

The role of lesser snow geese as nitrogen processors in a sub-arctic salt marsh

R.W. Ruess¹, D.S. Hik², and R.L. Jefferies²

¹ Biological Research Laboratories, 130 College Place, Syracuse University, Syracuse, NY 13244, USA

² Department of Botany, University of Toronto, Toronto, Ontario, Canada M5S 1A1

Summary. Ammonia volatilization losses from faeces of Lesser Snow Geese were measured during the summer of 1987 on the salt-marsh flats at La Pérouse Bay. Amounts of ammonia volatilized increased with increasing ambient temperature, and ranged from 1.0 to 15.1 mg N per 100 mg of nitrogen present as soluble ammonium ions at the start of the 8-h experiment. Using estimates of faecal deposition reported previously, the annual loss via volatilization was estimated at 0.08 g N m⁻², or 7.9% of the nitrogen present in goose faeces. Percent change in soluble ammonium ions in fresh faeces after 8 h ranged from -51.1% to +41.1%, indicating that net mineralization of organic nitrogen occurred in some of the faeces. Microbial respiration of fresh goose faeces increased exponentially with temperature. However, variable rates of net mineralization per unit rate of respiration indicated that the substrate quality affected microbial immobilization and thus net nitrogen mineralization. In feeding experiments, captive goslings grazed different types of vegetation, each with distinctive nutritional qualities. Forage quality had significant effects on goose feeding behavior and subsequent rates of nitrogen mineralization in fresh faeces. Net nitrogen mineralization rates in faeces from geese which grazed the three vegetation types ranged from 1.31 to 4.97 mg NH₄⁺-N g_{DW}⁻¹ 24 h⁻¹. Because plant growth in this salt marsh is nitrogen-limited, where swards are grazed, mineralization of organic faecal nitrogen represents an essential link in the maintenance of the flow of nitrogen into the sediments and the sustained growth of vegetation at a time when most required by the geese.

Key words: Ammonia volatilization – Nitrogen – Nutrient cycling – Forage quality – Lesser Snow Geese

Herbivores act as mineralizing agents by processing and recycling nutrients in plant biomass. The nutrients, which are returned to the soil as faeces or urine, are in forms that can be readily used by plants, thereby bypassing the rate-limiting step of the release of nutrients from litter. This recycling is essential for the regrowth of grazed swards (McKendrick et al. 1980; Coppock et al. 1983) and is likely to be of particular importance in habitats which are nu-

trient-limited. In addition to their direct role in nutrient cycling, herbivores may have indirect promotive effects on decomposition processes (Botkin et al. 1981; Naiman and Melillo 1984; Ruess and McNaughton 1987; Jefferies 1988a). Despite the fact that the process of food selection is an essential component of the ecology of herbivores (McNaughton and Georgiadis 1986), the link between herbivore feeding behavior and its influence on nutrient cycling processes within ecosystems remains an important, yet relatively poorly studied topic.

On the western shore of Hudson Bay, the tidal salt-marsh flats at La Pérouse Bay, Manitoba, are grazed intensively from early spring (mid June) to early August by adults and goslings of a breeding population of the Lesser Snow Goose (*Chen caerulescens caerulescens* L.). Primary production of ungrazed vegetation is severely nitrogen-limited (Cargill and Jefferies 1984a), but grazing by geese may stimulate net aboveground production by over 100%, as a result of the rapid recycling of nitrogen as faecal nitrogen (Bazely and Jefferies 1985). Although as much as 2 g N m⁻² may be incorporated into goose biomass each year (Cargill and Jefferies 1984b), much of this export is probably counterbalanced by nitrogen-fixation on the surface of the sediments, which is significantly higher in grazed swards than in ungrazed swards (Bazely and Jefferies 1988).

Bazely and Jefferies (1985) reported that amounts of soluble nitrogen in fresh faeces collected throughout the summer of 1983 averaged 9.5 mg NH₄⁺-N g_{DW}⁻¹ faeces⁻¹, or 53% of the total faecal nitrogen. When monitored over a 30-h period, the amount of nitrogen in faeces declined by approximately 62%, which they attributed to volatilization losses and leaching of ammonium into the sediments. Although nitrogen volatilization losses of this magnitude (33% of total nitrogen deposition) are within the range for many pastures and agricultural soils (Ball et al. 1979; Sherlock and Goh 1984; Ryden and McNeill 1984; Bouwmeester et al. 1985), they are well above those reported for landscapes with free ranging domestic livestock (Schimel et al. 1986), or environments with native large ungulates (Ruess and McNaughton 1988). In order to estimate the magnitude of volatilization losses from faeces deposited on the salt-marsh flats at La Pérouse Bay, rates of ammonia losses from fresh goose faeces were measured on different occasions throughout the growing season.

Once the faeces are deposited, further microbial activity

may result in the net mineralization of organic nitrogen and the release of soluble inorganic nitrogen into the sediments. Alternatively, the nitrogen which is released may be immobilized by the microbes where they are substrate-limited. In order to relate microbial activity in faeces to particular forage plants, we allowed captive goslings to feed on swards dominated by one of the three important forage species consumed by geese in the tidal marshes. We collected fresh faeces and determined rates of microbial respiration and rates of net nitrogen mineralization in these droppings.

Methods

The study site

All studies were conducted during the summer of 1987 at La Pérouse Bay (58° 04' N, 94° 03' W), 25 km east of Churchill, Manitoba. Approximately 7000 pairs of Lesser Snow Geese nest in the brackish and fresh-water marshes immediately inland from the coast (Cooke et al. 1982; Jefferies 1988a). After hatch, both adults and approximately 20000 goslings feed intensively on the vegetation of the tidal salt marshes. The vegetation in the marsh is dominated by the stoloniferous grass, *Puccinellia phryganodes* (Trin.) Scribn. and Merr., and the rhizomatous sedge, *Carex subspathacea* Wormsk., on which the geese feed (Jefferies 1979). Approximately 80% of the above ground primary production of the salt marsh is grazed by the geese (Cargill and Jefferies 1984b). In the upper marsh, particularly on mounds elevated by frost heave and in grassy turf inland from the strand line, *Calamagrostis deschampsiodes* is common. This coarser, turf-forming grass is grazed by the geese when supplies of the other sources of forage are limited (Jefferies 1988a, b).

Ammonia volatilization

Ammonia volatilization from fresh goose faeces was measured on a number of occasions from early June to early September 1987, near the research camp at La Pérouse Bay, utilizing a closed-chamber system equipped with acid gas traps (Sherlock and Goh 1984; Ruess and McNaughton 1988). PVC chambers (25.4 cm diameter * 18 cm length), driven into the soil to an 11 cm depth, were covered with plexiglass lids fitted with rubber O-rings. Ambient air was drawn continuously across the soil surface within the chambers through two small holes (1 cm diameter) in the chamber walls. A fraction of air from the chambers was bubbled through acid gas traps. Air flow through the system was maintained using a rotary vane vacuum pump coupled to a gasoline engine (Ruess and McNaughton 1988). Flow rates through the chambers and gas traps were regulated at 21.21 min⁻¹ and 1.91 min⁻¹ respectively, using gas flow meters (Dwyer Inst. Co., Michigan City, IN). Mean air velocity within chambers was 0.21 m s⁻¹. Gas traps consisted of 150 ml 2% boric acid/indicator solution, and were back titrated with 0.1 N HCl.

Fresh faeces were collected from sites where wild geese or captive goslings were feeding, and determinations were made of water and soluble ammonium contents of faeces immediately upon return to the field laboratory. Approximately 15 g (dry weight) of faeces were placed on the soil surface within each of the two experimental chambers at

the start of an experiment. The ammonia content of air which passed through a third chamber, devoid of faeces, was also measured. This amount was subtracted from each of the results obtained for the other two chambers. At the end of an experiment (8 h) the water and soluble ammonium contents of the faeces in the two chambers were determined. In order to obtain an estimate of the decline in rates of ammonia volatilization over several days, on four occasions faeces were left in chambers, the lids of which were removed, and resealed at approximately 24 and 48 h after the start of the initial 8-h experiment. Faeces were reweighed immediately before the start of each 8-h experiment, and faeces were also taken from the chambers at this time for determinations of amounts of water and soluble ammonium. Ammonia volatilization rates during the 8-h periods (i.e. 24 to 32 h and 48 to 56 h) were measured, as described above. In order to estimate loss of volatilized nitrogen as a percentage of the total nitrogen in the faeces, amounts of nitrogen were measured in oven-dried faeces before and after six experiments (see below).

The amount of ammonia volatilized during each experiment was expressed either as a percentage of the initial ammonium concentration in fresh faeces, termed "percent volatilization", or as nitrogen loss per gram dry weight faeces, termed "mass volatilization". Where total amounts of nitrogen in faeces were measured, loss of nitrogen after 8 h was expressed as a percentage of the faecal nitrogen present at the start of each experiment.

Incubation of goose faeces

Fresh goose faeces were incubated in the laboratory at near-constant temperature conditions, during which time microbial respiration and net nitrogen mineralization in fresh faeces were measured. Approximately 5 g (wet wt) of faeces were placed on a moistened sponge at the bottom of a 0.8–1 jar, together with a 20 ml scintillation vial containing 15 ml 1N NaOH to trap respired CO₂. The solution was changed after 12 h and after 24 h. Respiration rate was calculated from results of the titration of the NaOH solution with HCL. All chambers were kept in the dark, and a chamber without faeces served as the control treatment. Soluble ammonium was measured initially, and after the 24-h incubation; the difference taken as net nitrogen mineralization. Soluble ammonium ions present in faeces were extracted in 1N KCL (1:5 w/v) for 12 h at room temperature and amounts determined using the phenol-hypochlorite method (Solorzano 1969).

Feeding experiments

The feeding behavior of captive goslings when they grazed swards of either *Puccinellia*, *Carex*, or *Calamagrostis* was studied. Two measures of behavior were recorded: pecking rates and defecation rates. It is well known that when forage plants contain a high percentage of their dry weight as fiber, pecking rates are low and defecation rates are high. There is an inverse relation between passage rate and forage digestibility (Demment and Van Soest 1983). Measurement of the feeding behavior of the goslings, therefore, provides indirect evidence of the digestibility of the three forage species. Rates of microbial respiration and rates of the net mineralization of nitrogen in faeces produced by the goslings which fed on these three plant species were also examined.

The birds were taken from nests just after hatch in mid-June, and raised in captivity at the field station. Initially, the birds were kept in large boxes which were heated with infrared lamps; water and ground Purina duck chow were provided, as required. After a few days, the goslings were allowed to graze vegetation within a large outdoor pen close to the field station.

Feeding experiments were conducted on 11 July, 16 August and 27 August, 1987. At the beginning of Experiment 1, 18 goslings were randomly divided into three groups; six birds from a group were placed in a large pen where the plant sward was dominated by one of the three species indicated above. The goslings were allowed to "acclimate" to the vegetation for approximately 8 h; water was provided in trays and the birds were moved to a new pen when the vegetation was well grazed. In Experiments 2 and 3 the same procedure was used, except only 3 goslings were placed in each pen as the birds were larger. Pecking rates (pecks per minute) and defecation rates (faeces per bird per hour) were monitored on at least 2 occasions during the day. Faeces were collected from all plots between 2000 and 2100 h after 8 to 10 h of grazing, and taken immediately to the laboratory for analyses of the pH, water content and soluble ammonium content, and for use in the incubation experiments.

Fresh goose faeces were incubated for 24 h; rates of microbial respiration and net mineralization of nitrogen were measured as described above. Incubation temperatures of the three experiments conducted in early, mid and late season averaged $19.2^{\circ}\text{C} \pm 0.1$ (S.D.).

In all chemical analyses of faeces, the material was derived from goslings which fed on either *Puccinellia*, *Carex*, or *Calamagrostis*. Sodium and chloride in faeces and plant tissues were determined using neutron-activation analysis. All irradiations were conducted in the SLOWPOKE reactor at the University of Toronto. Quantities of acid-detergent fiber (Demment and Van Soest 1983) were analyzed by the Agri-Food Laboratories, Ministry of Agriculture and Food, Ontario, Canada. Total carbon and nitrogen in oven-dried faecal material and plant tissues were determined using a LECO CHN analyzer. All material was ground in a Wiley mill (mesh size 20) before analysis.

Data were analyzed using standard statistical procedures (SAS 1982), and unless otherwise stated, numbers represent means \pm standard errors.

Results

Ammonia volatilization

Ammonia volatilization expressed as a percentage of initial amounts of soluble ammonium in fresh faeces (percent volatilization) increased with increasing ambient temperature (Fig. 1). Initial losses ranged from 1.0 to 15.1 mg N loss $100\text{ mg NH}_4^+-\text{N}^{-1}\text{ h}^{-1}$, and rates decayed to zero within 48 h. The air temperature ranged from 5°C to over 30°C in these experiments. The mean maximum temperature in July was 15°C in Churchill, although on two days the temperature exceeded 30°C (Churchill Weather Office, Environment Canada). Nitrogen volatilization per gram dry wt faeces (mass volatilization) ranged from 0.020 to 0.550 mg N loss $\text{g}_{\text{DW}}\text{ faeces}^{-1}\text{ h}^{-1}$. This loss was unrelated to ambient temperature, but correlated positively with the percent

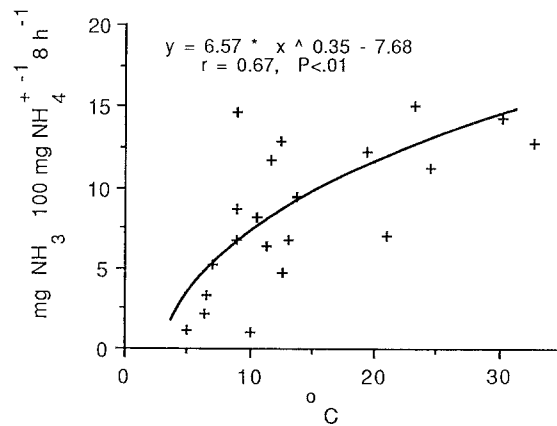


Fig. 1. Relationship between ammonia volatilization losses from fresh faeces and ambient temperature over 8-h periods taken throughout the summer 1987 at La Pérouse Bay. Each point represents the mean of two measurements of volatilization

of total nitrogen initially present as soluble ammonium ($P < 0.001$).

Percent change in soluble ammonium over the 8-h volatilization run (ammonium mass loss) ranged from -51.1% to $+41.1\%$, indicating that net mineralization of organic nitrogen occurred in some of the faeces. This ammonium mass loss was unrelated to percent volatilization, or ambient temperature, but correlated positively with initial ammonium concentration in faeces ($P < 0.05$) and with mass volatilization ($P < 0.05$).

Although there was a significant decline in both faecal ammonium concentrations and ammonium mass loss as the season progressed, these changes were a consequence of differences in the chemical composition of faeces from adults and goslings. We used adult faeces for studies of volatilization early in the season, a combination of adult and gosling faeces in July, and gosling faeces for the remainder of the season. Compared with adult faeces, gosling faeces had a lower initial ammonium concentration ($F_{1,19} = 22.9$, $P < 0.0001$), and a lower percentage nitrogen as soluble ammonium ($F_{1,10} = 6.8$, $P < 0.05$), which resulted in lower rates of mass volatilization ($F_{1,19} = 9.0$, $P < 0.01$).

Initial incubations of faeces

When fresh goose faeces were incubated for 24 h at constant temperatures, microbial respiration over a 24-h period increased exponentially with increasing incubation temperature (Fig. 2). Net rates of nitrogen mineralization (N_{min}) for the experiments ranged from -0.92 ± 0.14 to $9.86 \pm 1.02\text{ mg NH}_4^+-\text{N g}_{\text{DW}}^{-1}\text{ 24 h}^{-1}$ over the temperature range of 4.8 to 22.2°C , and the rates were linearly correlated with values of total respiration ($\text{Resp} = \text{mg CO}_2-\text{C g}_{\text{DW}}^{-1}\text{ 24 h}^{-1}$):

$$N_{\text{min}} = 0.15 (\text{Resp}) + 0.32 \quad r^2 = 0.56, P < 0.01 (n = 12)$$

However, there was some variation in rates of net nitrogen mineralization per unit rate of respiration which indicated that substrate quality affected the balance between microbial immobilization and net mineralization of nitrogen.

Feeding experiments

There were significant interspecific differences in the amounts of shoot nitrogen in the plants used in the grazing

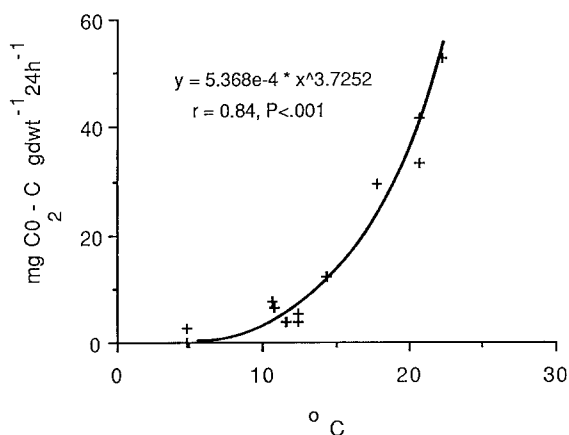


Fig. 2. Rate of microbial respiration in fresh goose faeces as a function of incubation temperature

experiments (Table 1). On average, *Calamagrostis* tissue contained lower amounts of nitrogen compared with corresponding values for *Carex* or *Puccinellia*, hence *Calamagrostis* had the highest C/N ratio. In contrast, *Puccinellia* had the highest mean nitrogen concentration and the lowest

C/N ratio in above-ground tissue. Amounts of sodium and chloride in *Puccinellia* were higher than amounts of these ions in tissues of the other two species (Table 1). There also were significant seasonal changes in plant phenology (Cargill and Jefferies 1984a, b). Shoot nitrogen declined from July to August while shoot carbon increased, resulting in an increase in shoot C/N ratio.

There were no significant differences in the weight of goslings of the three groups selected at random for each experiment (Table 2). Goslings feeding on *Calamagrostis* had lower pecking rates and higher defecation rates compared with corresponding rates for goslings feeding on *Carex* or *Puccinellia* (Table 2). Observations indicated that geese had difficulty biting the stiff stems and blades of *Calamagrostis*. The water content of faeces from goslings grazing on *Calamagrostis* was lower, and the C/N ratio higher, than corresponding data for faeces of goslings which fed on *Carex* or *Puccinellia* (Table 1). The pH of faeces varied between 6.6 and 7.3. The high C/N ratio of the faeces compared with the ratio in shoot tissue from goslings which fed on *Puccinellia* implies a high digestibility of this grass (Table 1). In contrast, corresponding ratios for shoots and faeces of *Carex* were similar to each other. Provisional data of amounts of acid-detergent fiber in shoots of the three

Table 1. Amounts of carbon (% dry wt), nitrogen (% dry wt), sodium (mol g_{DW}⁻¹) and chloride (mol g_{DW}⁻¹) in shoots of *Carex subspathacea*, *Puccinellia phryganodes* and *Calamagrostis deschampsoides*, and carbon (% dry wt), nitrogen (% dry wt), sodium (mol g_{DW}⁻¹) chloride (mol g_{DW}⁻¹), water (%) and soluble ammonium (mol g_{DW}⁻¹) in faeces of goslings of the Lesser Snow Goose which have fed on these species in three experiments conducted on 13 July, 13 August and 28 August respectively ($n=3$ for sodium and chloride, all others $n=9$). The carbon/nitrogen ratios of shoots and faeces are also shown. ANOVA results list proportion of variance explained by the two primary effects (SPECIES and EXPERIMENT) and their interaction (*, $P<0.05$; **, $P<0.01$, ***, $P<0.001$; ****, $P<0.0001$). Numbers within rows within treatments followed by different letters are significantly different at $P<0.05$

	Species			Experiment			Anova		
	<i>Carex</i>	<i>Puccinellia</i>	<i>Calamagrostis</i>	1	2	3	Species	Expt	Species*Expt
Shoots									
Carbon	44.1a	43.2b	41.6c	41.9b	43.4a	43.5a	44****	23**	26**
Nitrogen	2.52a	2.71a	2.05b	2.90a	2.26b	2.13b	23****	34****	39****
C/N	18.3b	16.7b	20.6a	15.7b	19.4a	20.5a	21**	34****	37****
Sodium	190b	485a	145b				88**		
Chloride	330b	526a	280b				74*		
Faeces									
Carbon	40.5b	42.0a	41.2b	40.2b	41.8a	41.8a	24*	42**	11
Nitrogen	1.97a	1.86ab	1.70b	1.61b	1.93a	1.98a	14*	31**	45**
C/N	20.7c	22.9b	25.4a	25.7b	22.0a	21.4a	23**	23**	45**
Sodium	281b	351a	122b				82**		
Chloride	545b	827b	380c				65*		
H ₂ O	88.7a	87.5a	84.7b	87.2a	87.0a	86.8a	48****	1	8
NH ₄ ⁺	2.25b	3.29a	2.66ab	2.40b	2.61ab	3.19a	28**	17*	10

Table 2. Gosling weight, pecking rate and defecation rate of goslings of the Lesser Snow Goose feeding on three forage species (*Carex subspathacea*, *Puccinellia phryganodes* and *Calamagrostis deschampsoides*) in three experiments conducted on 13 July ($n=18$), 13 August ($n=9$) and 28 August ($n=9$) respectively. Statistical notations follow Table 1

	Species			Experiment			Anova		
	<i>Carex</i>	<i>Puccinellia</i>	<i>Calamagrostis</i>	1	2	3	Species	Expt	Species*Expt
Goose Wt (g)	1397a	1394a	1320a	774c	1494b	1842a	1	89****	2
Pecking Rate ^a	117a	114a	77b	97b	102ab	109a	66****	6*	4
Defecation Rate ^b	8.5b	7.3b	10.1a	8.3a	9.4a	8.3a	34**	8	8

^a pecks min⁻¹

^b faeces h⁻¹

Table 3. Microbial respiration between 0 and 12 h and 0 and 24 h, net nitrogen mineralization between 0 and 24 h, and nitrogen mineralization efficiency (mineralization/respiration) of fresh faeces of goslings of the Lesser Snow Goose which fed on either *Carex subspathacea*, *Puccinellia phryganodes* or *Calamagrostis deschampsoides* in three experiments conducted on 13 July, 13 August and 28 August respectively ($n=3$)

	Species			Experiment			Anova		
	<i>Carex</i>	<i>Puccinellia</i>	<i>Calamagrostis</i>	1	2	3	Species	Expt	Species*Expt
Initial Respiration ^a	4.25a	1.45c	2.39b	2.41a	3.00a	2.67a	76***	3	8
Total Respiration ^b	23.47a	13.25b	13.79b	16.47a	16.93a	17.11a	63***	0	26*
N Mineralization ^c	4.97a	2.52b	1.31c	3.09b	1.49c	4.22a	54****	29***	10
N Mineralization Efficiency ^d	0.23a	0.20a	0.09b	0.17ab	0.10b	0.25a	26*	35*	17

^a mg CO₂ g_{DW}⁻¹ 12 h⁻¹

^b mg CO₂ g_{DW}⁻¹ 24 h⁻¹

^c mg NH₄⁺-N g_{DW}⁻¹ 24 h⁻¹

^d mg NH₄⁺-N mgCO₂⁻¹ g_{DW}⁻¹ 24 h⁻¹

species, and in faeces derived from each of the species support this suggestion. Mean values ($n=3$) of amounts of acid-detergent fiber as a percentage of the dry weight were, respectively, 24.0, 24.9 and 25.7% for shoots of *Puccinellia*, *Carex* and *Calamagrostis*. The corresponding percentages for faeces ($n=3$) derived from each of the plant species were 32.4, 29.2 and 30.6%, respectively. Apparent digestibility coefficients (Buchsbaum et al. 1986) based on these data were 26% for *Puccinellia*, 15.9% for *Calamagrostis* and 14.9% for *Carex*, although further measurements of acid-detergent fiber are required to substantiate these values.

The initial (first 12 h) and total (summed over 24 h) respiration rates in faeces from geese that grazed *Carex* were on average, appreciably higher than the rates measured in faeces derived from the other two species (Table 3). Rates of respiration based on 24 h were more than double the rates recorded for the first 12 h of incubation. This suggests that autolysis of cells occurred which led to rapid microbial growth as respiratory substrates were released.

Net nitrogen mineralization rates of faeces over the 24-h incubation ranged from 1.31 mg NH₄⁺-N g_{DW} faeces⁻¹ 24 h⁻¹ for geese grazing on *Calamagrostis*, to 4.97 mg NH₄⁺-N g_{DW} faeces⁻¹ 24 h⁻¹ for geese grazing on *Carex* (Table 3). This was equivalent to mineralization rates of 7.7, 13.6 and 25.2% respectively of the total nitrogen present in faeces from geese which fed on *Calamagrostis*, *Puccinellia* and *Carex*. The amount of nitrogen mineralized per unit CO₂ respired, termed "mineralization efficiency", was on average over twice as high in faeces from goslings which grazed *Puccinellia* and *Carex* compared with goslings which grazed *Calamagrostis* (Table 3).

Discussion

The magnitude of the gaseous ammonia flux from the sediment surface is highly dependent on a complex suite of factors which includes, the method of measurement, the substrate concentration in the sediments, micrometeorological conditions, soil moisture, soil pH, texture, cation exchange capacity and the buffering capacity of the soil (Bouwmeester et al. 1985; Ferguson and Kissel 1986; Black et al. 1987). In order to estimate seasonal volatilization losses from goose faeces on the tidal flats at La Pérouse Bay, we used estimates given in Table 2 of Cargill and Jef-

feries (1984b) of the quantities of faeces produced at the marsh in 1979 and in 1980. They divided the grazing season into ten periods and calculated total deposition of faeces for both adults and goslings during each period. Using values of 2.8 and 9.5 mg soluble NH₄⁺-N g_{DW} faeces⁻¹ for goslings and adults respectively, the estimate of the quantity of soluble nitrogen deposited in faeces during the season was 0.337 g NH₄⁺-N m⁻². Although the number of pairs of nesting geese has doubled since 1979 (Jefferies 1988a), the breeding colony occupies a much larger area of the coastal lowland in the vicinity of La Pérouse Bay, and thus, on the marsh (5.4 km²), the goose density has remained relatively unchanged during the summer. Seasonal volatilization losses were calculated using the equation in Fig. 1, assuming a mean daily temperature of 15° C, and that the rates of volatilization declined to zero within 48 h of the deposition of faeces on the sediment. This provided a seasonal volatilization loss estimate of 0.08 g N m⁻². Using 56.7 g_{DW} faeces m⁻² as a mean value of faecal deposition in the marsh per season (Cargill and Jefferies 1984b), and our estimate of the mean total nitrogen concentration in faeces of 1.84% (see below), this rate of volatilization is equivalent to a seasonal loss of 7.9% of the total nitrogen initially present in goose faeces.

Our extrapolations of rates of volatilization over 8 h to estimates of seasonal losses are, of course, approximations; nonetheless we believe they overestimate actual values for the following reasons. Using a mean annual temperature of 15° C and ignoring the diel, temperature-dependent effects on rates of volatilization over a 48-h period is likely to exaggerate estimates of losses (c.f. Fig. 1). Thus, although further detailed studies are required for more precise calculations of the nitrogen budget for the salt-marsh flats at La Pérouse Bay, the estimate of seasonal loss of nitrogen volatilized from faeces (0.08 g N m⁻² or 7.8% of the total nitrogen recycled by geese) is a low value. It is approximately 25 times less than the nitrogen exported in goose biomass (Cargill and Jefferies 1984b). Thus the loss appears to represent a relatively minor pathway for nitrogen in this system.

It is likely that a significant portion of the soluble faecal nitrogen unaccounted for by Bazley and Jefferies (1985) after 48 h in their experiments was immobilized by microbes present in the fresh faeces. The range of -51.1% to

+ 41.1% change in soluble ammonium over the 20 measurements of rates of volatilization (ammonium mass loss) in the present study, brackets the 47% loss they reported. Our initial laboratory incubations of fresh faeces indicated that, on average, at 15°C, respiration and mineralization rates in fresh faeces would be 12.9 mg CO₂-C g_{DW}⁻¹ 24 h⁻¹ and 2.3 mg NH₄⁺-N g_{DW}⁻¹ 24 h⁻¹ respectively, representing the potential for a significant net increase in the concentration of inorganic nitrogen in faeces. This measure is probably an underestimate of the rate of net mineralization, since it does not include nitrification. Jefferies (1988a) reported that, although rates of nitrification rates in the sediments were undetectable, nitrate was rapidly produced in sediment incubations if they were primed with ammonium, suggesting that nitrifiers were severely substrate-limited. The physical-chemical conditions in fresh faeces are suitable for nitrification, and nitrate generated in faeces may provide a significant source of nitrate for plant growth.

Significant changes in the digestive physiology of the geese occurred throughout the season, as indicated by the differences in faecal chemical compositions attributed to experimental effects (Table 1). During their period of rapid exponential growth, goslings retain a larger percentage of injected nitrogen than adults (Jefferies, unpublished work). This would account for the seasonal decline in faecal C/N ratio and the seasonal increase in faecal nitrogen and ammonium. These effects interact strongly with seasonal differences in plant phenology and interspecific differences in forage quality, explaining the large number of SPECIES*EXPERIMENT interactions, e.g. older plant tissue of lower nitrogen content and higher C/N ratio was less digestible.

The relatively large nutritive requirements of geese, coupled with their rapid processing of food, explains, in part, why geese are very selective feeders (Lief 1973; Prins et al. 1980; Thomas and Pevett 1980; Sedinger and Raveling 1984, 1988; Buchsbaum and Valiela 1987). We found that differences in the chemical compositions of the three forage species affected goose feeding behavior, the digestibility of the forage and the dynamics of microbial growth in the fresh faeces. The low nitrogen content and high C/N ratio in the above-ground tissue of *Calamagrostis* suggest that this plant is a low quality food source for the geese. At La Pérouse Bay, geese tend to avoid *Calamagrostis* in favor of *Puccinellia* or *Carex* (Jefferies 1988a, b). On the more northern nesting grounds at the McConnell River, near Eskimo Point, NWT., they graze *Calamagrostis deschampsoides* intensively, for lack of more favorable forage. The ability of adults and goslings to thrive on lower quality forage may be linked to increased foraging time (Sedinger and Raveling 1988), or changes in the gross anatomy of the gastrointestinal tract in response to increases in dietary fiber (Malone 1965; Miller 1975; Burton et al. 1979).

Although levels of soluble ammonium in fresh faeces were higher from birds which grazed *Puccinellia* than birds which grazed *Carex*, respiration and net nitrogen mineralization rates were highest in faeces of birds which grazed *Carex* (Tables 1 and 3). Two reasons may account for this difference in microbial activity. Firstly, the high amounts of sodium and chloride in *Puccinellia* tissue and in faeces derived from this grass may restrict microbial activity. Secondly, relatively few cells of the grass may be broken in the gut of a gosling, so that hydrolases and proteases are not released which can act on the cellular contents and provide substrates for microbial activity.

These studies indicate that selection for high-quality forage by geese has effects beyond the level of herbivore nutrition which influence both the pathways and rates of nitrogen movement in the system. Forage of high quality promotes faecal decomposition and nitrogen mineralization by microbes, and the data suggest that microbial nutrient uptake reduces ammonia volatilization losses. Bazely and Jefferies (1985) showed that during rainfall events, nitrogen is leached from goose faeces. Faeces are not incorporated into the sediments, but remain on the surface; leaching is the primary pathway of the return of nitrogen to the sediments. When high tides flood the salt-marsh flats in late July or early August, faecal material either is piled c. 30 cm high on the strandline, or else taken out to sea on the ebb tides. Faecal nitrogen which is not leached into the sediments by late summer is lost from the tidal flats. Therefore, in faeces where there is a rapid net mineralization of nitrogen, the microbial activity facilitates a return of this element to the sediments, before the faeces are removed by tides or winds. This input of nitrogen results in sustained net primary production of the forage species at a time when most required by the geese.

Acknowledgments. We gratefully acknowledge the tireless field assistance of Iris Frey, Tony Iacobelli, Alison Jefferies, Paul Mekiuniak and all the "goosers" at La Pérouse Bay. Part of this research was supported by NSF grants BSR 84-11093 to RW Ruess and BSR 85-05862 to SJ McNaughton. RL Jefferies thanks the Natural Sciences and Engineering Research Council of Canada, the Canadian Wildlife Service (Environment Canada), the Northern Heritage Foundation and the Department of Indian and Northern Affairs of the Government of Canada for financial support. F.S. Chapin and an anonymous reviewer provided many helpful suggestions on an early draft of the manuscript.

References

- Ball R, Keeney DR, Theobald PW, Nes P (1979) Nitrogen balance in urine-affected areas of a New Zealand pasture. *Agron J* 71:309-314
- Bazely DR, Jefferies RL (1985) Goose faeces: a source of nitrogen for plant growth in a grazed salt marsh. *J Appl Ecol* 22:693-703
- Bazely DR, Jefferies RL (1988) Lesser Snow Geese and the nitrogen economy of a grazed salt marsh. *J Ecol* (in press)
- Black AS, Sherlock RR, Smith NP (1987) Effect of timing of simulated rainfall on ammonia volatilization from urea, applied to soil of varying moisture content. *J Soil Sci* 38:679-687
- Botkin DB, Melillo JM, Wu LSY (1981) How ecosystem processes are linked to large mammal population dynamics. In: Fowler CW, Smith TD (eds) *Dynamics of large mammal populations*. John Wiley and Sons, New York, pp 373-387
- Bouwmeester RJB, Vlek PLG, Stumpe JM (1985) Effect of environmental factors on ammonia volatilization from a urea-fertilized soil. *Soil Sci Soc Am J* 49:376-381
- Buchsbaum R, Valiela I (1987) Variability in the chemistry of estuarine plants and its effect on feeding by Canada geese. *Oecologia* 73:146-153
- Buchsbaum R, Wilson J, Valiela I (1986) Digestibility of plant constituents by Canada Geese and Atlantic Brant. *Ecology* 67:386-393
- Burton BA, Hudson RJ, Bragg DD (1979) Efficiency of utilization of bulrush rhizomes by Lesser Snow Geese. *J Wildl Manage* 43:728-735
- Cargill SM, Jefferies RL (1984a) Nutrient limitation of primary production in a Sub-Arctic salt marsh. *J Appl Ecol* 21:657-668
- Cargill SM, Jefferies RL (1984b) The effects of grazing by Lesser Snow Geese on the vegetation of a Sub-Arctic salt marsh. *J Appl Ecol* 21:669-686
- Cooke F, Abraham KF, Davies JC, Findlay CS, Healey RF, Sa-

- dura A, Seguin RJ (1982) The La Pérouse Bay Snow Goose project – a 13 year report. Unpublished report, Biology Department, Queen's University, Kingston, Ontario
- Coppock DL, Detling JK, Ellis JE, Dyer MI (1983) Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal aboveground plant biomass and nutrient dynamics and plant species diversity. *Oecologia* 56:1–9
- Demment MW, Van Soest PJ (1983) Body size, digestive capacity, and feeding strategies of herbivores. Winrock Intl Livestock Res Pub, Morrilton, Arkansas
- Ferguson RB, Kissel DE (1986) Effects of soil drying on ammonia volatilization from surface-applied urea. *Soil Sci Soc Am J* 50:485–490
- Jefferies RL (1988a) Vegetational mosaics, plant-animal interactions and resources for plant growth. In: Gottlieb LD, Jain SK (eds) *Plant evolutionary biology*. Chapman and Hall, London, pp 341–369
- Jefferies RL (1988b) Pattern and process in arctic coastal vegetation in response to foraging by Lesser Snow Geese. In: Werger MJA (ed) *Plant form and vegetation structure, adaptation, plasticity and relation to herbivory*. SPB Academic Publishers. The Hague, pp 1–20
- Jefferies RL, Jensen A, Abraham KF (1979) Vegetational development and the effect of geese on vegetation at La Pérouse Bay, Manitoba. *Can J Bot* 57:1439–1450
- Lieff BC (1973) Summer feeding ecology and blue and Canada geese at the McConnell River, N.W.T. Unpublished PhD dissertation, Univ of Western Ontario, London
- Malone CR (1965) Dispersal of plankton: rate of food passage in mallard ducks. *J Wildl Manage* 29:529–533
- McKendrick JD, Batzli GO, Everett KR, Swanson JC (1980) Some effects of mammalian herbivores and fertilization on tundra soils and vegetation. *Arct Alp Res* 12:565–578
- McNaughton SJ, Georgiadis NJ (1986) Ecology of African grazing and browsing mammals. *Ann Rev Ecol Syst* 17:39–65
- Miller MR (1975) Gut morphology of mallards in relation to diet quality. *J Wildl Manage* 39:168–173
- Naiman RJ, Melillo JM (1984) Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). *Oecologia* 62:150–155
- Prins HH, Ydenberg RC, Drent RH (1980) The interaction of Brent Geese, *Branta bernicla*, and sea plantain, *Plantago maritima*, during spring staging: field observations and experiments. *Acta Bot Neerl* 29:585–596
- Ruess RW, McNaughton SJ (1987) Grazing and the dynamics of nutrient and energy regulated microbial processes of Serengeti grasslands. *Oikos* 49:101–110
- Ruess RW, McNaughton SJ (1988) Ammonia volatilization and the effects of large grazing mammals on nutrient loss from the Serengeti grasslands. *Oecologia* 77:382–386
- Ryden JC, McNeill JE (1984) Application of the micrometeorological mass balance method to the determination of ammonia loss from a grazed sward. *J Sci Food Agric* 35:1297–1310
- SAS Institute. 1982. SAS user's guide. SAS Institute Inc., Raleigh
- Schimel DS, Parton WJ, Adamsen FJ, Woodmansee RG, Senft RL, Stillwell MA (1986) The role of cattle in the volatile loss of nitrogen from a shortgrass steppe. *Biogeochem* 2:39–52
- Sedinger JS, Raveling DG (1984) Dietary selectivity in relation to availability and quality of food for goslings of cackling geese. *Auk* 101:295–306
- Sedinger JS, Raveling DG (1988) Foraging behavior of cackling Canada Goose goslings: implications for the roles of food availability of processing rate. *Oecologia* 75:119–124
- Sherlock RR, Goh KM (1984) Dynamics of ammonia volatilization from simulated urine patches and aqueous urea applied to pasture. I. Field experiments. *Fert Res* 5:181–195
- Solorzano L (1969) Determination of ammonia in natural waters by the phenol-hypochlorite method. *Limnol Oceanogr* 14:799–801
- Stewart BA (1970) Volatilization and nitrification of nitrogen from urine under simulated cattle feedlot conditions. *Environ Sci Technol* 4:579–582
- Thomas VG, Prevett JP (1982) The role of horsetails (Equisetaceae) in the nutrition of northern-breeding geese. *Oecologia* 53:359–363

Received May 18, 1988