long-distance migrants (Gwinner, 1996; McCormick et al., 1998), and relates to other life history events in Arctic vertebrates (van Oort et al., 2005). Despite close examination of the drivers and effects of reproductive phenological mismatches (e.g., Miller-Rushing et al., 2010) investigations of

mismatches in migration phenology have been largely limited to avian models (e.g., Both et al., 2009).

Caribou and wild reindeer (both *Rangifer tarandus*) are well known for their long-distance seasonal migrations between winter ranges rich in lichens, for which caribou are dietary specialists, and summer ranges with a greater diversity of forbs, graminoids, and dwarf shrubs (Skogland, 1985). The annual timing of arrival on summer ranges by caribou generally coincides with the onset of the plant growing season, which represents a resource pulse at a time of high resource demand when calves are born (Gunn and Skogland, 1997; Skogland, 1989). However, spatial and temporal patterns of plant phenology, especially emergence timing, are being altered dramatically by climate change in all of Earth's major biomes, particularly in the Arctic (Parmesan, 2006; Post et al., 2009, 2013; Root et al., 2003; Walther et al., 2002). The extent to which the timing of caribou migration, and most importantly timing of arrival on summer calving grounds, may or may not respond to climate change driven shifts in plant phenology is currently unknown, and constitutes the over-arching focus of this thesis. As many migratory ungulates maximize access to easily digested, high quality forage by utilizing seasonal ranges (Albon and Langvatn, 1992), climate-driven changes in plant phenology may be associated with changes migratory timing, or consequences for a lack thereof. The research described herein will examine the influence of the timing and spatial variability in resource availability on migration phenology of a migratory arctic vertebrate, caribou.

Methodology

The migratory Kangerlussuaq-Sisimiut caribou herd of West Greenland has been the focus of ongoing research on foraging ecology, behavior, reproductive phenology, and

population dynamics (Bøving and Post, 1997; Kerby and Post, 2013; Post and Forchhammer, 2002, 2008; Post and Stenseth, 1999; Post et al., 2003, 2008; Thing, 1984). Our study site is located between the village of Kangerlussuaq and Russell Glacier (60.1°N, 50.3°W), at the eastern extent of the herd's summer calving range.

Caribou in this region winter near the west coast of Greenland along the Davis Strait (Thing, 1984), where temperatures are warmer than nearer the inland ice sheet (Figure 1.1). Typically, inland temperatures exceed those along the coast seasonally beginning some time in late April, coincidental with caribou migratory timing. Caribou departure from the coastal winter grounds occurs around April 26-May 21, and arrival at the summer calving grounds occurs May 22-May 28; although recently, considerable variation in this timing has been observed from year to year. The migration period is typically 2-3 weeks and covers approximately 70 km (Thing, 1984) (Figure 1.2). Calving is largely confined to a core area near the center of the summer grounds. While their winter diet is lichen-rich, caribou transition to a forb-, shrub-, and graminoid-dominated diet in the summer months.

Despite considerable knowledge of the temporal aspects of this herd's reproductive phenology, little is known of the implications of spatial variability in the region's onset of spring, or vegetative growth. This work addresses the importance of a spatial context in studies of long-distance migratory populations by examining resource phenology from a sub-continental perspective. An applicable framework for such an investigation is the Green Wave Hypothesis, a perspective originally proposed for avian studies by Drent et al. in 1978 (Drent et al., 1978). The Green Wave Hypothesis in its original form held that birds migrate along a spatiotemporal flush of resource availability, but its use now extends to ungulate migrations as well (Bischof et al., 2012). As the caribou of the Kangerlussuaq-Sisimiut herd live in a predator-free environment, a

unique opportunity to explore the relationship between migratory animals and the resources along their migratory passageway exists in southwest Greenland.

The foundational assumption of the Green Wave Hypothesis is that the timing of peak resource availability progresses through space; this evolution is what propels herbivore populations during spring migrations (van der Graaf, 2006). Few detailed explorations of this assumption exist, primarily owing to the obvious logistical constraints of studying a population's entire migratory passage (Hebblewhite et al., 2008). This limitation can be overcome by analysis of remotely sensed reflectance satellite data, and such an approach constitutes the second chapter of this thesis. Many landscape-level phenological analyses compare random points between ranges or stopover points (e.g., Hird and McDermid, 2009; Sawyer and Kauffman, 2011), but fail to capture the spatially explicit pattern of the green wave phenomenon. Rather than comprising simply a series of ranges or spatially segregated points, I consider the green wave to be a surface of time, in which relief is symbolic of variation in the spatial onset of spring, projected across the full extent of a population's migratory corridor.

NASA's Moderate Resolution Imaging Spectroradiometer (MODIS) is a satellite-mounted multispectral sensor capable of recording surface reflectance data at resolutions as fine as 250m. The Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) are both effective satellite-derived proxies of spatial and temporal patterns in resource phenology (Zhang et al., 2003). While Landsat offers NDVI data at finer resolutions, the data is rendered ineffective in many timeframes by the influence of cloud cover, and is not available at the temporal frequency of MODIS. As neither form of satellite-derived vegetation phenology has the ability to differentiate between different vegetation types, this work relies on NDVI time series derived from the MODIS sensor. Annual time series of NDVI can be interpreted in a

phenological sense, articulated as the Green Wave Index (GWI) or Instantaneous Rate of Green-up (IRG). I demonstrate in Chapter 2 that across the range of the Kangerlussuaq-Sisimiut caribou herd, a green wave exists, and manifests variably across years. The relative timing of spring at each end of the migration route relates to local weather conditions, and the direction of the green wave as a whole depends upon the degree of synchrony exhibited by the departure and destination ranges.

In Chapter 3, I explore how interannual variability in the manifestation of spring at multiple scales relates to patterns in caribou arrival timing. Because of pan-Arctic declines in caribou populations (Bastille-Rousseau et al., 2013; McLoughlin et al., 2003; Post and Klein, 1999; Vors and Boyce, 2009), a statistical migratory signal could be relatively weak at present. Population size can have a significant impact on phenological measurements like first arrival dates (Miller-Rushing et al., 2008), potentially influencing conclusions drawn from long-term phenological datasets (Figure 1.3). The herbivore count data used in this investigation accordingly focuses on a more robust measure of arrival, the timing of peak density on the core calving range (Edwards and Richardson, 2004).

As I demonstrate in Chapter 3, a recent increase in interannual variation in arrival timing in this population coincides with a decline in population size and a shift in the onset of vegetation phenology at broad scales. However, across the duration of this study, no trend was detected in migration phenology. I conclude therefore that caribou migration is ultimately a photoperiod-entrained behavior, and arrival timing depends on a combination of proximate biotic factors including population density and broad-scale vegetation phenology. This work has revealed the importance of a broad-scale perspective in analyses of migration, in both a spatial and temporal context. Future efforts should take a finer approach by combining GPS-collar

movement data with satellite-derived vegetation phenology in order to explore the conditions organisms experience across the duration of their route, but should continue to take into account the full extent of the migratory corridor and maximize the potential of long-term datasets.

Figures

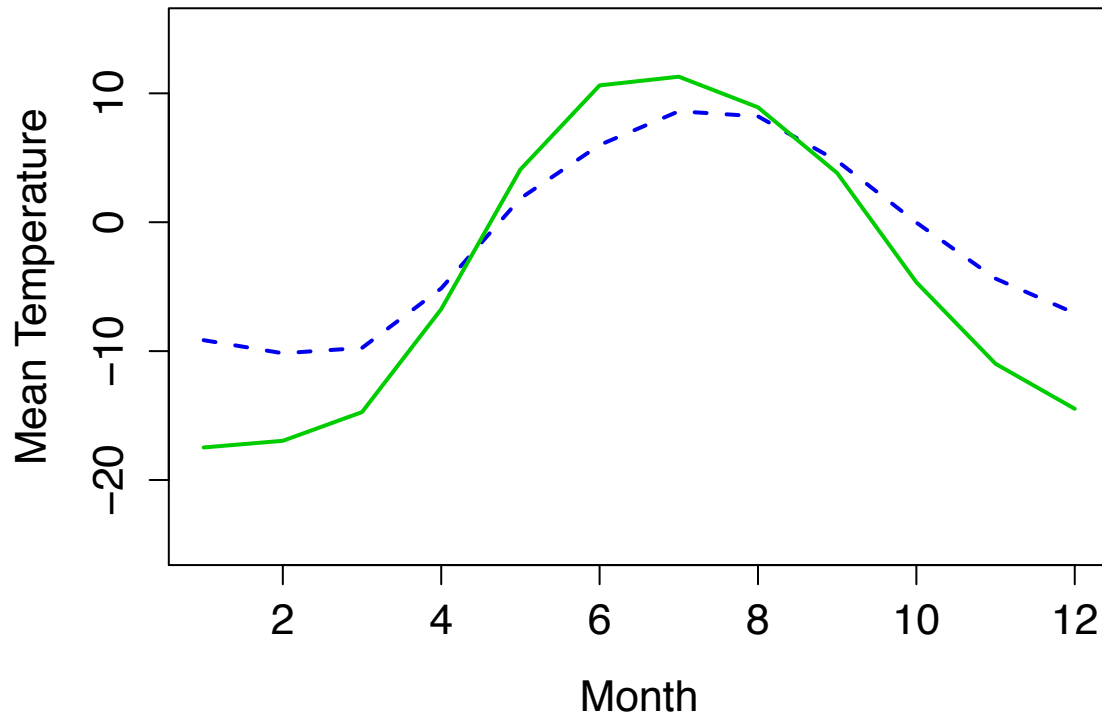


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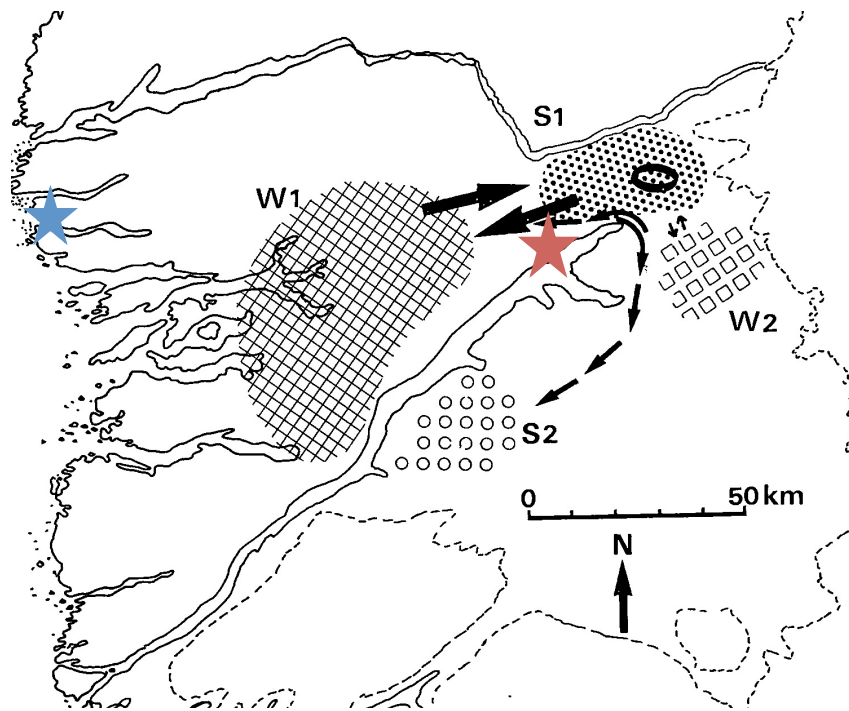


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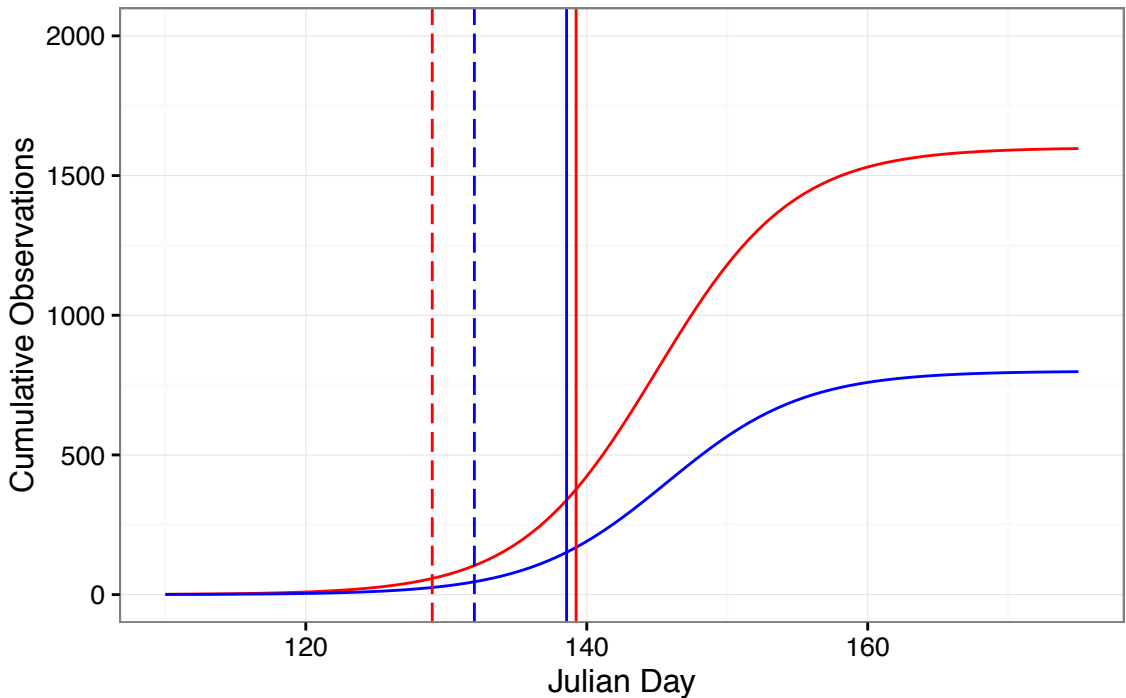


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Chapter 2 – Against the wave: when a migrant’s spring range phenology varies with warming

Introduction

Migration is a taxonomically widespread life history strategy in species inhabiting seasonal environments (Milner-Gulland et al., 2011), and one that is potentially subject to complex dynamical alteration by climate change (Bowlin et al., 2010; Seebacher and Post, 2015). The adaptive value of migration relates to the benefits that accrue to the individual organism in terms of spatial and temporal tracking of large-scale variation in resource availability and quality (Cresswell et al., 2011). Among ruminants, a taxonomic group in which seasonal migration and partial migration are widespread (McNaughton, 1985; Soest, 1994; Sinclair and Norton-Griffiths, 1995), this leads to a spatial and temporal partitioning of landscape utilization (Hebblewhite et al., 2008). Ideally, spatially and temporally synchronous patterns of variation in resource availability and herbivore distribution facilitate optimal use of a variable resource landscape on multiple scales. However, in many long-distance migrants representing numerous clades, the onset of migration is driven by a photoperiod cue (Gwinner, 1996; McCormick et al., 1998). In contrast, the timing of availability of forage resources for such species, including plants for migratory mammals and invertebrates for migratory birds, is cued by temperature. Hence, the dual challenge of timing migration toward spring breeding grounds according to photoperiodic cues on departure ranges, and synchronizing arrival timing on destination ranges where resources are cued by local temperature, may be vulnerable to mismatch under climate change (Visser, 2008; Visser and Both, 2005).

Consequences of temporal mismatches in reproductive phenology of migratory organisms have been extensively documented (Miller-Rushing et al., 2010). One approach to investigations of mismatch in migration phenology is the Green Wave hypothesis, which posits

that individuals of herbivorous species undergoing seasonal migration follow a spatiotemporal flush of greenness as spring plant growth commences and progresses across a landscape (Drent et al., 1978). Migrating along a green wave has obvious and well-documented benefits (Bischof et al., 2012; Visser et al., 2011), but is only possible in instances where a continuous flush of resource quality and availability exists, and unfolds in a predictable manner across the landscape. Interannual variation in the timing of onset and in the rate and directionality of propagation across the landscape of spring plant growth may pose challenges to optimal migratory timing for two reasons. First, while photoperiod, which cues departure timing in long-distance migratory herbivores such as caribou (*Rangifer tarandus*), is generally predictive of the seasonality of resource availability, it may not be predictive of high-frequency variation in resource timing on the destination range where offspring production occurs. In this case, static or generally fixed migratory timing would therefore not coincide with a variable resource pulse that is driven by variation in local abiotic conditions such as temperature and precipitation from year to year. Second, and relatedly, interannual variability in the directional aspect of a green wave, i.e., the direction or vector along which it propagates from the point or locale of onset, could induce both variation in the timing of green-up in the departure range as well as unpredictable timing of resource availability on the destination range, in addition to variation in inter-range phenology encountered along the migratory route.

Traditionally the Green Wave hypothesis has been used to explain avian migration, but it is increasingly being investigated as a driver of terrestrial herbivore migration as well (Bischof et al., 2012; van der Graaf, 2006; Lendrum et al., 2014; Najafabadi et al., 2015). Here, we extend such investigations to a large mammalian herbivore notorious for undertaking long-distance seasonal migrations, caribou. The migratory Kangerlussuaq-Sisimiut caribou herd of West

Greenland has been the focus of ongoing research on foraging ecology, behavior, reproductive phenology, and population dynamics (Kerby and Post, 2013; Post, 1995; Post and Forchhammer, 2002; Thing, 1984). The population is bounded on all sides by the Davis Strait, Nordre Isortoq, the inland ice sheet, and the Sukkertoppen ice cap (Thing, 1984) (Figure 2.S1). Despite considerable knowledge of the temporal aspects of this herd's reproductive phenology, little focus to date has been placed on implications of variation in seasonal range phenology for migratory arrival timing in this herd. Here we explore the relationship between climatic and terrain features on regional and range-specific plant phenology across the home range of the Kangerlussuaq-Sisimiut caribou herd.

Methods

Study Site

We analyzed interannual variation in spring green-up timing on seasonal ranges utilized by the Kangerlussuaq-Sisimiut caribou herd in southwest Greenland. This herd undergoes a partial seasonal migration between a winter range located near the village of Sisimiut along the west coast of Greenland and a summer range located approximately 150 km inland toward the village of Kangerlussuaq, near Greenland's Inland Ice (Thing, 1984) (Figure 2.S1). Because we are concerned here with spring green-up phenology in relation to the seasonal timing of migration by caribou toward the summer range where offspring production occurs, we hereinafter refer to the winter range as the departure range and the summer range as the destination range. The region is bounded on all sides by geographic barriers. Seasonal ranges were described by Thing (Thing, 1984); this map was manually georeferenced with a 30m ASTER Digital Elevation Model (DEM) in ArcGIS in UTM zone 22N (Land Processes

Distributed Active Archive Center (LP DAAC)). Across the entirety of the region, mean elevation is 513.8 m above sea level. The centroid of the core destination range lies 71.3 km east of that of the core departure range. Elevation in the destination range is on average 36 meters lower than that in the departure range.

Vegetation Index

The National Aeronautics and Space Administration (NASA) Terra satellite is equipped with a Moderate Resolution Imaging Spectroradiometer (MODIS), which collects twice-daily reflectance data at spatial resolutions as fine as 250m. Vegetation Index (VI) datasets are available in 16-day intervals, where the highest detected per-pixel VI is reported with an associated date of VI composite. We used the 1 km MOD13A2 Normalized Difference Vegetation Index (NDVI) dataset (Land Processes Distributed Active Archive Center (LP DAAC), 2000) for this investigation in order to minimize the potential for noise produced in finer resolution datasets to interfere with analyses. NDVI was selected for vegetation monitoring because it is less sensitive to errors caused by topographic variation (Matsushita et al., 2007), and does not rely on an interpolated 500 nm blue band, as the Enhanced Vegetation Index (EVI) does. NDVI data for southwest Greenland from 2001 through and including 2015 were downloaded and mosaicked using {pyModis}, a Python-based package built to provide a streamlined environment for MODIS data manipulation. The NDVI dataset was screened for and cleaned of poor-quality pixels, defined as Good Data pixels of only the Highest Quality (Didan, 2015). Final data preparation followed the methodology proposed by Beck (Beck et al., 2006), according to which winter NDVI is held constant and negative outliers are removed to correct for common false-low index values.

Plant Phenology

Annual regional NDVI time cubes were created by taking the pixel specific composite date for each observation, and arranging the data into a multidimensional array (e.g., Figure 2.S2). An annual double-logistic function (Beck et al., 2006) was fit to NDVI values in each pixel and interpolated for all days of the year using R package {phenex}. The Green Wave Index (GWI) is calculated by normalizing the interpolated NDVI value at time = t using Equation 1:

$$GWI = \frac{NDVI_t - NDVI_{min}}{NDVI_{max} - NDVI_{min}}$$

The Julian date of 50% GWI was extracted from the double logistic function to produce annual “green wave maps,” in which pixels with comparatively large digital numbers represent MODIS pixels featuring delayed 50% GWI. We used the annual date of 50% GWI to index the annual midpoint of spring green-up on each range. This index is intended as a large-scale, satellite-derived analog to the annual date of 50% green-up monitored by observation of species-specific emergence timing on multi-annual small-scale ($1m^2$) plots on the destination range. Data from these plots have demonstrated a rate of advance in the onset of the date of 50% green-up on the destination range of 16 days per decade since 2002 (Kerby & Post 2013; Post et al., in review).

We used kernel density estimation to explore the timing of the maximum onset of spring both regionally and within each range. This was accomplished by applying Gaussian kernels to the full distribution of pixel-specific Julian dates of 50% GWI, and extracting the timing of the global maxima of that function, thereby determining the date at which the largest portion of a given range experienced peak rate of greening. Density estimates were calculated with the R base package {stats} (R Core Team, 2014).

Green Wave Directional Analysis

The annual green wave maps were analyzed for directional phenological progression by calculating aspect using the 8-neighbor rule. Because areas with delayed satellite-derived vegetation phenology feature larger digital numbers, a Green Wave progresses from low to high values and therefore moves in the opposite direction of aspect. Annual range-wide aspect was produced by averaging all of the aspect values across the entirety of the region. Circular statistical analyses were performed with the R package {circular} using the methodology described by Zar (2010).

To explore geographic phenological trends, annual total range phenology was compared with the decimal degree latitude and longitude coordinates of each raster pixel. The effect of elevation on phenology was explored by resampling a 30m ASTER DEM to fit the resolution of the NDVI dataset using bilinear interpolation, and evaluating with a general linear model.

Herbivore Phenology

To estimate arrival timing by migratory caribou on the destination range, caribou counts were conducted on a near-daily basis between early spring (late April to early May) and early summer (mid to late June) from a set of fixed observation points located within the destination range (Post, 2013). Caribou counts were conducted from 2002-2015. The annual observation period encompassed the herd's arrival and calving period. Migratory arrival phenology was indexed as the annual date of maximum observed caribou density.

Local Weather Conditions

Monthly temperature and precipitation records were acquired from the Danish Meteorological Institute (<http://www.dmi.dk>) for both Kangerlussuaq and Sisimiut (2001-2015). These villages possess the nearest weather stations to the herd's primary destination (~10 km

from centroid) and departure (~60 km from centroid) ranges, respectively. Mean temperature and precipitation during the months preceding and during typical landscape green-up (April-June) were considered as potential predictors in this analysis.

Sea Ice

Sea ice conditions have far-reaching impacts on arctic ecosystems (Post et al., 2013), and previous evidence indicates that plant phenological dynamics at the study site may be associated with interannual dynamics of Arctic-Wide Sea Ice Extent (ASIE) (Kerby and Post, 2013; Post et al., 2016). Monthly ASIE was compiled from the National Snow and Ice Data Center (http://nsidc.org/data/seaice_index/archives.html). These data are available in tabular format for Arctic-wide sea ice extent and area, and are expressed in millions of square kilometers. ASIE data derive from 25x25km grid cells produced by passive microwave radiation sensors on the Nimbus-7 SMMR and DMSP SSM/I-SSMIS, and are calculated by summing the total area of grid cells covered by at least 15% ice concentration (Stroeve et al., 2012). Monthly anomalies were calculated by subtracting the annual month-specific ASIE from the 1978-2015 average month-specific ASIE.

Results

Range-Specific Phenology

Range-specific and regional phenology displayed considerable interannual variability across the duration of this study, but the mean date of 50% GWI was strongly correlated between the destination and departure ranges (see Figure 2.1 caption). Despite this correlation, the relative timing of spring green-up between ranges varied among years, with some years featuring earlier spring onset on the departure range others featuring earlier spring onset on the destination

range (Figure 2.2). The magnitude of the disparity between each range's green-up timing was significantly related to vegetation phenology across the total range (Figure 2.S3; $R^2 = 0.27$, $n = 15$, $F(1, 13) = 5.03$, $p = 0.04$). This suggests that the departure and destination ranges underwent nearly simultaneous green-up in years featuring earlier springs.

Local May temperature (i.e., the month preceding peak green-up) was the strongest predictor of green-up timing on both destination and departure ranges ($R^2 = 0.67$ and 0.69 respectively, $n = 15$, $F(1, 13) = 26.92$ and 29.51 respectively, $p < 0.001$). Mean local temperature in April was significantly related to green-up phenology in the departure range ($R^2 = 0.38$, $n = 15$, $F(1, 13) = 8.1$, $p = 0.01$) but not the destination range ($R^2 = 0.07$, $n = 15$, $F(1, 13) = 0.98$, $p = 0.34$), and mean local June temperature was not related to green-up timing in either range ($p > 0.05$). Departure range phenology was more closely associated with local temperature than was that of the destination range (Figure 2.3). Monthly precipitation was not significantly related to range phenology in any of the months as a standalone predictor, but in the destination range there was a nearly significant interaction between mean May temperature and May precipitation (total model: $R^2 = 0.75$, $n = 15$, $F(3, 11) = 10.8$, $p = 0.001$). A January + June ASIE model explained 40% of the variation in destination range phenology (total model: $R^2 = 0.41$, $n = 15$, $F(2, 12) = 4.19$, $p = 0.04$), but failed to predict departure range phenology ($p > 0.05$). Average May temperature was significantly related to the same ASIE model in Kangerlussuaq, but not Sisimiut ($R^2 = 0.49$ and 0.34 , $n = 15$, $F(2, 12) = 5.66$ and 3.07 , $p = 0.02$ and 0.08 , respectively).

Green Wave Phenology

Across the total range, the date of 50% GWI advanced by an average of 1.56 ± 0.04 days per 100 m elevation decrease. This trend was significant within all years ($p < 0.05$ in all years).

Across all years, the timing of green-up advanced by an average of 0.27 ± 0.03 days per 1° decrease in slope. The relationship between slope and green-up phenology was significant in all years. When terrain aspect was categorized into the 8 principal cardinal directions, an ANOVA revealed a significant association between aspect and green-up phenology in all years except 2010.

Over the period investigated, mean aspect of the Green Wave was generally northeasterly (Table 2.S1). That is, green-up progressed from northeast to southwest. Of the years in which Rayleigh tests were significant for aspect, the mean angle for green wave aspect was between -2 degrees and 72 degrees. The difference between destination and departure range phenology was significantly related to the green wave aspect, where years featuring a more westward-advancing wave experienced a comparatively later green-up in the departure range (Figure 2.4; $R^2 = 0.41$, $n = 15$, $F(1, 13) = 8.86$, $p = 0.01$).

Herbivore phenology

Over the period 2002-2015, caribou reached peak presence (i.e., maximum density) on the destination range on average on Julian Day 163 ± 7.4 (Figure 2.5). While inter-annual variability in observed peak arrival phenology increased over the course of the investigation, 33% of the variation in caribou arrival phenology could be explained by satellite-derived green-up phenology on the destination range ($R^2 = 0.33$, $n = 14$, $F(1, 12) = 5.98$, $p = 0.03$). Despite the positive correlation between caribou arrival phenology and destination range green-up phenology, caribou arrival lagged behind green-up by approximately two weeks on average; however, this lag was nearly 20 days in years with the earliest green-up and was as low as 10 days in years with the latest green-up (Figure 2.6). Caribou arrival timing did not correlate with

green-up phenology on the departure range or green-up phenology across the entire range ($p > 0.05$ in both cases).

Discussion

A variety of environmental factors appear to play a role in the variation of landscape-scale phenology in highly seasonal Arctic environments. Low elevation is associated with advanced phenology, so it is unsurprising that the caribou herd's lower-elevation destination range typically undergoes an earlier spring green-up. Though our data show a 1-day advance in plant phenology for every 3.62° increase in slope, it should be noted that terrain data were resampled in a resolution that may preclude meaningful analysis of some topographic influences on landscape phenology. While NDVI and terrain data were analyzed using 1 km pixels, it is likely that topographic features at much finer scales play significant roles in seasonal plant development. This limitation of satellite-derived vegetation data demonstrates the increasing need for data collection at multiple scales in ecological studies.

Regional phenology in 2013 exhibited numerous inconsistencies with trends that overwhelmingly applied in these analyses. During that year, the destination range featured a comparatively delayed period of peak green-up, and the influence of terrain characteristics such as slope and aspect were masked by some other driver of plant phenology, such as snowmelt phenology or atypical ablation events. The year 2013 also featured the least westward green wave progression and one of the latest herbivore arrival records in this dataset. While the mean May temperature in Sisimiut that year was relatively cold, Kangerlussuaq experienced its coldest May over the duration of this study (DMI, unpublished data).

Previous work provided mixed evidence of a role of local monthly temperature in plot-level green-up phenology (Kerby and Post, 2013; Post et al., 2016), however this work corroborates the utility of local temperature as a predictor of remotely-sensed, broad-scale vegetation phenology. Interannual variation in Arctic-wide sea ice extent is strongly associated with multi-annual phenological dynamics at the plot-scale at this study site (Kerby and Post, 2013), but this is the first study to our knowledge to find a significant relationship between satellite-derived vegetation phenology and sea ice extent, adding to other evidence indicating the ecological importance of sea ice decline in the Arctic (Post et al., 2013).

Inconsistency in relative differences in range-specific green-up phenology documented here suggests that in this site a Green Wave materializes with varying interannual intensity. Previous work has shown that expanding phenological mismatches between seasonal ranges impedes optimal migration timing in long-distance migrants (Clausen and Clausen, 2013). Our results indicate arrival timing for a population of arctic ungulates relates, albeit somewhat weakly, to green-up phenology on the destination range (Figure 2.6). However, the cues that drive the initiation of departure from the winter range, as well as those that determine the rate of migration between seasonal ranges, remain unclear. The fact that the lag between arrival timing and green-up phenology on the destination range appears to increase with earlier green-up on the destination range deserves further attention. This pattern would seem to indicate an additional element of spatial mismatch for this caribou population, in accordance with earlier results (Post et al., 2008) that could be exacerbated by additional warming.

Here we have shown that caribou in the study population apparently migrate against the spatiotemporal gradient characterizing the flush of springtime resource availability across the landscape. Though the timing of maximum occurrence of herbivore density in the calving range

is related to vegetation green-up phenology on that range, the regional propagation of landscape phenology is counterintuitive given known seasonal herbivore distributions. The influence of local temperature on spatially relative landscape phenology may have changed recently in an evolutionary timescale, resulting in a novel environmental condition associated with a previously consistent migration. This population now exhibits highly variable, and possibly increasingly variable, timing in the occurrence of peak density on its summer calving range, a condition potentially explained by increased unpredictability in seasonal resource availability. Further work should explore the intra-annual dynamics of migrant arrival timing, and the influence of departure range conditions on arrival and reproduction. Though the full extent of mal-timed migration implications is still unclear, this work presents a step toward understanding the suite of environmental factors influencing migration and vegetation phenology in the context of a widely held migration hypothesis.

Figures

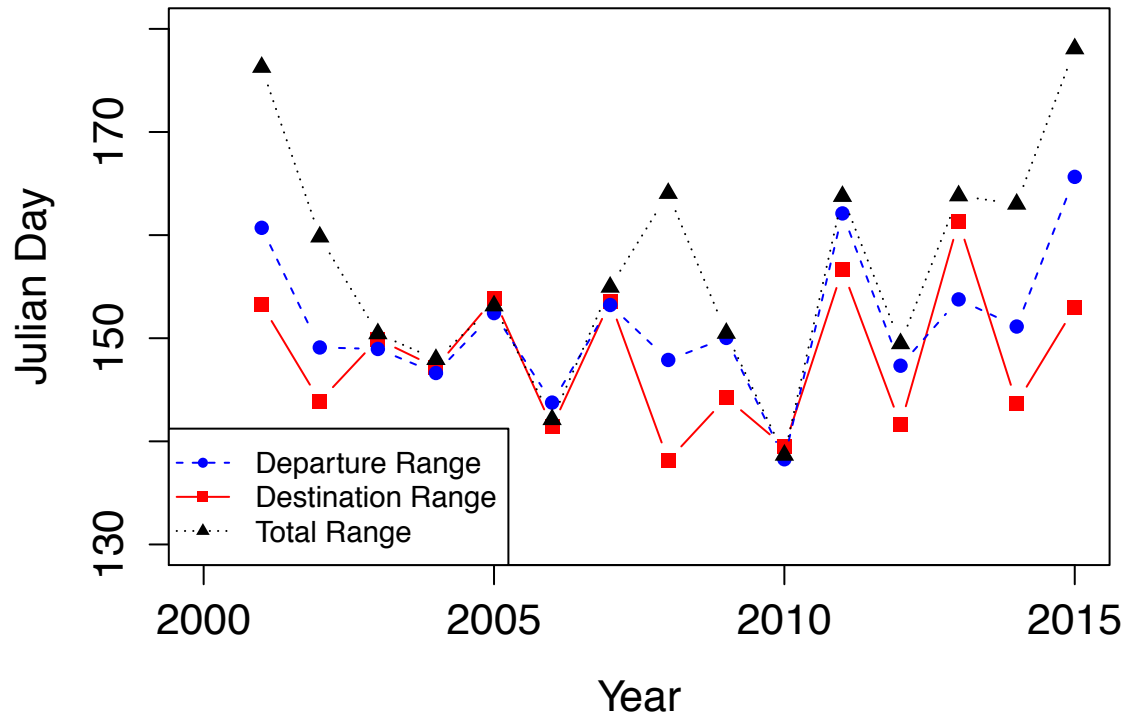


Figure 2.1. Satellite-derived phenology in destination and departure ranges, of the Kangerlussuaq-Sisimiut caribou herd, and across the region from 2001-2015. Pairwise inter-range correlations calculated using general linear models were: destination range:departure range ($r = 0.72$, $F_{1,13} = 13.84$, $p = 0.003$); destination range:region ($r = 0.49$, $F_{1,13} = 4.02$, $p = 0.07$); departure range:region ($r = 0.87$, $F_{1,13} = 39.42$, $p < 0.001$).

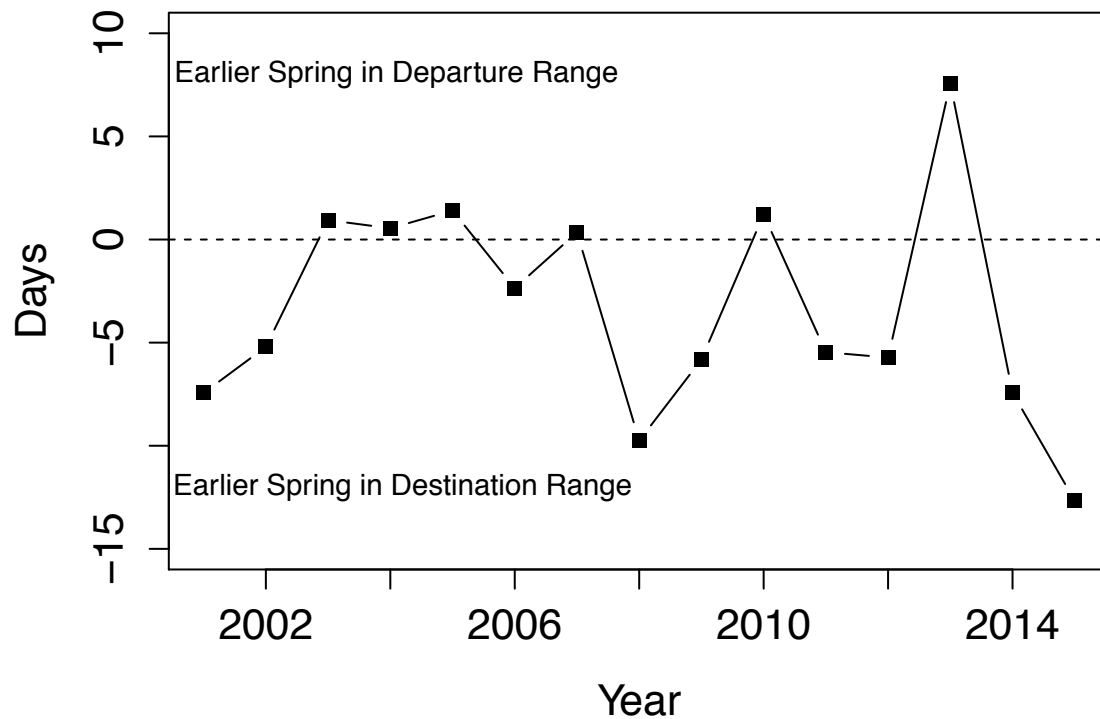


Figure 2.2. Difference in timing of spring onset on primary destination and departure ranges of Kangerlussuaq-Sisimiut caribou herd by year, 2001-2015. This difference is calculated as the (date of maximal destination range green-up) – (date of maximal departure range green-up) for each year in the analysis. Years with negative difference values feature comparatively earlier springs in the destination range, and years with positive differences feature earlier springs in the departure range. The difference in range phenology was significant to the $\alpha = 0.05$ level in all years (Welch 2-sample t-test).

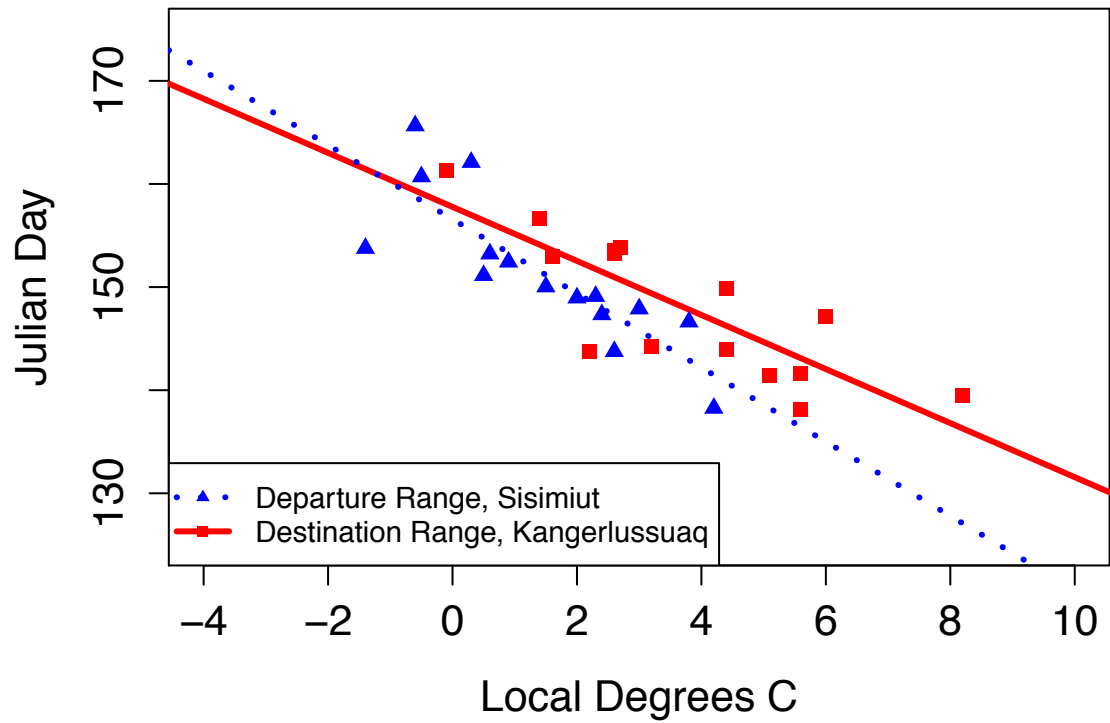


Figure 2.3. Departure range phenology (blue) and destination range phenology (red) in relation to May mean temperature in Sisimiut (departure range) and Kangerlussuaq (destination range), Greenland, 2001-2015.

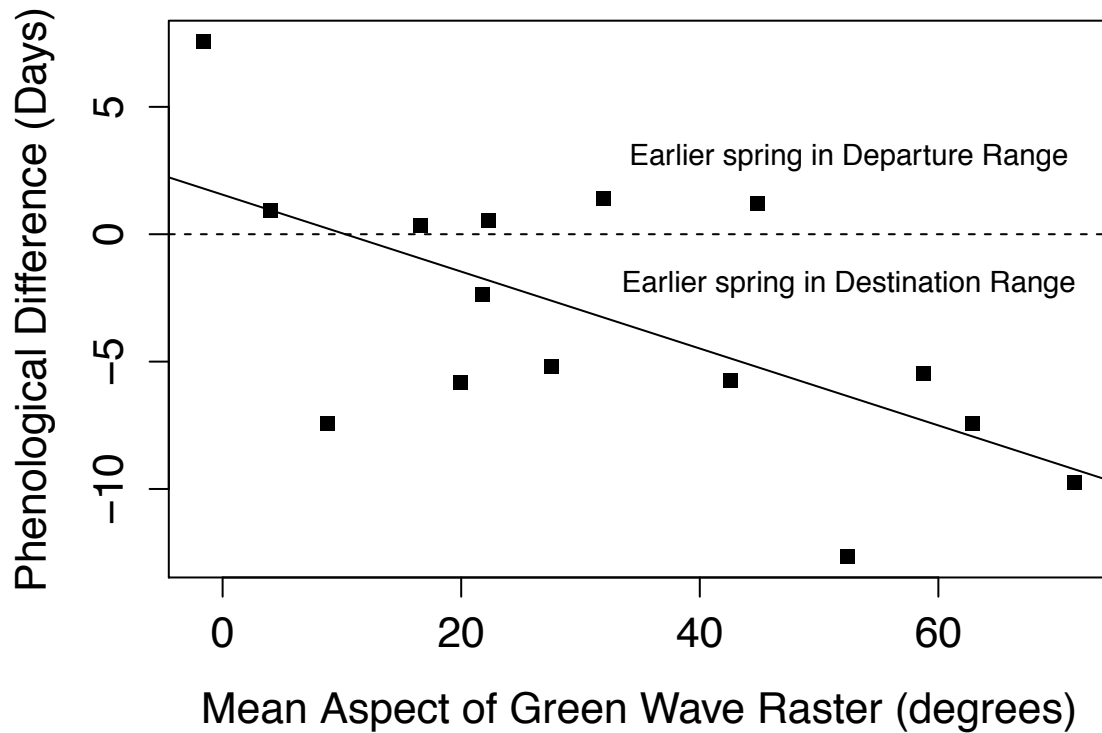


Figure 2.4. Difference in date of maximum occurrence of 50% GWI in primary seasonal ranges of Kangerlussuaq-Sisimiut caribou herd, vs. mean aspect of green wave surface, 2001-2015. 0° aspect indicates wave progresses south; 90° aspect indicates westward wave.

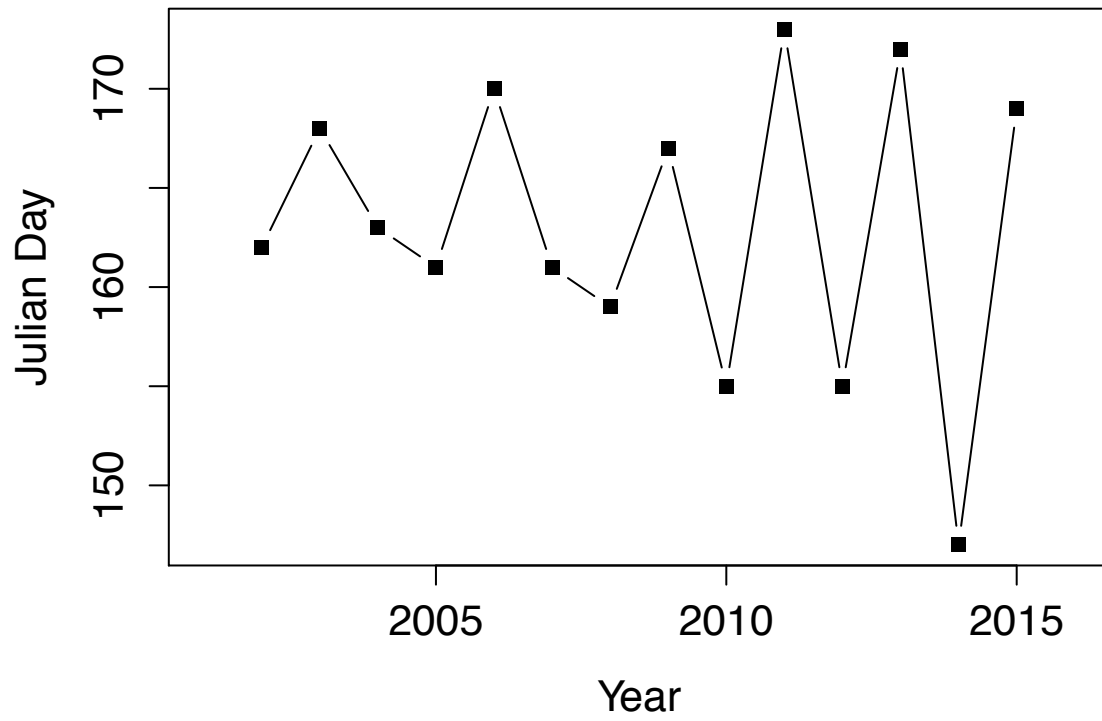


Figure 2.5. Date of maximum observed caribou density in the summer calving range near Kangerlussuaq, Greenland, 2002-2015.

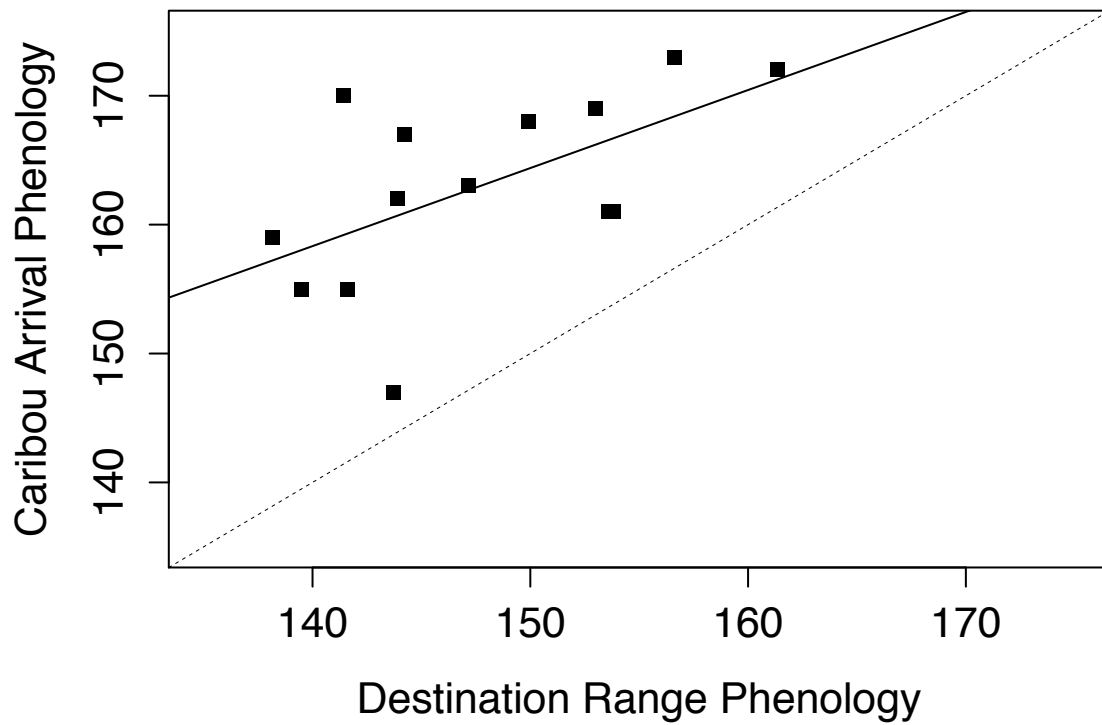


Figure 2.6. Caribou arrival phenology vs. destination range green-up phenology near Kangerlussuaq, Greenland, 2002-2015. Units are expressed in Julian Days.

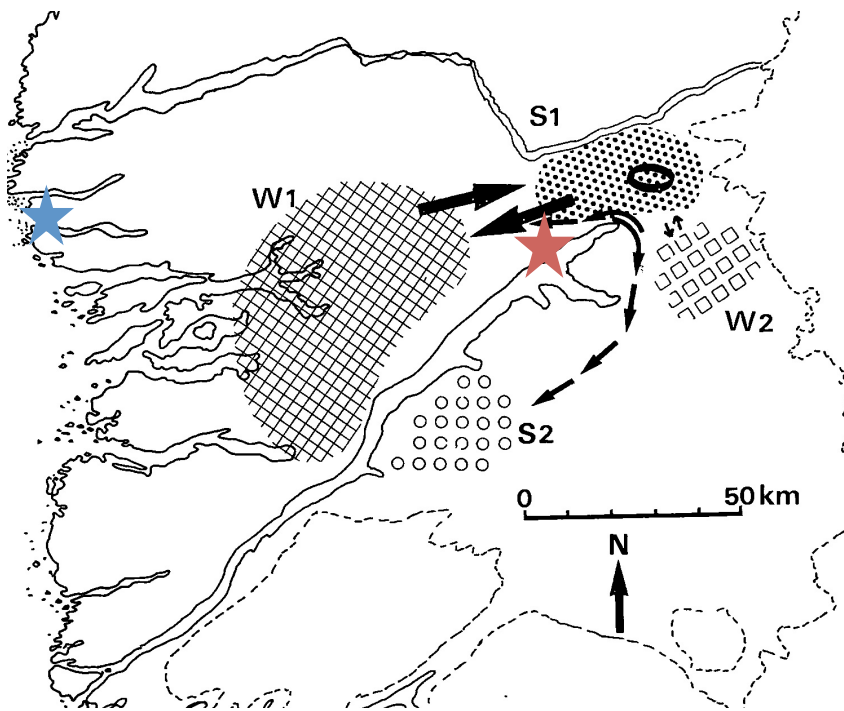


Figure 2.S1. Southwest Greenland map; bounded to west by Davis Strait, to east by Inland Ice Sheet, to north by Nordre Isortoq, and to south by Sukkertoppen Ice cap. Seasonal ranges of Kangerlussuaq-Sisimiut caribou herd indicated by S1, S2, W1, and W2, indicating the primary (1) and secondary (2) summer (S) and winter (W) ranges. Image reproduced from Thing (1984). Stars indicate nearby villages (red = Kangerlussuaq; blue = Sisimiut).

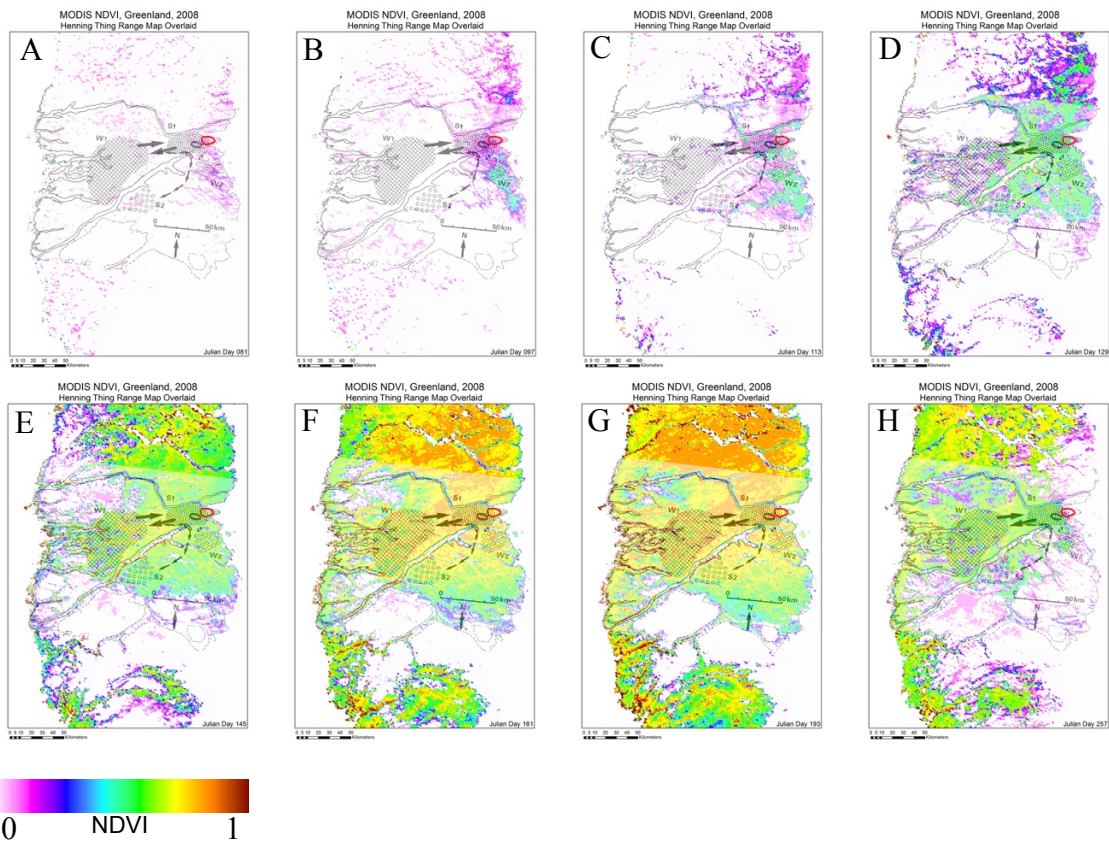


Figure 2.S2. Example annual time-series NDVI in southwest Greenland derived from MODIS 16-day composites, 2008. Imagery complete for spring green-up period (frames A-F); along with late summer (G) and early winter (H). A) Julian Day 081; B) Julian Day 097; C) Julian Day 113; D) Julian Day 129; E) Julian Day 145; F) Julian Day 161; G) Julian Day 193; H) Julian Day 257.

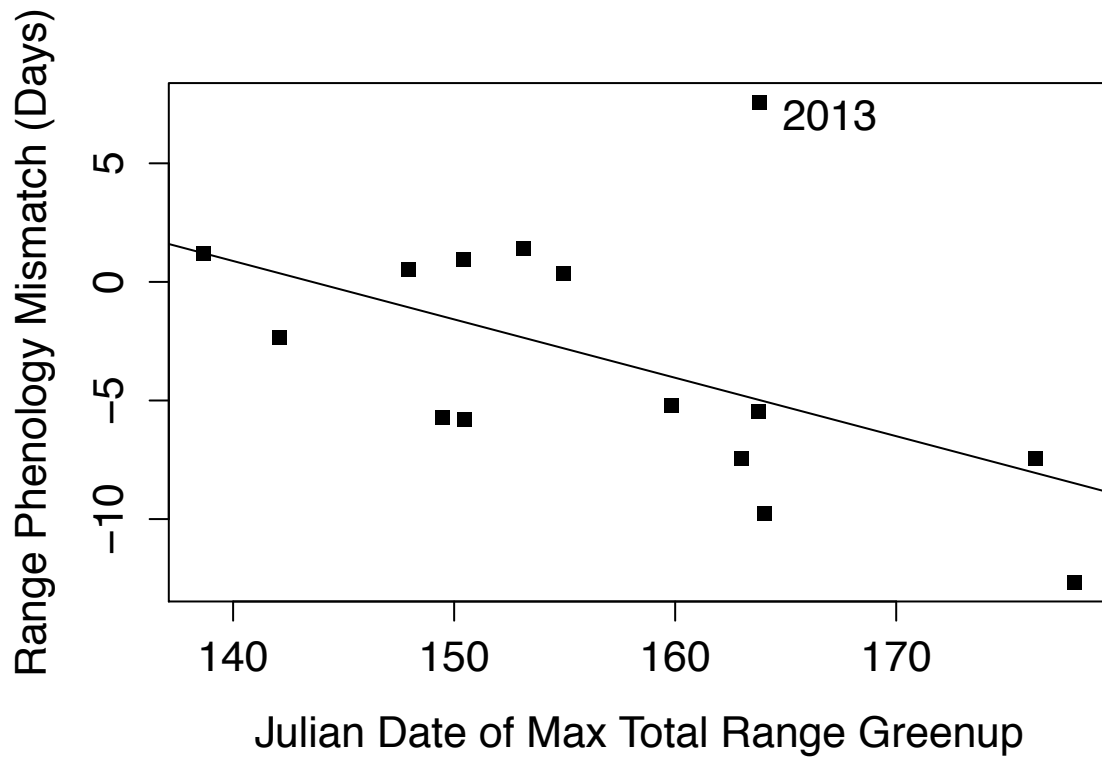


Figure 2.S3. Magnitude of difference in phenology between departure and destination ranges of the Kangerlussuaq-Sisimiut caribou herd, 2001-2015, related to the timing of regional green-up. Mismatch calculated by subtracting the date of maximum departure range green-up from the date of maximum destination range green-up.

Table 2.S1. Circular statistics for annual green wave aspect.

<u>Year</u>	<u>Mean Angle</u>	<u>Angular Deviation</u>	<u>Rayleigh's z</u>	<u>p-value</u>
2001	62.857	1.397	0.024	2.33E-05
2002	27.585	1.396	0.026	4.34E-06
2003	4.014	1.407	0.010	1.59E-01
2004	22.250	1.390	0.033	1.34E-09
2005	31.937	1.396	0.025	8.47E-06
2006	21.825	1.399	0.021	2.75E-04
2007	16.617	1.398	0.022	1.05E-04
2008	71.432	1.396	0.026	3.20E-06
2009	19.944	1.395	0.027	1.20E-06
2010	44.807	1.402	0.017	4.66E-03
2011	58.772	1.400	0.020	5.05E-04
2012	42.611	1.405	0.013	4.14E-02
2013	-1.590	1.397	0.024	2.59E-05
2014	8.761	1.393	0.030	3.67E-08
2015	52.421	1.396	0.026	2.91E-06

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Chapter 3 – Destabilization of migration phenology associated with a shift in resource phenology

Introduction

Patterns of plant phenology are driven in time and space by a suite of abiotic factors (Hwang et al., 2011; Parmesan, 2006; Walther et al., 2002). As the rate of climatic warming continues to increase, many areas of the globe are experiencing earlier springs and altered temporal relationships between species at adjacent trophic levels (“trophic mismatch”) (Both et al., 2009a; Burthe et al., 2012; Thackeray et al., 2010, 2016). The potential for differential rates of phenological advance between resource and consumer species is especially pronounced in the Polar Regions, where the timing of activity by primary producers is cued by photoperiod and temperature, while that of primary- and higher order consumers is constrained primarily by photoperiod (Moe et al., 2009; Moline et al., 2008; Post, 2016; Post and Forchhammer, 2008; Shultz et al., 2009).

For migratory organisms, shifting plant phenology may induce a modification of migratory timing (Visser and Both, 2005), but this response is made difficult for long-distance migrants because of unpredictable conditions in their destination range (Both et al., 2009b; Clausen and Clausen, 2013). In the Polar Regions, endogenous rhythms driven by photoperiod make adjusting to interannual variation in resource phenology difficult (van Oort et al., 2005). For caribou (*Rangifer tarandus*), recent advancements in resource phenology can result in an expanding trophic mismatch between reproductive timing and resource availability, leading to reduced calf production (Kerby and Post, 2013; Post and Forchhammer, 2008).

Previous investigations of factors influencing the timing of seasonal migrations in terrestrial herbivores indicate that, while reducing risk of predation on offspring may have been important in the evolution of migratory strategies (Sinclair, 1985), vegetation phenology may be

an important proximal driver of the timing of arrival by ungulates on reproductive ranges (Albon and Langvatn, 1992; Bartlam-Brooks et al., 2013; Bischof et al., 2012; Boyce, 1989; Hebblewhite et al., 2008; Maddock, 1984). Interannual variability in the onset of spring could therefore disrupt migratory timing in ungulates inhabiting seasonal environments, leading to an advance, delay, or destabilization of the timing of seasonal range arrival. While much has been done to explore the implications of climate change for reproductive phenology, few studies have attempted to explore the effect of the former on migratory timing in high-latitude ungulates (Pettorelli et al., 2005).

Here we explore the timing of spring arrival in a migratory caribou population in relation to factors preceding and during the herd's reproductive season. We propose four predictive scenarios aimed at disclosing the role of environmental cues influencing migratory arrival timing in caribou. These scenarios can be inferred by two possible changes in arrival timing along two axes (Box 3.1). First, if photoperiod is the main driver of migration phenology and other consistently variable factors influence interannual variability, we expect that arrival timing at the calving range, and interannual variation in arrival time, should remain constant from year to year. Second, if photoperiod is the main driver, but other dynamically variable factors influence interannual variability in migratory phenology, arrival timing should not undergo a multiannual trend but should undergo a change in variance. If, however, photoperiod is not the ultimate driver of migration phenology, two alternative scenarios exist. First, if arrival timing is influenced by biotic factors such as the timing of resource availability or density dependence, we may expect arrival timing to exhibit multiannual trends and changes in interannual variation in concert with such factors. This could appear in two ways – with increasing or decreasing variance over time – providing insight on the specific proximate driver. Because photoperiod is

a key driver in other facets of the annual life cycle in caribou, we consider a photoperiodic entrained migration to be the default null hypothesis. On the basis of an analysis of 14 years of data on arrival timing by caribou at their calving range, we find that no multiannual trend exists, but that increasing variation in arrival timing relates ostensibly to changes and fluctuation in population density and vegetation phenology on the destination range.

Methods

Study Site

This work was conducted in a low-Arctic study site in southwest Greenland, near the village of Kangerlussuaq. The site includes the core calving area of the migratory Kangerlussuaq-Sisimiut caribou herd, in the primary summer range (hereinafter, “destination range”). This herd undergoes an annual migration from its primary winter (“departure”) range near the coastal town of Sisimiut to the inland calving area in late May – early June. Calving occurs in early June (Kerby and Post, 2013; Post and Forchhammer, 2008; Post et al., 2003; Thing, 1984).

Herbivore Phenology

Near-daily herbivore counts were conducted in and around the core calving area from 2002 to 2015 (Post, 2013). Observers used a series of promontories from which animals could be enumerated by visual line of sight with the aid of binoculars and a 60x spotting scope without the possibility of disturbing individuals. Within years, observation effort was consistent from day to day. Because phenological measures such as first arrival date are sensitive to population size (Miller-Rushing et al., 2008; Tryjanowski and Sparks, 2001) and caribou populations are declining globally (Vors and Boyce, 2009), we instead chose to use the date of the maximum

daily count as an index of peak herbivore presence in the core calving area (Edwards and Richardson, 2004).

Plant Phenology

Twelve permanent plots (0.5 m²) arranged across elevations and aspects were used to monitor plant phenology with the same frequency and regularity as herbivore censusing. The daily number of species emergent at each plot was compared with the final plot-specific number of species emergent on Julian Day 174 to generate annual time series of plant emergence. This was then averaged across all plots and fit with a nonlinear regression model described elsewhere (Post and Klein, 1999; Post et al., 2003) to index the date of 50% community emergence.

To explore range-wide trends in plant phenology, a satellite-derived approach was used to examine vegetation patterns across the caribou herd's destination range as well as specifically encompassing the entire core calving area. NASA's MODIS Terra satellite reports Normalized Difference Vegetation Index (NDVI) data on 16-day intervals. A 50% Green Wave Index (GWI) was used to index remotely sensed phenology, as documented elsewhere (Beck et al., 2006; John and Post *in prep*). Satellite-derived phenology was analyzed for three separate datasets: To explore broad-scale trends in resource phenology, 1-km resolution 50% GWI was calculated for the departure and destination ranges (MOD13A2; Land Processes Distributed Active Archive Center (LP DAAC), 2000a). To explore an intermediate scale between the observational and 1-km satellite-derived datasets, 50% GWI was calculated for 250-m resolution NDVI in the core calving area (MOD13Q1; Land Processes Distributed Active Archive Center (LP DAAC), 2000b).

Trends in and associations among caribou arrival timing and biotic factors

To test for trends in caribou arrival timing and plant phenology on the calving range, we separately regressed our indices of each against "year". To test for changes in interannual variability in timing of caribou arrival and plant phenology on the calving range, we applied a Zivot-Andrews test of stationarity to each time series (Zivot and Andrews, 1992). We then tested for associations between caribou arrival timing and two biotic factors: plant phenology and caribou density, in two ways. First, we used simple linear regression to test for associations between caribou arrival timing and plant phenology and density. Phenology was included either as 50% GWI at 1km or 250m scales, or as 50% community-level emergence on observational plots. Caribou density was indexed as the maximum number of caribou observed each year on the calving range. Second, we applied a first-order autoregressive [AR(1)] model with caribou arrival timing as the dependent variable and annual dates of 50% GWI or community-level emergence, and caribou density, as predictor variables. We applied an AR(1) model to account for autocorrelation in the caribou arrival time series to avoid spurious detection of associations between arrival timing and predictor variables (Post et al., 2001). First-order, or lag-one, autocorrelation in phenology time series data may arise as a consequence of indirect influences of resource availability or density dependence on the timing of life history events (Post et al., 2001). Previous applications of this model framework have proven useful in disclosing the influences of such factors on both interannual variability and trends in arrival timing by migratory birds (e.g., Forchhammer et al., 2002). Hence, the combination of simple linear regression, which tests for individual and combined influences of resource phenology and density on caribou arrival timing, and autoregression, which tests for the influences of these factors after accounting for autocorrelation in arrival timing, represents a complementary

approach. If a significant predictor variable identified by simple linear regression does not remain significant in an autoregressive model, we may conclude that it contributed to autocorrelation in the dependent variable rather than to variation in it (Forchhammer et al., 2002; Post et al., 2001).

Results

The mean date of occurrence of peak caribou density (arrival timing) in the core calving area was June 11 \pm 7.42 days. Arrival timing in the core calving area did not advance significantly over the study period ($R^2 = 0.014$, $n = 14$, $F_{1,12} = 0.17$, $p = 0.69$), but did exhibit increasing interannual variability (Figure 3.1). The time series demonstrated significant lag-one negative autocorrelation (Figure 3.S1). Peak density on the destination range decreased significantly over the course of the study, from a maximum of 595 caribou in 2006 to a low of 93 in 2014 ($R^2 = 0.43$, $n = 14$, $F_{1,12} = 9.22$, $p = 0.01$).

The two indices of vegetation phenology on the calving range produced time series with differing trends (Figure 3.2). The long-term, plot-level observational dataset indicated an advance in the timing of 50% community emergence of -12.7 ± 3.4 days/decade over the study period ($R^2 = 0.54$, $n = 14$, $F_{1,12} = 13.98$, $p = 0.003$). Satellite-derived estimates of 50% GWI indicate, however, no significant trend for either the destination range as a whole or the core area of the destination range. However, the detrended observational time series correlated strongly with both detrended satellite-derived phenology time series (Figure 3.S2; observational:rangewide $R^2 = 0.48$, $n = 14$, $F_{1,12} = 11.21$, $p = 0.006$; observational:core area $R^2 = 0.42$, $n = 14$, $F_{1,12} = 8.79$, $p = 0.01$).

The timing of caribou arrival on the core calving range occurred significantly later than 50% emergence or green-up on the calving range. Caribou arrival occurred on average 15.3 ± 1.67 days after the maximum occurrence of range-wide 50% GWI (paired t-test; $t_{13} = 8.58$, $p < 0.001$), and 14.1 ± 2.22 days after plot-level 50% community emergence (paired t-test; $t_{13} = 5.95$, $p < 0.001$).

Simple linear regression analysis revealed that satellite-derived vegetation phenology in the destination range was a significant predictor of the timing of caribou arrival (Figure 3.3; $R^2 = 0.33$, $n = 14$, $F_{1,12} = 5.98$, $p = 0.03$), while finer-resolution remotely sensed phenology in the core area was not ($R^2 = 0.004$, $n = 14$, $F_{1,12} = 0.04$, $p = 0.85$). The annual date of plot-level 50% community-level emergence on the calving range based on long-term observational data was a similarly poor predictor of caribou arrival timing ($R^2 = 0.07$, $n = 14$, $F_{1,12} = 0.93$, $p = 0.35$). Likewise, satellite-derived vegetation phenology in the departure range was not related to timing of peak caribou density in the destination range ($R^2 = 0.20$, $n = 14$, $F_{1,12} = 2.94$, $p = 0.11$).

A simple linear regression model including broad-scale destination range phenology and caribou density revealed that both factors contributed significantly to variation in caribou arrival timing (total model: $R^2 = 0.55$, $n = 14$, $F_{2,11} = 6.70$, $p = 0.01$). Neither predictor was, however, significant in the same model with fine-scale phenology and density or with plot-level 50% community emergence and density ($p > 0.05$ in both cases). Density alone was not a significant predictor of arrival timing ($p > 0.05$). However, after accounting for significant first-order autocorrelation in caribou arrival timing through application of the AR(1) model, caribou arrival timing was significantly positively associated with density (AR(1): $t = -5.16$, $p < 0.001$; density: $t = 2.72$, $p = 0.02$; full model $R^2 = 0.77$), but not with phenology on the calving range using any metric of the timing of green-up ($p > 0.05$ in all cases).

Finally, a Zivot-Andrews test identified a potential structural break in the caribou arrival time series in 2010 ($t = -13.08$), indicating an increase in interannual variability in arrival timing from that year forward. The same test identified a potential change in stationarity of the range-wide NDVI time series beginning in the same year, notably identifying a significant change in the trend occurring in 2010 ($t = -10.28$).

Discussion

Migration facilitates the ability of individuals to capitalize on spatially variable resource availability, but its adaptive value depends upon the ability of the individual to synchronize their migration timing to coincide with the timing of resource availability on the destination range (Maddock, 1984). While previous work has demonstrated the nutritional and reproductive benefits of ungulate migrations (Albon and Langvatn, 1992; Bischof et al., 2012; White et al., 2014), few studies have attempted to quantify contributions of variation in resource phenology to both long-term trends and interannual variability in migratory arrival timing. Our results indicate that arrival timing on a calving range by caribou in this population has not undergone a trend over the past 14 years, suggesting that migration phenology in this instance is ultimately driven by photoperiod. The increase in interannual variability in arrival timing over this period, however, suggests that other factors may contribute proximally to variation from year-to-year in arrival timing. This result appears consistent with the prediction deriving from a scenario in which migration timing is cued by an interaction between photoperiod, which has not changed, and biotic factors that have changed over the course of the study.

Interestingly, our conclusions relating to the influence of biotic factors on arrival timing in this caribou population are strongly dependent on the method of analysis employed. For

instance, caribou arrival timing correlated fairly strongly with a broad-scale metric of phenology on the calving range. However, finer resolution satellite-derived and observational metrics of plant phenology were not predictive of caribou arrival timing. This might suggest that broad-scale patterns in resource availability are more important than fine-scale, local conditions for caribou migration phenology. Similarly, departure range phenology was not related to arrival timing, although this is not entirely unexpected given evidence that the caribou of this herd migrate against a green wave (John and Post, *in prep*). Peak caribou arrival occurred approximately 2 weeks after 50% GWI on the range, and in years with particularly early green-up, caribou arrival was as much as 3 weeks behind 50% GWI (John and Post, 2016 *in prep*).

After accounting for negative first-order autocorrelation in caribou arrival timing, however, no index of plant phenology on the calving range was predictive of caribou arrival. Instead, caribou density in the focal population emerged as the sole significant predictor of arrival timing. Though direct conclusions regarding density dependence in the timing of caribou arrival on the calving grounds cannot be drawn from our data, population density has been shown to play an important role in ungulate migration phenology at high latitudes (Hansen et al., 2010; Mysterud et al., 2011). Furthermore, density of caribou at the study site has declined markedly over the focal period, from a peak of nearly 600 animals in 2006 to approximately 100 in 2015 (Post, unpublished data). The positive association between caribou arrival timing and density on the calving range suggests earlier arrival in years of lower density and later arrival in years of higher density. This pattern is consistent with density-dependent competition for forage resources along the migratory route. Furthermore, that resource phenology was a significant predictor of caribou arrival timing in a simple linear model, but no longer remained significant after application of the AR(1) model, suggests that variation in resource phenology may be the

source of first-order autocorrelation in caribou arrival dates. Indeed, our time series of resource phenology indexed by range-wide 50% GWI displayed significant negative first-order autocorrelation (-0.57 ± 0.24 ; $p = 0.018$). The increasing variability in caribou arrival timing since 2010 may therefore be indicative of overcompensation by individuals in this population in attempting to adjust for interannual variation in plant phenology from one year to the next.

While a causal link between the coincidental change in broad-scale plant phenology and interannual variability in caribou arrival timing cannot be established from these analyses, our findings suggest the contribution of environmental predictability to migratory consistency warrants further investigation. While mixed evidence exists relating climatic predictability to breeding phenology (Gaillard, 2007; Loe et al., 2005), predictability of vegetative phenology has not been a focus in migration phenology literature. Our work indicates that environmental predictability could play a role in migration phenology. If unpredictable destination conditions drive a destabilization of herbivore phenology, the annual migration, and the benefits that accrue from it, could become diminished.

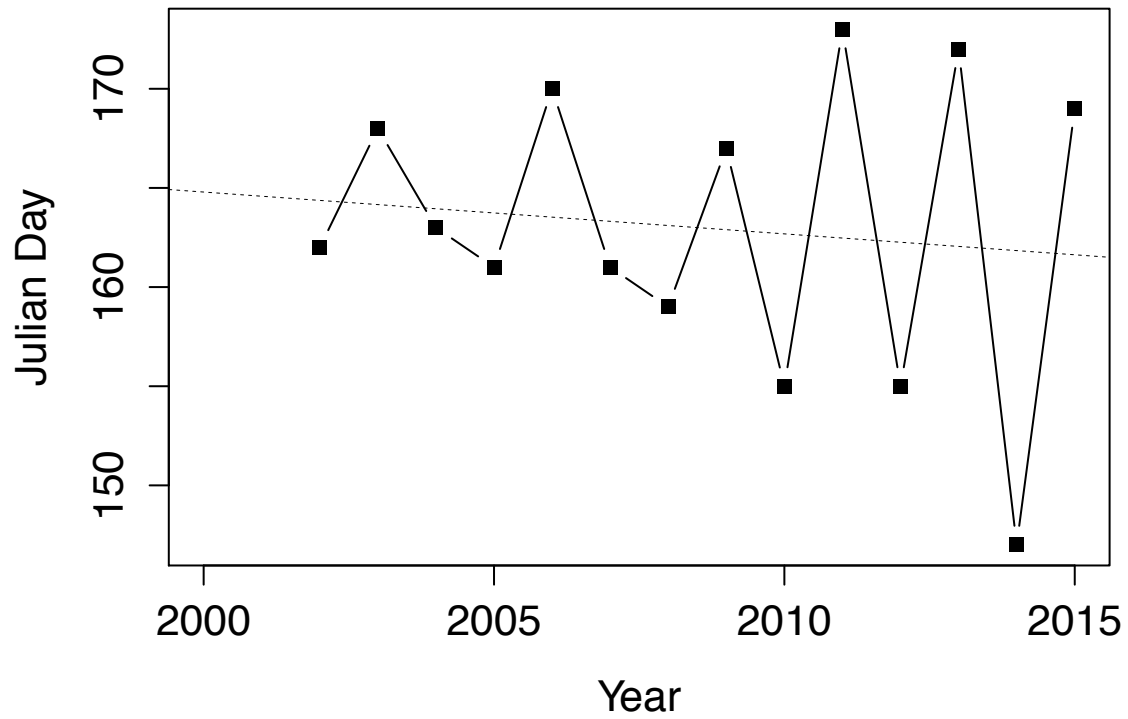


Figure 3.1. Annual dates of caribou arrival at the core calving (i.e., destination) range near Kangerlussuaq, Greenland, 2002-2015. Phillips-Perron Unit Root test and Augmented Dickey-Fuller test reject stationarity in the time series (PP: $DF = -12.75$, $p = 0.01$; ADF: $DF = -2.0$, $p = 0.57$).

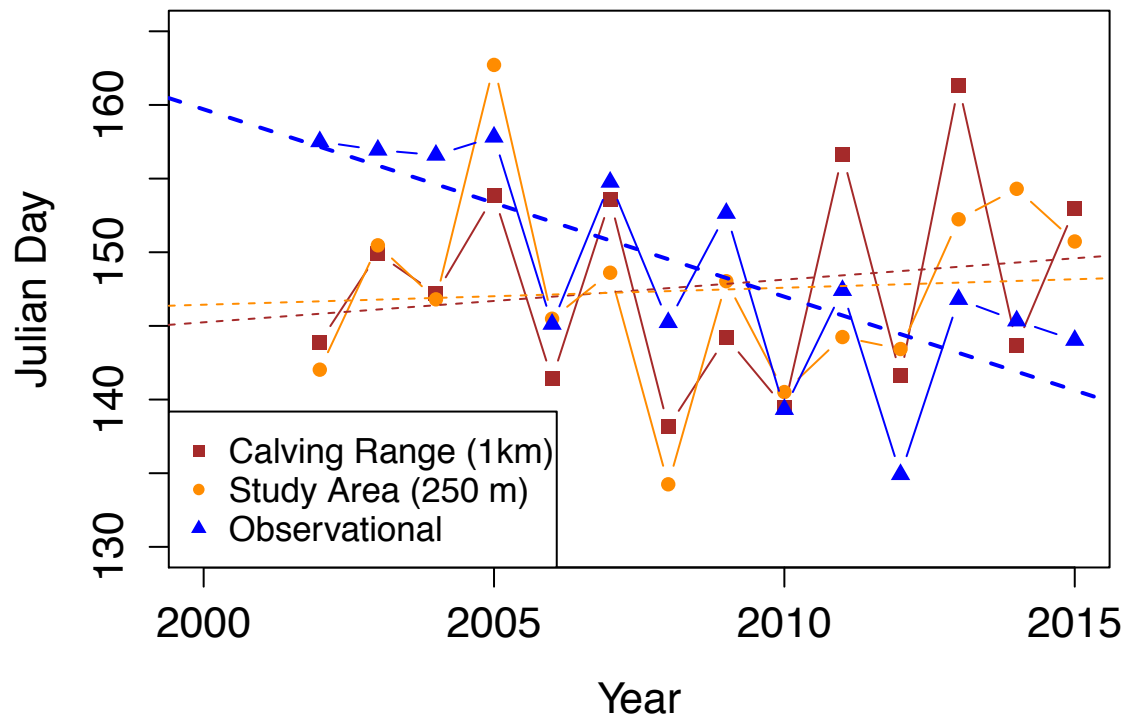


Figure 3.2. Dissimilar trends in observational versus satellite-derived vegetation phenology indices, 2002-2015. A significant trend was detected through time in the observational dataset ($R^2 = 0.54$, $n = 14$, $F_{1,12} = 13.98$, $p = 0.003$) but not in either satellite-derived dataset (Range-wide: $R^2 = 0.03$, $n = 14$, $F_{1,12} = 0.36$, $p = 0.56$; Local 250m: $R^2 = 0.005$, $n = 14$, $F_{1,12} = 0.06$, $p = 0.81$). Coarse and fine-scale satellite observations were highly correlated ($r = 0.59$, $n = 14$, $F_{1,12} = 6.53$, $p = 0.03$), but neither satellite-derived phenology metric correlated strongly with the observational phenology dataset (Range-wide:observational $r = 0.34$, $n = 14$, $F_{1,12} = 1.56$, $p = 0.24$; study area:observational $r = 0.39$, $n = 14$, $F_{1,12} = 2.14$, $p = 0.17$).

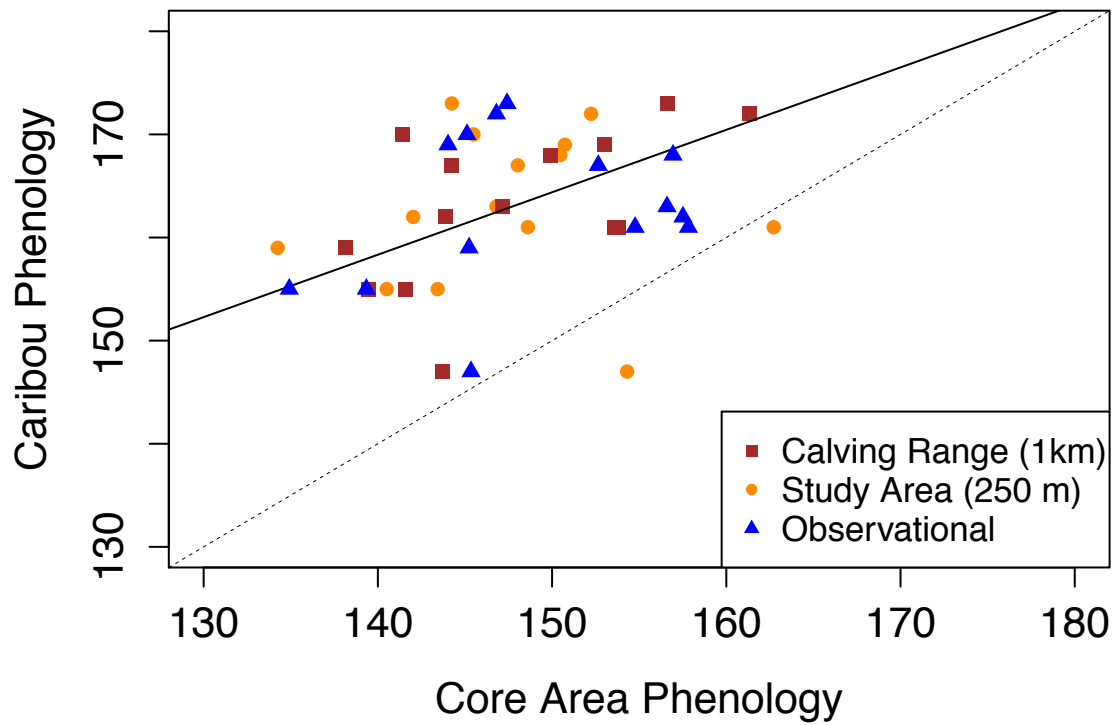
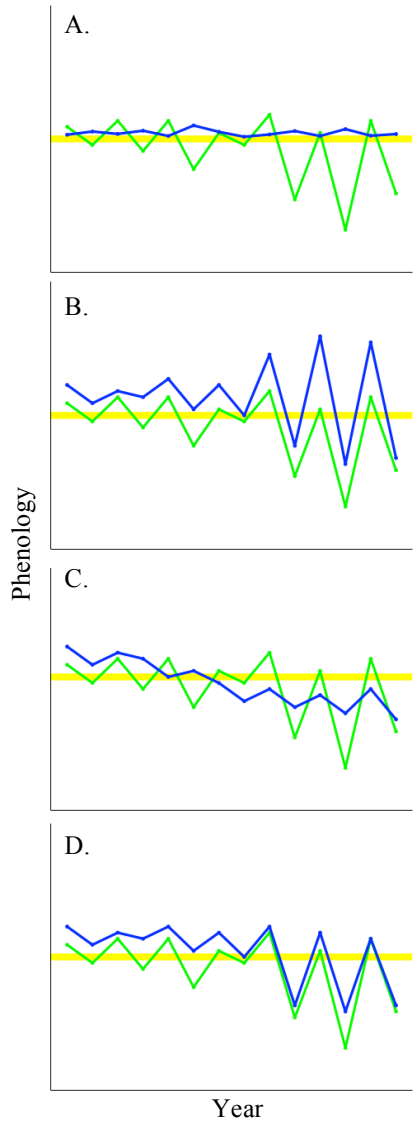


Figure 3.3. Timing of peak density of Kangerlussuaq-Sisimiut caribou herd in the core summer calving area from 2002 to 2015. Caribou arrival phenology relates to satellite-derived vegetation phenology of the destination range, but not that of the core calving area or that based on plot-level observations.



	Variance constant	Variance changes
No Trend	<p>A. Migration driven by photoperiod</p> <p>Arrival variability driven by static variability in proximal factors</p>	<p>B. Migration driven by photoperiod</p> <p>Arrival variability driven by variability in proximal factors that underwent change in interannual variation</p>
Trend	<p>C. Migration driven by trends in other factors</p> <p>Arrival variability driven by static variability in proximal factors</p>	<p>D. Migration driven by trends in other factors</p> <p>Arrival variability driven by variability in proximal factors that underwent change in interannual variation</p>

Box 3.1. Four hypothetical scenarios depicting interactions between photoperiodic and proximal biotic influences on migration phenology. In the first scenario (**A**), no trend is detected in migration phenology (blue) despite multiannual patterns in biotic factors such as resource phenology or population density (green). In the second (**B**), no trend in migration phenology exists but a change in interannual variation occurs midway through the time series. In the third scenario (**C**), migration phenology undergoes a trend but no change is detected in interannual variation over time. In the final scenario (**D**), an advance in migration phenology and a change in interannual variation occur within the time series. The yellow line indicates the time at which the diel light:dark ratio reaches an arbitrary value that triggers migration.

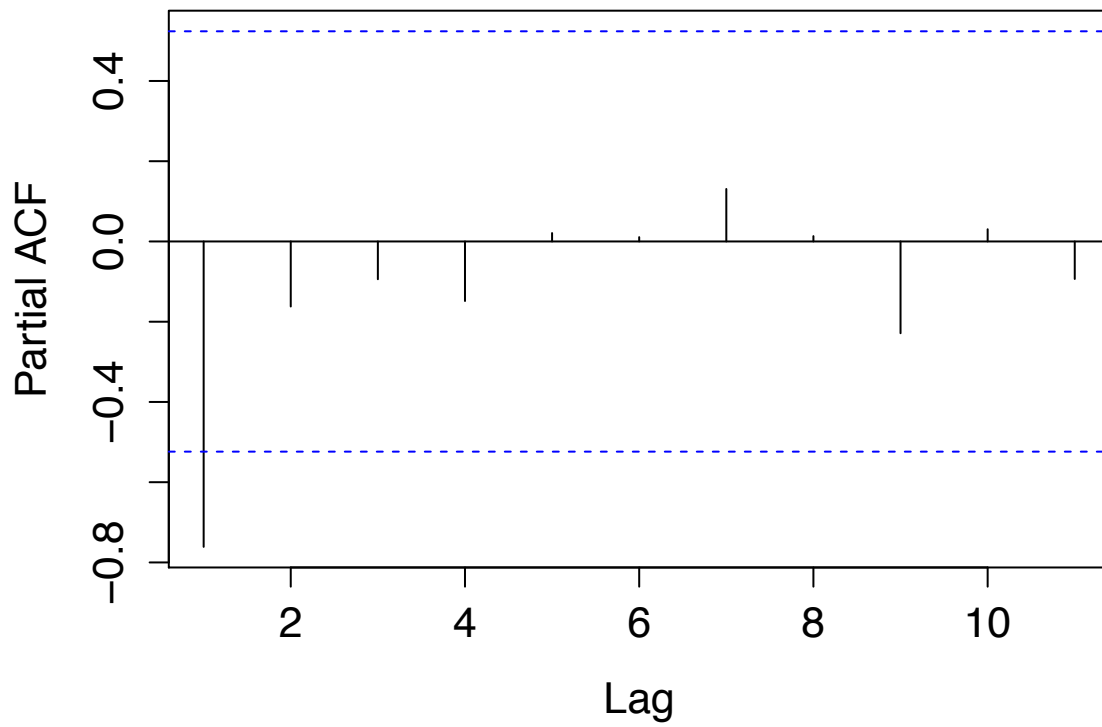
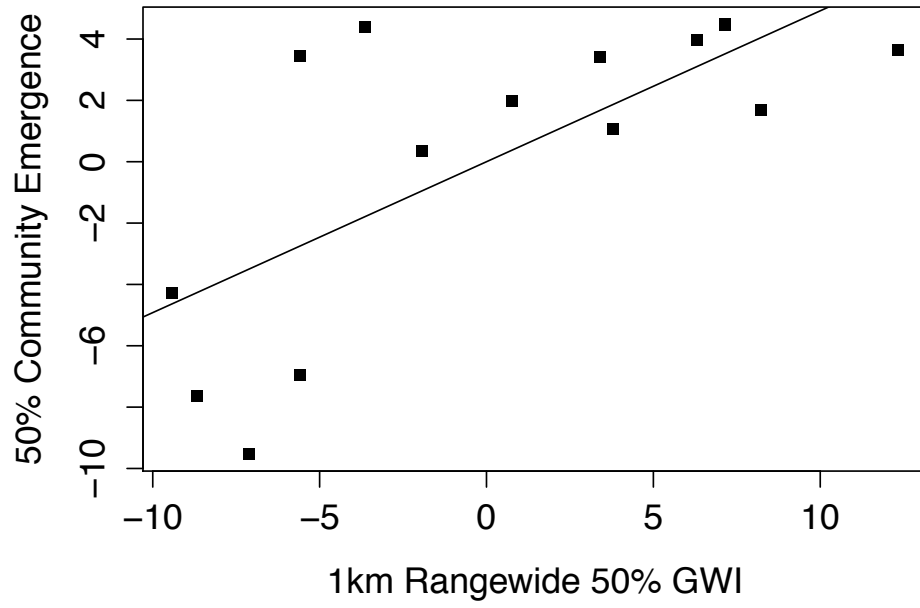


Figure 3.S1. Partial autocorrelation plot of Kangerlussuaq-Sisimiut caribou herd arrival phenology on core summer calving grounds, 2002-2015.

A



B

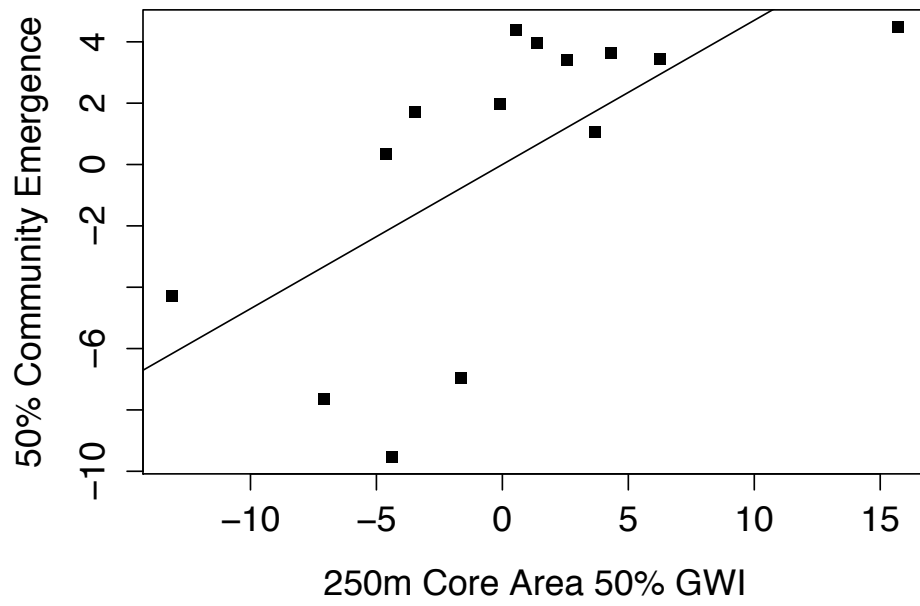


Figure 3.S2. Detrended satellite-derived and observational phenology datasets, 2002-2015.

A: Comparison of plot-level community emergence in SW Greenland study site and satellite-derived vegetation phenology for destination range of Kangerlussuaq-Sisimiut caribou herd.

B: Comparison of plot-level community emergence (same as A) and satellite-derived vegetation phenology from core calving area of Kangerlussuaq-Sisimiut caribou herd. Statistical coefficients reported in text.

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Chapter 4 – Phenology is a surface: The multidimensionality of time in landscape ecology

Introduction

Much of the theoretical basis of the work described in Chapters 2 and 3 of this thesis comes from two foundational concepts of movement ecology, the Forage-Maturation Hypothesis (FMH), and the Green Wave Hypothesis (GWH). These represent separate, but not mutually exclusive views on why and when animals and populations move. The FMH arose from the seminal works of McNaughton, and Hobbs and Swift (Hobbs and Swift, 1988; McNaughton, 1984, 1986), and holds that large herbivores move in aggregations in order to maintain immaturity in vegetation by applying a grazing pressure on optimally mature plants. Because there is a certain degree of maturity which confers maximum nutritional value and digestibility (Hamel et al., 2009; van Soest, 1994), moving from patch to patch and returning after an ideal elapsed time allows herbivores to capitalize on optimal vegetation phenology throughout a range (Fryxell, 1991).

The GWH arose from a somewhat older body of work beginning with the observation by Drent (Drent et al., 1978) that the annual boreal migration of barnacle geese coincides with a latitudinal burst of primary productivity now referred to as “the Green Wave” (van der Graaf, 2006; Kölzsch et al., 2015). The concept has been used to show that herbivores migrate along springtime bursts of productivity that can exist on multiple axes, including latitude (van der Graaf, 2006; Si et al., 2015) and elevation (Bischof et al., 2012). The fundamental realization of the GWH is similar to the FMH in that both hypotheses posit that herbivores move along a gradient of optimal resource availability.

The principal difference between these hypotheses is scale, in the sense of both space and time. While the FMH deals with day-to-day activities of a population in a range, the GWH deals

with annual journeys that cover hundreds, and sometimes thousands, of kilometers. In the most basic sense, though, these concepts complement each other independent of scale. The remainder of this chapter seeks to explore how a perspective of movement ecology that is flexible in scale unites two formerly disparate ecological concepts in dimension, evaluation, and interpretation.

Phenology as a surface

Let us first consider a surface representative of a hypothetical landscape. The x -axis and y -axis are indicative of Cartesian direction, but rather than terrain relief, the z -axis is a measure of time (Figure 4.1). Each point on the surface is a reflection of the time point at which the x - y coordinate has reached its optimal degree resource supply – that is, when the vegetation in that position is most digestible and nutritious for passing herbivores. In order for an upcoming analogy to make sense, we must first invert the time axis; so that a point featuring delayed phenology lies at a z -value lower than a point featuring advanced phenology. Thus, the hypothetical surface features an earlier period of peak resource availability in the southeast region, and optimal resources appear progressively later as one moves toward the northwest.

It should be noted that the surface described in Figure 4.1 has no finite x , y , or z limits. This is because it is intended to act as a flexible tool: the x - and y -dimensions could represent a space of 1 km^2 just as easily as they could represent one of 1000 km^2 . Similarly, the z -dimension can be equally representative of a week or a year (Figure 4.2).

Herbivores as particles

Let us now consider either of two ecological entities that undergo active movement. First, individuals walk, swim, or fly from point A to point B. In a predator-free environment, this motion is presumably driven by a quest to maximize resource intake. Just as an individual is like a particle moving through space, it moves through time. Second, populations move from region to region in the same pursuit for resources, but on a broader spatial and temporal scale. Like the motion of the individual particle, gregarious populations are like viscous liquids, changing position, density, and distribution according to the external forces acting on the aggregation. The degree of gregariousness of the population is proportional to the degree of viscosity of the liquid.

Relationship between particles (herbivores) and surface (phenology)

From this point forward, only the term “particle” will be used to describe herbivores, but it should be noted that the following arguments apply to individuals and populations. In an ideal scenario, herbivores move through an environment by continuously tracking vegetation that is at its optimal phenological stage. In the example of the hypothetical landscape surface (Figure 4.1), this translates to a particle that moves in the x - and y -direction in such way that it remains in contact with the surface while descending through time. Any x - or y -movement that causes the particle to become removed from the surface is therefore reflective of a departure from optimal foraging territory. Because our perspective of Earth and its inhabitants is one restricted by three dimensions, and fixed in the temporal sense, particles can only move in a descending manner, progressing at a fixed rate through the z -dimension. Like the force of gravity, time propels the hypothetical particle through one dimension, while active decisions regarding movement propel

it through the others. The distance covered on the x- and y-axis relative to that of the z-axis is a measure of speed (Figure 4.3):

$$speed = \frac{a}{b}$$

where a is the length of the hypotenuse of the triangle created by x- and y-movement (in kilometers, for example), and b is the elapsed time experienced by z- movement (in days, for example). In elementary mechanics, instantaneous speed is often described as the derivative of position vs. time, in that the slope is calculated as a change in the y-axis (position) relative to that of the x-axis (time). Here I have merely inverted this relationship by placing time along the vertical axis, and added an additional dimension for position.

Just as the speed of particulate movement is measured by time and distance, the “speed” at which a propagation of resources presents itself can be measured as the elapsed time in the appearance of a phenophase between one position and the next. The degree to which a particle moves in synchrony with the surface of optimal resource represents the degree to which animal movement is reflective of both the FMH and GWH. Local variation in the topography of the surface represents variability in the timing of peak production, and serves as a buffer against mistimed movement, as particles moving imperfectly along the general gradient of the surface are subject to more interactions with the surface itself as a function of the degree to which autocorrelation in the surface exists. Deviations in movement from the expected “optimal” surface present opportunities to explore patterns of movement unrelated to a pursuit of resources.

An example of the optimal forage surface

The caribou population described in the previous chapters of this thesis exists in a predator-free environment, simplifying the framework required to advance an understanding of the relationship between herbivores and forage. In an attempt to ascertain the degree to which herbivores track resource pulses, it became imperative to view the world of a migratory ungulate from a Tralfamadorian perspective, and thus it was fitting to compress time into something perceivable, and therefore something that could be explored in concert with space. By exploring a landscape wherein the optimal time of resource availability is projected in space, one can predict the way in which herbivores should move through a landscape, on spatiotemporal scales both great and small.

Based on the previous knowledge that caribou of the Kangerlussuaq-Sisimiut herd migrate from coast to inland (Thing, 1984), it was expected that a Green Wave of spring vegetation production would serve as the underlying driver of the migration itself. It became immediately apparent, though, that an inverse wave exists, which propagates toward the coast (Figure 4.4). This presents a unique problem in migratory phenology: How can caribou undergo an annual migration in a landscape without a pursuable pattern of resource phenology? The deductions presented in the previous chapters of this thesis suggest that photoperiod is the ultimate driver of this migration, a conclusion consistent with findings from similar systems (van Oort et al., 2005).

Concluding remarks

One interesting caveat of the FMH is that animals modify the surface on which they exist to create new pockets of immature vegetation toward which they can mobilize in the future. This adds an additional dimension related to time, in which the contours of the optimal forage surface

evolve as a function of the grazing pressure of individuals and populations. A region left unperturbed by herbivores will reach its point of optimal forage condition only once per year, but one subjected to multiple revisits will experience optimal conditions repeatedly during a growing season as herbivores feed at a site, then depart as the vegetation replaces itself before returning at a later time when forage has returned to its optimal state.

This approach to movement ecology marries well with the ecological theory of time (Post, 2017). Here, rather than exploring time as a thing to be competed for, I consider time as a dimension to be navigated just as space. After all, we are the products of how we choose to spend our time.

Figures

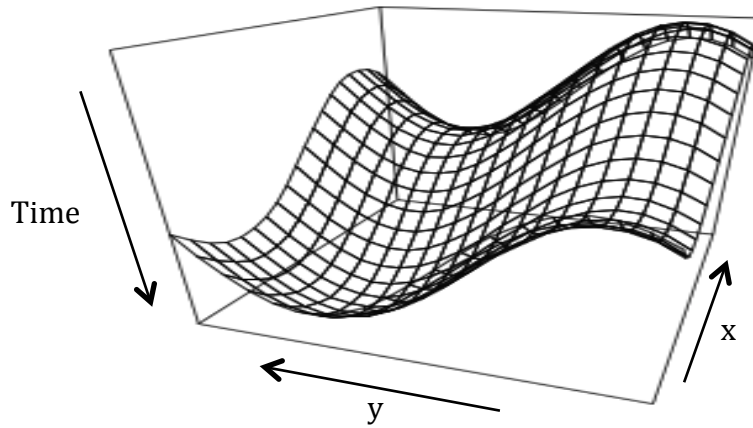


Figure 4.1. A hypothetical phenological surface. Note that the time axis has been inverted so that earlier events are at a shallower position than later events.

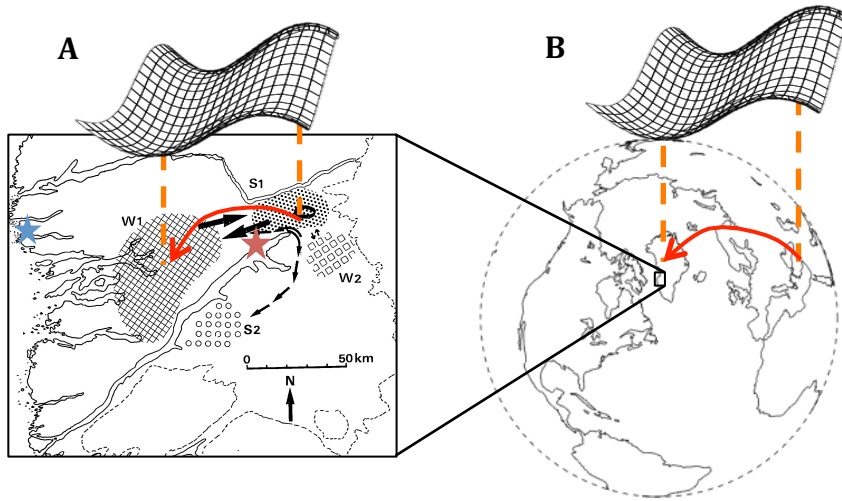


Figure 4.2. The optimal forage surface at multiple scales. At a sub-continental scale (A), a migration following the green wave would be expected to travel from east to west. At a global scale (B), a migration following the expectation would travel from south to north.

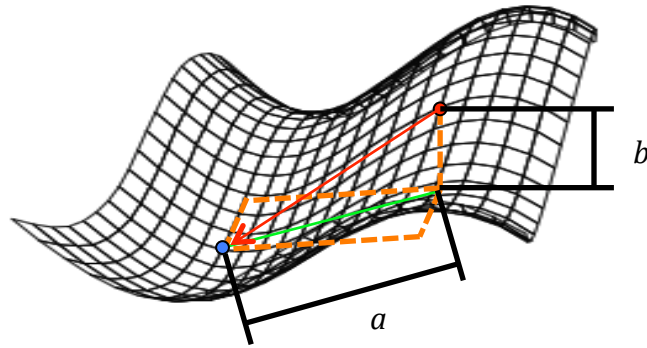


Figure 4.3. Speed is a function of distance and time. Here, distance is measured as Cartesian distance traversed (a) by a particle between time t_0 (red dot) and t_1 (blue dot) and time is measured as the linear drop (b) between the two points.

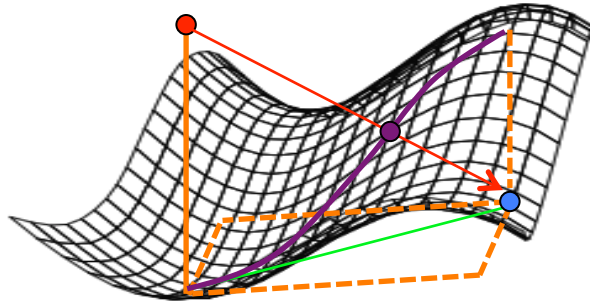


Figure 4.4. The unexpected nature of migration in the Kangerlussuaq-Sisimiut caribou herd.

Travelling from an area of delayed resource phenology, the herd's motion interacts with the optimal forage surface at only one point (purple dot) during its migration (red arrow) from departure range (red dot) and destination range (blue dot). An optimal (expected) migratory route based on this surface would instead follow the path of the purple curve, descending through time in relation to the progression of peak forage availability.

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Appendix A

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Van den Bogaard, E.H., Podolsky, MaA., Smits, J.P., Cui, X., **John, C.**, Gowda, K., Desai, D., Amin, S.G., Schalkwijk, J., Perdew, G.H., and Glick, A.B. 2015. Genetic and Pharmacological Analysis Identifies a Physiological Role for the AHR in Epidermal Differentiation. *Journal of Investigative Dermatology*. 135(5) 1320-28.

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