

EFFECTS OF SIMULATED CLIMATE CHANGE
ON THE REPRODUCTIVE PHENOLOGY OF TUSsock COTTONGRASS:
IMPLICATIONS FOR GROWTH AND REPRODUCTION
OF REINDEER AND CARIBOU ON THE SEWARD PENINSULA, ALASKA

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A
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By

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Abstract

I investigated the experimental effects of manipulations of snowmelt on the flowering phenology and forage chemistry (digestibility and nitrogen concentration) of tussock cottongrass on the Seward Peninsula, Alaska. The early snowmelt treatment (1) accelerated reproductive phenology by 11 days, and (2) resulted in higher floral digestibility but is associated with decreased nitrogen concentration in flowers. Therefore, changes in climate that lead to changes in the timing of snowmelt can alter the timing of flowering of *E. vaginatum* and, consequently, its value as reindeer and caribou forage. I then used relationships between forage chemistry and body weight gain of caribou derived from White (1983) to model the possible effects of altered forage chemistry on food intake and growth in reindeer. Reindeer foraging on cottongrass flowers can potentially increase their intake of digestible dry matter and therefore energy, by selecting to forage on early-emergent inflorescences over late-emergent ones. The multiplicative effects of forage quality and food intake can result in large increases in the rate of body weight gain that have positive feedbacks on the health and reproductive status of reindeer at both the individual and population level. Comparison of effects on reindeer and caribou populations on the Seward Peninsula indicate that early emergence of cottongrass flowers may confer a greater benefit on reindeer.

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General Introduction

Climate-driven changes in seasonal patterns that affect the development of primary producers affect primary consumers. Some of these primary consumers, or herbivores, depend on seasonally available forage that makes them sensitive to the timing of availability of forage plants. If access to seasonal food is adequate, then it should lead to healthy individuals that grow rapidly and reproduce at a higher rate.

An increasing number of studies indicates that changes in climatic regimes are occurring in the arctic. Most of the Arctic has warmed in recent decades (Serreze *et al.* 2000, Folland *et al.* 2001). Since the 1960s, the melt date in northern Alaska has advanced by approximately eight days (Stone *et al.* 2002). Early snowmelt has subsequently contributed to the lengthening of the active growing season (Myneni *et al.* 1997), affecting the timing of emergence of forage plants in the spring. Trees in the northern hemisphere have shifted spring phenology by three days earlier, on average (Root *et al.* 2002).

This study focused on the flowering phenology of tussock cottongrass (*Eriophorum vaginatum*) in relation to simulated changes in climate manifested by changes in the timing of snowmelt. Tussock cottongrass is a common arctic sedge (Britton 1966, Walker *et al.* 1982) and is an important forage plant for reindeer and caribou in early spring (Kelsall 1968, Wein 1973, Thompson and McCourt 1981). This plant emerges early during snowmelt and may represent up to 77% of caribou diet during calving (Thompson and McCourt 1981). Studies have been conducted on its vegetative growth and production (Archer and Tieszen 1980,

Shaver and Laundré 1997, Walsh *et al.* 1997) but the interaction between reproductive phenology and chemistry, and the subsequent value of cottongrass inflorescences as forage to reindeer and caribou has yet to be determined. This study investigated the effects of experimental advance and delay of snowmelt on the flowering phenology and nutrient characteristics of this arctic sedge, and the possible effects that such variation in cottongrass flowering phenology and chemistry might have on reindeer and caribou growth and productivity.

The availability of nutritious forage is particularly critical to female reindeer and caribou during calving. Reindeer with access to high quality forage produce more milk (Chan-Mcleod *et al.* 1994) and recover faster from winter loss of body condition (Adamczewski *et al.* 1987, Chan-Mcleod *et al.* 1994). Changes in forage availability that increase energy intake of reindeer and caribou during calving increase milk production and body condition. However, major differences exist between reindeer and caribou that may result in different effects from changes in forage availability in the spring.

Though reindeer and caribou are of the same species, they differ in two major aspects. First, reindeer are short-distance migrants while caribou may travel long distances between summer and winter ranges. This difference, however, has minor effect on body condition because *Rangifer* is an efficient locomotor (Fancy and White 1985). The second difference between reindeer and caribou is in their time of calving. Reindeer in the Seward Peninsula calve in late April (Chetkiewicz 1993) and Western Arctic Herd (WAH) caribou calve in early June (Davis and Valkenburg 1978). This difference is of significance in relation to the

timing of snowmelt and the availability of high quality spring forage because of nutritional demands during calving and lactation. Coincidence of early snowmelt and calving allows access to high quality forage by growing calves and lactating females.

In chapter 1, I describe the effects of changes in the timing of snowmelt on the timing of emergence of tussock cottongrass flowers and their nutritional quality. I show that advancing the timing of snowmelt can advance the timing of flowering of tussock cottongrass and increase digestibility but is associated with decreased nitrogen concentration of the flowers.

In chapter 2, I examine the scenario of early emergence of tussock cottongrass flowers in relation to energy intake, growth, and productivity of female reindeer and caribou on the Seward Peninsula. I contend that early availability of tussock cottongrass flowers will increase the energy intake of female reindeer during a critical time when the energetic demand for lactation and maintenance is high. I develop a scenario of the likely positive feedback of early emergence of tussock cottongrass flowers on reindeer on the Seward Peninsula.

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Chapter 1

Changes in timing of snowmelt alters timing of flowering and floral chemistry of tussock cottongrass (*Eriophorum vaginatum*)

Abstract

I investigated the effects of manipulating snowmelt on the reproductive phenology and chemistry of tussock cottongrass (*Eriophorum vaginatum*) on the Seward Peninsula, Alaska. The early snowmelt treatment initiated reproductive phenology 4 days earlier than control and 11 days earlier than the late snowmelt treatment but did not alter the rate of phenological development *per se*. In vitro dry matter digestibility and nitrogen concentration of cottongrass inflorescences were highest in early phenological stages irrespective of date of snowmelt. Early snowmelt resulted in lower nitrogen concentration in flowers at phenological stage 2, but the average rate of decline in tissue nitrogen (8%) was slower than that for the late-emergent flowers (37%). In contrast, early-emergent flowers exhibited the highest digestibility at phenological stage 2, which then declined at a lower rate (8%) than those from the late snowmelt plots (14%). I conclude that (1) changes in climate that result in early snowmelt can advance the timing of flowering of *E. vaginatum* and that (2) early emergence of cottongrass flowers increases their digestibility but is associated with decreased nitrogen concentration.

Key words: Alaska, caribou, climate change, digestibility, *Eriophorum vaginatum*, nitrogen, range ecology, *Rangifer tarandus*, reindeer, tundra

Introduction

Environmental changes can influence growth characteristics of forage plants in the Arctic. Forage plants that are exposed to changes in climate may respond by changing their timing of development and their nutrient characteristics that affect herbivores. Understanding factors that affect the relationship between growth of forage plants and climate change is a fundamental aspect of ecosystem ecology, especially in light of changes in the timing of snowmelt in the Arctic (Myneni *et al.* 1997, Overpeck *et al.* 1997).

Recent changes in climate have been documented in the arctic. Much of the arctic has warmed in recent decades (Serreze *et al.* 2000, Folland *et al.* 2001), and warmer winters in high latitudes are predisposed to greater snowfall (Barry 1992), especially in late winter and spring (Jefferies *et al.* 1992, Houghton *et al.* 2001). Increasing cloud cover (Austin *et al.* 1992) and decreasing solar radiation absorbed by snow (Choudhury and Kukla 1979, Jefferies *et al.* 1992) may delay snowmelt, resulting in delayed and shortened growing seasons. On the other hand, the warming currently observed in the arctic has advanced the melt date in northern Alaska by approximately 8 days since the 1960s (Stone *et al.* 2002), and accelerated the decline of minimum ice extent in the Arctic over the last 50 years (Chapman and Walsh 1993, Johannesson *et al.* 1995). Early snowmelt has subsequently contributed to the lengthening of the active growing season (Myneni *et al.* 1997), and trees in the northern hemisphere have advanced spring phenology, averaging 3 days earlier per decade over the last 50 years (Root *et al.* 2003).

The purpose of this study was to examine the interaction between reproductive phenology and inflorescence chemistry of tussock cottongrass (*Eriophorum vaginatum*) in relation to timing of snowmelt. I predicted that advancing the onset of snowmelt would advance and accelerate cottongrass floral phenology and would result in increased quality (digestibility and nitrogen concentration) of the inflorescences.

I focused my study on tussock cottongrass inflorescences because of the importance this forage has on herbivores such as reindeer and caribou in early spring. Ecologists have studied tussock cottongrass vegetative growth (Archer and Tieszen 1980, Chapin and Shaver 1996, Shaver and Laundré 1997, Walsh *et al.* 1997) but the interaction between reproductive phenology and chemistry, and the subsequent value of cottongrass flowers as forage has yet to be determined. Tussock cottongrass is a common arctic sedge (Britton 1966, Walker *et al.* 1982) whose inflorescences are an important forage for reindeer and caribou during early spring (Kelsall 1968, Wein 1973). Tussock cottongrass is much sought after by *Rangifer* during snowmelt due to its high nutritional quality relative to other plant species, and may represent up to 77% of the diet of caribou during calving (Thompson and McCourt 1981).

Tussock cottongrass is adapted to growing in the Arctic environment. The tussock growth form acts as a solar collector and can be as much as 8°C warmer than the air above it (Kielland unpublished). Tussocks of *E. vaginatum* also are warmer than soils of comparable depth between tussocks (Chapin *et al.* 1979) favoring enhanced nutrient uptake (Marion and Kummerow 1990). Tussock cottongrass can also photosynthesize under the thawing spring snow (Starr and Oberbauer 2003). As in most other arctic graminoids, floral initiation

occurs in the year prior to flowering (Bliss 1971, Shaver and Kummerow 1992). These adaptations help tussock cottongrass emerge early in the spring.

Spring is a critical time for many arctic herbivores. Compared to *Rangifer* winter diet of lichen, moss, and woody stems, emerging plants confer a large change in both forage biomass and forage quality for ungulates such as reindeer and caribou. Winter diet of reindeer in the Seward Peninsula consists of approximately 50% lichen, 25% shrub stems, 15% moss, and 10% sedges (Finstad and Kielland unpublished). When plants begin to emerge from under the snow in the spring, nutrients stored in below-ground plant parts are translocated to above-ground growing plant parts. These growing plant parts provide highly digestible, nutrient-rich forage for reindeer and caribou. The timing of emergence and nutrient translocations is particularly important to female *Rangifer* because of their increased energetic demands during calving and lactation (Robbins 1993).

Previous experimental manipulations of early snowmelt have shown temporal adjustment in floral development of various plants (Galen and Stranton 1995, Price and Waser 1998, Starr *et al.* 2000). Early floral development would necessitate early translocation of nutrients from belowground stores to developing plant parts. Growing plant parts provide highly nutritious forage in May, providing much-needed energy and nutrients for reindeer and caribou compared to winter forage (Johnstone *et al.* 2002). Changes in climatic regimes that affect the timing of plant emergence in the spring and alter chemistry of forage are thus likely to be critical to reindeer and caribou productivity.

Methods

The research was conducted in May and June of 2001 and 2002 on McCarthy's Marsh near the confluence of the Fish River and the Pargon River (64° 59' 37" N lat., 163° 06' 16" W long.) on the Seward Peninsula, Alaska, approximately 48 km north of the village of White Mountain (Figure 1.1). Classified as Ecological Site # 42B (Swanson *et al.* 1985), the site is composed predominantly of low-lying tussock tundra with patches of taiga within small riparian corridors. Microtopography results in variation between poorly-drained tussock bogs and somewhat drier tussock fields.

In 2001, I established three replicate experimental blocks in tussock tundra. Each block contained three 5 x 25 m² plots separated by 5-m buffer strips. Within each block, plots were randomly assigned the following treatments: control, early snowmelt, and late snowmelt. Due to logistical problems, only two snow fences were erected. Early snowmelt was achieved by placing black Typar[®] mesh fabric on top of the snow in early May for two weeks or until snowmelt, whichever came first. Two late snowmelt plots were established using 20-m long, 1.2 m tall snow fences erected perpendicular to the prevailing northeast winter wind to examine the effect of delayed snowmelt on the flowering phenology of *E. vaginatum*. Snow within five meters of the snow fence constituted my delayed snowmelt plots (designated late snowmelt). Snow depth measurements were taken both at the snow fence and obtained from a Natural Resource Conservation Service (NRCS) snow telemetry (SNOTEL) station at the project site. Air temperature measurements were also downloaded from the NRCS SNOTEL weather station on site through a web interphase at <http://www.ambcs.org>.

All plots were monitored for *E. vaginatum* reproductive development from 15 May 2002 until seed set in late June 2002. Phenological stages were recorded according to protocol established by Finstad and Kielland (unpublished; Table 1.1). Ten flowers were randomly collected from each plot at every reproductive phenological stage starting from stage 2. Stages 0 and 1 occurred under the snow and consequently were not recorded. Sampling commenced upon protrusion of floral buds above the snow cover. The flowers, including the peduncle, were plucked manually from the lowest point above-ground and oven-dried for 24 hours at 60° C using a Precision Scientific model 845 oven. The ten flowers from each treatment plot were pooled and constituted one analytical sample due to weight requirements for nitrogen (0.01 g) and in-vitro dry matter digestibility (IVDMD; 0.25 g) chemical analyses.

In the laboratory, the samples were redried for 48 hours at 60°C, and then ground in a Wiley mill using a size 20 mesh. IVDMD of *E. vaginatum* flowers was analyzed using a modified Van Soest method (Tilley and Terry 1969, Handl and Rittenhouse 1975, Van Soest 1976). Rumen extract was obtained from captive reindeer fed a diet of *E. vaginatum* for four days prior to the digestibility trials. Dried samples (0.25 g) were placed in sterile Ankom[®] rumen filter bags, weighed, then added to the buffered rumen content and allowed to digest for four days in a Daisy[®] incubator. The filter bags were subsequently removed from the rumen extract, treated with pepsin, dried, and weighed. Nitrogen concentration of *E. vaginatum* flowers was measured using a LECO 200 CNS elemental analyzer. Subsamples of

approximately 0.01 g were weighed into aluminum foil cups and then combusted at 800°C to convert elemental nitrogen into N₂.

Statistical analysis

Data did not deviate markedly from assumptions of normality. Statistical analyses included an ANCOVA on nitrogen, and IVDMD data using treatment and stage as class variables and date as covariate. A two-factor ANOVA was used to analyze biomass and timing of flowering using treatment and stage as class variables. Type IV Sum of Square Error was used in the analyses due to empty cells (Neter *et al.*, 1996; SAS Institute, 2001).

Results

Timing of flowering. Snowmelt manipulations changed the timing of flowering of *E. vaginatum* (ANOVA, $p < .0001$, $\alpha = .05$, $df = 4$; Figure 1.2). On average, inflorescences in the control plots initially emerged from under the snow during stage 2 on 17 May 2002. The early snowmelt treatment advanced the emergence of stage 2 *E. vaginatum* flowers by 4 days relative to control. Stage 2 flowers from the snow fence plots emerged 7 days after those from the control plots. The dates when the flowers transitioned into each phenology stage were different among treatments at all stages (ANOVA, $p < .0001$, $\alpha = .05$, $df = 18$).

Development from stage 2 to stage 4 took 6 days in the early snowmelt plots compared to 8 days in the late snowmelt plots. However, flowers in the snow fence plots moved from stage 4 to stage 5 in 17 days, 6 days longer than those in the early snowmelt plots. No differences were observed in the overall rate of phenological development among treatments (Figure 1.2).

Forage chemistry. Snowmelt manipulations had a significant but opposite effect on digestibility and floral nitrogen concentrations (ANCOVA, $p=0.0016$, $\alpha=0.05$, $df=4$; Figure 1.3). At stage 2, flowers from the late snowmelt plots had 17% higher nitrogen concentration than those from the early snowmelt plots. However, by stage 5, flowers from the late snowmelt plots had 19% lower nitrogen concentration than those from the early snowmelt plots. Nitrogen concentration of flowers from the late snowmelt plots declined 37% from stage 2 to stage 5 compared to an 8% decline in the early snowmelt plots for the same interval. There was a significant interaction between treatment and phenology stage (ANOVA, $p=0.0037$, $\alpha=0.0037$, $df=10$).

Snowmelt manipulations also had a significant effect on IVDMD (ANCOVA, $p=0.0270$, $\alpha=0.05$, $df=4$; Figure 1.4). At stage 2, early snowmelt flowers were 4% more digestible than late snowmelt flowers. But by stage 5, early snowmelt flowers were 9% more digestible than late snowmelt flowers. Digestibility of early snowmelt flowers declined 9% from stage 2 to stage 5 compared to a 17% decline in flowers from the late snowmelt plots for the same interval.

No differences were detected in floral mass among treatments at stage 2, 3, and 4 (Figure 1.5). By stage 5, however, flowers from the late snowmelt plots had increased by 79% in mass from stage 2 while flowers from the early snowmelt plots had gained 35% for the same interval.

Discussion

Snowmelt manipulations changed the time cottongrass flowers emerged from under the snow. However, the flowers from all treatment plots emerged from under the snow at the same phenological stage irrespective of treatment. With the snow cover removed and the tussocks exposed to the sun, advancing snowmelt resulted in early flowering of *E. vaginatum*, while delaying snowmelt delayed flowering. Similar findings of temporal adjustment in floral development coincident with manipulations of early or late snowmelt have been documented for *Polygonum bistorta* (Starr *et al.* 2000), *Ranunculus adoneus* (Galen and Stranton 1995), *Androsace septentrionalis* (Inouye *et al.* 2003), and other subalpine meadow species (Price and Waser 1998). Late snowmelt may also delay vegetative phenology in *E. vaginatum* (Walsh *et al.* 1997). However, in a long-term experiment (9 years) at Toolik Lake, Alaska using open top greenhouses in the summer, the increase in ambient temperature did not affect the date at which *E. vaginatum* flowering buds opened (Chapin and Shaver 1996).

The rate of overall development did not differ between treatments, indicating that there is an apparent fixed time required for floral development. Flowers from all treatments exhibited rapid development from bud emergence (stage 2) to full flower (stage 4) then slower development from stage 4 to seed set (stage 5). The fast development from stage 2 to stage 4 supports the idea of a flowering mechanism resulting from natural selection which better adapts arctic sedges to their northern environment. Pollen production was complete within one week of flower emergence regardless of treatment. Development from stage 4 to stage 5 took two weeks, on average, allowing the fruit to develop and disperse in time for the surrounding ground to be snow-free.

Since cottongrass flowers initiate growth the prior autumn and lie dormant under the snow until the following spring, nitrogen concentration at stage 2 is largely determined by what is stored in the floral bud and what may have already been translocated from below-ground stores. It is unlikely that root uptake contributed to nitrogen concentration in flowers from the early snowmelt plots because the soil was still frozen even though the tops of the tussocks were already snow-free. On the other hand, the late snowmelt plots were the only experimental plots that still had snow 11 days later, on 24 May 2002 - the first day stage 2 flowers emerged from under the snow in the late snowmelt plots (Figure 1.7) and seven days after control plots were snow free. Yet, nitrogen concentration in flowers from the late snowmelt plots was higher than that from other treatment plots at stage 2. The high nitrogen concentration in late emerging flowers at stage 2 could be due to root uptake of nutrients in meltwater coming from the already snow-free area outside the snow fence plots or retranslocated from below-ground stores. With high temperatures (9°C) the area surrounding the snow fences was already snow-free and the ground under the delayed snowmelt plots may have allowed nutrient influx in meltwater from outside the plots.

The rapid decline in nitrogen concentration in flowers in the late snowmelt plots between stages 4 and 5 could be due to dilution of nitrogen by the increased amount of structural tissue accumulated at that stage. Because I included the peduncle as part of the sampling unit, floral biomass measurements included more structural tissue accumulated towards the later part of the growing season. Despite having similar biomass from stage 2 to stage 4 (Figure 1.5), flowers from the late snowmelt plots had the highest biomass at stage 5,

possibly due to larger peduncles. Though I did not weigh peduncles separately from the flowers, visual inspection of the samples at stage 5 suggested that flowers from the late snowmelt plots tended to have longer peduncles than those from the other treatment plots.

The interaction between nitrogen concentration and phenology stage indicates that nitrogen concentration declined at a faster rate in flowers from the late snowmelt plots than those in the early snowmelt plots. The increase in floral biomass may explain the rapid decline in nitrogen concentration possibly because of what appears to be the enlargement of peduncles in flowers from the late snowmelt plots, especially at stage 5.

Digestibility of flowers from the early snowmelt plots was higher than that of flowers from the late snowmelt plots, suggesting higher fiber concentration in flowers from the late snowmelt plots. Flowers from the late snowmelt plots were under snow cover 11 days longer than those from the early snowmelt plots, potentially allowing them to lengthen the peduncles while under the snow. The insulative properties of snow along with the ability of tussock cottongrass to photosynthesize under the thawing spring snow may have influenced growth of the peduncles. Peduncles from the late-emerging flowers may have been larger than those from the early-emerging flowers, increasing structural carbon that could lower digestibility in the late-emerging flowers. However, because the peduncles were not measured, this assertion remains to be quantified. Nevertheless, the difference in IVDMD between early-emerging flowers and late-emerging flowers indicates that delaying snowmelt decreased the digestibility of *E. vaginatum* flowers through mechanisms that are not clear. These small differences in forage digestibility may ultimately have larger significance in

herbivores that selectively graze on that particular forage (“multiplier effect”; White 1983; discussed in Chapter 2).

In conclusion, changes in climate that lead to changes in the timing of snowmelt alter the timing of flowering of *E. vaginatum* and, consequently, its value as reindeer and caribou forage. In this study, I was able to manipulate cottongrass to emerge 4 days ahead of or 7 days after controls. It is likely that earlier snowmelt will result in even earlier emergence of cottongrass flowers. What remains to be determined is how plastic the reproductive phenology of tussock cottongrass is in light of the warming trend in the Arctic.

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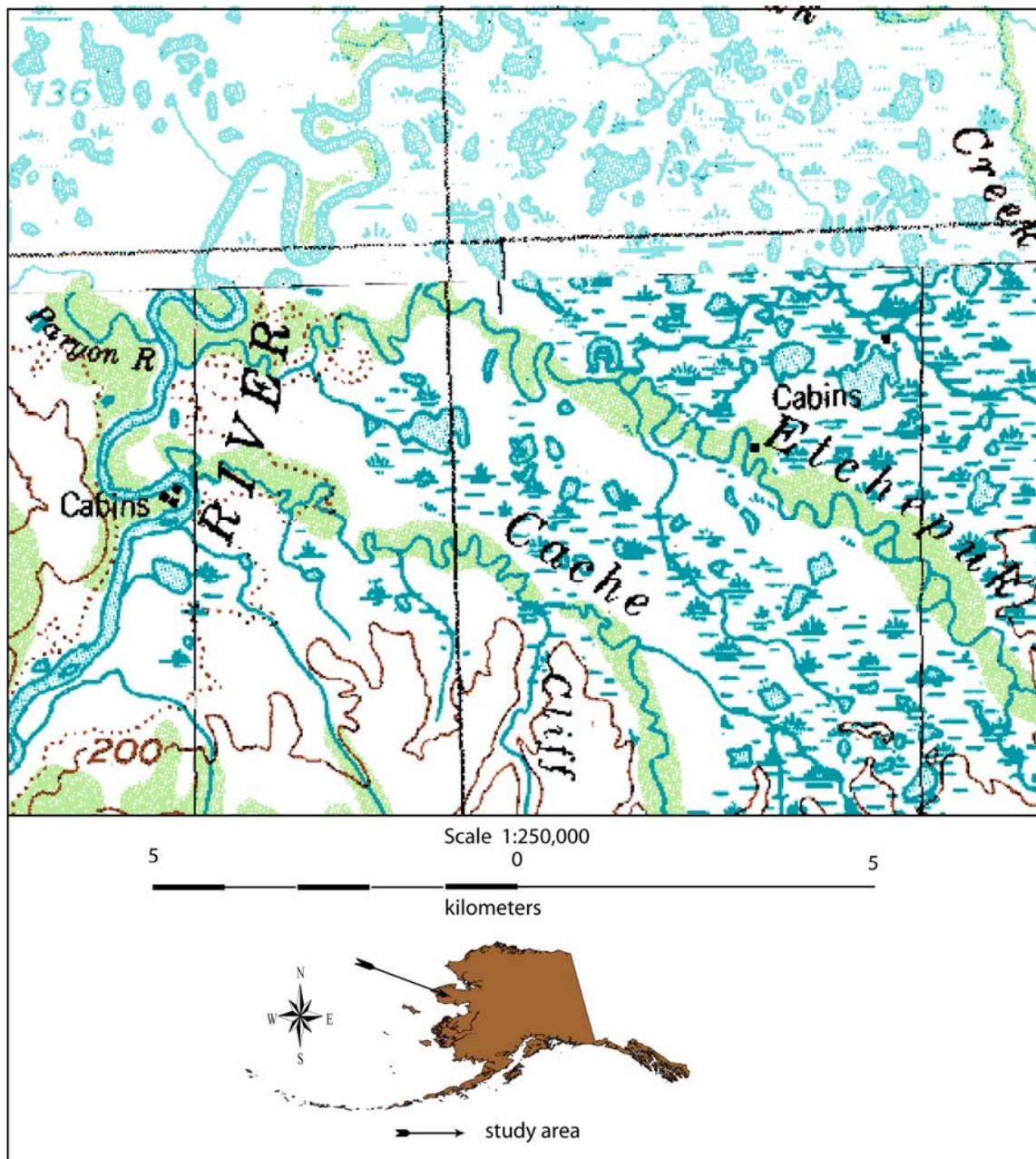


Figure 1.1. Map of project site on the Seward Peninsula. In the spring of 2002, plant collections were made at the confluence of the Pargon River and the Fish River and another site 8 km up the Etchepuk River.

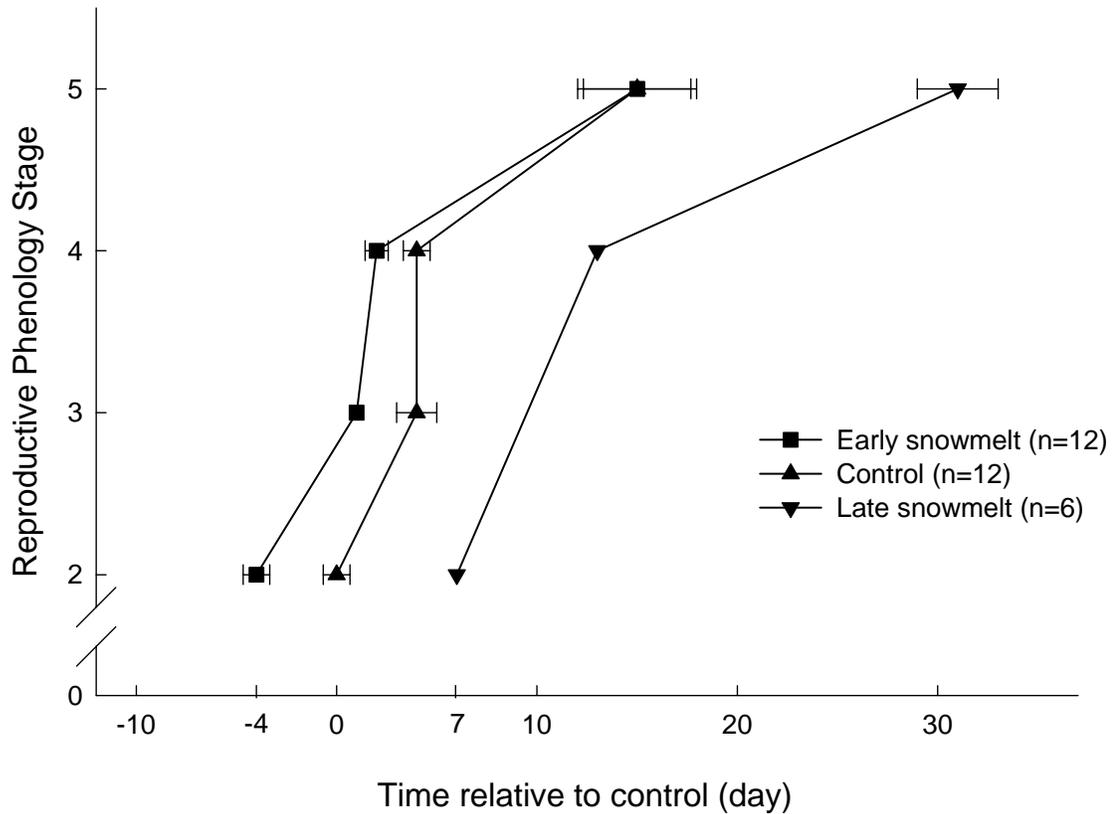


Figure 1.2. Relationship between time relative to *E. vaginatum* flowering in the control plots at stage 2 and the progression of reproductive phenology for the three treatments. Data are means and standard errors.

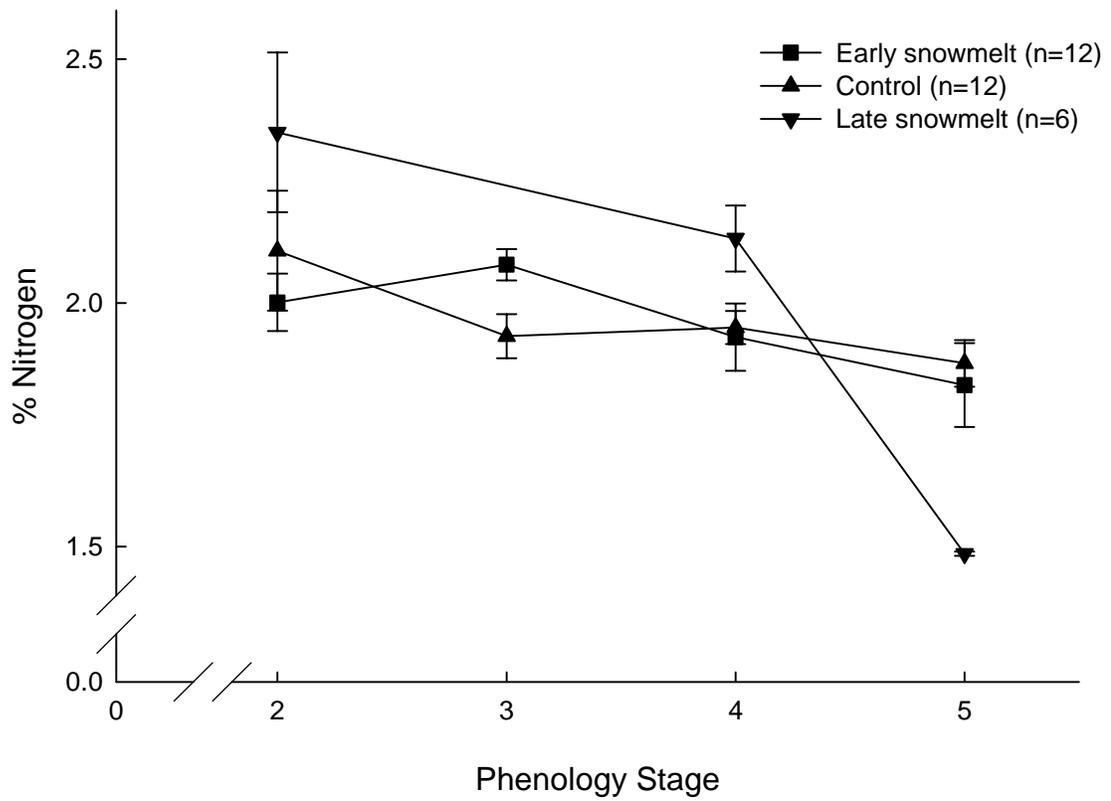


Figure 1.3. Relationship between reproductive phenology and nitrogen concentration in *E. vaginatum* inflorescence for the three treatments. Data points are means with standard errors.

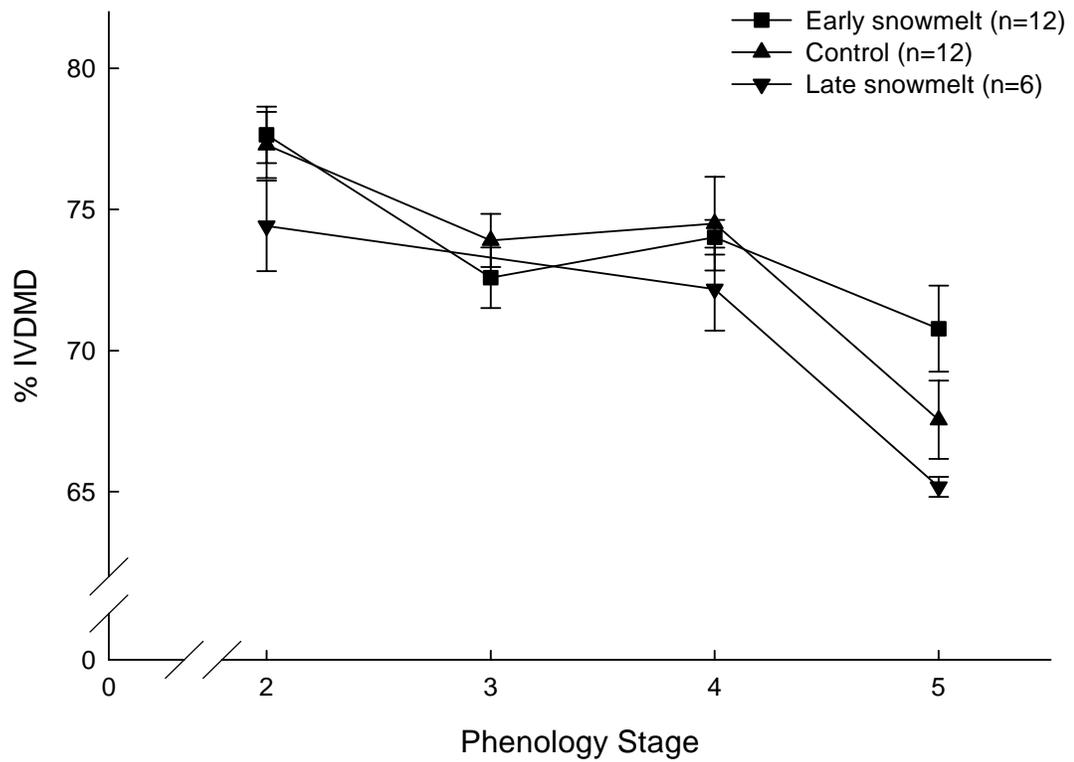


Figure 1.4. Relationship between reproductive phenology and in-vitro dry matter digestibility of *E. vaginatum* for the three treatments. Data are means and standard errors.

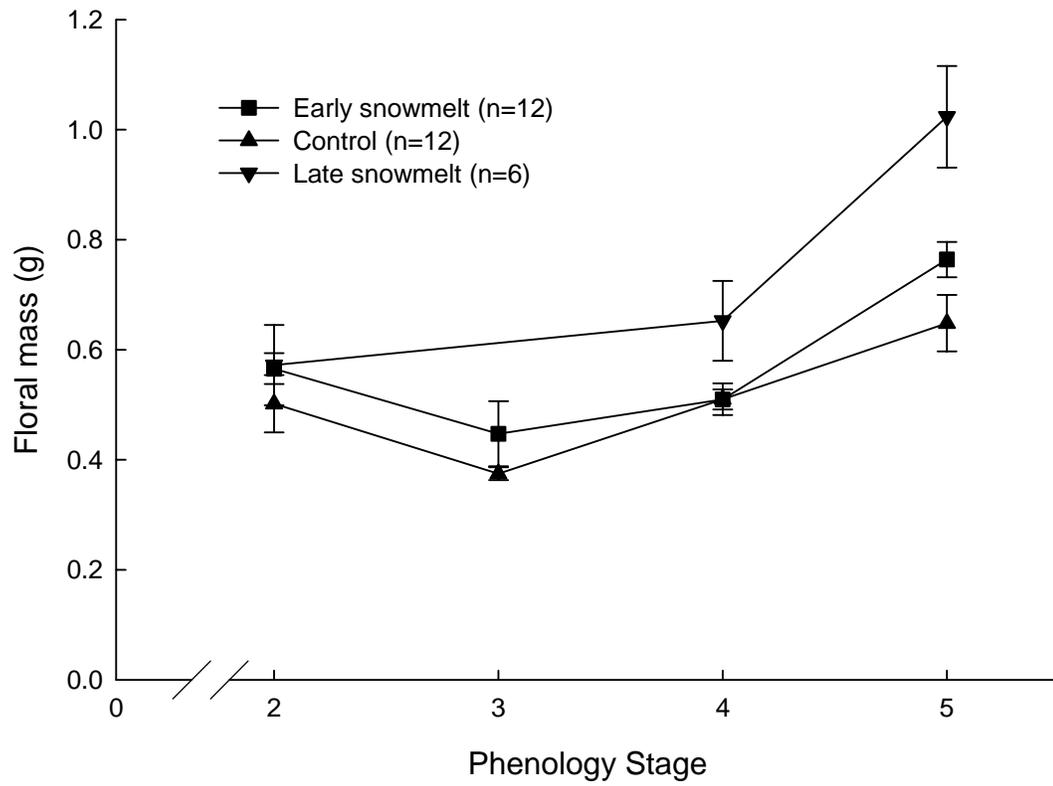


Figure 1.5. Relationship between reproductive phenology and mass of *E. vaginatum* flowers for the three treatments. Data are means with standard errors.

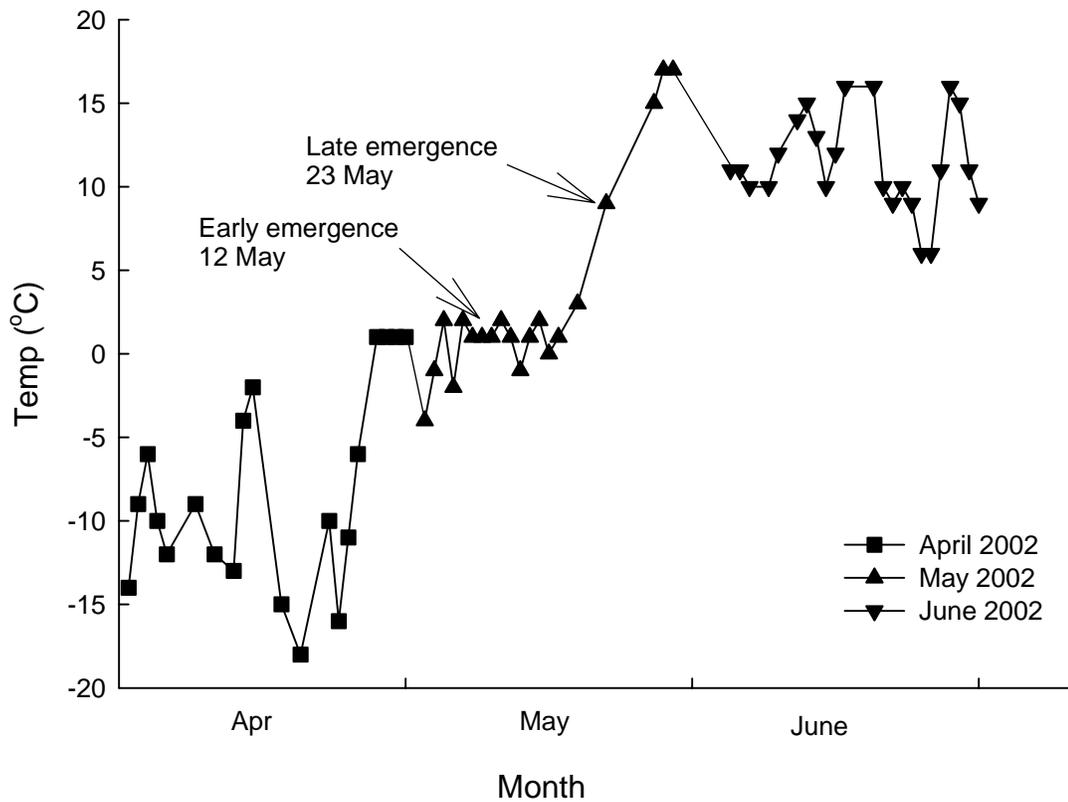


Figure 1.6. Temperature measurements at Pargon Creek for the period 1 April – 30 June 2002. Temperatures at cottongrass flower emergence in the early and late snowmelt plots are indicated with arrows. SNOTEL data are telemetry readings from www.ambcs.org archives.

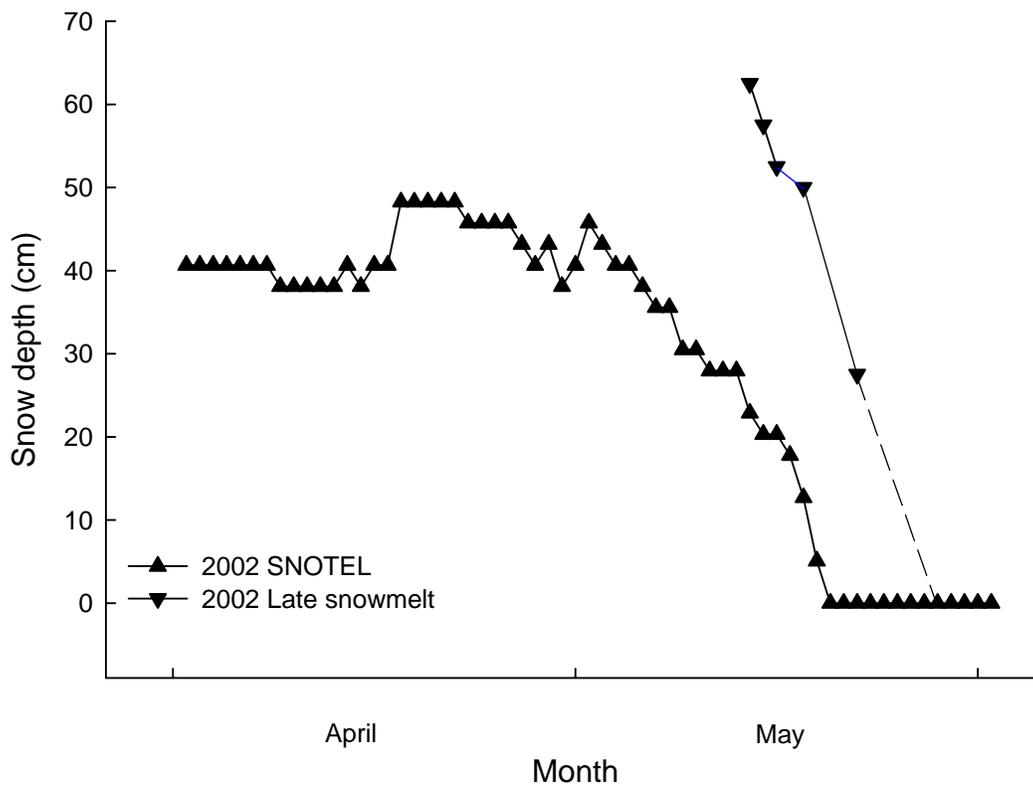


Figure 1.7. Snow depth measurements at Pargon Creek for the period 1 April – 31 May 2002. Snow depth at late snowmelt plots are from 13 May - 22 May 2002 . Late snowmelt data points are mean of two plots measured 0.5 m from the midpoint of the late snowmelt. SNOTEL data are telemetry readings from www.ambcs.org archives.

Table 1.1. The reproductive phenology protocol established by the Reindeer Research Program, University of Alaska Fairbanks, as adapted from Finstad and Kielland (unpublished).

Growth stage	Description
0	Dormant, no new floral buds or floral buds closed
1	Floral buds forming or swelling
2	Flowers opening
3	Full flower / anthesis
4	Post flower, fruit or pod developing (females), pollen has been shed (males)
5	Mature fruit / seed set (females), flowers senesced (males)
6	Fruits, seeds dispersed (females), flowers senesced (males); fruits (females), flowers (males) may have fallen off plant

Chapter 2

Effects of changes in forage chemistry on potential growth and reproduction in reindeer on the Seward Peninsula, Alaska

Abstract

I investigated through simple models the potential effects of altered forage digestibility due to changes in the timing of flowering of *Eriophorum vaginatum* on reindeer (*Rangifer tarandus*) herds on the Seward Peninsula, Alaska in early spring. Changes in forage chemistry resulting from advanced reproductive phenology increase the rate of weight gain in female reindeer disproportionately relative to increases in forage quality due to the multiplier effect of foraging behavior. I found that foraging on early-emergent cottongrass flowers that confer a 4% increase in forage digestibility may result in a near doubling in the rate of body weight gain in female reindeer. Thus, small changes in forage chemistry can have far-reaching implications for productivity at both the individual as well as the population level.

Key words: Alaska, caribou, climate change, forage quality, productivity, *Rangifer tarandus*, reindeer, Seward Peninsula

Introduction

Changes in forage availability and chemistry can influence growth characteristics of herbivore populations through feedback mechanisms pertaining to foraging behavior and energy gain (White 1983). Herbivores with access to highly digestible forage with high nitrogen concentration generally respond with increased growth and higher potential rates of reproduction (Robbins 1993, Van Soest 1994). Understanding factors that affect the relationship between forage availability and chemistry and herbivore population processes is fundamental to the understanding of ecosystem ecology in the Arctic, especially in light of changing forage chemistry through the very short growing season.

It is generally agreed that changes in climate are already manifested in the Arctic. Much of the Arctic has warmed in recent decades (Serreze *et al.* 2000, Folland *et al.* 2001). Snowmelt has advanced in northern Alaska by approximately 8 days since the 1960s (Stone *et al.* 2002). Green-up is also occurring earlier in northern Alaska (Keeling *et al.* 1996, Myneni *et al.* 1997, Jones *et al.* 1997, Root *et al.* 2003). These environmental changes are likely to affect forage availability and forage chemistry that, in turn, may influence herbivore populations such as reindeer and caribou.

The purpose of this study was to examine the potential effects of changes in forage availability and plant chemistry in early spring with respect to reindeer growth and productivity on the Seward Peninsula, Alaska. I used relationships between forage chemistry and body weight gain derived from White (1983) and from experimental plots to model the possible effect of altered forage chemistry on food intake and growth in reindeer. I also

discuss the possible consequences of early snowmelt on the demography of reindeer and caribou populations on the Seward Peninsula in light of the fundamental difference in calving dates between these *Rangifer* subspecies.

In Chapter 1, I discussed the potential effects of simulated climate change on the reproductive phenology of tussock cottongrass. Specifically, I showed that early snowmelt can increase the digestibility of cottongrass flowers. In order to put my findings in a larger ecological context, I used ideas developed by White (1983) regarding what he termed "multiplier effects", where small changes in forage quality may have large consequences in terms of body weight change in reindeer. His study with reindeer compared the effects of different forage quality on behavioral changes in forage intake that in turn affected how much body weight reindeer gained. In brief, selective foraging by reindeer increases overall diet quality (as measured by forage digestibility). This increase in forage quality triggers increased appetite and food intake by the animal. Because body weight gain is a function of the multiplicative effects of forage quality and food intake, small changes in forage quality are amplified through behavioral changes that can result in large increases in the rate of body weight gain. These are the relationships underlying the so-called multiplier effects (White 1983).

Conversion of energy from forage to body weight begins with intake. Total forage intake is affected by intake rate, which for reindeer I used $117 \text{ g/kg}^{0.75}/\text{day}$ for consistency with White (1983). Metabolic body weight (0.75 power of body weight) is widely accepted for use in comparing basal metabolic rates of different placental mammals (Robbins 1993). I used this

factor in my model for consistency with the literature and to avoid further conversions from reported results cited in this modeling exercise. Daily dry matter intake (DMI) is the amount of forage ingested by reindeer per day. The product of DMI and dry matter digestibility (DMD) is digestible dry matter intake (DDMI) and is an index of energy intake. Metabolism of DDMI above maintenance requirements results in body weight (BW) gain.

I focused my study on tussock cottongrass (*Eriophorum vaginatum*) because it is an important forage species for reindeer and caribou in the spring (Kelsall 1968, Wein 1973, Thompson and McCourt 1981). It provides high energy forage during a critical time for females because of high post-partum nutritional demands for milk production as well as for gaining body mass in preparation for the next winter (Boertje 1990, Chan-McCleod *et al.* 1994). Characteristics including the ability to collect solar heat, allow cottongrass flowers to emerge early from under the thawing spring snow (Chapin *et al.* 1979, Starr and Oberbauer 2003). However, variation in the timing of snowmelt influences when the flowers emerge from under the snow, thus influencing the availability of cottongrass flowers for reindeer and caribou.

Domesticated reindeer (*Rangifer tarandus tarandus*) were introduced from Russia to the Seward Peninsula by missionaries in the late 1890s when caribou abundance was very low. One fundamental difference is that caribou leave the Seward Peninsula in May and travel to their calving grounds north of the Brooks Range. Another difference between reindeer and caribou is timing of calving. Reindeer calve in late April, approximately a month earlier than caribou (Davis and Valkenburg 1978, Chetkiewicz 1993).

The idea that small changes in forage quality can affect body growth substantially is not new. A comparison of growth rates in three reindeer populations showed that favorable foraging conditions can lead to higher rates of growth (Reimers *et al.* 1983). White (1983) showed that selective grazing by adult reindeer resulted in a 268% (273 g/day) increase in body weight gain in a foraging experiment at Atkasook, Alaska. Other studies further suggest that variation in body weight is related to forage quality. My modeling exercise attempted to link changes in climate and changes in body weight gain in reindeer through slight changes in forage quality. Here, I build upon the ideas proposed by White (1983), but try to link climatic variability to changes in reindeer growth and reproduction through empirical relationships between forage quality and animal physiology.

Methods

I used data from a snowmelt manipulation study (Chapter 1) and dry matter intake rate (117 g/kg^{0.75}/day; where kg^{0.75} = metabolic body weight) for reindeer (White 1983) to derive digestible dry matter intake of *E. vaginatum* inflorescences as affected by the date of snowmelt. *E. vaginatum* flowers were collected at predesignated reproductive phenology stages (Chapter 1) through the growing season. I computed potential weight change of reindeer based on predicted values of DDMI of reindeer foraging on *E. vaginatum* flowers under simulated climate change scenarios given the equation

$$\text{Body Weight (BW) Change (g/d)} = -507 + 10.5 \times (\text{DDMI}) \quad (1)$$

Linear regression equations were developed from relationships between forage quality, dry matter intake, and rate of body weight gain based on White (1983) as follows:

$$\% \Delta \text{DMI} = 1.93 \times (\% \Delta \text{DMD}) \quad (2)$$

$$\% \Delta \text{BW} = -10.47 + 10.51 \times (\% \Delta \text{DMI}) \quad (3)$$

These equations allowed me to estimate proportional changes in potential DMD, DMI, and body weight change of reindeer under earlier versus later emergence of *E. vaginatum* inflorescences.

I also compared the dates of emergence of cottongrass flowers from the snowmelt manipulations study to the calving dates of reindeer and caribou. I then created model scenarios of (1) cottongrass flowers emerging one week earlier than usual, and (2) changes in weight due to changes in forage quality on the Seward Peninsula.

Results

Early emergence of cottongrass inflorescences that have 4% higher digestibility than late-emerging inflorescences translates into an 8% increase in potential DMI by reindeer (Figure 2.1). This increase in DMI, in turn, can confer a 78% increase in daily weight gain for reindeer foraging on early-emergent cottongrass flowers (Figure 2.2). Moreover, increase in forage digestibility confer a proportional change in body weight 20-fold that of the proportional change in forage digestibility (Figure 2.3). Thus, small changes in forage quality can be greatly amplified through animal behavior and physiology.

Discussion

Reindeer foraging on early-emergent cottongrass flowers can potentially have higher intake of digestible dry matter and, therefore, energy, than when they forage on late-emergent ones.

This modest increase in energy intake could result in increased body weight gain (Robbins 1993, Van Soest 1994). Using White's (1983) proportional relationships between forage quality, intake, and body weight change, small increases (4%) in forage quality due to differences in timing of snowmelt can be expected to produce large increases (78%) in weight gain. Indeed, as reindeer graze through the landscape, foraging on cottongrass flowers as they emerge, a higher potential rate of weight gain may be achieved early in the growing season.

Forage selection is one mechanism through which changes in forage quality may affect reindeer weight gain. Selection of higher quality forage over low quality forage multiplies the effects of forage quality on body weight gain. In the case of early snowmelt where high quality forage is available to reindeer early in the spring, selection may occur between what is available in late winter (moss, lichen, woody stems) and tussock cottongrass flowers.

Increase in body weight has been correlated with increased reproductive success in female reindeer (Reimers *et al.* 1983, Cameron *et al.* 1992, Adams and Dale 1998). Since reindeer calves are born before vegetation has initiated growth, females require body stores to transfer sufficient energy and protein to their calves (Reimers *et al.* 1983, Crête and Hout 1993). The availability of cottongrass earlier in the spring allows *Rangifer* to replenish stores quicker and gain weight earlier. In a study of caribou in Denali National Park, Adams and Dale (1998) reported that female caribou that produced calves as 2-year-olds averaged 5 kg heavier in the prior fall than those that did not. Therefore, a potential reproductive advantage could be gained by foraging on early-emergent cottongrass flowers.

I used DDMI in order to calculate potential weight gain of reindeer foraging on early versus late emergent cottongrass flowers. The difference in DDMI between early and late emergent cottongrass flowers was small, and the DDMI of cottongrass flowers was almost twice that of the intake for maintenance (Figure 2.4). An 80 kg female reindeer foraging on early-emergent cottongrass flowers would have approximately 700 g/day more weight gain than a similar female foraging on what is available in late winter. Providing they stay in those different planes of nutrition, in approximately two weeks these reindeer females would differ in body weight by 5 kg. This difference is particularly significant in light of the observation that such variation in body weight among female *Rangifer* could represent the difference between reproducing or not as two-year-olds the following spring (Adams and Dale 1998).

Earlier snowmelt and flowering of *E. vaginatum* brought about by climate change may result in earlier availability of higher quality forage for reindeer recovering from winter losses of fat and protein and for females during lactation. High energy intake increases protein deposition in the adult female and increases fat deposition in non-breeding adult female *Rangifer* (Cameron et al. 1993, Crête and Hout 1993, Chan-McLeod et al. 1994). However, another benefit of a high energy diet for lactating females is the increased production of milk (Chan-McLeod et al. 1994). Reindeer calves, therefore, also stand to gain from early availability of tussock cottongrass. With greater milk production from the mother, calf growth increases (Loudon and Kay 1984, White and Luick 1984), which in turn confers higher calf survival (Guinness *et al.* 1978, Skogland 1985). After weaning, intake of high

energy forage increases calf growth (Verme and Ozoga 1980) that greatly affect the probability of reproducing in females at two years of age (Adams and Dale 1998).

So far I have depicted scenarios with *E. vaginatum* as the only available spring forage affecting *Rangifer*. As the growing season progresses, other forage plants emerge and become available. For example, *Carex aquatilis* flowers also have high digestibility, but emerge approximately a month later than *E. vaginatum* flowers (Figure 2.6). But with reindeer foraging on high quality plants early in the season, their physiological system is already conditioned to take advantage of high quality forage as the season progresses. Selective foraging by *Rangifer* on early phenology plant parts thus allows for maximum utilization of higher energy forage. The first plants that leaf out in the spring are deciduous shrubs such as willow (*Salix* sp.) and birch (*Betula nana*). These shrubs are not as digestible as cottongrass flowers.

One of the differences between reindeer and caribou populations on the Seward Peninsula that I mentioned earlier is that of calving time. If the current warming trend in the Arctic persists, availability of early-emergent cottongrass flowers may approach coincidence with reindeer calving time (Figure 2.5). Availability of high quality forage close to calving dates hastens body weight gain and may increase milk production, benefiting calves as well as adult female reindeer. Thus the availability of high quality forage close to when resource demand during lactation is high in reindeer compared to caribou may confer greater benefit on reindeer.

The scenarios shown here illustrate that shifts in timing of phenological development of a primary forage species result in changes in *Rangifer* energy intake that ultimately have consequences for growth and productivity at the individual and population levels. The effects of early availability of high quality forage on reindeer may be more pronounced if the current trend towards earlier greenup in the Arctic continues.

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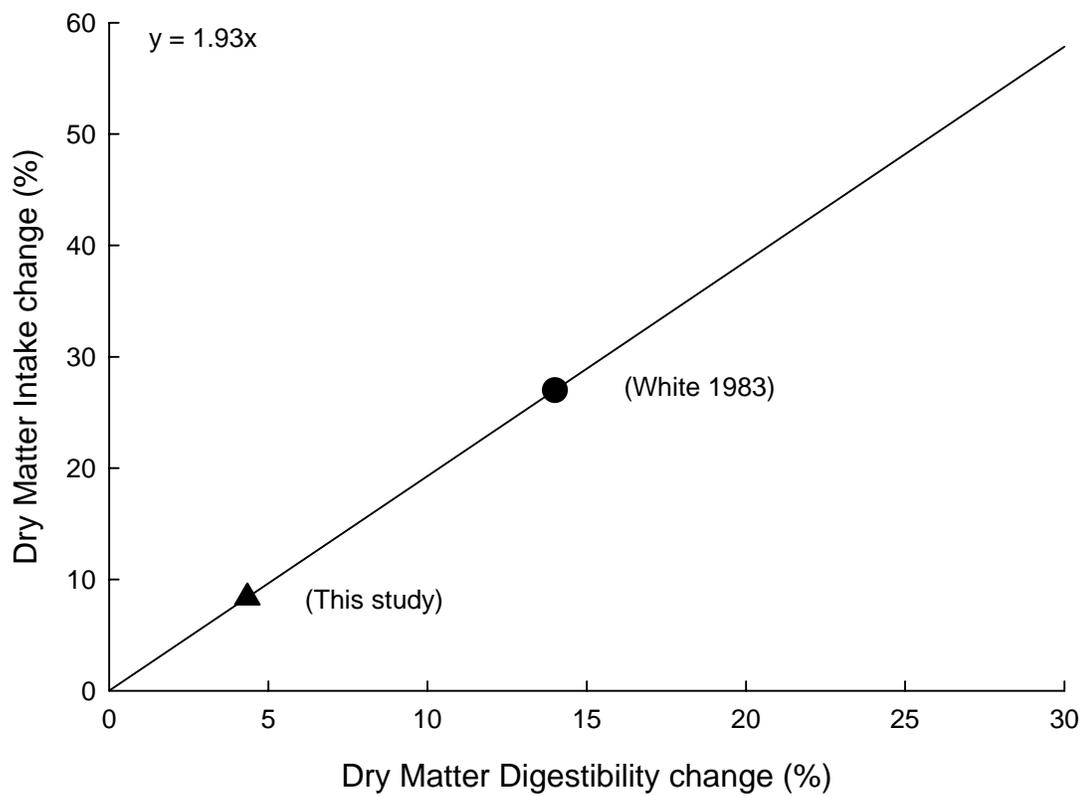


Figure 2.1. Relationship between % change in dry matter digestibility of *E. vaginatum* flowers and % change in dry matter intake by reindeer under different snowmelt simulations using data from this study and from White (1983).

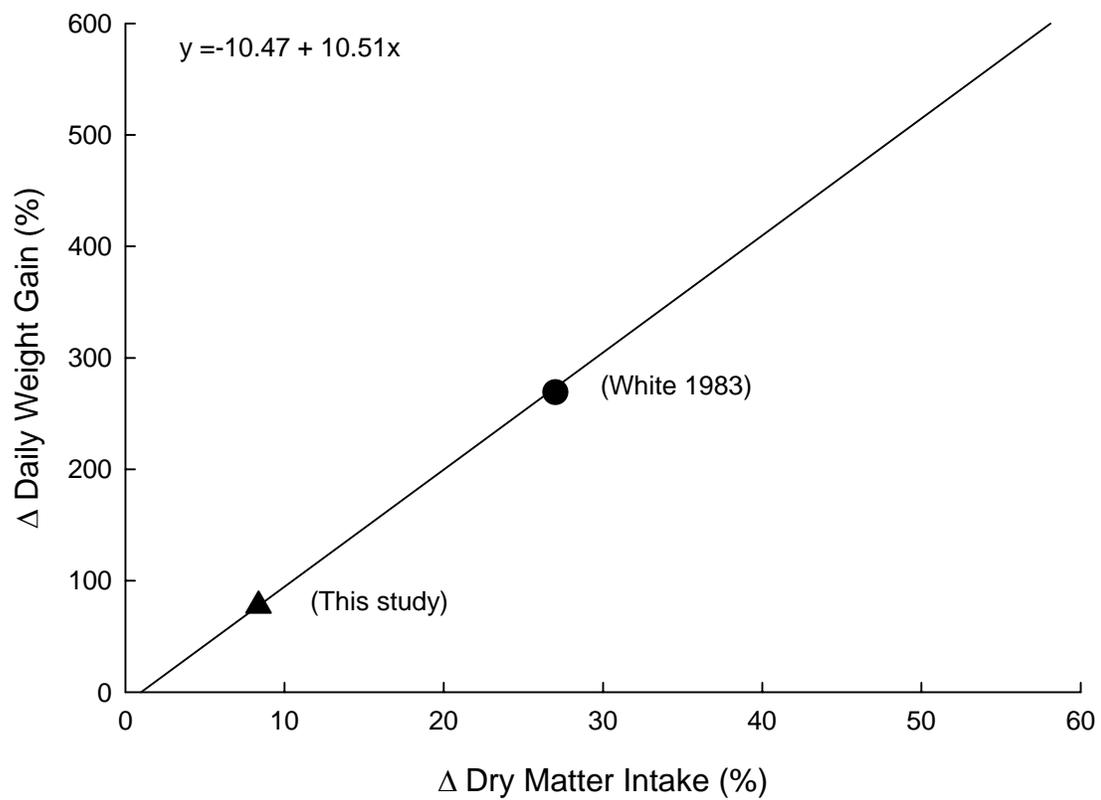


Figure 2.2. Relationship between % change in dry matter intake and % change in daily weight gain for reindeer.

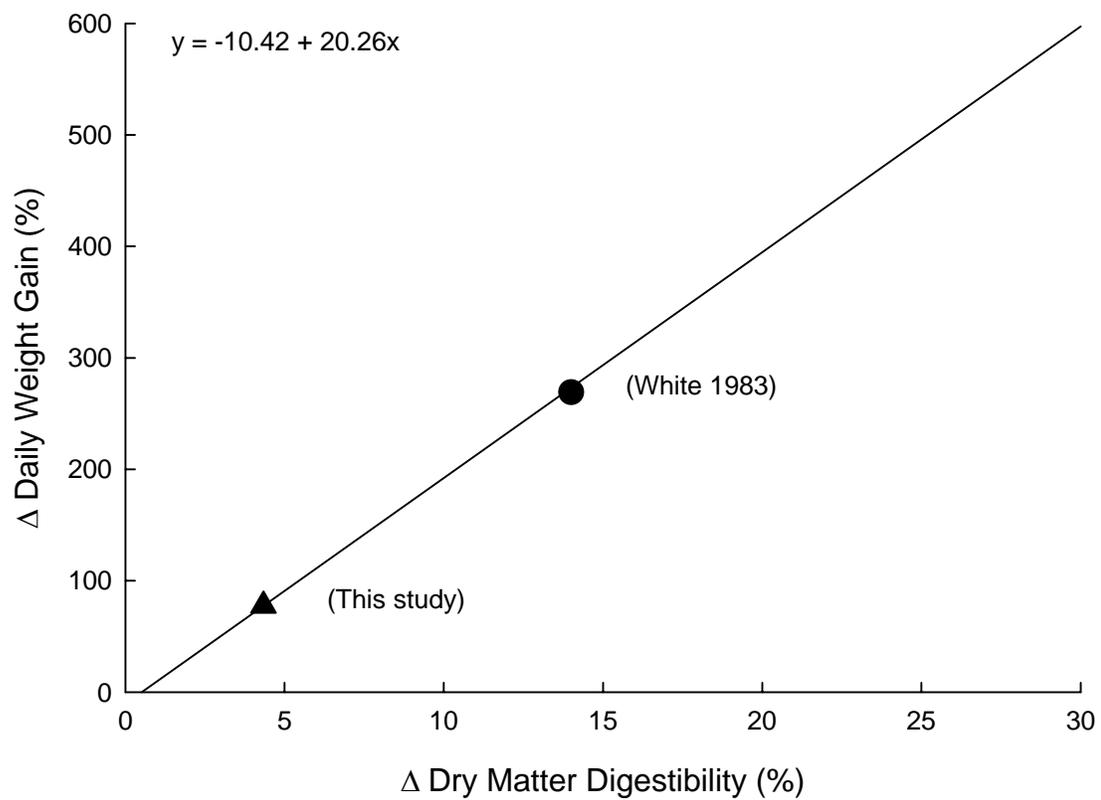


Figure 2.3. Relationship between % change in dry matter digestibility of cottongrass flowers and % change in daily weight gain.

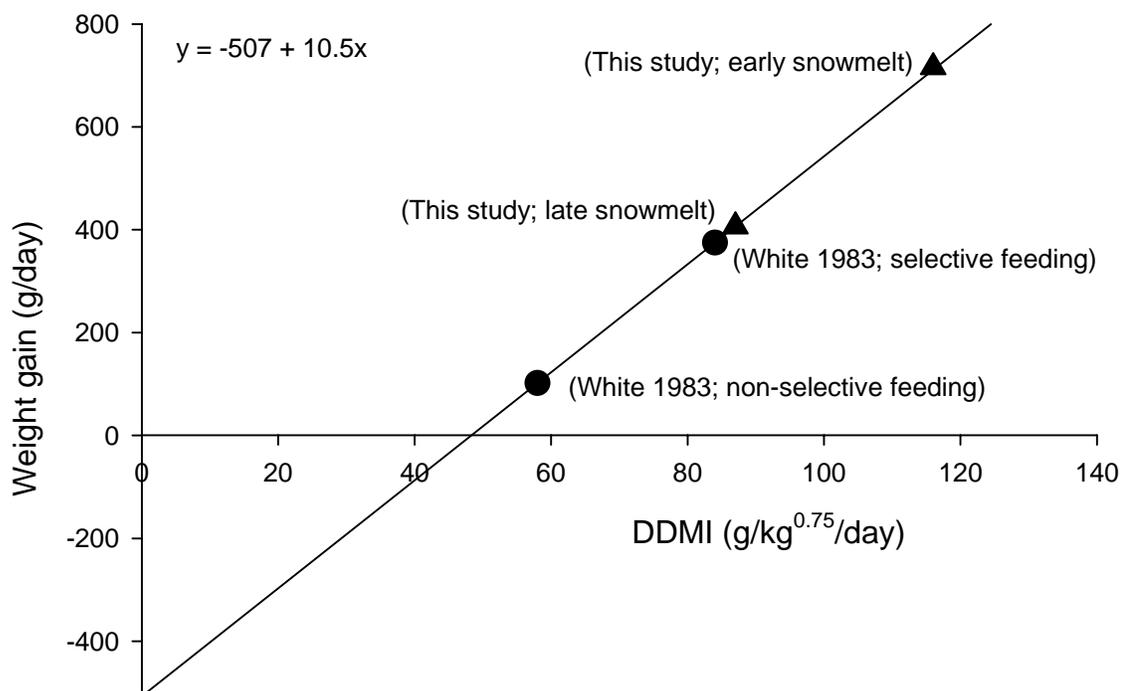


Figure 2.4. Relationship between digestible dry matter intake (DDMI) and potential weight gain for reindeer based on White (1983).

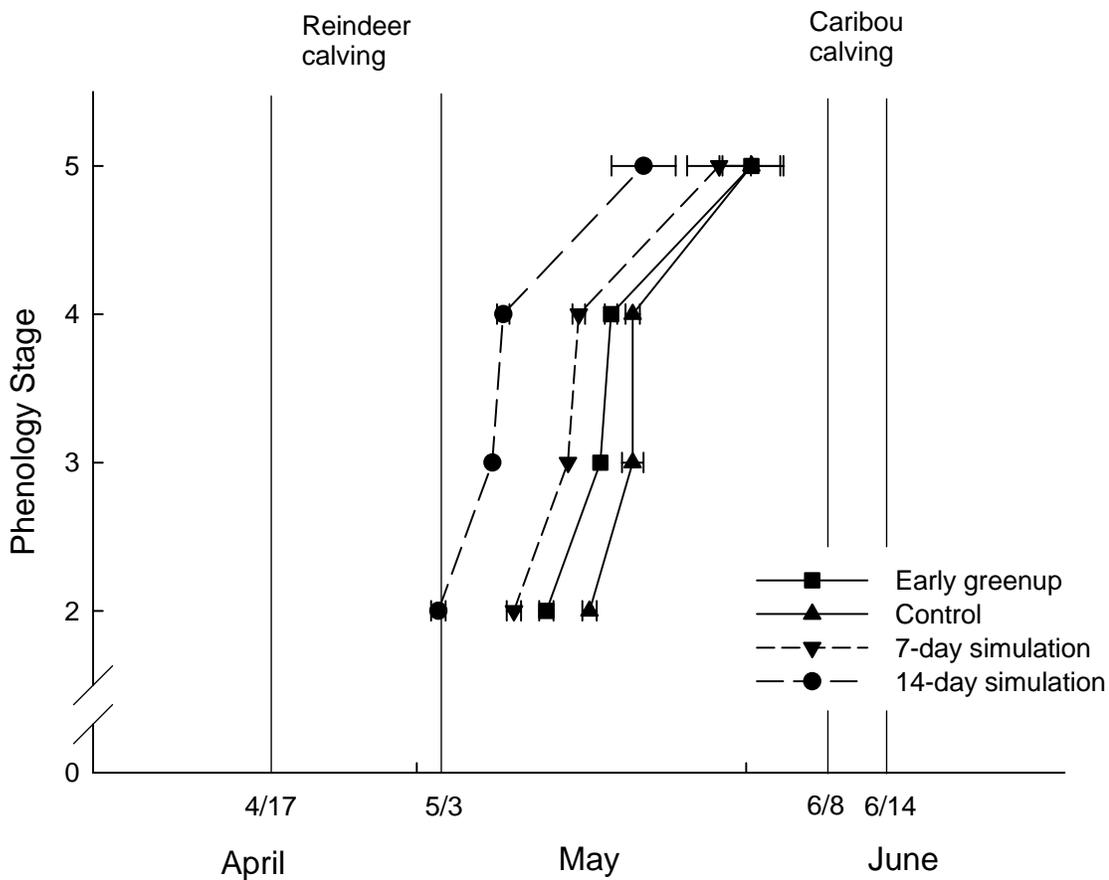


Figure 2.5. Relationship between *E. vaginatum* reproductive phenology and calving time for Seward Peninsula reindeer (Chetkiewicz, 1993) and Western Arctic Herd caribou (Davis and Valkenburg, 1978). Dashed lines are model simulations of seven and fourteen day advances in greenup.

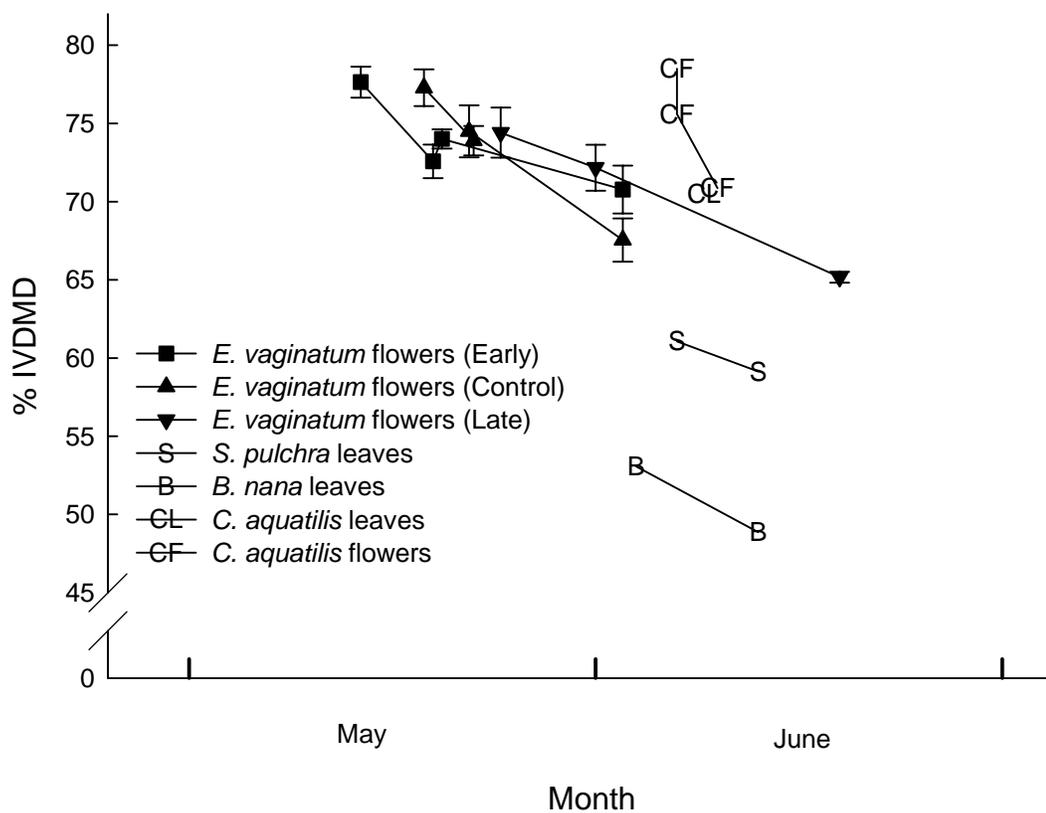


Figure 2.6. Relationship between in-vitro dry matter digestibility and date for *E. vaginatum* and *C. aquatilis* flowers, and *S. pulchra*, *B. nana*, and *C. aquatilis* leaves. Data for *E. vaginatum* are means and standard errors from Chapter 1. Data for *C. aquatilis*, *S. pulchra*, and *B. nana* are means only.

General Conclusion

The early emergence of tussock cottongrass in light of early snowmelt is only indicative of how other forage plants will respond to potential climatic changes in the Arctic. Associated changes in forage quality may have different effects on various herbivores, but reindeer in the Seward Peninsula likely stand to gain as I have shown here. However, the basic pathways linking climatic changes and growth and reproductive success of other herbivores on the Seward Peninsula will likely be through phenological and chemical changes in key forage plants.