

Effects of elevated CO₂ on keystone herbivores in modern arctic ecosystems

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“Current atmospheric CO₂ enrichment represents a dietary change of the biosphere not preceded in the past 0.5 million years.” (Korner 2000)

A central theme of this chapter is that elevated atmospheric CO₂ will directly alter growth and nutrient quality of arctic plants as well as indirectly change climate especially at high latitudes. Determining how this environmental change will affect arctic ecosystems requires an understanding of the physiological ecology of arctic biota as well as the strength and nature of biotic interactions. For example, changes in plant abundance and quality associated with elevated atmospheric CO₂ could negatively affect herbivores and so alter the competitive interplay between species and thus the ecological community.

Since much has recently been written about the effect of elevated CO₂ on the physiology and ecology of arctic plant communities (Chapin et al. 1992; Oechel and Vourlitis 1996; Oechel 1997; Dormann and Woodin 2002), in this chapter we primarily focus on the potential effects of these environmental changes on key consumers in Arctic ecosystems, specifically herbivores. Thus, a second theme of this chapter is that elevated CO₂ will affect the interaction between herbivores in arctic ecosystems and their plant food supply. We primarily focus on keystone herbivores in extant arctic ecosystems because they provide important insights into the effect of changes in plant quality and quantity on herbivore populations, specifically, and arctic ecosystems, in general.

1.1 Elevated atmospheric CO₂ will change climate especially at high latitudes

Carbon availability to plants has increased at least 30% during the past 150 years due to burning of fossil-fuels and forest destruction – this same level of increase in carbon availability has occurred historically, but over ca. 500,000 years (Petit and al. 1999). This acceleration of CO₂ enrichment with industrialization is projected to continue so that by the end of the 21st century the concentration of CO₂ in the earth’s atmosphere will have doubled compared to preindustrial concentrations (IPCC 1996).

Increased availability of carbon affects plant growth (via fertilization) and plant quality, as discussed in the next section (Section 1.2). Besides this fertilization effect of CO₂ enrichment, increased atmospheric CO₂ will also contribute to global warming because CO₂ is one of the “greenhouse gases” (e.g., (Crowley 2000)). The effect of global warming on arctic ecosystems, the region north of the latitudinal treeline, is difficult to ascertain because many other components of the climate system besides the greenhouse gases will also change (e.g., hydrological processes)(Korner 2000). However, current predictions suggest that global warming will vary across the globe with relatively small changes in temperature near the equator and the most substantial changes (>4 °C) occurring at high latitudes such as the arctic. These types of large-scale increases in temperature in the arctic would change the seasonal phenology of arctic biota (Penuelas and Filella 2001; Lucht et al. 2002), cause substantial changes in distribution and abundance of plants (Davis and Shaw 2001) and animals (Walker et al. 2001), and may

alter the significant amount of carbon now stored in arctic soils thus further elevating atmospheric CO₂ (Oechel and Billings 1992).

Changes in seasonal phenology would have profound effects on the fauna in arctic ecosystems. For example, the breeding season of many arctic herbivores coincides with periods of maximal availability of young plant tissue that is most nutritious (e.g., (Raveling 1978; Sedinger and Raveling 1986; Prop and de Vries 1993; Gunn and Skogland 1997)). Increased ambient temperature would increase plant growth rate and so reduce the time period during which high-quality immature forage is available (Ayres 1993) and also directly affect the nutrient quality of forage plants (Tolvanen and Henry 2001). This can create a phenological mismatch between consumer and consumed that negatively affects reproduction (Dunn and Winkler 1999; Both and Visser 2001) and hence their populations (Boyd and Madsen 1997; Prop et al. 1998; Inouye et al. 2000; Price and Root 2000; Root and Schneider 2002).

The primary prediction regarding changes in plant distribution and abundance with climate change is that shrub-tundra and taiga communities will spread northward and replace tussock-tundra (Bliss and Matveyeva 1992). Such a change in plant communities would decrease the abundance of tundra graminoids that, in turn, would adversely affect populations of arctic grazers. For example, large-scale climatic variability associated with the North Atlantic Oscillation between 1928 and 1977 was significantly related to plant phenology and interannual changes in growth, fecundity, and population trends for seven species of northern ungulates (Post and Stenseth 1999). If habitat preferences of contemporary herbivores remain fixed as plant distribution and abundance changes, then browsing mammals currently inhabiting taiga (e.g., moose, snowshoe hare) will likely replace browsing mammals currently inhabiting shrub-tundra (e.g., caribou) as well as vertebrate grazers (e.g., voles, lemmings, geese) in the arctic (Bryant and Reichardt 1992; Kerr and Packer 1998; Walker et al. 2001).

In the remainder of this chapter, we primarily focus on the direct effect of CO₂ enrichment on arctic ecosystems (versus indirect effects of CO₂ enrichment such as global warming (Chapin et al. 1992; Arft et al. 1999)).

1.2 Effects of elevated CO₂ on growth and nutrient quality of arctic plants

Our understanding of how elevated CO₂ affects plant growth and quality is largely based on studies of plants that are endemic to mid-latitudes and not high-latitudes (Bazzaz 1990; Mooney et al. 1991). However, some studies have focused on the direct effects of elevated CO₂ on arctic plants in intact arctic ecosystems (reviewed by (Oechel and Billings 1992; Dormann and Woodin 2002)(Table 1). Elevated CO₂ has a short-term (days to weeks) positive effect on plant productivity, but over longer timescales (months to years) there is often a complete homeostatic adjustment that results in similar rates of photosynthesis in plants exposed to ecologically relevant but different levels of ambient CO₂ (Tissue and Oechel 1987; Oechel and Vourlitis 1996). In general, these studies reveal that elevated CO₂ has relatively minor direct effects on photosynthesis and net

primary productivity of arctic plants with the level of plant response primarily depending on temperature, and water and nutrient availability (Oechel and Billings 1992; Oechel and Vourlitis 1997).

Although elevated CO₂ has relatively minor direct effects on photosynthesis and net primary productivity of arctic plants, elevated CO₂ significantly changes plant quality (Bryant and Reichardt 1992). In general, the carbon:nitrogen ratio in plants increases with CO₂ enrichment (Ayres 1993; Cotrufo et al. 1998; Korner 2000). The increased carbon availability is often used by plants to increase the amount of carbon-based secondary compounds such as tannins (especially in C₄ woody plants) (Jonasson et al. 1986; Bryant and Reichardt 1992), or fiber (in C₃ plants) (Ayres 1993). Nitrogen limitation is often associated with CO₂ enrichment so that plants have less tissue protein (Berendse and Jonasson 1992; Cotrufo et al. 1998). Thus, from an herbivore's perspective, the increased plant fiber or secondary compounds, and decreased protein in plants grown in conditions of elevated CO₂ directly reduces the nutritional quality of the plants (Ayres 1993). As discussed in the next sections, these changes in plant resource allocation associated with elevated CO₂ are predicted to affect growth and condition of herbivores, herbivore population dynamics, and the reciprocal interactions between arctic herbivores and the plant communities upon which they depend.

Although we focus in this review on the direct effects of elevated CO₂ on plant quality and how this will affect certain herbivores, it is worth emphasizing that elevated CO₂ will directly and indirectly influence interactions between plants and herbivores. For example, the increased carbon availability to plants with elevated CO₂ will likely interact with the effect of elevated CO₂ on ambient temperature and its effect on plant quality (Oechel and Billings 1992). Increased ambient temperature would likely increase nutrient availability in the arctic ecosystem so that plants may then route available carbon to growth rather than the production of carbon-based fiber or secondary compounds. Increased ambient temperature would also directly affect herbivore energy and nutrient requirements, development, and survival. Thus, elevated CO₂ will certainly affect plant-herbivore interactions in several ways (Ayres 1993). We focus here on one dramatic effect of elevated CO₂ on plant-herbivore interactions: how changes in plant quality can directly affect keystone herbivores in arctic ecosystems.

1.3 Top-down and bottom-up processes: the importance of keystone herbivores in arctic ecosystems

Understanding how elevated CO₂ will affect arctic ecosystems requires knowledge of how elevated CO₂ will directly influence plant growth and quality, and how these changes in plant growth and quality will, in turn, influence consumers in higher trophic levels. Biotic communities in arctic ecosystems are primarily organized in linear food chains with distinct trophic levels (i.e., "trophic ladders") rather than in food webs with less distinct trophic levels (i.e., "trophic webs") (Strong 1992). Since arctic ecosystems have relatively low species diversity (Hansell et al. 1998), low annual primary production (Bliss 1986), and are organized in multiple trophic ladders, predicting how changes in

primary producers will influence consumers should be relatively straightforward. However, even for the relatively simple arctic ecosystem, there are multiple controls on ecosystem processes that complicate our ability to predict the effect of perturbations such as elevated CO₂.

According to Drent and Prins (1987), the distribution and abundance of arctic herbivores is largely determined by “bottom up” processes such as nutrient availability to plants. Thus, increased plant growth associated with elevated CO₂ would increase primary productivity and, in turn, would support more herbivores. However, the simultaneous decrease in plant quality associated with elevated CO₂ would nutritionally challenge some arctic herbivores and likely compromise their ability to numerically respond to the predicted increase in plant growth (see section 1.5).

There are also “top down” processes such as herbivory and predation in arctic ecosystems that are important in influencing how the biota responds to elevated CO₂. Arctic ecosystems are unusual in that some herbivores such as geese are “keystone” species (Kerbes et al. 1990; Jefferies 1999) meaning they have a significant and disproportionately large impact on the ecosystem (Paine 1966; Paine 1969; Power et al. 1996). Keystone species in other ecosystems are usually predators (e.g., sea otters, starfish) near the top of the food chain rather than mid-level consumers such as herbivores (Strong 1992; Bond 1994).

The role of geese as keystone species in arctic ecosystems is described in the next section. The important point here is that the population density of keystone herbivores in arctic ecosystems affects the relative strength of top-down and bottom-up forces. At high population densities, keystone herbivores exert strong top-down influences on forage plants that can lead to runaway consumption and destruction of the arctic vegetation (Jefferies 1997; Jefferies 1999; Handa et al. 2002). In contrast, at lower herbivore population densities, resources available to plants may limit their productivity which then will exert strong bottom-up control of herbivore populations (Drent and Prins 1987). In short, keystone herbivores in arctic ecosystems are of central ecological importance and so must be considered when determining how elevated CO₂ affects arctic ecosystems.

1.4 Geese as keystone herbivores in arctic ecosystems and trophic cascades

Herbivores in extant arctic ecosystems include relatively small populations of large mammals (e.g., muskox, caribou), large and often cyclic populations of small mammals (e.g., voles, lemmings), resident galliformes (e.g., grouse, ptarmigan), and migratory waterfowl (e.g., geese and a few duck species) (Bliss 1975; Batzli et al. 1980; Bliss 1986; Jefferies et al. 1992). Muskox and caribou are the only two ungulate species that are resident in the northernmost regions of the world (Klein 1986). Muskox are relatively unselective, bulk feeders that can eat plants high in fiber, whereas caribou are selective grazers whose performance is strongly affected by forage quality (White 1983; White and Fancy 1986). Voles and lemmings are also selective grazers, their population dynamics are directly influenced by plant quality and quantity, and their grazing can have dramatic

affects on the habitat (Batzli et al. 1980; Batzli 1983; Oksanen 1983; Bliss 1986). Grouse and ptarmigan as well as medium-sized mammals such as arctic hares do not occur at sufficiently high densities in arctic ecosystems to have major impacts on the vegetation (Batzli et al. 1980).

For the purposes of this review, we have chosen to focus on geese that inhabit primarily coastal salt marsh and adjacent uplands in arctic ecosystems for three main reasons: (1) avian herbivores such as geese require relatively high-quality forage and so changes in plant quality, like that predicted to occur with elevated CO₂, should rapidly affect their distribution and abundance; (2) coastal regions, in general, and those in the arctic, in particular, are especially vulnerable to changes in sea level like that predicted to occur with elevated CO₂ and global warming; and (3) geese are keystone species in this system (Kerbes et al. 1990; Jefferies 1999) that can consume as much as 90% of the net aboveground primary production (Cargill and Jefferies 1984). Thus, we focus on arctic-nesting geese because these keystone herbivores and their primary habitat are both likely to sensitively respond to the environmental change predicted with elevated atmospheric CO₂.

Body size is thought to put limits on the quality of foods that can be eaten by herbivores. In general, as body size of herbivores declines so does the fiber level of the selected diet and the proportion of energy requirements satisfied by energy yield from fermentation (Illius and Gordon 1993; Cork 1994). This pattern of decline in reliance on fiber with decreasing body size in vertebrate herbivores is thought to occur because of unequal allometries of energy requirements and gut capacity (Demment and Van Soest 1985). The relative rarity of avian herbivores (i.e., only 3% of extant bird species) suggests these allometric constraints are especially difficult to circumvent for birds (McWilliams 1999). True geese are exceptional birds in that they eat leaves throughout their life cycle and they are strong flyers with associated high metabolic rates. Thus, geese are expected to sensitively respond to changes in plant quality and quantity because they require relatively high-quality and quantity of forage to satisfy their relatively high energy and nutrient requirements (McWilliams 1999).

Evidence for geese as “keystone herbivores” in Arctic ecosystems (Kerbes et al. 1990; Jefferies 1999) includes the effect of their grazing on plant primary production (Cargill and Jefferies 1984; Bazely and Jefferies 1985; Jefferies 1988b; Hik and Jefferies 1990; Gauthier et al. 1995; Person et al. 1998), on plant succession (Bazely and Jefferies 1986; Drent and Wal 1999), and the dramatic effect of changing density of geese on the plant community (Srivastava and Jefferies 1996; Zacheis et al. 2001) as well as ecosystem properties (Ruess et al. 1989; Bazely and Jefferies 1997; Jefferies 1999).

Overgrazing by lesser snow geese has caused large-scale, long-term changes in quality and quantity of preferred arctic plants in coastal salt-marshes throughout southern Hudson Bay and James Bay, Canada (Kerbes et al. 1990; Jefferies 1997; Handa et al. 2002). This large-scale impact of geese on the vegetation is primarily the result of improved survival and habitat on the wintering areas (in the mid-southern U.S.) which has effectively

removed what historically was the primary, density-dependent limitation on arctic-nesting goose populations (Batt 1997). These large-scale effects of overabundant geese on arctic plant communities has, in turn, negatively affected goslings attempting to grow up in arctic breeding areas with reduced plant quality and quantity (Cooch et al. 1991; Cooch et al. 2001).

The positive feedback responses between grazing goslings and their forage plants that occurs at low to moderate grazing intensities breaks down at higher grazing intensities (Jefferies 1999). Destructive removal of below-ground parts of plants and overgrazing of above-ground plant parts by geese creates bare patches of sediment which then become hypersaline during summer due to increased rates of soil evaporation (Srivastava and Jefferies 1996)(Fig. 1). The hypersaline soil conditions depress growth and inhibit recolonization of the salt-marsh graminoids so that an alternative vegetational state develops that is dominated by *Salicornia borealis*, a salt-tolerant plant species that is not eaten by geese and persists for many decades. This process is called a “trophic cascade” by ecologists and refers to runaway consumption and dominance by species at higher trophic levels (in this case by geese) that has dramatic effects through the food chain (Jefferies 1999). Trophic cascades are rare in terrestrial systems but when they do occur they are found where species diversity is low and food chains are linear (e.g., arctic ecosystems)(Strong 1992).

Clearly, understanding how elevated CO₂ will affect arctic ecosystems requires knowledge of how changes in plant growth and quality affect these “keystone herbivores” that dominate this ecosystem. We expect keystone herbivores such as geese to sensitively respond to changes in plant growth and quality because of the allometric constraints associated with being a bird that flies and eats leaves.

1.5 Reciprocal interactions between plants and herbivores in arctic ecosystems

In this section and the next, we discuss the interplay between arctic herbivores and their food plants and emphasize how changes in food quality affect plant-herbivore interactions. The reciprocal interactions between arctic herbivores and their food plants demonstrate how changes in plant quality, like those predicted to occur with elevated CO₂, can affect key consumers in arctic ecosystems.

In arctic ecosystems, plant chemistry (e.g., secondary compounds) controls herbivory on woody vegetation (Bryant and Kuropat 1980; Batzli 1983), and deciduous woody plants that are browsed respond to herbivory by changing their plant chemistry (Bryant and Reichardt 1992). Vertebrate herbivores such as the arctic hare browse deciduous woody plants (i.e., they eat shoots and leaves) whereas insect herbivores eat primarily just the leaves. When deciduous woody plants are browsed, more nutrients (e.g., nitrogen) are available for the remaining shoots so that leaf growth increases and available carbon is used to support increased plant growth rather than the production of carbon-based secondary compounds. In contrast, when leaves are repeatedly eaten from deciduous woody plants by insect herbivores, then less nutrients are available for new leaf growth

and this nutrient-limitation causes a surplus of available carbon that can be used to support increased production of secondary compounds or fiber. Thus, woody plants that are browsed are higher in quality (i.e., more nitrogen, less secondary compounds) than woody plants that are defoliated by insects, and these differences in quality subsequently influence future herbivory (e.g., (Danell and Huss-Danell 1985)).

Such an interplay between arctic plants and herbivores is also evident for vertebrate grazers that eat herbaceous (nonwoody) plants. For example, flocks of arctic-nesting brent geese revisit certain areas of coastal salt marsh at intervals of time that maximize plant quality and quantity (a phenomena known as “cyclic grazing”; (Prop 1991; Rowcliffe et al. 1995; Drent and Wal 1999)). Given the time required for plants to recover from being grazed and the intake rates achieved by brent geese on swards of certain biomass, the frequency of revisitation by these geese coincided with that which maximized their intake on a given sward (Fig. 2). Thus, cyclic grazing by brent geese effectively increased the amount of high-quality forage plants available to the geese within a season (Drent and Wal 1999).

Moderate grazing by geese increases the quality of forage because newer, younger plant tissue is higher in nitrogen and lower in fiber (Fig. 3). For example, grazing by lesser snow goose goslings increased net above-ground primary productivity by up to 100% and increased nitrogen concentration in forage plants, in large part because the droppings produced by feeding goslings increased available nitrogen for plant growth (Cargill and Jefferies 1984; Bazely and Jefferies 1985). Thus, goslings modulate nitrogen flow in this arctic ecosystem by their grazing and so increase the quality and quantity of available forage (Jefferies 1988b; Jefferies 1988a; Jefferies 1999).

1.6 How keystone herbivores respond to reduced plant quality like that predicted to occur with elevated CO₂.

As discussed above, elevated atmospheric CO₂ consistently causes changes in plant quality that generally reduce the plant’s nutritional value for herbivores. Since the effects of CO₂ enrichment on the forage quality of plants is predicted to be especially evident in C₃ plants, which predominate in arctic ecosystems, the effect of reduced forage quality on arctic herbivores is particularly pertinent yet poorly understood (Dormann and Woodin 2002). Most research on the response of herbivores to CO₂–treated plants has focused on insect herbivores inhabiting temperate systems (reviewed by (Lincoln et al. 1993; Lindroth 1996)). We are unaware of any research that focuses on the response of arctic herbivores to changes in plant quality directly caused by elevated atmospheric CO₂. Thus, we will focus here on how arctic herbivores respond to forage with increased plant fiber and decreased protein since these are the expected changes in quality of plants grown under conditions of elevated CO₂.

During the breeding season in the Arctic, adult geese and goslings select plant species and plant parts that are high in protein and low in fiber (Sedinger and Raveling 1984; Gauthier and Bedard 1990; Krapu and Reinecke 1992; Fox 1993; Laing and Raveling

1993; Manseau and Gauthier 1994). High-quality forage (low fiber, high protein) is needed by geese and goslings during this time to satisfy the high nutrient requirements for breeding and growth, respectively (Sedinger and Raveling 1986; Sedinger 1992). Protein content is an important nutrient because nitrogen is typically a limiting nutrient for herbivores (Mattson 1980) especially during growth and reproduction (Robbins 1993), and geese are relatively inefficient at retaining dietary protein (Sedinger 1997). Fiber content is important because it largely determines digestibility of forage and may limit food intake (Sedinger and Raveling 1988; Sedinger 1997).

The requirement for high-quality forage should make it difficult for avian herbivores such as geese to survive when plant quality and quantity diminishes as predicted with elevated CO₂. Few studies have directly tested how wild herbivores respond to reduced forage quality. Small mammalian herbivores (e.g., voles) increase intake and passage rates and reduce fiber digestibility when eating higher fiber diets (Batzli et al. 1994; Cork 1994; Owl and Batzli 1998). This potentially important adjustment in intake and digestibility in response to changes in dietary fiber has rarely been studied in avian herbivores (McWilliams 1999). In one of the few such studies, Japanese quail increased daily food intake with increased dietary fiber, as predicted, although digestibility did not change (Savory and Gentle 1976a; Savory and Gentle 1976b).

To address how extant avian herbivores respond to reduced forage quality, we fed Canada goose and lesser Snow goose goslings from hatch until at least 100 days old on one of six diets that were a factorial combination of two levels of fiber and three levels of protein. All birds received the same dietary fiber levels (either 45% or 30% neutral detergent fiber (NDF)) throughout growth. Levels of dietary protein were high (18%), medium (14%), or low (10%) for goslings after 21 days old. The levels of dietary protein and fiber were chosen based primarily on ecological relevance and nutritional adequacy. In short, the lower level of dietary fiber was representative of selected foods of wild goslings whereas only a few selected wild foods contained as much fiber as those in our higher level of dietary fiber (Sedinger 1992). We expected this higher level of dietary fiber to increase processing time and thus potentially limit food intake of goslings. The levels of dietary protein were at or below expected protein requirements (ca. 18%) of young growing goslings based on studies of domestic waterfowl (NRC 1984).

All diets were formulated from the same five ingredients: beet sugar (*Beta vulgaris altissima*), soybean (*Glycine max*) meal, orchard grass (*Dactylis glomerata*) hay, oat (*Avena sativa*) hulls, and wheat (*Triticum aestivum*) middlings (a flour-byproduct). Use of these ingredients insured that the dietary fiber was primarily from grasses as it is for wild goslings (Sedinger 1992). The following measurements were made on each gosling every 2-3 days after hatch until they were at least 100 days old or until growth was complete: body mass, culmen, tarsus, head length, and length of 9th primary (Dzubin and Cooch 1992).

Diet quality affected survival of Snow goslings especially early in growth, whereas diet quality had less effect on survival of Canada goslings (Fig. 4). For Snow goslings but not Canada

goslings, survival was consistently lower for birds fed the two 10% protein diets and for birds fed the higher fiber diet at each level of dietary protein. There were also important differences in survival between Snow and Canada goslings fed the same diets. Survival of Snow goslings fed the two 10% protein diets was lower than Canada goslings fed the same diets (LP/HF diet: $\chi^2 = 16.0$, d.f.=1, $p=0.0001$; LP/LF diet: $\chi^2 = 5.6$, d.f.=1, $p=0.02$). Similarly, survival of Snow goslings fed the high protein, high fiber diet was lower than Canada goslings fed the same diet ($\chi^2 = 5.3$, d.f.=1, $p=0.02$). These results suggest that Snow geese have higher protein requirements during growth (>10%) than Canada geese, and that Canada goslings can survive better than Snow goslings when eating diets with more fiber. These results suggest that Snow goslings require a higher quality foraging environment than Canada goslings for normal growth.

Diet quality also affected growth rate and size of Snow and Canada geese (Fig. 5). Growth rate and structural size, as indexed by tarsus length, were significantly reduced for both Canada and Snow geese fed the low protein diets. Feather growth, as indexed by length of ninth primary, was also delayed for both goose species fed the low protein diets. We detected no significant effects of dietary fiber on growth of goslings, suggesting geese were able to compensate for this aspect of reduced diet quality (see next section).

For arctic-nesting geese, slower growth, smaller body size, and delayed feather growth of goslings is associated with reduced survival and fitness (Cooke et al. 1995; Cooch et al. 2001) and so these effects of reduced diet quality can have major impacts on goose population dynamics. If elevated CO₂ generally reduces forage quality of arctic plants as expected, then the interspecific differences in nutritional requirements and growth rates of Snow and Canada goslings would suggest that Snow geese would be more affected by reduced forage quality than Canada geese. Thus, the response(s) of such avian herbivores to changes in plant quality and quantity associated with elevated CO₂ is likely to be strongly negative and species-specific.

1.7 Genetic variation and phenotypic plasticity influence an organism's response to environmental change

The ability of plant and animal species to respond to environmental change depends on the level of genetic variability within species as well as the ability of specific genotypes to flexibly respond as the environment changes. Arctic plants exhibit substantial ecotypic variation which increases the chances that some populations will survive when the environment changes (reviewed by (McGraw and Fetcher 1992)). Arctic herbivores such as Canada geese (*Branta canadensis* subsp) also have substantial ecotypic variation with at least 11 or >100 recognized subspecies depending the authority (Bellrose 1980; Shields and Cotter 1998).

Phenotypic plasticity may also enable individuals to favorably respond to environmental change. Recent work with arctic-nesting geese has demonstrated considerable phenotypic flexibility in their digestive system that has important ecological implications (McWilliams and Karasov 2001). For example, Snow and especially Canada goslings

increase their food intake with increased dietary fiber to compensate for the decrease in digestibility of the higher-fiber diet (Fig. 6). A reduction in diet quality is also associated with an increase in digestive capacity (Fig. 7) which allows goslings to eat more of the lower quality diet while maintaining retention time of digesta and metabolizability of the diet relatively constant (McWilliams et al. 2000). These same patterns of digestive response in relation to diet quality have been documented for other relatively small herbivores (Cork 1994; Iason and Wieren 1999).

We know little about the extent of phenotypic plasticity in different species living in arctic ecosystems and its ecological implications. Presumably, species that can flexibly respond are more likely to successfully adapt to environmental changes compared to other species that are inflexible (Pigliucci 1996; Piersma and Lindstrom 1997). Our results indicate that arctic-nesting geese have significant phenotypic flexibility in their digestive system yet there is clearly a limit to this flexibility as indicated by their slow growth and reduced survival when fed diets high in fiber and low in dietary protein. For most birds, maximum size of the digestive tract is likely limited by constraints associated with flying (McWilliams and Karasov 2001). Thus, arctic-nesting geese can flexibly respond to short-term changes in diet quality, but the extent of change in forage quality expected with elevated CO₂ may well exceed their capacity.

1.8 Migration and mobility influence an organism's response to environmental change

Migration of both plants and animals will play a role in the redistribution of arctic biota in response to elevated CO₂ (Davis and Shaw 2001). In general, evidence from past climatic change demonstrates that species migrate individualistically rather than as assemblages, so that autoecological studies should be useful for predicting response(s) of extant biota to future environmental change (Cronin and Schneider 1990; Graham and Grimm 1990; Davis and Shaw 2001).

Arctic herbivores vary tremendously in their mobility with the most sedentary (e.g., voles and lemmings) exhibiting dramatic and often cyclic population fluctuations, whereas the most mobile (e.g., migratory geese) apparently are able to find preferred habitat when it is available (Boyd and Madsen 1997). If responding to changes in plant quantity and quality simply involves spatially and temporally tracking preferred habitat, then animal species that can outpace the rate of environmental change will survive and those that cannot will perish. Arctic ecosystems are characterized by short growing seasons with high daily rates of plant production (but low annual productivity) even when ambient temperatures are only slightly above freezing (Bliss 1986). Birds especially use their mobility afforded by flight to capitalize on the brief pulse of productivity during the arctic summer – an impressive 15% of the world's bird species breed in the arctic but then spend the nonbreeding period in more hospitable temperate or tropical climes (Hansell et al. 1998). Thus, arctic-nesting birds provide good examples of highly mobile animals that can effectively track their preferred habitat over relatively large spatial scales (Boyd and Madsen 1997).

However, major changes in plant quantity and quality, and interactions between predators, herbivores, and primary producers are expected with elevated CO₂ that may affect Arctic wildlife populations even if they are highly mobile (Root and Schneider 2002). For example, breeding during the short arctic summer requires relatively fast growth rates for especially larger animal species such as geese. Faster growth rates of goslings increase short-term nutritional requirements. Thus, although arctic-nesting geese are quite mobile, their life history is such that large-scale reductions in plant quality and quantity or changes in plant phenology would negatively affect gosling growth and survival unless adaptation was to occur. Undoubtedly, the responses of arctic plants and animals to the effects of elevated CO₂ will involve an interplay of both adaptation and migration (Davis and Shaw 2001).

1.9 Summary

Elevated atmospheric CO₂ generally decreases plant quality (i.e., lower protein, increase fiber) especially of C₃ plants like those that dominate arctic ecosystems. Predicting how changes in the quality and distribution of plants will affect higher trophic levels in arctic ecosystems requires knowledge of the reciprocal interactions between keystone herbivores and their food plants. We review contemporary studies of one group of keystone herbivores in arctic ecosystems, arctic-nesting geese, and their response to changes in plant quality and quantity.

Arctic-nesting geese are good indicators of the health of arctic ecosystems because the ecological limitations associated with being an avian herbivore require them to sensitively respond to changes in plant quality and quantity. Field studies have demonstrated that goslings that grow up in areas with poor habitat quality are smaller as adults and have reduced survival and fitness compared to geese in good quality habitat. Recent captive-rearing experiments with goslings have elucidated some of the important mechanisms that cause reduced survival, size, and fitness of geese raised on poor quality forage. This recent work emphasizes the importance of phenotypic flexibility in the digestive system of keystone herbivores, and of digestive constraints in determining the lowest quality of food eaten by such herbivores. Thus, predicting the effects of elevated atmospheric CO₂ on arctic ecosystems requires understanding the interplay between phenotypic flexibility, adaptation, and migration of the arctic biota.

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Table 1. Effects of elevated atmospheric CO₂ on characteristics of arctic plants and the arctic ecosystem depend on timescale (short-term is days to months, intermediate is months to years, and long-term is decades to centuries). Symbols denote whether the plant or ecosystem response to elevated CO₂ was higher (+), lower (-), or the same (0) compared to a control (i.e., the plant or ecosystem exposed to ambient CO₂). Data are from (Oberbauer et al. 1986; Tissue and Oechel 1987; Grulke et al. 1990; Mooney et al. 1991; Oechel and Vourlitis 1996).

Plant or Ecosystem Effect	Time-scale of response		
	Short-term	Intermediate	Long-term
Plant Effect			
Growth and Production			
Photosynthesis	+	0	0
Transpiration	+	0	0
Biomass production	+	+ / 0	?
Shoot growth	+	0	?
Root:shoot ratio	+	?	+
Tillering	+	+	?
Tissue composition			
Nitrogen concentration	-	-	-
Carbon:nitrogen ratio	+	+	+
Starch content	+	+	+
Ecosystem Effect			
Evapotranspiration	+	0	0
Net ecosystem flux	+	0	?
Net carbon storage	+	+ / 0	+ / 0
Soil enzyme activity	+	+ / -	+ / -
Soil solution nitrogen	-	- / 0	- / 0

Figure legends

Figure 1: Overgrazing and grubbing by arctic-nesting geese in the low arctic saltmarsh ecosystem of Hudson Bay, Canada, has led to reductions in plant cover, increased soil evaporation and salinity, and thus to further reduction and degradation of the saltmarsh ecosystem. This trophic cascade has led to dramatic, large-scale changes in coastal saltmarsh vegetation from a vegetation community that supported large populations of vertebrate herbivores to a system with few if any plants that herbivores find palatable. Geese are clearly keystone herbivores in this system and so must be considered when determining the effects of elevated CO₂ on arctic ecosystems. From (Srivastava and Jefferies 1996; Jefferies 1999). Reprinted with permission from Blackwell Science.

Figure 2: Keystone herbivores such as geese sensitively respond to changes in plant quantity. Available biomass of a preferred forage plant (*Plantago maritima*) initially increases with less grazing by brent geese (*Branta bernicla*) (as indexed by how often they graze the sward; for example, every day, every other day, etc.). Maximum harvest by the geese is achieved when they return to a given sward every 7 days since this allows the plant enough recovery time to allow the geese to maximize their intake rate. Too little grazing of the sward by geese allows the plants to grow beyond the optimal size for maximum harvest (based on a model by Prop (1991). The measured frequency of visits by brent goose flocks to specific swards (shown by the histogram) coincides with maximum harvest but is skewed towards slightly earlier harvest (Prop 1991). From Drent and van der Wal (1999). Reprinted with permission from Blackwell Science.

Figure 3: Grazing by keystone herbivores such as geese improves plant quality. Nitrogen content of three arctic plant species ((a) *Puccinellia phryganodes*, (b) *Carex subspathacea*, and (c) *Festuca rubra*) normally decreases during the growing season when plants are ungrazed (open circles). Moderate grazing by geese (solid circles and lines) delays the decline in nitrogen content of the three plant species and hence extends the period of time with good forage quality. During the summer breeding season, more days with high protein, low fiber forage increases growth, survival, and productivity of geese. Data for 1978 are from Cargill and Jefferies (1984) and the data for 1979 are from (Ydenberg and Prins 1981). From Drent and van der Wal (1999). Reprinted with permission from Blackwell Science.

Figure 4: Survival probability of Snow geese (A) and Canada geese (B) fed grass-based diets with either high protein and high fiber (HP,HF), high protein and low fiber (HP,LF), low protein and high fiber (LP,HF), or low protein and low fiber (LP,LF) (see text for descriptions of diets). All geese were fed these diets from hatch until they were at least 100 days old. Survival of Snow goslings was significantly affected by both dietary protein and fiber, whereas survival of

Canada goslings was less affected by diet (Kaplan Meir estimates of survival were compared using a log-rank test).

Figure 5: Body size (as indexed by tarsus length) and feather growth (as indexed by length of ninth primary feather) of growing Canada geese (A) and lesser Snow geese (B) fed grass-based diets with either high protein (solid circles) or low protein (open circles) (see text for descriptions of diets). All geese were fed these diets from hatch until they were at least 100 days old. There was no significant effect of dietary fiber on growth rates (not shown), while geese of both species fed low dietary protein grew slower than geese fed high dietary protein. No standard errors are shown for Snow geese fed low dietary protein because only one Snow goose survived to at least 60 days when fed that diet.

Figure 6: Daily food intake (adjusted for goose body mass using ANCOVA) and apparent metabolizable energy of 8-week old Canada geese and lesser Snow geese fed grass-based diets with either high fiber or low fiber (see text for descriptions of diets). All geese were fed these diets from hatch until the total collection digestibility trials were conducted when they were 8 weeks old. Canada and Snow geese digested less of the available dietary energy and ate relatively more when fed higher fiber diets. However, the smaller body-sized Snow geese increased their food intake only 11% while the larger Canada geese increased their food intake 115% when fed the low fiber compared to the high fiber diets. This suggests that food intake of Snow geese may be constrained when they consume high-fiber forage.

Figure 7: Phenotypic flexibility in digestive organs of Canada and lesser Snow geese in response to dietary fiber (see text for descriptions of diets). Gizzard mass, small intestine length, and the combined length of both caeca increased when geese were fed high-fiber diets compared to low-fiber diets (Factorial ANOVA; Goose species effect: $P < 0.0001$ for gizzard and small intestine, $P = 0.96$ for caeca; Dietary fiber effect: $P < 0.0001$ for gizzard, $P = 0.019$ for small intestine, $P = 0.004$ for caeca). There was no significant effect of dietary protein on digestive organs (not shown).

Figure 1

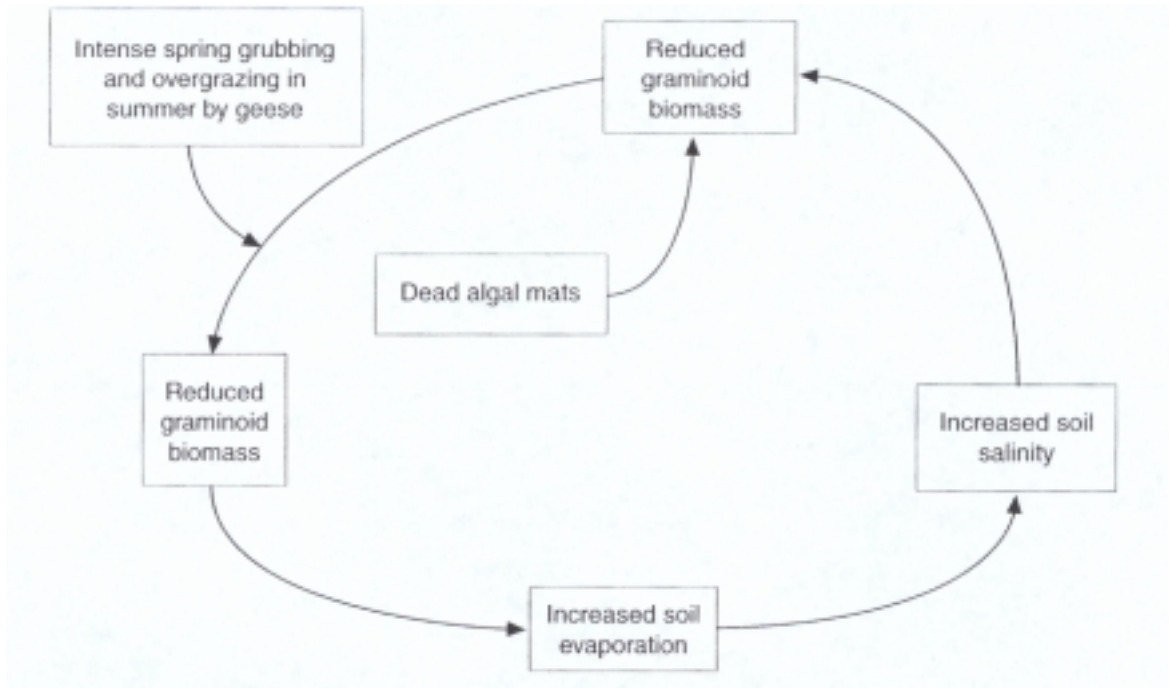


Figure 2

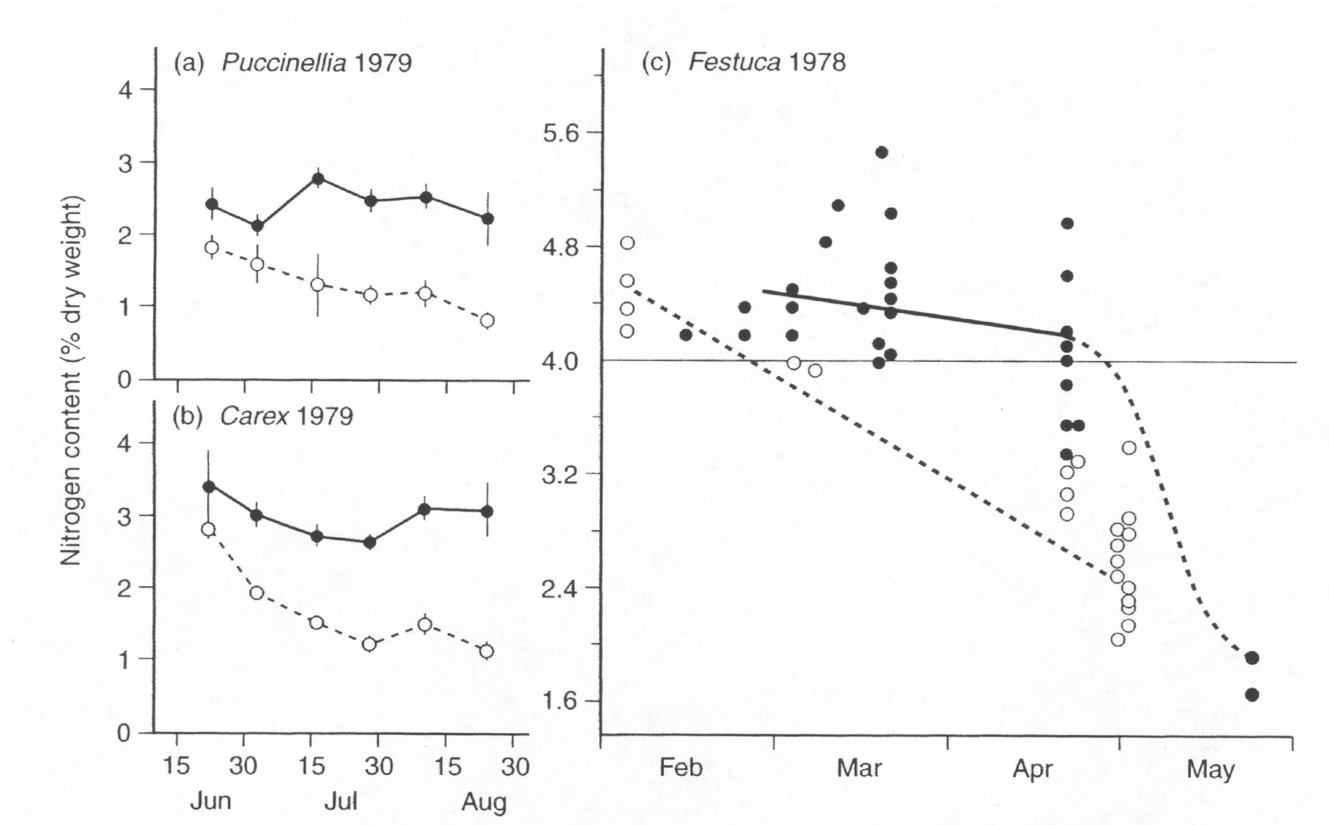


Figure 3

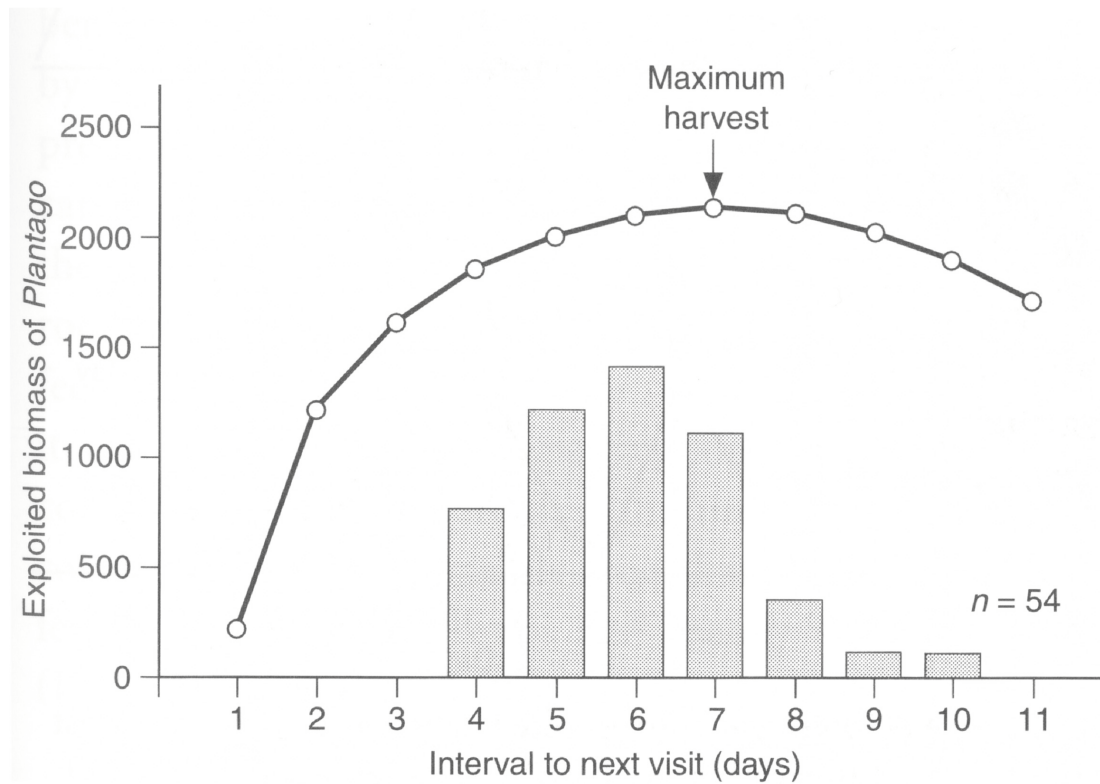


Figure 4

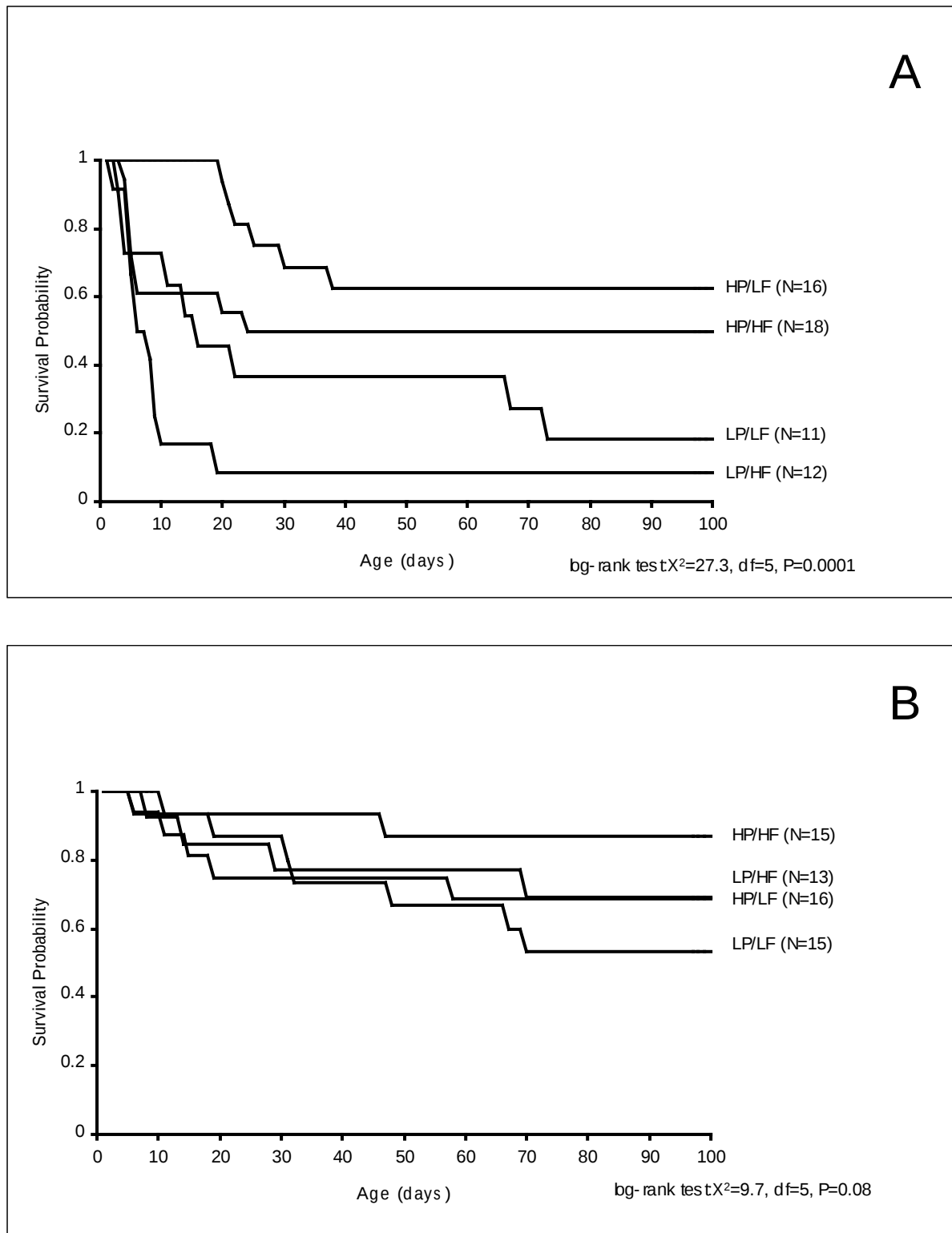


Figure 5

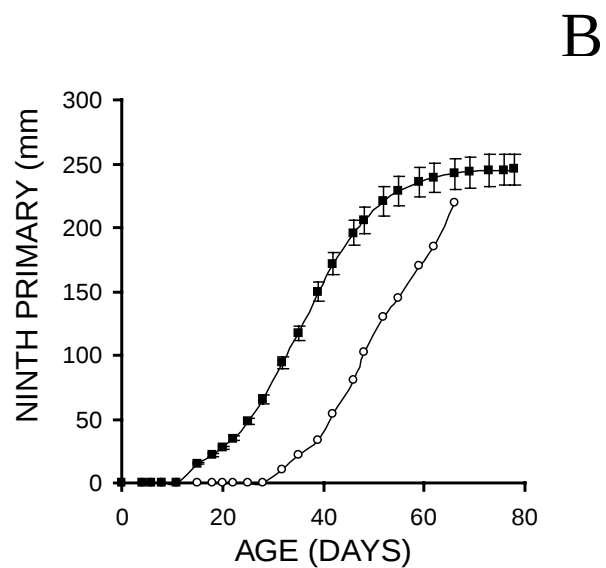
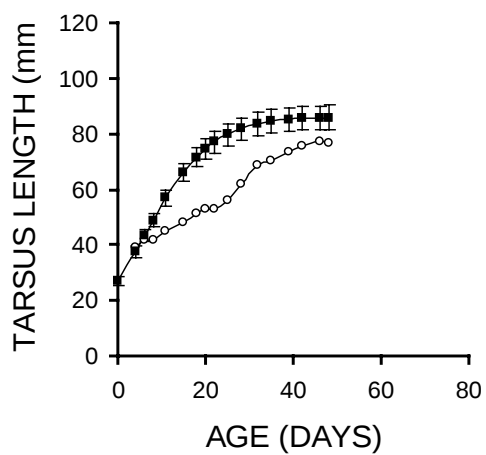
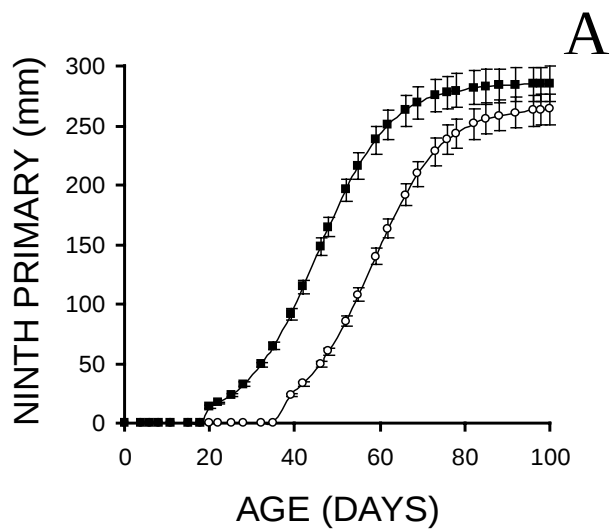
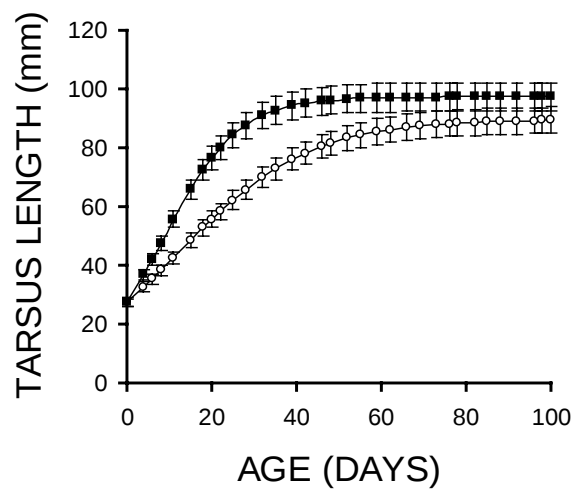
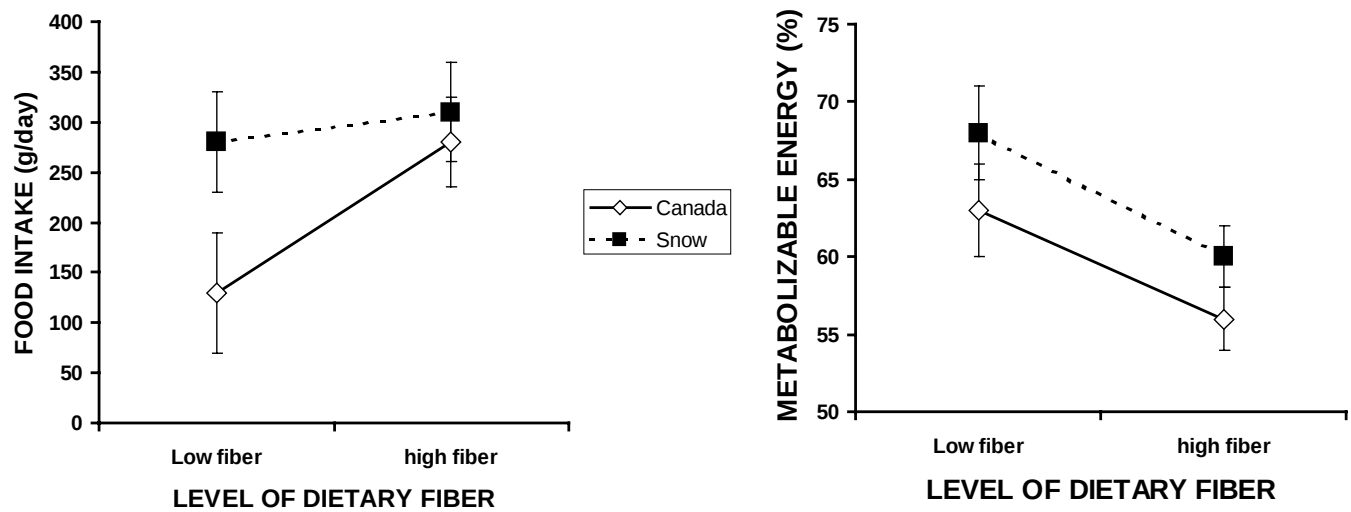


Figure 6



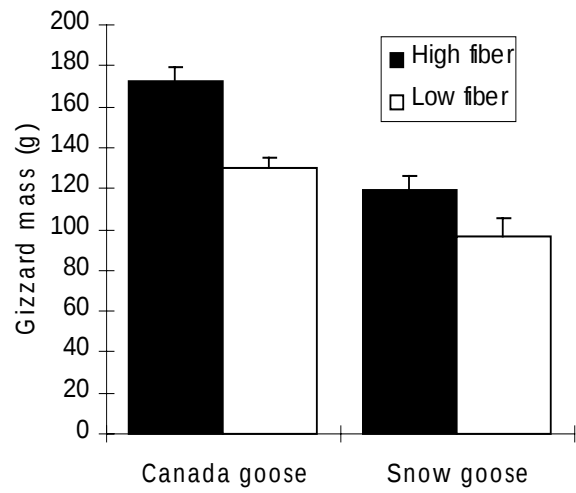


Figure 7

