ECOGRAPHY 23: 367–373. Copenhagen 2000

Recovery of tall cotton-grass following real and simulated feeding by snow geese

J. W. Hupp, D. G. Robertson and J. A. Schmutz

Hupp, J. W., Robertson, D. G. and Schmutz, J. A. 2000. Recovery of tall cotton-grass following real and simulated feeding by snow geese. – Ecography 23: 367–373.

Lesser snow geese *Anser caerulescens caerulescens* from the western Canadian Arctic feed on underground parts of tall cotton-grass *Eriophorum angustifolium* during autumn staging on the coastal plain of the Beaufort Sea in Canada and Alaska. We studied revegetation of sites where cotton-grass had been removed either by human-imprinted snow geese or by hand to simulate snow goose feeding. Aerial cover of cotton-grass at sites ($n = 4$) exploited by human-imprinted snow geese averaged 60 and 39% lower than in undisturbed control plots during the first and second year after feeding, respectively. Underground biomass of cotton-grass stembases and rhizomes in hand-treated plots was 80 and 62% less than in control plots 2 and 4 yr after removal, respectively ($n = 10$ yr^{-1}). Aerial cover and biomass of common non-forage species such as *Carex aquatilis* did not increase on treated areas. Removal of cotton-grass by geese likely reduces forage availability at exploited sites for at least 2–4 yr after feeding but probably does not affect long-term community composition. Temporal heterogeneity in forage abundance likely contributes to the large spatial requirement of snow geese during staging.

J. W. Hupp (jerry_hupp@usgs.gov), D. G. Robertson, and J. A. Schmutz, U.S. Geological Survey, Alaska Biological Science Center, 1011 E. Tudor Road, Anchorage, AK 99503, USA (present address of D. G. R.: Harding Lawson Associates, 601 E. 57th Place, Anchorage, AK 99518, USA).

Removal of underground parts of plants by geese can reduce primary productivity and alter species composition in arctic and subarctic plant communities (Giroux and Bédard 1987, Kerbes et al. 1990, Iacobelli and Jefferies 1991, Boyd 1995, Abraham and Jefferies 1997, Esselink et al. 1997, Gauthier et al. 1997). The effects of goose foraging on tundra plant communities have been studied primarily on brood-rearing areas (Cargill and Jefferies 1984, Hik et al. 1991, Iacobelli and Jefferies 1991, Gauthier et al. 1995, Ruess et al. 1997). However, geese can also consume large amounts of forage on arctic staging areas (Hupp et al. 1996) as they acquire energetic reserves for autumn migration. About 500000 lesser snow geese *Anser caerulescens caerulescens* that nest in the western Canadian Arctic (Abraham and Jefferies 1997) use the coastal plain of the Beaufort Sea as an autumn-staging area in late August and September (Hawkings 1987, Johnson and Herter 1989). The coastal staging area extends across 700 km of arctic tundra from the Parry Peninsula, Northwest Territories to the Arctic National Wildlife Refuge (ANWR) in Alaska (Robertson et al. 1997) and is large compared to autumn staging areas of geese at lower latitudes (e.g. Giroux and Bédard 1988, Reed et al. 1989). The population may use an extensive staging area because geese consume a large quantity of forage in a spatially heterogeneous environment (Walker et al. 1982, 1989) where feeding habitat is patchily distributed and comprises a small portion of the landscape (Hupp and Robertson 1998).

Snow geese also may require a large staging area if their feeding reduces forage abundance at exploited sites for ≥ 1 yr, thus lowering foraging success should they use the same sites in successive years. Under those

Accepted 21 October 1999

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ISSN 0906-7590
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conditions flocks might need to search for feeding sites in different regions as plants in previously exploited sites recover. Snow geese may affect availability of a major forage species, tall cotton-grass *Eriophorum angustifolium* (Brackney and Hupp 1993), in years following feeding because they uproot cotton-grass tillers and consume the underground stembase and rhizomes from which the plant regenerates in spring (Fox et al. 1990, Hupp and Robertson 1998). Geese discard the uneaten aerial portion of cotton-grass at feeding sites, disturb the upper 5 cm of the active layer, and temporarily alter composition of the plant community. Common non-forage species such as *Carex aquatilis* and *Arctograstis latifolia* are typically left undisturbed. Availability of forage at exploited sites could be reduced during subsequent staging periods if cotton-grass does not recover in the first growing season after feeding or if abundance of non-forage species increases. Alternative foods may not be readily available because most aboveground forage is senescent, and the diet during autumn staging is constrained to a small number of items (Brackney and Hupp 1993).

We tested the hypothesis that aerial cover and underground biomass of cotton-grass were reduced for ≥ 1 yr after removal of plants. We also examined whether removal of cotton-grass increased production of other graminoid species. We used human-imprinted snow geese to study the effects of feeding on aboveground cover of graminoids, and removed cotton-grass by hand to simulate snow goose feeding and measure the response of underground biomass.

Methods

We conducted all studies on the coastal plain of the ANWR. The region is a sedge and shrub-dominated low arctic tundra (Webber 1974) previously described by Walker et al. (1982), Felix and Raynolds (1989), and Jorgenson et al. (1994).

Effects of feeding by human-imprinted snow geese

We measured regrowth of cotton-grass during 2 yr following feeding by human-imprinted snow geese. We collected snow goose eggs from the Anderson River nesting colony in the Northwest Territories, Canada and imprinted hatched young on human observers. Geese were acclimated to foraging on cotton-grass during two summers prior to this experiment. In 1991, we selected four thermokarst pits (Walker et al. 1980) that had vigorous stands of cotton-grass along the flooded edges and were similar to sites selected by autumn-staging snow geese (Hupp and Robertson 1998). The pits were in a region of high-centered polygons and were separated by 50–100 m. We established two 0.5×2.0-m plots in areas of flooded cotton-grass along the edge of each pit. We used a point frame to measure aerial cover of vegetation in plots (200 points/plot) in mid-August, 1991.

After measuring pre-treatment cover, we randomly chose one plot in each pit as a control and constructed a wire exclosure around the plot to exclude geese. We formed exclosures by wrapping strands of wire around 50-cm tall posts placed near the corners of a plot, and crossing wire over the top (Boyd 1995). The exclosed area included a 25-cm buffer. We erected a poultry wire fence around each thermokarst pit and included both plots in the penned area. We placed 6 human-imprinted snow geese in each fenced area for 4 h during the first week of September, 1991. Geese fed intensively and removed most cotton-grass from unprotected (exploited) plots, but did not disturb vegetation in exclosed control plots. We removed the pen after geese had fed and constructed an exclosure around the exploited plot. We maintained exclosures at control and exploited plots through 1993 to prevent the confounding effects of further feeding by wild snow geese. Exclosures would not have deterred microtines. In early August, 1992 and 1993, we measured aerial cover of vegetation in exploited and control plots with a point frame. We measured regrowth via point frame to avoid destructive sampling techniques that might affect plant growth.

We used a paired t-test to determine whether aerial cover of cotton-grass was similar between adjacent plots prior to feeding in 1991. We used a repeated measures analysis of variance (ANOVA) to determine if aerial cover in exploited and control plots differed between the onset of the study and the 2 yr of post-treatment measurement. The interaction between year and treatment was a test of whether aerial cover in exploited plots was similar to control plots across years.

Effects of simulated snow goose feeding

In August, 1989 we removed cotton-grass tillers by hand to simulate snow goose feeding on underground plant parts. We monitored recovery of underground biomass in the affected areas over 4 yr. We selected two 20-m^2 sites ca 150 m apart in a water track (Walker et al. 1980). Each site was a relatively homogeneous stand of cotton-grass that included a small amount ($< 10\%$ aerial cover) of *Carex aquatilis*. Sites were either saturated or flooded with 1–5 cm of water and were similar to water track habitats where snow geese often fed on cotton-grass (Hupp and Robertson 1998). We established 15 pairs of 0.5×0.5-m plots at each site. Members of a pair shared a common border. Plots were arranged in 3 rows of 5 pairs, with 1 m separating each row, and 20 cm separating pairs in a row.

At the start of the study we randomly selected 5 pairs at each site for a pre-treatment comparison of underground biomass in neighboring plots. We used the remaining 10 pairs at each site to compare regrowth of cotton-grass in removal plots versus adjacent undisturbed control plots. We removed all cotton-grass tillers and attached underground stembases and rhizomes from both plots of the 5 pairs selected for the pre-treatment comparison, and from 1 randomly selected plot in each of the remaining 10 removal-control pairs. We removed cotton-grass by feeling down a tiller, grasping the underground stembase, and moving the tiller back and forth until the soil was loosened and the entire plant could be freed. We felt that technique most closely resembled feeding activity by snow geese and minimized disturbance to the active layer. We severed the underground portion from the aerial shoot of each harvested plant ca 1 cm above the stembase to collect the portion of cotton-grass consumed by snow geese (Brackney and Hupp 1993). We oven-dried samples at 60°C and weighed underground material collected from each plot. We fertilized each removal plot with 2–3 feces collected from captive snow geese.

We revisited the sites in August 1991 and 1993 to measure recovery of cotton-grass in removal plots after 2 and 4 yr, respectively. In 1991 we harvested cotton-grass in removal and adjacent control plots at 5 randomly selected pairs in each site. Cotton-grass was harvested by hand and underground biomass measured as in 1989. Upon completion of the study in 1993, we used a shovel to harvest underground biomass in the remaining removal-control pairs. We dug plots in 1993 so that we could collect all underground material and determine whether underground biomass of *Carex* differed between treatment and control plots. We washed and separated underground biomass by genera. We were able to identify a large proportion of the underground material because rhizomes and stembases were often attached to live tillers. We only retained stembases and rhizomes that we believed were alive (firm, with solid interiors, and attached fine roots). We dried and weighed harvested material.

We used a paired t-test to determine if the underground biomass of cotton-grass was similar between neighboring plots at the onset of the study. We used an ANOVA to test the effects of treatment (removal vs control) and years of recovery (2 vs 4) on underground biomass of cotton-grass. We blocked the analysis by site. Harvest of cotton-grass in removal plots in 1989 may have reduced competition for light and nutrients, and could have stimulated graminoid production in adjacent control plots. To control for that potential bias, we also calculated the biomass of cotton-grass harvested from removal plots in 1991 and 1993 as a proportion of mass initially taken from those same plots in 1989. We used an ANOVA to assess the effects of years of recovery and site on proportional regrowth of cotton-grass. We used a paired t-test to determine if the underground biomass of *Carex* spp. differed between removal and control plots upon conclusion of the study in 1993.

Table 1. Repeated measures analysis of variance of cotton-grass cover in 4 pairs of 0.5 × 2.0-m plots on the Arctic National Wildlife Refuge, 1991–93. Cover in paired plots was measured in 1991 prior to feeding by human-imprinted snow geese in the treatment plots. Cotton-grass cover was remeasured in treatment and control plots 1 and 2 yr following feeding by snow geese.

Source of variation	DF	MS	F	p
Between groups				
Treatment	1	4428	3.7	0.10
Error	6	1209		
Within groups				
Years since treatment	2	2672	8.0	0.006
Years × treatment	2	1545	4.6	0.03
Error	12	334		

Results

Effects of feeding by human-imprinted snow geese

Aerial cover of cotton-grass was similar (paired $t = -0.28$, $DF = 3$, $p = 0.80$) between paired exploited (mean = 48.3%, SE = 6.0) and control plots (mean = 46.7%, SE = 6.6) before captive snow geese fed at sites in 1991. Combined aerial cover of *Carex aquatilis* and *Arctograstis latifolia* was < 9% at all sites. Aerial cover of cotton-grass was lower ($p = 0.03$) in exploited plots than in control plots in each of the 2 yr following feeding by snow geese (Table 1, Fig. 1). Aerial cover in

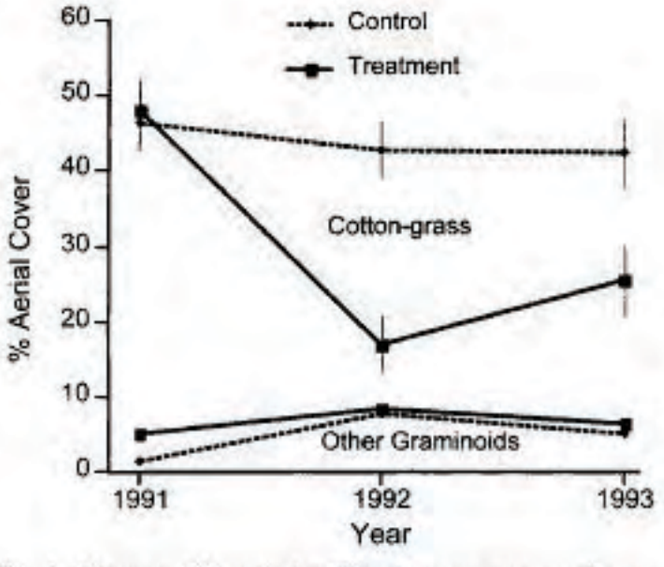

Fig. 1. Mean aerial cover (± SE) of cotton-grass and combined cover of *Carex aquatilis* and *Arctograstis latifolia* at 4 pairs of 0.5 × 2.0-m treatment and control plots, Arctic National Wildlife Refuge, Alaska, 1991–93. Snow geese were allowed to feed in treatment plots following measurement of cover in 1991.

Table 2. Analysis of variance of the effects of treatment (cotton-grass removal vs undisturbed control), years since treatment (2 vs 4) and site on underground biomass of cotton-grass in 0.5 × 0.5-m plots, Arctic National Wildlife Refuge, Alaska. Cotton-grass in treatment plots was removed by hand in 1989 and regrowth measured in treatment and paired control plots in 1991 and 1993 (n = 5 pairs/site/year).

Source of variation	DF	MS	F	p
Treatment	1	5059	112.9	≤0.0001
Years since treatment	1	1468	32.8	≤0.0001
Year × treatment	1	58	1.3	0.27
Site	1	244	5.5	0.03
Error	35	45		

exploited plots was greater ($F = 12.63$, $DF = 1, 3$, $p = 0.038$) 2 yr after feeding than in the first year after feeding (Fig. 1). Aerial cover of *Carex aquatilis* and *Arctograstis latifolia* was similar between exploited and control plots ($p > 0.4$) in both years following feeding by snow geese (Fig. 1).

Effects of simulated snow goose feeding

Underground biomass of cotton-grass did not differ between paired plots (mean = 22.7 g, SE = 3.5 vs mean = 19.8 g, SE = 1.5) at the onset of the simulated feeding study in 1989 ($t = 0.81$, $DF = 9$, $p = 0.44$). The underground biomass of cotton-grass that we harvested from removal plots at the start of the study was similar ($t = -1.2$, $DF = 18$, $p = 0.28$) between the two sites (Site 1 mean = 17.5 g, SE = 3.1; Site 2 mean = 21.8 g, SE = 2.2).

Harvest of cotton-grass in 1989 significantly reduced underground biomass of cotton-grass in removal plots compared to control plots for 2 and 4 yr at both sites (Table 2, Fig. 2). Underground biomass in removal plots averaged 23 (SE = 5.0) and 38% (SE = 4.8) of that in paired control plots in 1991 and 1993, respectively. We obtained more cotton-grass from all plots in the fourth year after treatment (Table 2, Fig. 2) when we used a shovel to harvest underground material. After 2 and 4 yr, biomass of cotton-grass in removal plots averaged 33 (SE = 8.4) and 73% (SE = 9.2), respectively of that originally removed from the plots in 1989. The difference between years was significant ($F = 9.5$, $DF = 1, 17$, $p = 0.007$). There was no difference in proportional regrowth between sites ($F = 0.5$, $DF = 1, 17$, $p = 0.49$). Proportions in both years were significantly < 1.0 (1-tailed t-test; $t = -7.9$, $DF = 9$, $p \leq 0.001$ for 1991; $t = -3.0$, $DF = 9$, $p = 0.01$ for 1993) indicating that biomass in removal plots had not fully recovered to levels present at the start of the study. We observed no differences (paired $t = -1.4$, $DF = 9$, $p = 0.19$) in underground biomass of *Carex* between treatment (mean = 52.5 g, SE = 4.5) and control plots (mean = 65.1 g, SE = 7.8) in 1993.

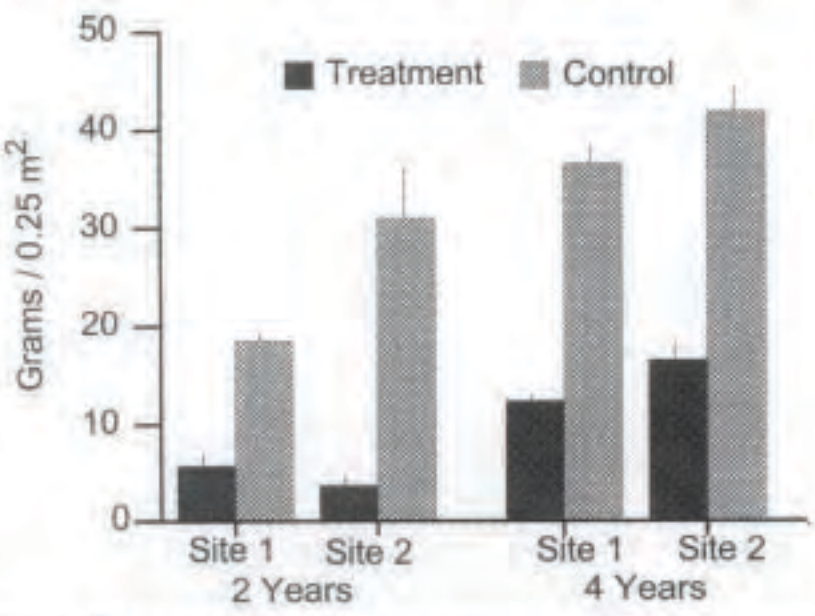

Fig. 2. Mean (± SE) underground biomass of cotton-grass in paired 0.5 × 0.5-m treatment and control plots at 2 (1991) and 4 yr (1993) intervals following hand removal of cotton-grass in treatment plots, Arctic National Wildlife Refuge, Alaska. Cotton-grass in 5 pairs of treatment and control plots was harvested at each of 2 sites at each time interval.

Discussion

Assumptions

We assume that feeding by human-imprinted snow geese simulated removal of cotton-grass plants by wild snow geese. Foraging behaviors of human-imprinted geese were similar to those we observed in wild geese. Captive geese fed almost exclusively on underground parts of cotton-grass and rarely removed tillers of *Carex aquatilis* or *Arctograstis latifolia*. The penned areas resembled patches that were heavily exploited by wild snow geese; most cotton-grass tillers in flooded areas had been removed, the upper 5 cm of soil at feeding sites had been disturbed, and discarded cotton-grass shoots were left at feeding sites (Hupp and Robertson 1998).

Hand removal of cotton-grass was a controlled perturbation that was similar to feeding by snow geese because we removed underground parts of cotton-grass and left other species undisturbed. However, unlike snow geese, we did not return the aerial shoots to the treatment sites after we had removed underground material because we were concerned that surface flows of water would wash discarded shoots onto control plots. Discarded cotton-grass shoots may provide a source of organic material that could affect nutrient cycling at feeding sites, and establishment of new plants from discarded fragments is possible for some species (Chou et al. 1992). However, we did not mimic those effects. We do not know if harvest of cotton-grass from removal plots in 1989 stimulated cotton-grass production in the adjacent control plots. If so, our comparison of removal to control plot biomass was biased and under-

estimated recovery of cotton-grass. However, the alternative comparison of second and forth year biomass harvested from removal plots to mass initially removed was not subject to that bias. That comparison was probably a more conservative measure of effects of forage removal because we removed cotton-grass by hand in 1989, but more completely harvested underground material by digging in 1993. We probably recovered more biomass by digging because we periodically broke stembases and rhizomes during hand removal. Also, we likely harvested material at greater depths while digging, and collected rhizomes from tillers that were outside the sample plot.

Effects of forage removal

Feeding by captive snow geese and removal of plants by hand reduced cotton-grass abundance for at least 2 yr. Aerial cover of cotton-grass had recovered more fully in the second year after feeding by captive geese compared to the first post-treatment year, but was still 39% lower on exploited plots than on control plots. After 2 yr, underground biomass at hand removal plots was 80% less than in control plots and was 67% less than the biomass initially removed from plots in 1989. After two years, sites exploited by captive geese appeared to have recovered more fully than hand-treated sites. However, aerial cover of cotton-grass may return to prefeeding levels more quickly than underground biomass because stembases accumulate material as tillers age (Billings et al. 1978).

Four years after hand removal, cotton-grass biomass in hand-treated plots was 27% less than the mass originally removed in 1989. Thus, even the more conservative comparison of forth year biomass at removal plots to material initially removed indicated that cotton-grass had not fully recovered after four years. We acknowledge that hand removal did not completely mimic feeding by snow geese and that our results should be interpreted cautiously. However, the major objective of our study was to determine if cotton-grass recovered in the first growing season after removal, and therefore whether geese could successfully exploit feeding sites in successive years. Because both real and simulated feeding reduced cotton-grass abundance for 2 yr, we conclude that foraging success would probably be reduced if snow geese returned to a feeding site in the year following exploitation. Cotton-grass requires at least 2 yr, and possibly up to 4 yr to recover after exploitation. This assumes that initial exploitation occurs in relatively homogeneous stands of cotton-grass ($\geq 40\%$ aerial cover) that have a high standing crop (≥ 80 g m^{-2}) of underground stembases and rhizomes.

We are not aware of published reports of revegetation following underground herbivory in tundra communities similar to those we studied. However, other studies have also found that tundra plant communities recover slowly from perturbation. Intensive grazing of aboveground vegetation can reduce production of tundra graminoids for 1–3 yr (Thompson 1955, Tieszen and Archer 1979, Webber et al. 1980, Batzli 1981). Human disturbance of arctic soils can affect vegetation for a substantially longer period (Bliss and Wein 1972, Ebersole 1985, Walker et al. 1987, Felix and Raynolds 1989, Emmers et al. 1995). Intensive grubbing by snow geese in subarctic salt marshes in eastern Canada may affect community composition for decades (Iacobelli and Jefferies 1991).

Following removal, aerial cover and underground biomass of cotton-grass increased over time as sites revegetated. In arctic plant communities, small patches of disturbed ground are typically recolonized by vegetative shoots that grow from the edge of the disturbed area (Ebersole 1985, Felix and Raynolds 1989). Snow geese primarily exploit cotton-grass in small, flooded patches of habitat (Hupp and Robertson 1998). Cotton-grass in upland sites on the edge of exploited patches would provide a source of plants for revegetation. Neither aerial cover nor underground biomass of species other than cotton-grass changed in the treated areas. *Carex aquatilis* was the most common species that occurred in treatment areas, but despite reduced competition from cotton-grass, *Carex* abundance did not increase. *Carex aquatilis* and cotton-grass are best adapted to different edaphic conditions (Chapin et al. 1980) and removal of cotton-grass at snow goose feeding patches apparently did not create conditions that were more suitable for growth of other species. Also, cotton-grass grows well in disturbed sites (Bliss and Wein 1972, Chapin et al. 1980, Ebersole 1985, Felix and Raynolds 1989, Emmers et al. 1995), and feeding by snow geese may create conditions conducive to its growth. Periodic removal of cotton-grass by snow geese probably does not alter long-term composition of vegetation at feeding patches but may affect short-term (2–4 yr) productivity of graminoids in small, discontinuous patches of habitat on the ANWR staging area (Hupp and Robertson 1998). In contrast, intensive grubbing by snow geese in subarctic salt marshes of the eastern Canadian Arctic can affect long-term composition of plant communities (Iacobelli and Jefferies 1991) across large regions (Kerbes et al. 1990, Abraham and Jefferies 1997, Jano et al. 1998).

Although feeding by snow geese may not alter long-term community composition, it does increase temporal variation in habitat quality by reducing forage abundance at exploited sites for at least 2, and possibly up to 4 yr. After an area has been exploited, geese may need to search for unexploited habitat in other regions of the coastal plain until cotton-grass recovers. Temporal and spatial variation in forage abundance caused by feeding in previous years may contribute to high annual variation in goose distribution observed by Robertson et al.

(1997). However, snow cover and other weather conditions also influence goose distribution on the staging area (Johnson and Herter 1989, Robertson et al. 1997). Hupp and Robertson (1998) concluded that the western Canadian Arctic population of snow geese required a large staging area because geese fed on a patchily distributed resource. A large staging area may also be necessary to allow geese to move among different regions as forage in previously exploited areas recovers. Temporal heterogeneity in forage abundance should be considered when assessing arctic habitat requirements of expanding snow goose populations (Ankney 1996, Abraham and Jefferies 1997).

Acknowledgements – This study was funded by the Alaska Biological Science Center of the U.S. Geological Survey. Considerable logistical support was provided by the Arctic National Wildlife Refuge, U.S. Fish and Wildlife Service. We appreciate field assistance from A. V. Badyaev, M. Blake, E. G. Burns, A. J. Chappelle, J. L. Dinsdale, C. B. Gougen, J. Ramsey, D. J. Sausville, and M. D. Romano. The manuscript was improved by comments from D. V. Derksen and A. B. Zacheis.

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