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Feedback dynamics of grazing lawns: coupling vegetation change with animal growth

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Abstract We studied the effects of grazing by Black Brant (*Branta bernicla nigricans*) geese (hereafter Brant) on plant community zonation and gosling growth between 1987 and 2000 at a nesting colony in southwestern Alaska. The preferred forage of Brant, *Carex subspathacea*, is only found as a grazing lawn. An alternate forage species, *C. ramenskii*, exists primarily as meadow but also forms grazing lawns when heavily grazed. We mowed plots of ungrazed *C. ramenskii* meadows to create swards that Brant could select and maintain as grazing lawns. Fecal counts were higher on mowed plots than on control plots in the year after plots were mowed. Both nutritional quality and aboveground biomass of *C. ramenskii* in mowed plots were similar to that of *C. subspathacea* grazing lawns. The areal extent of grazing lawns depends in part on the population size of Brant. High Brant populations can increase the areal extent of grazing lawns, which favors the growth of goslings. Grazing lawns increased from 3% to 8% of surface area as the areal extent of *C. ramenskii* meadows declined between 1991 and 1999. Gosling mass was lower early in this time period due to density dependent effects. As the goose population stabilized, and area of grazing lawns increased, gosling mass increased between 1993 and 1999. Because larger goslings have increased survival, higher probability of breeding, and higher fecundity, herbivore-mediated changes in the distribution grazing lawn extent may result in a numerical increase of the population within the next two decades.

Keywords *Carex* · Geese · Phenotypic plasticity · Plant-animal interactions · Salt marsh

Introduction

High grazing pressure on preferred resources force herbivores either to switch to alternative foods or to move to areas that have greater resource availability (Vickery et al. 1995). Breeding geese switch to alternative foods that are lower in quality when preferred resources are depleted because they demonstrate both fidelity to their breeding grounds and a faithfulness to brood rearing areas (Cooch et al. 1993; Hughes et al. 1994; Gadallah and Jefferies 1995; Lindberg and Sedinger 1998). However, herbivory can either increase or decrease a habitat's capacity to support secondary production (Kerbes et al. 1990; McNaughton et al. 1997). Herbivores influence, and in some cases can regulate, forage quality and availability through changes in plant growth, community composition, and rates and pathways of nutrient cycling (Coppock et al. 1983a; Bazely 1986; Ruess et al. 1989; Hik and Jefferies 1990; Pastor and Naiman 1992; van de Koppel et al. 1996; Mulder and Ruess 1998). These effects can have positive or negative feedbacks on herbivore populations depending on the spatial and temporal magnitude of tissue removal and successional state of the ecosystem (Kerbes et al. 1990; Pastor et al. 1997; van der Wal et al. 2000). In terrestrial grazing systems, feedbacks to herbivore nutrition, growth, and life history have been inferred through modeling changes in animal condition and fecundity, and changes in the availability and quality of forage (Hobbs and Swift 1985; Coughenour and Singer 1996; Pastor and Cohen 1997; Singer et al. 1997; van der Wal et al. 2000). Perhaps the best understanding of these feedbacks comes from studies of the interactions between geese and the foods on which they rely. Gosling growth is sensitive to the quality and per capita availability of food, and population dynamics can be followed using marked individuals (Cooch et al. 1991; Larsson and Forslund 1991; Sedinger and Flint

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1991; Lindholm et al. 1994). For example, size of goslings at fledging influences first year survival, adult body size, and adult fitness (Cooch et al. 1993; Larsson and Forslund 1991; Sedinger et al. 1995). It follows that the effects of herbivory on vegetation quality and availability may scale-up to the demography and size of herbivore populations (Oosterheld et al. 1992; Cooch et al. 1993).

Like other terrestrial herbivores (McNaughton 1984; Coppock et al. 1983b), geese often create and maintain grazing lawns, defined here as vegetation swards dominated by a high density of grazing-tolerant plant species with high nutrient concentrations. Grazing lawns range from a few square meters (Person et al. 1998) to square kilometers (McNaughton 1983, 1985), influenced principally by herbivore species, herbivore densities and landscape structure. The structural and functional stability of grazing lawns is sensitive to the activities of herbivores (Bazely and Jefferies 1985; McNaughton et al. 1997), abiotic factors such as soil salinity and precipitation (East 1984; Srivastava and Jefferies 1995), and human impacts (Oosterheld et al. 1992; Jefferies et al. 1994). Despite the close association between herbivores and their food resources in systems where grazing lawns are a prominent feature of the ecosystem, a direct link between exploitation of grazing lawns and the dynamics of wild populations has not been documented.

Black Brant (*Branta bernicla nigricans*) geese (hereafter Brant) breeding in western Alaska rear their young on grazing lawns of *Carex subspathacea* (Person et al. 1998). Brant grazing pressure increased on existing *C. ramenskii* meadows over the past decade (Ruess et al. 1997). We tested if Brant would select remaining *C. ramenskii* tissues as a food source after mowing ungrazed *C. ramenskii* meadows and revisited these plots to determine if Brant could maintain these swards as grazing lawns for 5 years. These plot-based experiments were scaled-up to determine if the areal extent of grazing lawns increased over the past decade concurrent with a decrease in ungrazed *C. ramenskii* meadows throughout the Tutakoke River Brant colony. We then tested for a positive relationship between gosling mass and grazing lawn extent between 1991 and 1999 despite observations that the population appeared to be at an equilibrium below historic densities. If the extent of grazing lawns were dependent on population size and density dependent effects on animal growth could be modified by herbivores, these herbivore-mediated changes could translate into a numerical increase in this population.

Materials and methods

Study system

Population dynamics and nutritional considerations.

This study was conducted at the Tutakoke River Brant colony (61°15'N, 165°30'W) at the mouth of the Kashunuk River and Angoyaravak Bay. Approximately 30% of the Brant breeding at

Tutakoke are individually identifiable from leg bands (Sedinger et al. 1995). Historically, Brant nested in a band that stretched from the present colony to approximately 20 km up the Kashunuk River drainage (Spencer et al. 1951; King and Derksen 1986). The population was reduced from 7,400 to 1,100 nesting pairs during the late 1970s and early 1980s coincident with heavy arctic fox (*Alopex lagopus*) predation and the advent of outboard motors into the subsistence culture of the people of this region (Raveling 1986; Anthony et al. 1991, 1995; Sedinger et al. 1993; Sedinger 1996). The population has increased and stabilized at about 5,500 breeding pairs after reductions in both harvest and predation (Raveling 1989; Sedinger et al. 1993; Anthony et al. 1995). Density dependent reductions in growth, body size, and clutch size in Brant nesting at Tutakoke initially accompanied the population increase (Sedinger et al. 1998). These density dependent effects may be associated with changes in the forage base at Tutakoke if grazing lawn extent is dependent on the size of the population (Ruess et al. 1997; Person et al. 1998; Sedinger et al. 1998).

Taxonomic issues and plant communities in the Tutakoke River colony

The Yukon Kuskokwim (YK) Delta encompasses over 75,000 km² of wetlands between the Yukon and Kuskokwim Rivers. Throughout the coastal fringe of the YK Delta, *C. subspathacea*, the preferred forage of Brant, occurs as nearly monospecific grazing lawns that are maintained by grazing, whereas *C. ramenskii* occurs as a taller sedge with lower nutritional quality than that of *C. subspathacea* (Sedinger et al. 1995; Ruess et al. 1997; Person et al. 1998). These two sedges were classified as conspecifics until the late 1930s at which time they were re-classified as separate species based largely on their tiller length and floral position (Hultén 1941, 1990).

Three plant communities dominate areas used by Brant at the Tutakoke River colony: a slough levee community, *C. subspathacea* grazing lawns, and *C. ramenskii*-dominated meadows. The slough levee community occurs on elevated beach ridges and depositional levees along drainages that dissect the region. Geese forage selectively in this community for *Triglochin palustris* (Mulder et al. 1996; Mulder and Ruess 1998). *C. subspathacea* is maintained by Brant as short (0.5–3 cm height) grazing lawns occurring along coastal margins, riparian mudflats, and inland pond margins. Brant spend a disproportionate amount of time foraging on this community relative to its distribution and consume over 90% of the annual net aboveground primary productivity (NAPP) with no apparent negative effects on NAPP even though standing crop biomass is greatly reduced (Person et al. 1998). When protected from herbivores for 2 years, *C. subspathacea* can reach an aboveground biomass, nutritional quality, and growth form that does not differ from *C. ramenskii* (Person 2001). *C. ramenskii*-dominated meadows comprise the greatest areal extent of the three communities and *C. ramenskii* constitutes 60–70% of the aboveground live biomass of this community (Person 2001).

Shifts in the morphology of *C. ramenskii* and *C. subspathacea*

Mowing experiment

In 1995, we initiated an experiment in which we mowed and removed clippings from plots within *C. ramenskii* meadows in three locations across the Tutakoke River colony. We attempted to create swards that Brant would select and subsequently maintain as grazing lawns in three locations. In two locations we established four 15×15 m square treatment plots, in the third location finely dissected plant community zonation necessitated smaller plots that summed to 225 m² for each of the four treatments. The mowing treatments were applied in early June and mid-July of 1995 only. At each location we established an ungrazed plot within meadows of *C. ramenskii* that had not been converted to a grazing lawn (ungrazed control), a natural grazing plot in which geese were

already feeding on *C. ramenskii* (grazed control), an artificial grazing plot adjacent to the grazed control plot mowed to a canopy height of 5 cm (adjacent initiated), and an artificial grazing plot 150 m away from the other plots in an ungrazed *C. ramenskii* meadow (distant initiated). We included the distant initiated treatment plots because geese may have chosen and maintained the adjacent initiated plots simply because these plots were adjacent to areas already grazed, as opposed to selecting an artificially-created forage patch in the middle of a previously ungrazed meadow.

Biomass was sampled by clipping vegetation to the soil surface within five 10×10-cm quadrates. Vegetation samples were washed in fresh water, sorted to species (Hultén 1990) and standing dead biomass (SDB), dried in a field laboratory at 60°C, and stored for shipment to the University of Alaska Fairbanks, where they were dried to constant mass at 60°C and weighed to the nearest 0.001 g. We estimated NAPP using five randomly placed 30-cm diameter exclosures within all treatment plots two and three times in 1996 and 1997, respectively. We estimated NAPP as the difference between biomass within short-term exclosures and unexclosed biomass sampled at the time exclosures were established, divided by interval days (McNaughton et al. 1996). Vegetation within exclosures was sampled and processed as previously described. In 2000, we re-visited all plots but only sampled standing crop biomass (SCB) and grazing intensity from plots at one of the three locations. Vegetation at the other locations was not visibly different from the *C. ramenskii* meadows surrounding the manipulated plots, hence these plots were not maintained as a grazing lawn by Brant.

Nitrogen and carbon content of *C. ramenskii* was measured using a LECO CNS 2000 autoanalyzer after grinding vegetation through a 20-mesh size Wiley Mill. We report the carbon to nitrogen ratio (C:N) of *C. ramenskii* because higher C:N ratios represent poorer quality forage for geese (Sedinger and Raveling 1988). Fecal counts are used as an estimate of grazing intensity (Jefferies and Rockwell 2002). Fecal counts were made within randomly thrown 1-m² quadrates and statistical analyses were performed on fecal counts measured at the end of each growing season.

Our experiment was a randomized complete block design with location as the level of replication. Data were analyzed using ANOVA with year and location as class variables, 1996 and 1997 only. We included all two- and three-way interactions and removed them if they were not significant. We found a significant year × treatment × location interaction when either aboveground biomass or fecal counts were dependent variables. Therefore, these data were analyzed using one-way ANOVA followed by Tukey's honest significant difference (HSD) multiple comparisons when a significant treatment effect was found. Data were analyzed using General Linear Model procedures (SAS Institute 1990). Data were rank transformed, where necessary, in order to meet model assumptions.

Manipulation of grazing pressure on *C. subspathacea*

In 1994 we established six 1-m⁻² exclosures within *C. subspathacea* grazing lawns, and six unfenced 1-m⁻² control plots in both *C. ramenskii* meadows and swards of *C. subspathacea*. Vegetation was sampled and processed as described above. We sampled aboveground biomass from within one, 10×10-cm quadrate from each plot at the time plots were established in June 1994, again in July 1997, and in July 2001. In 1997, we removed the exclosures from the *C. subspathacea* plots which allowed wild geese to feed on the vegetation which had been protected since 1994.

Changes in the zonation of plant communities

We estimated the areal extent of plant communities at the Tutakoke colony from aerial videography tapes filmed to estimate the number of Brant nesting at the approximately 10 km² Tutakoke colony (Anthony et al. 1995). Videography was recorded by attaching a Hi

8 colour video camera to a fixed wing aircraft (Anthony et al. 1995). Between 1991 and 1999, 27 different random transects, each approximately 3 km long, were flown annually. Transects were not flown in 1996. Vegetation type was identifiable on each video image except in 1992, which was not analyzed. We estimated the percent cover of physiographic features and plant communities throughout the Tutakoke colony by taping a clear plastic sheet printed with 100 1.0-mm-diameter circles to a viewing monitor. We then identified plant communities within each circle as either grazing lawn, *C. ramenskii*-dominated meadows, or slough levee communities. We also identified the areal extent of lakes, rivers and tidal sloughs, mudflats, and miscellaneous features (e.g. driftwood) which were classified as 'other'. When a transect began we randomly paused the tape and identified the community type or feature within each printed circle. We then systematically advanced and sampled the tape every 3 s along each transect. This resulted in approximately 250 samples of the areal extent of plant communities and physiographic features for each year. Percent cover of each community type was regressed against time to test for an increase in the areal extent of *C. subspathacea* grazing lawns concurrent with a decline in the extent of *C. ramenskii*-dominated meadows. We tested for an inverse relationship between these models by comparing the absolute values of the slopes from the *C. subspathacea* and *C. ramenskii* regression models using a Z-test (Zar 1996). Data were arcsine transformed and analyzed using regression procedures (SAS Institute 1990).

Changes in gosling mass

We searched 67 random 50-m diameter plots for Brant nests annually between 1985 and 1997. We also attempted to find all nests associated with a marked male or female Brant both on and off plots. All nests and eggs within clutches were marked when found (Sedinger et al. 1995). At hatch, we revisited all marked nests and attempted to mark all goslings with a uniquely numbered fish-fingerling tag stapled through the web of their foot as they were hatching. Approximately 32 days later, we herded flightless geese into temporary corrals on a sample of brood rearing areas used by Brant families from the Tutakoke River colony. Sex was determined by cloacal examination on all goslings and gosling mass was measured (±5.0 g) with a spring scale. Goslings were then banded and released after all birds had been processed for a particular banding drive. We tested for variation in gosling mass using ANCOVA (SAS Institute 1990), with gosling sex and year as class variables, gosling age as a covariate, and possible age × year interactions.

Estimating the number of families reared from the Tutakoke river colony

We estimated the number of families reared from the Tutakoke river colony using a Lincoln-Peterson index (Poole 1974). We used the number of marked females observed during nesting as an initial sample of the number of nesting pairs using brood rearing areas that we sampled approximately 32 days later. We then used a ratio of the number of unmarked and marked females captured during banding drives to calculate an index of the number of families using brood rearing areas (Sedinger et al. 1998). The Lincoln-Peterson method conservatively estimates the breeding population because population estimates do not include those birds whose nests were destroyed by predators or abiotic events such as storm surges; therefore, we also used estimates of the number of Brant nesting in mid-June at the Tutakoke River colony between 1991 and 2000 (Anthony 2001; Anthony et al. 1995) as an additional measure of population size.

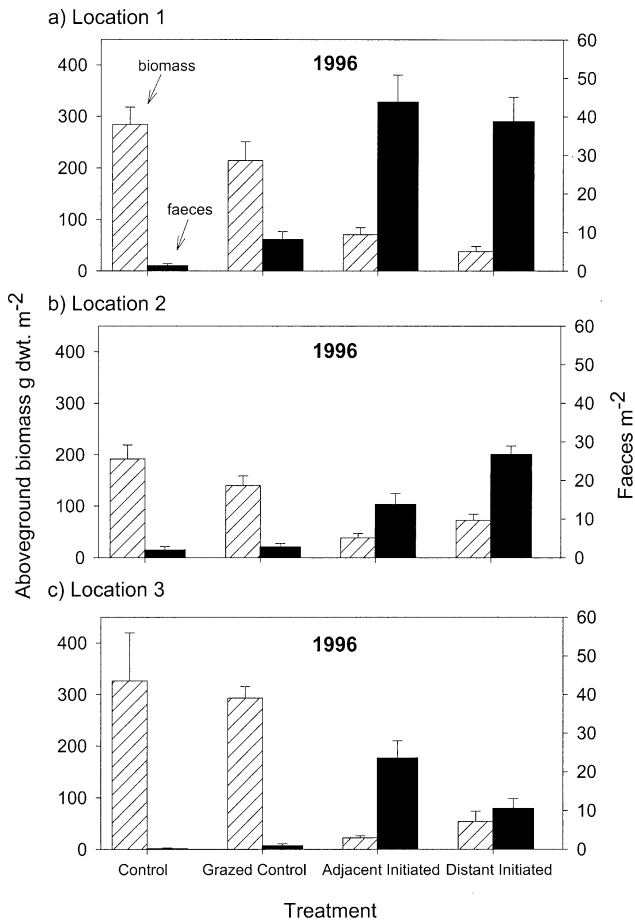


Fig. 1 Mean (\pm SE) aboveground biomass and grazing intensity, as indexed by fecal counts, at the end of the 1996 growing season in locations 1, 2, and 3. Data follow mowing treatments applied 1 year earlier to the *Carex ramenskii* community at three locations within the Tutakoke River Black Brant (*Branta bernicla nigricans*) colony on the Yukon-Kuskokwim Delta, Alaska

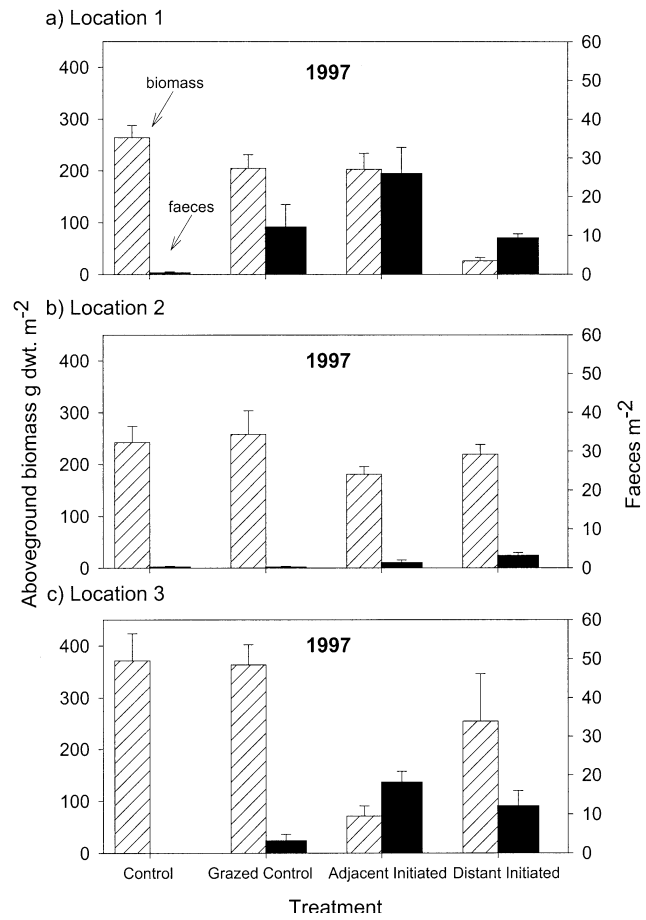


Fig. 2 Treatment differences in aboveground biomass and grazing intensity, as indexed by fecal counts, at the end of the 1997 growing season. Data follow mowing treatments applied 2 years earlier to the *Carex ramenskii* community at three locations within the Tutakoke River Black Brant colony on the Yukon-Kuskokwim Delta, Alaska. Data represent mean \pm SE

Results

Shifts in the morphology of *C. ramenskii* and *C. subspatheacea*

Mowing experiment

We found a significant year \times treatment \times location interaction for aboveground biomass ($F_{14,119}=3.7$; $P<0.0001$) and for grazing intensity ($F_{14,179}=5.6$; $P<0.0001$). To identify the variation associated with each term in this interaction we analyzed each location and year separately. In 1996, aboveground biomass was lower across all locations in plots that had been initiated the previous year (all P values <0.0003) (Fig. 1a–c). There was over 5 times more aboveground biomass in control plots than in either initiated plot when averaged across all locations. Grazing pressure was substantially higher on the adjacent initiated and distant initiated treated plots across all locations in the 1996 growing season (all P values <0.0001) (Fig. 1a–c). Grazing pressure was lowest on the ungrazed control

plots, which when averaged across all locations contained 1 ± 0.1 feces m^{-2} compared to 4 ± 0.7 feces m^{-2} in grazed control plots, and 27 ± 7.0 and 25 ± 7.0 feces m^{-2} in adjacent initiated and distant initiated treatment plots, respectively.

Fecal counts tended to be higher in both the adjacent initiated and the distant initiated treatments when compared to both control plots across all locations in 1997 (all P values <0.0001). Aboveground biomass was higher in both adjacent initiated and distant initiated treatments in 1997 when compared to 1996 (Fig. 2a–c). The negative relationship between fecal density and aboveground biomass was weaker in 1997 ($r^2=0.11$; $P=0.049$) than in 1996 ($r^2=0.49$; $P<0.0001$). Vegetation in the initiated- and control plots did not visibly differ from the surrounding *C. ramenskii* meadows in two of the three locations in 2000, 5 years after the treatments were applied. In one of the three locations there still were differences in SCB and grazing intensity where geese had maintained initiated swards as grazing lawns (Fig. 3).

NAPP did not differ among treatments while geese were incubating ($F_{3,11}=2.3$; $P=0.18$), or throughout the brood

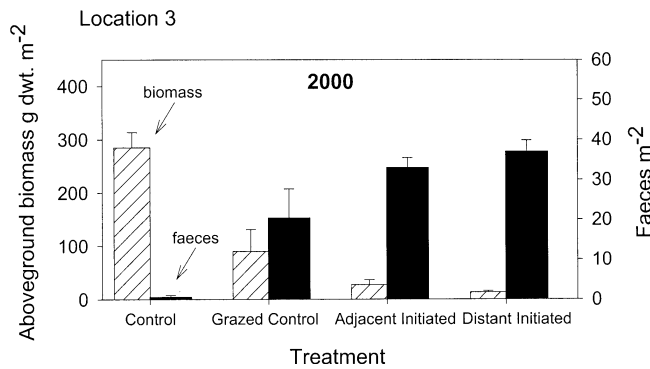


Fig. 3 Treatment differences in aboveground biomass and grazing intensity, as indexed by fecal counts, at the end of the 2000 growing season. Data follow mowing treatments applied 5 years earlier to the *Carex ramenskii* community at one of the three locations within the Tutakoke River Black Brant colony on the Yukon-Kuskokwim Delta, Alaska. Vegetation in locations 1 and 2 did not visibly differ from the surrounding *C. ramenskii* meadows therefore we did not sample it or grazing intensity. Data represent mean \pm 1 SE

rearing period of 1996 ($F_{3,11}=0.09$; $P=0.97$) (Table 1). NAPP tended to be lower in both initiated plots than in both control plots throughout the 1997 growing season (Table. 1). However, NAPP did not differ among treatments during the late brood rearing period in 1997 ($F_{3,11}=1.11$; $P=0.35$).

We found a significant year \times treatment interaction when nitrogen concentration, carbon concentration, and

C:N ratio of *C. ramenskii* sampled at the end of the growing seasons were entered as dependent variables (all P values <0.001), therefore years were analyzed separately. In 1996, *C. ramenskii* in the adjacent initiated and distant initiated treated plots had both a higher nitrogen concentration and a lower C:N ratio when compared to both controls (overall treatment P values <0.007) (Table 2). Nutritional characteristics of *C. ramenskii* tended not to differ among treatments in 1997. Vegetation in the treated plots had a higher nitrogen concentration and lower C:N ratios in 2000 when compared to control plots (Table 2).

Manipulation of grazing pressure on *C. subspathacea*

SCB within excluded *C. subspathacea* swards increased from 14 ± 1.2 g m⁻² in 1994 to 369 ± 74 g m⁻² following 3 years of protection. We removed these exclusions in 1997. After 4 years of grazing pressure the biomass in these plots was similar to *C. subspathacea* control plots. SCB in control *C. subspathacea* plots averaged 22 ± 5 g m⁻² in 2001 compared to 18 ± 2 g m⁻² in *C. subspathacea* plots that had been made re-available to geese. SCB within control *C. ramenskii* plots was similar between 1994 and 2001 and averaged 296 ± 17 g m⁻².

Table 1 Mean net aboveground primary productivity (NAPP) of *Carex ramenskii* from the mowing experiment conducted at the Tutakoke River Black Brant (*Branta bernicla nigricans*) colony on the Yukon-Kuskokwim Delta, Alaska, during the 1996 and 1997

Treatment	NAPP during incubation		NAPP during brood rearing		NAPP during late brood rearing 1997
	1996	1997	1996	1997	
Ungrazed control	5.4 \pm 1.2 a	2.5 \pm 0.2 ab	-0.1 \pm 1.6 a	6.3 \pm 0.8 a	4.9 \pm 1.3 a
Grazed control	5.2 \pm 0.8 a	1.6 \pm 0.3 b	2.7 \pm 1.5 a	6.8 \pm 0.9 a	4.2 \pm 1.6 a
Adjacent initiated*	4.1 \pm 0.5 a	2.2 \pm 0.2 ab	2.7 \pm 1.4 a	3.2 \pm 0.7 b	2.3 \pm 0.7 a
Distant initiated*	3.8 \pm 0.5 a	2.9 \pm 0.4 a	3.6 \pm 0.9 a	3.8 \pm 0.6 ab	4.3 \pm 1.6 a

* Plots were mowed in 1995 only

growing seasons. Results are from ANOVA, Tukeys HSD method. Letters shared within columns are not statistically different at $\alpha=0.05$. Values represent mean \pm SE g dwt m⁻² day⁻¹

Table 2 Treatment differences in carbon and nitrogen concentration and the carbon to nitrogen ratio (C:N) of *Carex ramenskii* harvested at the end of the 1996–1997 and 2000 growing seasons. Letters shared within columns and years do not differ statistically at $\alpha=0.05$ (Tukeys HSD). Data are means \pm 1 SE

Year	Treatment	Nutritional characteristics		
		Carbon	Nitrogen	C:N
1996	Ungrazed control	43.5 \pm 0.2 a	1.8 \pm 0.1 a	24.2 \pm 0.6 ab
	Grazed control	44.2 \pm 0.1 a	1.8 \pm 0.1 a	24.7 \pm 0.8 a
	Adjacent initiated*	43.7 \pm 0.3 a	2.5 \pm 0.2 b	18.6 \pm 1.3 bc
	Distant initiated*	40.6 \pm 1.1 a	2.8 \pm 0.1 b	14.5 \pm 0.9 c
1997	Ungrazed control	43.9 \pm 0.1 a	1.8 \pm 0.4 a	24.3 \pm 0.6 a
	Grazed control	44.0 \pm 0.1 a	1.8 \pm 0.1 a	24.9 \pm 0.6 a
	Adjacent initiated*	43.6 \pm 0.1 ab	1.9 \pm 0.1 a	23.9 \pm 1.4 a
	Distant initiated*	43.5 \pm 0.2 b	1.9 \pm 0.1 a	24.0 \pm 1.1 a
2000	Ungrazed control	44.7 \pm 1.9 a	1.8 \pm 0.1 a	24.8 \pm 1.6 a
	Grazed control	48.6 \pm 3.6 a	2.2 \pm 0.2 a	22.6 \pm 1.8 a
	Adjacent initiated*	43.5 \pm 0.2 a	4.0 \pm 0.4 b	11.3 \pm 1.0 b
	Distant initiated*	43.7 \pm 0.3 a	4.4 \pm 0.3 b	10.2 \pm 0.8 b

* Plots were mowed in 1995 only

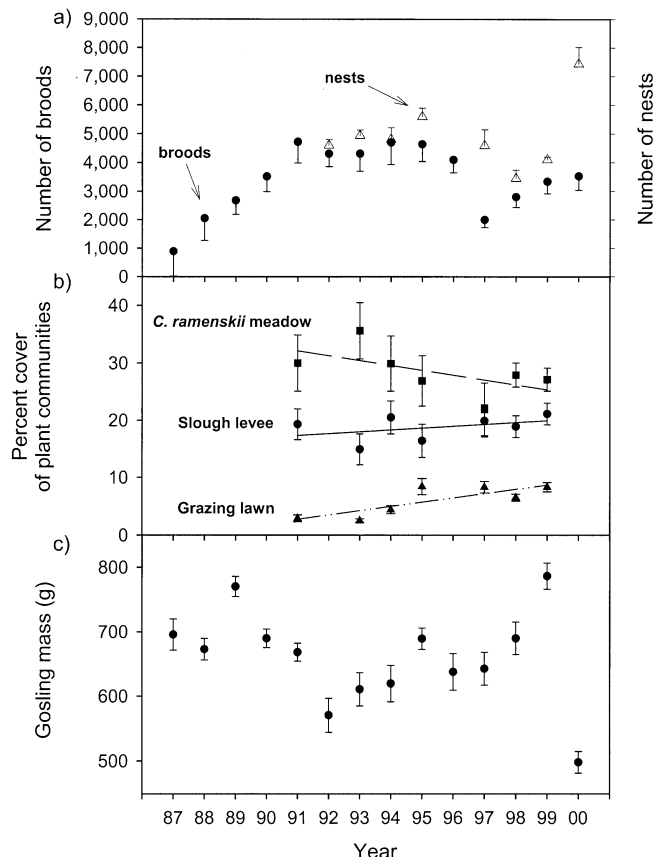


Fig. 4 **a** Lincoln-Peterson estimates of the number of Brant families using brood-rearing areas on which adults and goslings reared from the Tutakoke River colony were recaptured and weighed between 1987 and 2000, data represent mean \pm SE; Δ number of Brant nests 2–3 weeks prior to mean hatch between 1991 and 2000, data represent mean \pm SE. **b** Changes in the percent coverage of the three community types comprising the Tutakoke River Black Brant colony on the Yukon-Kuskokwim Delta, Alaska. **c** Changes in known-age gosling mass over years in which population size and aerial coverage of plant communities comprising the Tutakoke River colony were changing. Symbols represent least squared means \pm SE after controlling for sex, age, and year differences

Estimating the number of families reared from the Tutakoke river colony

The number of families reared from the Tutakoke colony increased from 885 to 4,165 between 1987 and 1991 (Fig. 4a). Between 1991 and 1996 the number of families reared from Tutakoke was relatively constant, fluctuating by approximately $\pm 10\%$. In 1997, a storm surge of the Bering Sea inundated a large portion of the Tutakoke colony when geese were incubating. This resulted in low nesting success and a 61% decrease in the number of families using brood rearing areas in 1997 compared to 1996 (Fig. 4a). By 2000, the population of Brant nesting at Tutakoke had increased to 7,437 \pm 584.

Table 3 Percent cover of the dominant physiographic features at the Tutakoke River Black Brant colony on the Yukon-Kuskokwim Delta, Alaska. Physiographic features in the “Other” category (e.g. observation towers, driftwood) represented $\leq 0.8\%$ and are not shown below. Data represent mean \pm 1 SE

Year	Physiographic features		
	Mud	Lake	River/slough
1991	31.2 \pm 5.0	13.5 \pm 3.1	3.1 \pm 0.8
1993	29.9 \pm 5.1	12.9 \pm 3.0	5.4 \pm 1.4
1994	30.4 \pm 5.3	11.1 \pm 2.6	3.7 \pm 1.5
1995	32.5 \pm 5.8	14.3 \pm 3.2	2.5 \pm 0.9
1997	32.2 \pm 5.8	12.4 \pm 3.1	6.0 \pm 1.8
1998	26.2 \pm 2.4	15.1 \pm 1.6	5.1 \pm 1.2
1999	22.8 \pm 2.0	10.1 \pm 1.2	10.8 \pm 1.5

Changes in the zonation of plant communities

The areal extent of grazing lawns increased from 2.9 \pm 0.6 to 8.3 \pm 0.8% between 1991 and 1999 ($y=0.007x-0.63$; $P<0.0001$) (Fig. 4b). In contrast, the areal extent of *C. ramenskii*-dominated meadows decreased from 30.0 to 27.1 \pm 2.0% over the same time period ($y=-0.014x+1.75$; $P=0.001$). There was no difference in the inverse relationship between the absolute value of the slopes between these regression models ($Z=0.24$, $P>0.5$), suggesting an inter-conversion between the two community types. The areal extent of the slough levee community ranged in cover from 19.3 \pm 2.7% in 1991 to 21.1 \pm 1.9% in 1999 ($y=0.01x-1.73$; $P=0.014$) (Fig. 4b). Mudflats, lakes, tidal rivers, and tidal sloughs comprise approximately 50% of the 10 km² Tutakoke colony landscape and their extent remained stable throughout this period (Table 3).

Changes in gosling mass

Between 1987 and 2000 we marked and subsequently recaptured 1,482 known-age goslings on a sample of brood rearing areas. Gosling mass varied among years ($F_{13,1466}=10.8$; $P<0.0001$) (Fig. 4c). Goslings were largest when the number of families reared from the Tutakoke colony was first beginning to recover from harvest and predation pressures in the late 1980s (Fig. 4c). Gosling mass declined from 770 to 570 g between 1989 to 1992 coincident with the stabilization of the number of broods produced from the Tutakoke colony. In contrast, gosling mass increased 200 g between 1992 and 1999 (Fig. 4c) despite observing a population equilibrium throughout much of this time frame (Fig. 4a). The increase in mass was positively related to the areal extent of grazing lawn between 1991–1999 ($y=559+17.8x$; $F_{1,5}=3.4$, $P=0.14$; $r^2=0.46$) (Fig. 5).

Feedbacks between population size and grazing lawn extent

It required 4 years for geese to revert our previously excluded *C. subspathacea* plots back to a grazing lawn

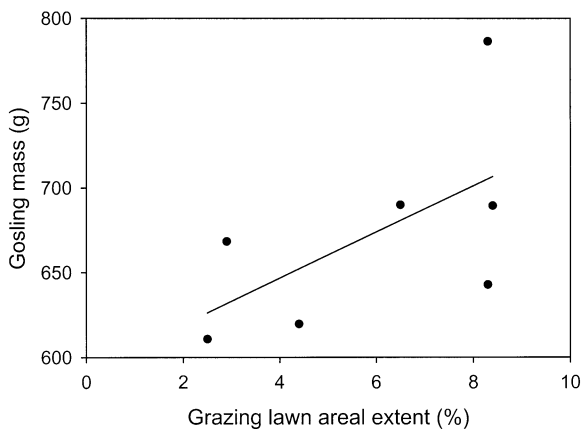


Fig. 5 The relationship between gosling mass (least square mean \pm SE) and areal extent of grazing lawns (%) within the Tutakoke River colony between 1991 and 1999 ($y=559x+17.8$; $r^2=0.46$)

that was similar to control plots (see Manipulation of grazing pressure on *C. subspathacea*), therefore we chose a priori to examine the 4-year lagged relationship between the number of families and lagged grazing lawn extent. We found a positive relationship between the size of the population and grazing lawn extent when lagged 4 years ($y=0.25+0.002x$; $F_{1,6}=13.1$, $P=0.015$; $r^2=0.72$). The a priori decision to use a 4-year time lag was compared with the results obtained from all other lagged and non-lagged models. A 4-year lag is as likely to be the best fitting model as a 5-year time lag ($r^2=0.76$) and is a better fitting model than each of a 2-, 3-, 6-year, and non-lagged relationship.

Discussion

Because size of young is a strong determinant of recruitment and future fecundity, the interplay between population size and the areal extent of grazing lawns will likely result in a numeric increase in this population. Gosling mass was greatest when the population of Brant breeding at Tutakoke was low in the late-1980s, and decreased as the population began to recover from harvest and predation pressures. Between 1989 and 1992 gosling growth, structural size, and clutch size decreased concurrent with an increase in the population from 885 to 4,300 broods (Sedinger et al. 1998). However, gosling mass increased between 1992 and 1999 while the population was stable, but below historic densities. We attribute the recent increase in gosling mass to the feedbacks between herbivory and grazing lawn zonation. We found a positive relationship between the number of broods and the areal extent of grazing lawns within the Tutakoke colony landscape. Increasing grazing pressure on preferred resources beginning in 1988 forced herbivores to switch from *C. subspathacea* grazing lawns to less nutritious *C. ramenskii* meadows. Grazing pressure on these meadows

resulted in an increase in grazing lawn extent throughout the Tutakoke colony which then led to increased gosling mass (Fig. 5).

Such a population response is subject to time lags that are intrinsic to the breeding population. For example, fewer goslings reared during the early 1990s would have bred, and those recruited into the breeding population would have produced fewer offspring because these cohorts consisted of small goslings. Breeding propensity, clutch size, and age at first breeding are positively correlated with female body size in Brant (Sedinger et al. 1995). A time lag also occurs because individuals do not reach peak breeding probability until they are 4 years old because clutch size is reduced until this age (Sedinger et al. 1995).

Variation in factors extrinsic to the breeding population will also delay detection of an increase in the population. Storm-surges on the breeding grounds and high predation pressures such as those that reduced the number of families reared from Tutakoke in 1997 will add stochasticity to a numeric increase in the population of Brant breeding at Tutakoke. Effects such as inclement weather on the wintering grounds, such as those that reduced all breeding Brant populations by approximately 20% in 1998 would also affect the rate of a numerical response of Brant to changes in the extent of grazing lawns (Anthony 2001; Schamber 2001). Thus, we predict that the herbivore-mediated changes in plant community zonation will impact the size of the Brant population breeding at Tutakoke within one to two decades unless extrinsic factors reduce the Tutakoke breeding population. The feedbacks we've described are not the only factors which may regulate this population. However, the feedbacks between population size, grazing lawn extent, and the subsequent effects on gosling size likely contribute to the regulation of the carrying capacity of these breeding grounds.

Our data contrast with goose-vegetation dynamics in the eastern Canadian subarctic where increasing populations of lesser snow geese (*Anser caerulescens caerulescens*) have destroyed vast expanses of *C. subspathacea* and *Puccinellia phryganodes* grazing lawns along the Hudson and James Bay coast (Kerbes et al. 1990). The expansion of this population has resulted from changes in land-use patterns in lower latitudes which led to over-winter subsidies in the diet of lesser snow geese. Destruction of breeding-ground habitat is the principal result of spring grubbing for belowground tissues, a foraging behaviour not exhibited by Brant. Lesser snow goose gosling growth and survival declined coincident with increases in the population and decline in habitat (Cooch et al. 1993), in contrast to the increase in Brant gosling mass over the past decade. When preferred food resources are limiting, Brant and lesser snow geese are forced to select alternative foods to maintain a positive energy and nitrogen balance because both species demonstrate intra- and inter-annual faithfulness to brood rearing areas (Cooch et al. 1993; Lindberg and Sedinger 1998). Lesser snow geese switch from *C. subspathacea*



Fig. 6 A grazing lawn that was created 5 years earlier by mowing and removing aboveground tissues of *C. ramenskii*. Vegetation in the foreground is an example of *C. ramenskii* that is in a short morphology, it is indistinguishable from *C. subspathacea*. The enclosure in the center of the photograph was not manipulated in 1995 and is representative of the tall-ungrazed morph of *C. ramenskii* that dominated this area prior to treatment application. This is one of the distant initiated treatment plots at location 3

and *P. phryganodes* grazing lawns to forage species lower in quality and less tolerant of grazing (Zellmer et al. 1993; Gadallah and Jefferies 1995). Differences in the foraging ecology of these goose species, coupled with isostatic rebound of the region and hypersalinization of soils are perhaps the most marked differences between these two colonies (Gadallah and Jefferies 1995; Srivastava and Jefferies 1995). Increased grazing pressure by lesser snow geese has led to the collapse of an ecosystem. In contrast, increases in Brant grazing pressure has created and maintained grazing lawns along the Bering Sea coast.

Brant feed on less nutritious *C. ramenskii* tissues under high population conditions because the abundance of their preferred forage, *C. subspathacea*, is likely inadequate to sustain a large population. However, removing aboveground tissues of *C. ramenskii* results in a sward that Brant prefer to graze and can maintain as a grazing lawn. On the sward scale (e.g. 225 m²) the resulting lawn attains a prostrate growth form that is morphologically and nutritionally indistinguishable from a *C. subspathacea* grazing lawn (Fig. 6). Aboveground biomass of *C. ramenskii* ranged from 9 to 72 g m⁻² when it was heavily grazed and this is the same range reported for *C. subspathacea* grazing lawns (Person et al. 1998). The nutritional quality of grazed *C. ramenskii* is also similar to that of *C. subspathacea*. C:N ratios range from 19 to 8 for grazed *C. ramenskii* and from 20 to 11 for *C. subspathacea* (Person et al. 1998). Thus, under high grazing pressures these sedges appear to converge in their nutritional characteristics. Given that these sedges were once classified as the same species, the ecological evidence presented here indicates that genetically characterizing these morphological types is warranted.

The shift in character states of *C. ramenskii* and *C. subspathacea* is bi-directional. *C. subspathacea* standing

crop biomass did not differ from that of control *C. ramenskii* plots after 3 years of protection from grazing pressure. Similarly, the combined influences of the spring storm surge and above-average arctic fox predation (J. Sedinger, unpublished data) in 1997 resulted in a 61% decrease in the number of families using brood rearing areas when compared to 1996. The consequent decrease in grazing pressure likely allowed vegetation in our manipulated plots to revert to the tall *C. ramenskii* growth form at locations 1 and 2.

Grazing lawns are created through phenotypic plasticity or ecotypic differentiation within local plant populations subjected to chronic grazing pressures (Coughenour 1985; Painter et al. 1993). Grazing tolerant ecotypes retain their morphology when protected from grazing for several growing seasons (Carmen and Briske 1985; Painter et al. 1989) while phenotypically plastic species rapidly change character states in response to herbivory (McNaughton 1984; Stearns 1992; Painter et al. 1993). Thus, a fundamental distinction exists in that grazing lawns dominated by ecotypes should buffer a food web against disturbances that temporarily remove or reduce consumers from a system. In contrast, a plastic response of vegetation to the removal of consumers likely introduces time lags in feedbacks between consumer-induced changes in the structure of a food web, and the subsequent numerical response of the herbivore population.

The plastic response to herbivory by *C. ramenskii* offers a mechanism through which this ecosystem shifts between alternate states. We believe there was a state shift of this system when the Brant population declined from 7,400 to 1,100 pairs. The corresponding decrease in grazing pressure likely resulted in the reduction of the areal extent of grazing lawns due to the plastic response of *C. ramenskii* similar to what we observe when *C. subspathacea* swards are protected. As the Brant population increased between 1989 and 1992, gosling mass and structural size were reduced (Sedinger et al. 1998). This suggests that the population was controlled by bottom-up forces, specifically, a low areal extent of grazing lawn relative to the population of Brant.

After 1992, we observed an increase in mass of goslings reared from the Tutakoke colony while the population of Brant fluctuated by only 10%. Our data suggest that Brant have exerted top-down control over ecosystem processes at the Tutakoke colony over the past 6 years through the increase in the areal extent of grazing lawns. Bottom-up forces in this ecosystem occur at an annual time scale due to the high plasticity of *C. ramenskii*, (i.e., a constant presence of Brant is required to maintain grazing lawns) and that top-down control by Brant resulting in avian population feedbacks occurs on the order of decades. Removing consumers from this system for 2–3 years could significantly reduce the extent of grazing lawns. In contrast, it probably requires a decade for herbivore-mediated increases in grazing lawn extent to be manifested in an increase of this population. The long-term carrying capacity of this system is likely higher than current population estimates of Brant breed-

ing at Tutakoke reflect because *C. ramenskii* dominated meadows are widely distributed throughout the coastal zone of the YK Delta and grazing lawn extent could increase by an order of magnitude. These data emphasize the importance of understanding the stochasticity of population dynamics and the resulting feedbacks to the foods on which herbivores rely when evaluating the assumption of density dependence in a population.

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