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## TIMING OF NESTING BY CANADA GEESE IN RELATION TO THE PHENOLOGY AND AVAILABILITY OF THEIR FOOD PLANTS

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### SUMMARY

(1) This study examined seasonal variation in the foraging behaviour of cackling Canada geese (*Branta canadensis minima*) and in the nutrient content and availability of tundra grasses and sedges (graminoids) and arrowgrass during the nesting and brood-rearing periods, 1977–79 on the Yukon-Kuskokwim Delta, Alaska.

(2) Nitrogen concentrations in nearly all graminoids and arrowgrass began to decline either prior to, or during, hatching of cackling goose clutches. Grazing or clipping of vegetation resulted in higher and prolonged peaks in nitrogen concentration but peak nitrogen levels in these plants still occurred within a week of the end of the hatching period.

(3) Standing crops of graminoids increased until early August while the standing crop of arrowgrass (the most nutritious plant in the diet) in preferred foraging habitat began to decline in mid-July due to grazing by geese.

(4) Peck-rates of adult cackling geese tended to decline as brood-rearing progressed, indicating that preferred foods declined in availability during this period. Also, late in brood-rearing, preferred foraging areas were used less and arrowgrass comprised a smaller proportion of the diet.

(5) Changes in plant nutrient levels and shifts in diet and habitat use reduced the nutritional quality of the diet as brood-rearing progressed. Thus, as a result of both the natural phenology of tundra plants and grazing by geese, late hatching broods were at a nutritional disadvantage compared to those hatching early.

(6) We conclude that a seasonal decline in the quality of foraging conditions is probably an important factor favouring early nesting by geese.

### INTRODUCTION

Arctic nesting geese arrive on their breeding areas in early spring when little food is available; thus they are forced to rely heavily on stored reserves for both maintenance and egg formation (Barry 1962; Ankney 1977a; Ankney & MacInnes 1978; Raveling 1979). Whenever the spring thaw is late, average clutch size of these geese is reduced (for various species and populations, see Cooch 1958; Barry 1962; MacInnes *et al.* 1974; Mickelson 1975; Owen & Norderhaug 1977; Raveling & Lumsden 1977; Findlay & Cooke 1982; Ely & Raveling 1984), probably because females have devoted reserves to maintenance prior to

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egg-laying, instead of to egg formation and incubation. Since a later return to breeding areas could theoretically result in maximum clutch size production every year, regardless of the timing of the thaw, there must be counter-selective factors which prevent such a delay from evolving.

Two, not necessarily mutually exclusive, hypotheses, have been proposed to explain early arrival by geese on their nesting areas. Murton & Kear (1973) and MacInnes *et al.* (1974) suggested that early nesting evolved to synchronize grazing by goslings and post-breeding adults with the availability of food of the highest nutritional quality. During the brood-rearing period, geese obtain most, if not all, of their food from green plants (Barry 1967; Owen 1980; Sedinger & Raveling 1984). In addition, the brood-rearing period must be important in the annual protein budget of geese because it represents one of two segments of the annual cycle (the other being the spring pre-migration and migration period, McLandress & Raveling 1981) during which relatively high-protein green plants comprise a large proportion of the diet (see Owen 1980 for review of the annual cycle of food consumption). As yet, however, only Hardwood (1977) has published data which can be used to compare the phenology of plant nutrient composition with the phenology of the breeding season of geese and there are no data available to evaluate the effect of the geese themselves on the availability of the highest quality foods.

The second hypothesis states that the primary function served by geese nesting early is to allow enough time for young-of-the-year to fledge and gain strength for migration prior to freeze-up in the autumn (Cooch 1958; Ryder 1967). Two observations by Barry (1962, 1967) of flightless young brant, *Branta bernicla hrota* and *B. b. nigricans*, which had died when autumn freeze-up occurred, provide the primary evidence supporting this hypothesis. However, early arrival and nesting is observed in geese that nest at lower latitudes with longer growing seasons (MacInnes *et al.* 1974; Mickelson 1975; Raveling & Lumsden 1977; Cooper 1978). If length of the breeding season is the major factor that ultimately determines timing of egg-laying, a delay in nest initiation might be beneficial for these geese. Thus, it seems that the first hypothesis provides a more reasonable explanation for the early arrival on nesting areas, at least for geese that do not nest in the high arctic.

We undertook this study to compare the breeding phenology of cackling geese, *B. canadensis minima* Ridgway, with the phenology and availability of their principal food plants in order to examine the importance of these factors in influencing the timing of nesting by geese. The study was conducted during the nesting and brood-rearing periods from 1977 through 1979.

## STUDY AREA AND METHODS

### *Study area*

Our study area was on the Yukon-Kuskokwim (Y-K) Delta, Alaska, in the vicinity of the U.S. Fish and Wildlife Service field station at Old Chevak (61°N, 165°W). The principal study plot was a 40.4 ha area between the Onumtuk Slough and Kashunuk River (see Mickelson 1975 for further details) that surrounded a cabin and attached observation tower, which could be reached from the cabin without the observer being seen by geese.

We classified the habitat on the study area as either upland or lowland. Upland habitat consisted of relatively well drained areas from about 0.5 m up to about 1.5 m above mean high tide levels, characterized by lichens, moss, *Sphagnum* spp., *Empetrum nigrum*, *Rubus chamaemorus*, *Salix fuscescens* and *Ledum palustre* (Hulten 1968). Areas about 0.5 m above mean high tide levels were defined as lowland. We recognized two subtypes of

terrestrial lowland habitat: mudflat and meadow. Mudflats, which were adjacent to ponds, comprised 5% of terrestrial lowland habitat. These areas were characterized by bare mud or small, nearly pure, patches of either *Puccinellia phryganodes* or *Carex subspathacea*, both of which were less than 5 cm tall. Nearly pure stands of *C. mackenziei* and *Hippuris tetraphylla* also occurred adjacent to ponds and mudflats. Meadows consisted of vegetation up to 20 cm in height, dominated by *C. rariflora*, *C. ramenskii*, *Calamagrostis deschampsoides* and *Dupontia fisheri*. Scattered individuals of *C. mackenziei* and *Triglochin palustris* (arrowgrass) occurred in both mudflats and meadows and arrowgrass also occurred in stands of *C. mackenziei*.

#### Hatch dates

We determined hatch dates of cackling goose clutches either by visiting nests during hatching, or by visiting nests during egg-laying and assuming a 26-day incubation period and an egg-laying rate of one per day (Mickelson 1975). We added 1 day to the laying period for clutches of more than four eggs to account for 'skip-days' between eggs in larger clutches (MacInnes 1962; Mickelson 1975; Cooper 1978).

#### Vegetation sampling and analysis

In order to estimate vegetation biomass (standing crop) and to provide samples for chemical analyses, we established exclosed and unexclosed areas (7.6 × 7.6 m in 1977 and 3 × 5 m in 1978 and 1979) in a variety of vegetation types (Table 1). Exclosures were constructed of 1 m high plastic mesh (2 cm between strands). Mixed-meadow samples were

TABLE 1. Number of exclosed and unexclosed areas placed in each vegetation type during 1977–79

Vegetation type	1977		1978		1979	
	Excl.	Unexcl.	Excl.	Unexcl.	Excl.	Unexcl.
Mixed-meadow	3	—	3	—	—	—
Mixed-mudflat	—	—	2	—	2	2
<i>Carex mackenziei</i>	—	—	1	—	1	1
<i>C. subspathacea</i>	1	—	1	—	—	—

TABLE 2. Sample sizes for estimation of standing crop and nitrogen content

Sample type	Standing crop*					% Nitrogen†		
	1977E	1978E	1978U	1979E	1979U	1977	1978	1979
Mixed-meadow	3	6‡	4	—	—	3	3**	—
Mixed-mudflat	—	4§	4	4¶	4¶	—	2**	2
<i>Carex subspathacea</i>	1	2	—	—	—	1	1	—
<i>C. mackenziei</i>	—	2	—	2	2	—	1	2

\* Sample sizes in 1977 equal the number of exclosures. Sample sizes in 1978 and 1979 result from three (in two of three mixed-meadow exclosure and both mixed-mudflat exclosures on 13 June 1978) or two quadrats (all other areas and dates) clipped in each area. Table 1 contains the number of exclosures and unexclosed areas in each vegetation type.

† Samples from quadrats clipped within the same treatment (e.g. mixed-meadow exclosure on the same date were combined prior to Kjeldahl analysis, except in 1978 when samples from one mixed-meadow exclosure were analysed separately from those from the other two. See above for numbers of quadrats per treatment.

‡  $N = 8$  on 13 June.

§  $N = 2, 5$  and  $2$  on 7, 13 and 25 June, respectively.

¶  $N = 3$  on 7 July.

\*\*  $N = 2$  and  $1$ , for mixed-meadow and mixed-mudflat, respectively, on 7 June.

comprised of the species occurring in meadows while mixed-mudflat samples consisted almost entirely of *Puccinellia phryganodes*.

Samples of grasses and sedges were clipped to litter level at 7–12 day intervals from 0.01 m<sup>2</sup> (1977) or 0.1 m<sup>2</sup> (1978, 1979) quadrats randomly placed within each of the exclosed or unexclosed areas. No quadrats were clipped more than once. The irregular sampling interval allowed us to clip vegetation coincident with aircraft supply flights so samples could be transported out of the field. Plant sampling from exclosed and unexclosed areas was begun on 23, 7, and 12 June and terminated on 12, 7, and 9 August, in 1977, 1978, and 1979, respectively. Numbers of samples clipped from each area are indicated in Table 2. Exclosures provided samples of vegetation that were ungrazed while vegetation from unexclosed areas and hand-collected samples were available to grazing geese. Standing crop is reported here on a dry weight basis.

Individual arrowgrass plants were removed from 1978 mixed-meadow samples to provide a 'pure' sample of meadow arrowgrass for that year. All other arrowgrass samples were hand-collected from individual plants, in areas grazed by geese, on ten dates through the summer of 1979. The amount of material was insufficient for separate analyses representing each date, however. Therefore, five composite aliquots were formed for both mudflat and meadow arrowgrass by combining material collected on the following pairs of dates: 24 and 30 June, 4 and 7, 17 and 21, 28 and 31 July, and 9 and 12 August.

Productivity of graminoids was determined in 1978 by repeatedly clipping to litter level 0.1 m<sup>2</sup> quadrats (initially randomly selected) in the *C. mackenziei*, both mixed-mudflat exclosures and in two of three mixed-meadow exclosures. Productivity was estimated as the growth (g dry weight) since the previous clipping.

Plant samples were frozen within 24 h and kept frozen until ready for analysis at the University of California, Davis, where they were blotted lightly with paper towels, weighed, and freeze-dried to constant weight. Dry samples were ground in a Wiley Mill to pass a 40 mesh per inch sieve. Nitrogen content was determined by the macro-Kjeldahl method. Sedinger & Raveling (1984) provide more detail regarding sampling and analytical procedures.

The lengths of the longest leaves on individual arrowgrass plants available for grazing were measured (one leaf per individual) to the nearest mm as plants were encountered in mudflats and meadows used by geese. Measurements of the lengths of ungrazed arrowgrass individuals were made on all individuals in five 0.01 m<sup>2</sup> quadrats in the meadow exclosures and on individuals in one of the 3 × 5 m mudflat exclosures. Arrowgrass productivity was estimated by measuring the growth (mm) between clippings to litter level of all individuals within five 0.01 m<sup>2</sup> quadrats in the meadow exclosures and within a subarea of the same 3 × 5 m mudflat exclosure used to measure lengths of ungrazed arrowgrass individuals.

### Foraging behaviour

Habitat utilization by cackling geese was estimated by recording approximately once each day, the habitat (meadow, mudflat, or upland) occupied by all feeding cackling goose families on our principal study area. Habitat use was recorded between 04.00 and 24.00 h (the period when geese were actively foraging) immediately upon entering the observation tower, if four or more goose families were visible. If more than one habitat type was occupied by members of a family, the habitat occupied by the majority of family members was recorded.

Rate of pecking at food items by adults of both sexes of cackling geese (peck-rate) was determined by recording on a hand counter the number of pecks which occurred during a continuous bout of feeding, timed to the nearest 0.1 s. We used only those feeding bouts that were uninterrupted by alert behaviour (i.e. intervals in which the head was continuously down searching for, or consuming food). Feeding bouts of less than 5 s were excluded from the analysis because errors in estimation of peck-rate due to miscounting by one peck were >10% for short bouts. Adult males and females were distinguished by the larger body size (cf. Raveling 1978a) and greater frequency of alert and aggressive behaviour exhibited by males (Raveling 1970).

### *Statistical analyses*

We used linear regression followed by *t*-tests to test for significance of seasonal trends in plant protein content and biomass, goose peck-rate and habitat use. Analysis of covariance was used to compare both slopes and adjusted mean levels of regression lines. We compared nitrogen concentrations and standing crops in exclosed *v.* unexclosed vegetation using two-way ANOVA.

## RESULTS

### *Date of hatch*

Cackling goose clutches hatched significantly later in 1977 than in 1978 or 1979 ( $\chi^2_3 = 43.4$ ,  $P < 0.001$ , 1977 *v.* 1978 and  $\chi^2_3 = 60.4$ ,  $P < 0.001$ , 1977 *v.* 1979, Fig. 1). Peak of hatching occurred on 4 July, 21 and 20 June in 1977, 1978, and 1979, respectively. The proportion of clutches hatching late was greater in 1978 than in 1979 ( $\chi^2_2 = 7.59$ ,  $P < 0.025$ ).

Hatching was highly synchronous, especially in 1977, the year of delayed nesting, when 93% of the clutches hatched over an 8-day period between 30 June and 7 July (Fig. 1). Hatching was less synchronous during 1978 and 1979 with 70% and 83% of clutches, respectively, hatching between 18 and 27 June.

### *Plant phenology*

Standing crop of vegetation on mudflats was greater within exclosures than within unexclosed areas during 1978 ( $F_{1,36} = 19.57$ ,  $P < 0.001$ , Fig. 2). Standing crops in exclosed *v.* unexclosed areas did not differ significantly for any other vegetation type  $\times$  year combination.

Standing crop tended to increase between early June and early August for all vegetation types except 1978 unexclosed mixed-mudflat. These increases were significant ( $P < 0.05$ ), except for 1977 exclosed mixed-meadow, 1978 exclosed mixed-mudflat and 1979 exclosed and unexclosed *C. mackenziei*. Standing crops were smaller (four areas) or unchanged (one area) on the last compared to the penultimate sampling date in five of twelve areas, suggesting that above-ground standing crops began to decline in August.

Nitrogen content of vegetation (per cent of dry weight) was not different in exclosed *v.* unexclosed areas for any year or vegetation type ( $P > 0.29$ , all comparisons), so results from the two treatments were combined. Peak concentrations of nitrogen in plants either preceded (five cases) or coincided with (four cases) the hatching period of geese in nine of eleven vegetation type  $\times$  year categories (Figs 3,4). Peak nitrogen concentrations in arrowgrass from meadows in 1978 and mudflats in 1979 may have preceded the hatching period but no arrowgrass samples were collected from those habitats prior to the beginning

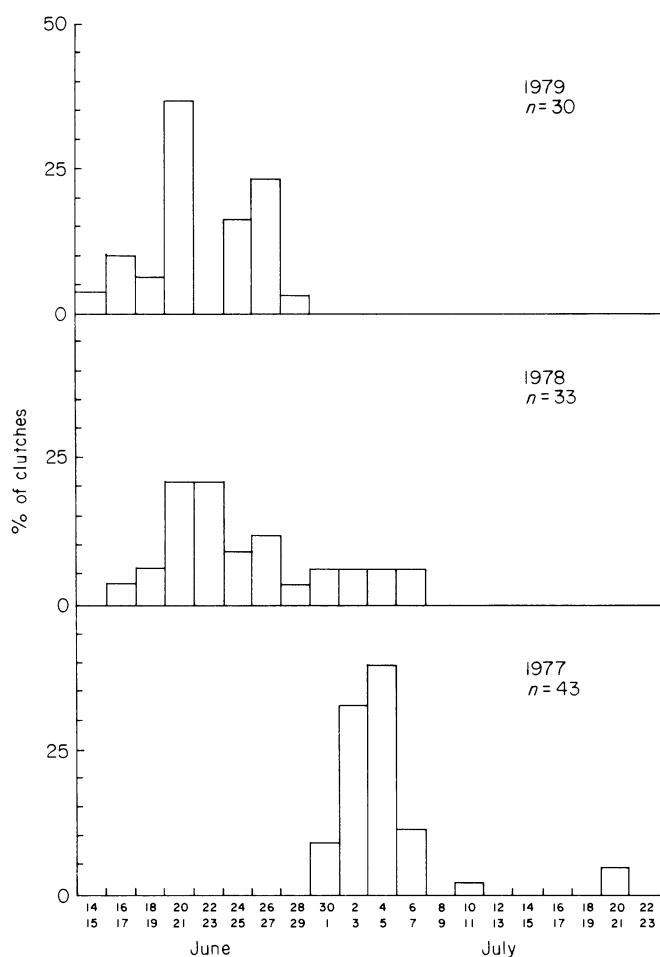


FIG. 1. Hatching dates of cackling goose clutches.

of hatch. Maximum measured nitrogen concentrations in 1978 mixed-mudflat vegetation and 1979 arrowgrass from mudflats occurred approximately 11 and 7 days following the respective hatching periods in the 2 years. Plant nitrogen concentrations declined during brood-rearing (i.e. following the peak of hatch) in all sequences of vegetation samples, significantly so in six of the eleven sequences ( $P < 0.05$ , Figs 3,4). Maximum nitrogen concentrations for vegetation  $\times$  year categories ranged from 2.6% (1978 mixed-meadow) to 5.4% (1979 arrowgrass from mudflats), while minimum nitrogen concentrations ranged from 1.4% (1977 mixed-meadow) to 3.9% (1979 arrowgrass from mudflats). Maximum nitrogen concentrations in repeatedly clipped grasses and sedges occurred in early July on both mudflats (4.0%) and meadows (3.3%, Fig. 5).

Growth rates of grasses and sedges peaked in mid-July at between 0.08 (mixed-mudflat) and 0.17 g 0.1 m<sup>-2</sup> day<sup>-1</sup> (*C. mackenziei*, Fig. 6). Maximum productivity of arrowgrass in meadows occurred in late June (Fig. 6). Growth rate of arrowgrass in mudflats was not



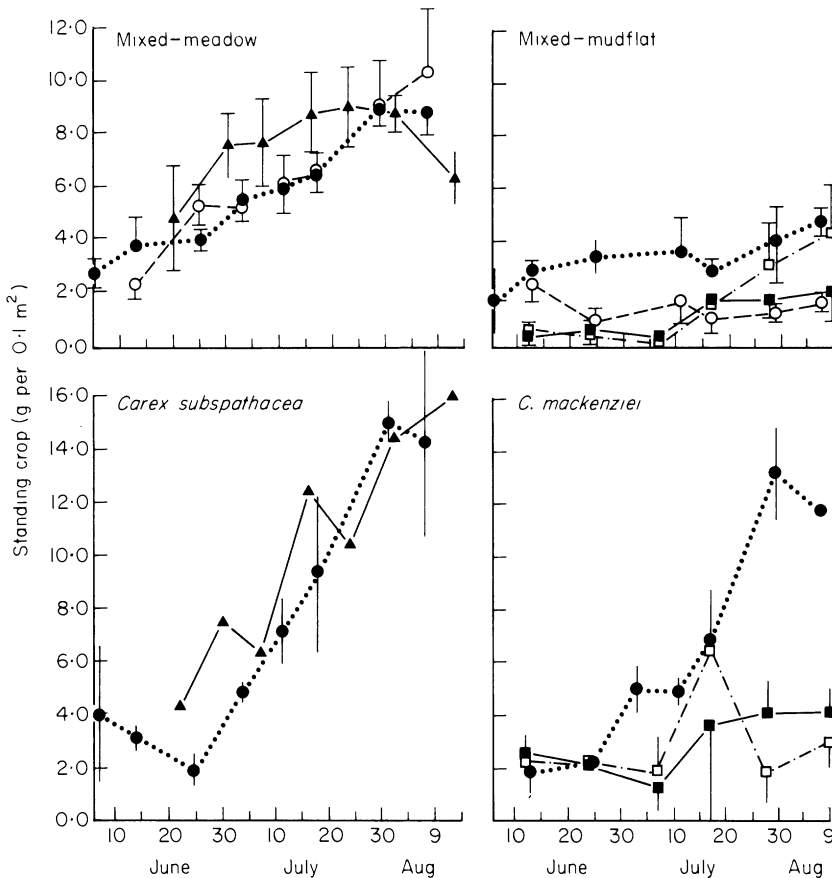


FIG. 2. Seasonal variation in standing crops of graminoids, 1977-79: (▲) 1977, (●) 1978, (■) 1979; open and closed symbols represent exclosed and unexclosed areas, respectively). Each point represents  $\bar{X} \pm \text{S.E.}$  ( $n > 2$ ) or  $\bar{X} \pm \text{range}$  ( $n = 2$ ). Sample sizes are in Table 2. Standing crops from 1977 are calculated from results from three 0.01 m<sup>2</sup> quadrats from each enclosure.

measured prior to early July but maximum recorded growth rate occurred during that period (Fig. 6).

The length of arrowgrass leaves protected from grazing increased until the end of July, then began to decline on both mudflats and meadows (Fig. 7). Those leaves subject to grazing, however, declined in length on mudflats in mid-July. Leaf lengths of grazed arrowgrass plants were significantly shorter ( $P < 0.05$ ) than those of ungrazed arrowgrass plants over the entire sampling period on mudflats. Grazed arrowgrass leaves in meadows were not sampled during July but were significantly shorter ( $P < 0.05$ ) than ungrazed leaves during August.

#### Foraging behaviour

Use of mudflats by cackling geese declined as brood-rearing progressed during all 3 years of the study, significantly so in 1977 and 1979 (Fig. 8). Rate of decline did not vary significantly among years ( $F_{2,73} = 2.42$ ,  $P > 0.05$ ) but the average per cent of foraging time spent on mudflats was greater in 1979 than in either 1977 or 1978



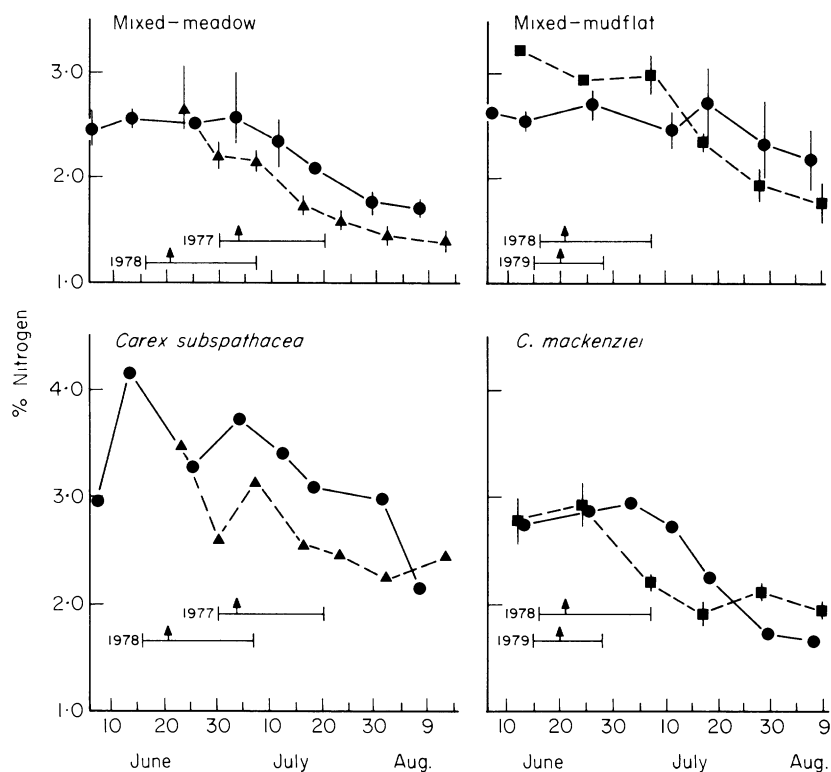


FIG. 3. Seasonal variation in nitrogen content (per cent of dry weight) of graminoids: (▲) 1977, (●) 1978, (■) 1979. Points and vertical bars represent means and ranges, respectively. Sample sizes are in Table 2. Arrows and horizontal bars represent the hatching peaks and hatching periods, respectively.

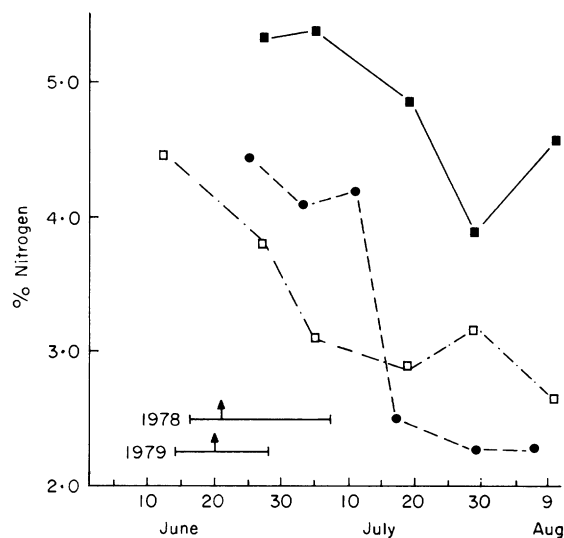


FIG. 4. Seasonal variation in nitrogen content (per cent of dry weight) of arrowgrass (*Triglochin palustris*) leaves from both mudflats (■) and meadows: (●) 1978, (□) 1979. Arrows and horizontal bars as in Fig. 3.

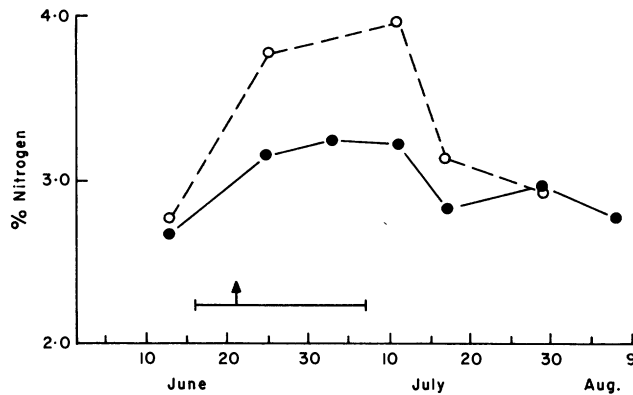


FIG. 5. Seasonal variation in nitrogen content (per cent of dry weight) of repeatedly clipped graminoids in 1978: (●) mixed-meadow, (○) mixed-mudflat. Arrow and horizontal bar as in Fig. 3.

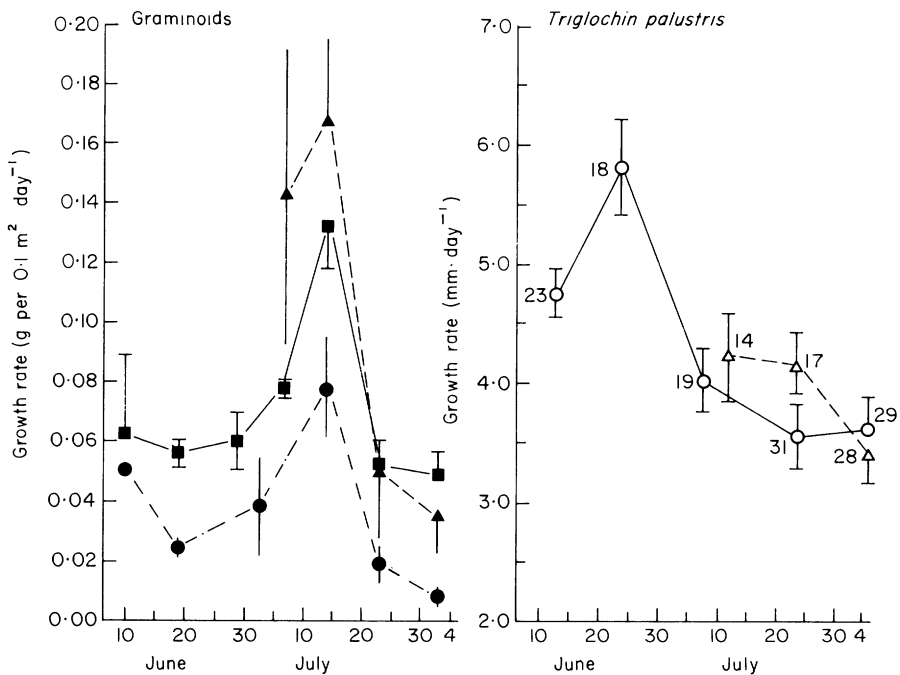


FIG. 6. Productivity (dry weight) of repeatedly clipped graminoids ( $\text{g } 0.1 \text{ m}^{-2} \text{ day}^{-1}$ , (●) mixed-mudflat, (■) mixed-meadow, (▲) *C. mackenziei*); and arrowgrass ( $\text{mm per day}$ , (○) from meadows, (△) from mudflats) during 1978 and 1979, respectively. Points are plotted on the midpoints of intervals over which growth occurred. Sample sizes for arrowgrass (number of leaves measured) are adjacent to plotted points. Sample sizes for graminoids (number of quadrats clipped) are  $n = 2$ , for mixed-mudflat and *Carex mackenziei*, and  $n = 6$  for mixed-meadow. Exceptions are 10 June mixed-meadow and mixed-mudflat ( $n = 4$  and 1, respectively) and 14 July mixed-meadow ( $n = 5$ ).

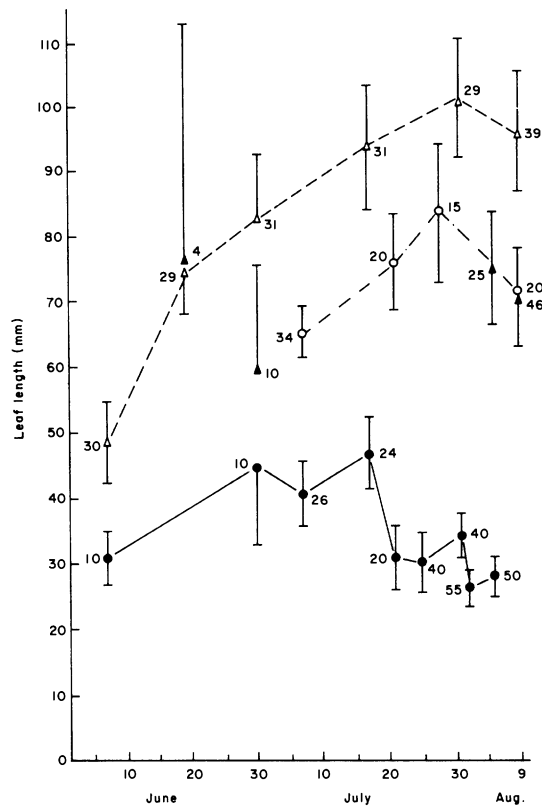


FIG. 7. Seasonal variation in *Triglochin palustris* leaf lengths on mudflats (● unexclosed, ○ exclosed) and meadows (▲ unexclosed, △ exclosed) during 1979. Vertical bars represent 95% C.L. Sample sizes are adjacent to plotted points.

( $F_{2,75} = 17.66, P < 0.001$ ). We did not detect any difference in foraging habitat use among different periods of the day for any year of the study ( $P > 0.1$  for all 3 years, Kruskal-Wallis Tests). Therefore, daily differences in the time at which habitat use was recorded did not bias our results.

Feeding bout lengths incorporated into the analysis of peck-rates varied from 5 to 50 s and from 5 to 53.2 s for males and females, respectively. Mean lengths of these bouts varied from 10.9 s (males feeding on mudflats in 1979) to 14.1 s (females feeding on mudflats in 1978). Length of feeding bout did not affect our estimate of peck-rate because number of pecks was linearly related to bout length. Thus, long bouts provided the same estimates of peck-rates as short bouts.

Peck-rates of both sexes of adult cackling geese in meadows declined during the brood-rearing periods of both 1978 and 1979, although the relationship was not significant for males in 1979 (Fig. 9). Adjusted mean peck-rates in meadows were higher in 1979 than in 1978 for both males ( $F_{1,155} = 6.45, P < 0.025$ ) and females ( $F_{1,200} = 6.79, P < 0.025$ ). Peck-rates of geese feeding on mudflats also tended to decrease during brood-rearing for both males and females in 1979 and for males in 1978 although the relationships were

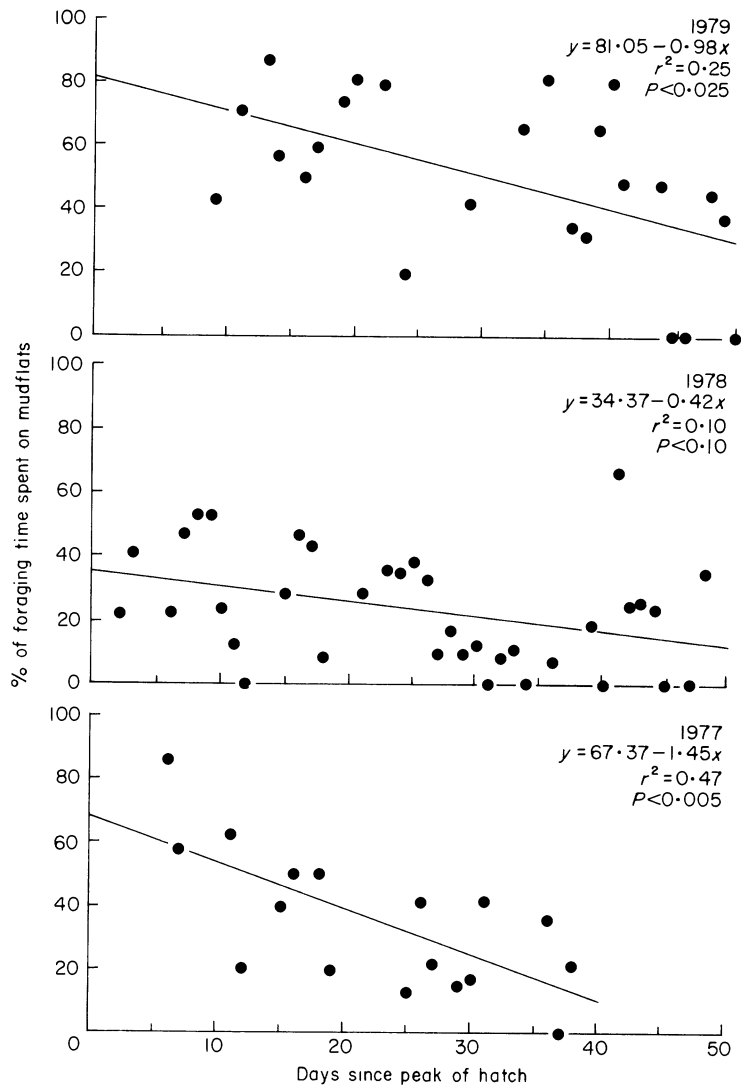


FIG. 8. Per cent of foraging time spent on mudflats by broods of cackling geese, 1977–79. Each point is the percentage of foraging broods on mudflats during mapping of broods (see methods). Mean numbers of broods (with ranges in parentheses) represented by each data point are 12.5 (6–24), 18.9 (5–48) and 9.5 (4–35) for 1977, 1978 and 1979, respectively.  $P$  is the probability that slopes differ from 0 by chance.

significant only for 1978 males and 1979 females (Fig. 10). Adjusted mean female peck-rates on mudflats were higher in 1979 than 1978 ( $F_{1,152} = 19.44$ ,  $P < 0.001$ ), while there was no between year difference for males feeding on mudflats ( $F_{1,161} = 1.20$ ,  $P > 0.10$ ). Peck-rates of geese were higher, on average, on mudflats than on meadows for males in both 1978 ( $F_{1,109} = 36.10$ ,  $P < 0.001$ ) and 1979 ( $F_{1,207} = 45.73$ ,  $P < 0.001$ ) and for females in 1979 ( $F_{1,223} = 48.21$ ,  $P < 0.001$ ). We did not make this comparison for females in 1978 because the slopes of the peck-rate *v.* time relationships differed between mudflats and meadows.

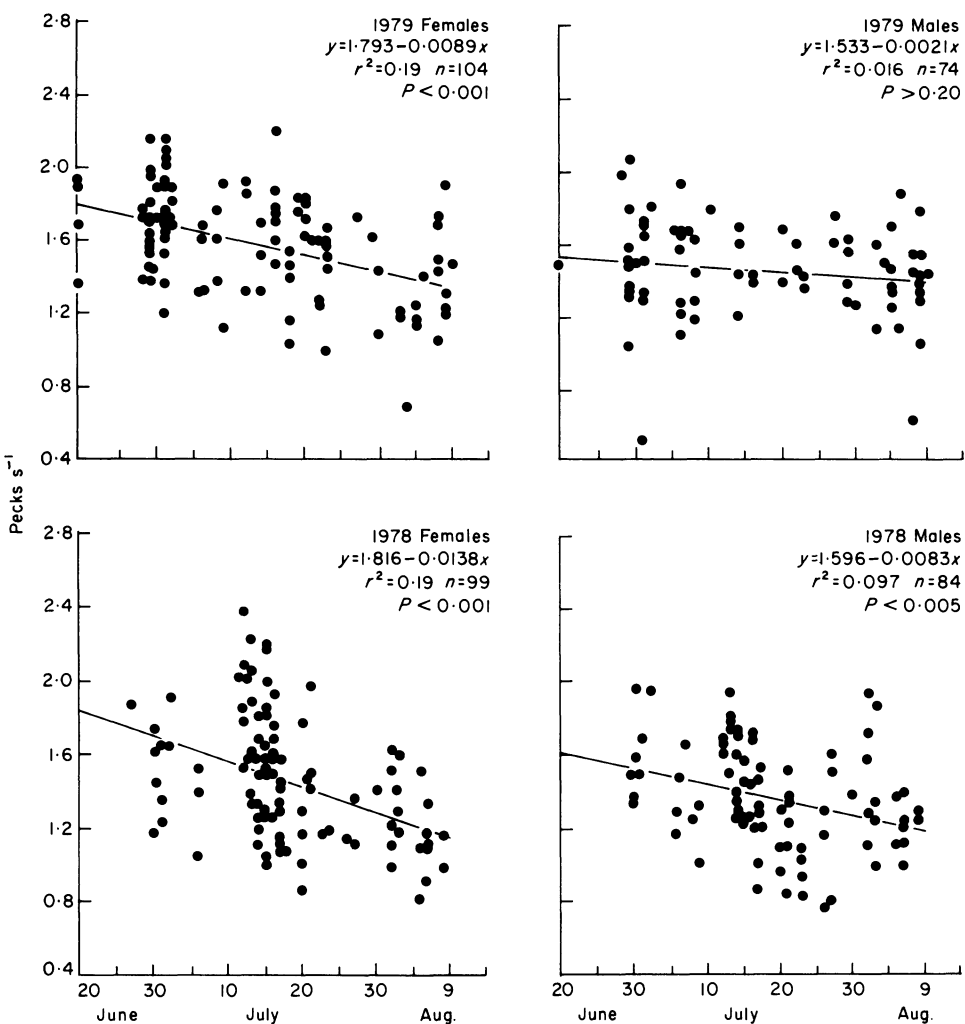


FIG. 9. Seasonal variation in pecking rates (pecks per s) of adult cackling geese foraging on meadows during 1978 and 1979. Day 0 for regressions corresponded to 20 and 21 June, for 1979 and 1978, respectively. *P* as in Fig. 8.

DISCUSSION

*Plant phenology*

Declining nitrogen, hence protein, concentrations in tundra graminoids, beginning shortly after spring emergence, have been documented at Barrow, Alaska (Chapin 1978) and on the west coast of Hudson Bay (Cargill 1981). High above-ground nitrogen concentrations in graminoids following the spring thaw result from rapid mobilization of nitrogen stored in below-ground organs which maximizes growth during the long days surrounding the summer solstice (Dennis, Tieszen & Vetter 1978). Nitrogen concentrations of whole plants decline because of the ‘dilution’ of rapidly growing tissue by more mature leaves (Chapin 1978; Mooney & Gulman 1982) and are maintained below potential levels because inorganic nitrogen is in short supply in many tundra areas (Ulrich & Gersper 1978; Chapin *et al.* 1981; Cargill 1981).

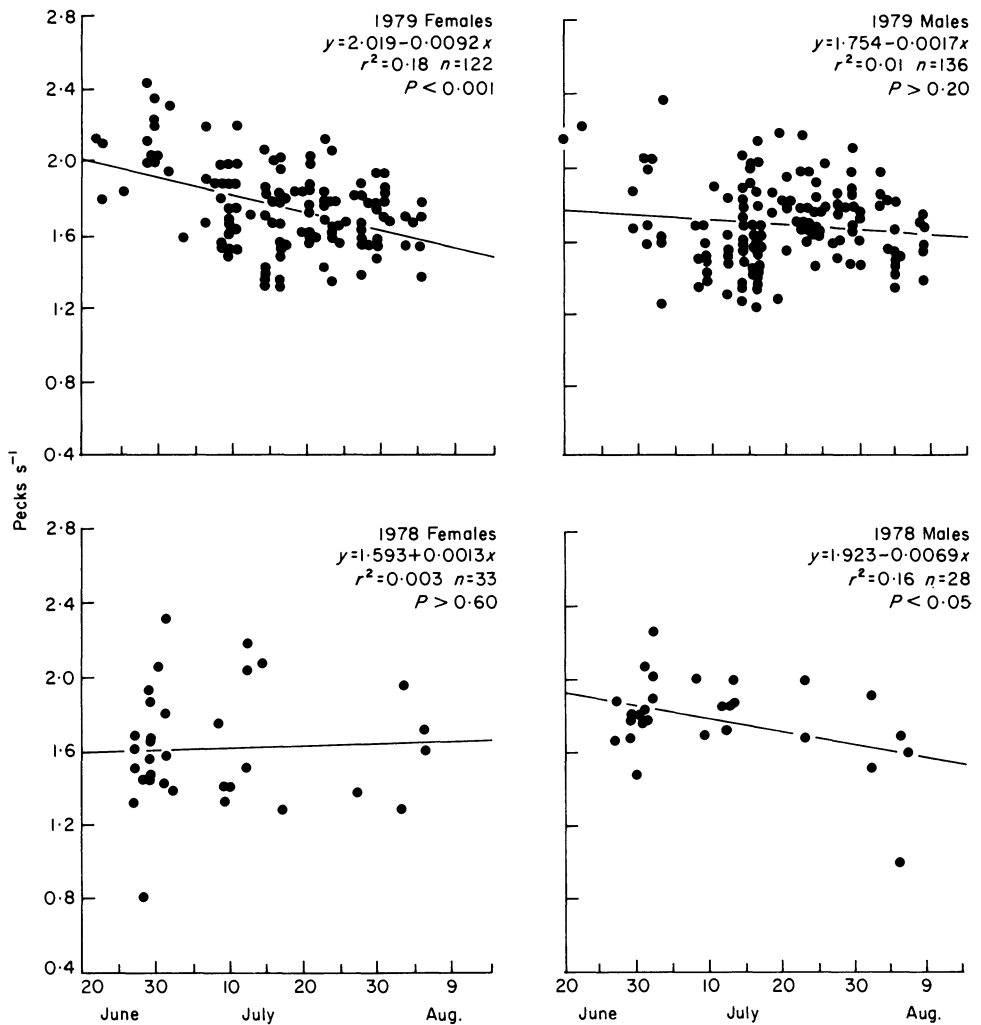


FIG. 10. Seasonal variation in pecking rates (pecks per s) of adult cackling geese foraging on mudflats during 1978 and 1979. Analysis as in Fig. 9.

Grazing may maintain relatively high nitrogen concentrations in graminoids during the growing season (Jameson 1963; Harwood 1977; Cargill 1981; Ydenberg & Prins 1981). This was true in our study as indicated by the delayed nitrogen peak in repeatedly clipped grasses and sedges (Fig. 5) compared with most other samples (Fig. 3). Also, in arrowgrass, which was more heavily grazed on mudflats than on meadows (Fig. 7), the nitrogen concentration peak was higher and lasted longer on mudflats than on meadows (Fig. 4). This delayed decline in nitrogen concentrations in grazed or clipped vegetation may have resulted in higher nitrogen levels in plants when goslings hatched than would have been predicted from data from our exclosures. However, the peak nitrogen concentration in heavily grazed arrowgrass still occurred within a week of the end of hatching in 1979 (Fig. 4), and the decline in nitrogen concentration in repeatedly clipped grasses and sedges began either during or within 4 days of the 1978 hatching period (Fig. 5).

The phenology of arctic graminoids results in their reaching peak nitrogen concentrations from 10 days (at Barrow, 71° N, Chapin, Van Cleve & Tieszen 1975) to an average of between three and seven weeks (La Parouse Bay, 58°N, Cargill 1981; Y-K Delta, 61° N, this study) following the initiation of spring growth which is approximately coincident with snow melt (Tieszen 1972, 1974). Since the initiation of nesting in Canada geese is also usually coincident with or immediately follows snow melt (MacInnes 1962; MacInnes *et al.* 1974; Mickelson 1975; Raveling 1978b) and a minimum of about 31 days (5 days for laying plus 26 days for incubation in cackling geese) is required for a female to hatch a clutch, most plant foods are already declining in nitrogen content before late-hatching broods start feeding. Since all arctic and subarctic species of geese begin nesting at about the time of snow melt (see Owen 1980 and Bellrose 1982 for reviews), these relationships should have general applicability to their foraging ecology.

Hatch date may be even later relative to peak nitrogen content when nesting is delayed by a late spring thaw, as happened in 1977 (Fig. 1). Peak nitrogen concentrations in *C. subspathacea* and mixed-meadow vegetation, however, were not noticeably later in 1977 than in 1978 (Fig. 3). Plant nitrogen levels thus tended to be lower at a given gosling age in 1977 than in 1978 (and probably 1979).

Variation in nitrogen concentrations among parts of individual plants might have provided opportunities for geese to select foods higher in nutrient content than were our samples, which represented averages of the entire above-ground parts of plants. The nutrient content of various above-ground fractions (e.g. individual leaves, stems, etc.) needs to be measured but available evidence indicates that within-plant variation in above-ground nutrient content may be limited. The known duration of leaf exsertion in arctic sedges ranges from 20 to about 60 days (Tieszen 1978; Chapin 1981) and some new leaves could have appeared during the first 3 weeks of the brood-rearing period. However, younger leaves do not necessarily have systematically higher rates of photosynthesis (Tieszen 1978) and rates of photosynthesis are highly correlated with leaf nitrogen levels because 50–80% of leaf protein consists of ribulose-1,5-biphosphate carboxylase, which fixes CO<sub>2</sub> (Friedrich & Huffaker 1980; Camp *et al.* 1982). Thus, our present knowledge of plant growth dynamics indicates that a steady supply of high protein content food was probably not provided by later exserted leaves. Furthermore, protein concentrations in those plant tissues actually available to geese may have been lower than our estimates (for the area we sampled) because meristem tissue, which was high in protein content (Williams *et al.* 1976), was located at the bases of stems and leaves (Rechenthin 1956) where it was less available to grazing geese. Thus, phenological patterns in plant foods probably resulted in declining nitrogen concentrations in available foods as brood-rearing progressed, especially in those plants that were not grazed until late in brood-rearing. We believe that higher nitrogen concentrations in oesophageal *v.* clipped samples (see below) were due to geese foraging in areas where plants had higher nitrogen concentrations (Ulrich & Gersper 1978).

#### *Intraspecific competition in cackling geese*

Arrowgrass predominated in the diet of goslings less than 24 days old (44% and 98% of the diet in 1978 and 1979, respectively. See Sedinger & Raveling 1984 for a description of the diet). Arrowgrass was eaten at four (on meadows) to five (on mudflats) times its frequency of occurrence in the environment which was related to its higher protein levels (compare Figs 3 and 4) and lower cell wall levels (23.7–29.1% of dry weight) than grasses and sedges (47.6–58.3%, Sedinger & Raveling 1984).



Availability of arrowgrass on mudflats declined in mid-July 1979 (Fig. 7). This was the result of grazing by geese, as indicated by shorter leaf lengths of arrowgrass in grazed *v.* ungrazed areas (Fig. 7). Growth rates of repeatedly clipped arrowgrass peaked in late June (meadows) or early July (mudflats) (Fig. 6). Thus, the absolute decline in arrowgrass biomass by mid-July 1979 was the result of cropping rate exceeding growth rate during this period. This probably occurred even earlier in 1977 and 1978 because brood densities were higher in those years (twelve broods on our principal study area in 1979 *v.* seventeen and twenty-three broods in 1977 and 1978, respectively, J. S. Sedinger & D. G. Raveling, unpublished). Cackling geese also reduced the leaf lengths of arrowgrass in meadows (Fig. 7) which, in conjunction with increasing biomass of less preferred plants, caused the declining peck-rates in meadows later in the summer (Fig. 9).

Reduction in availability of arrowgrass had at least three effects. First, peck-rates declined (meadows, Fig. 9) or had a slight tendency to do so (mudflats, Fig. 10), thus reducing rate of intake. Second, mudflats were used less as brood-rearing progressed (Fig. 8). Finally, arrowgrass comprised a steadily declining proportion of the diet during brood-rearing (17% of the diet of goslings more than 41 days old in 1978, Sedinger & Raveling 1984). The magnitudes of all three of these factors were related to brood densities. Peck-rates were higher in 1979 (lowest brood density year) than in 1978 for females feeding on mudflats (Fig. 10) and for both sexes feeding on meadows (Fig. 9). Mudflats were also used more by feeding broods in 1979 than in 1978 or 1977 (Fig. 8) and arrowgrass comprised a larger fraction of the diet in 1979 than in the other 2 years (Sedinger & Raveling 1984). Because mudflat arrowgrass was the most nutritious food available to cackling geese, these shifts in diet and habitat use and the lower rates of intake resulted in poorer foraging conditions later in brood-rearing and when brood density was high.

We calculated the nitrogen content of the diet of goslings during the brood-rearing period (Fig. 11), taking the following factors into account: per cent of each food type in the diet (arrowgrass, *Carex mackenziei*, mixed-meadow, mixed-mudflat and *Carex* seeds; data

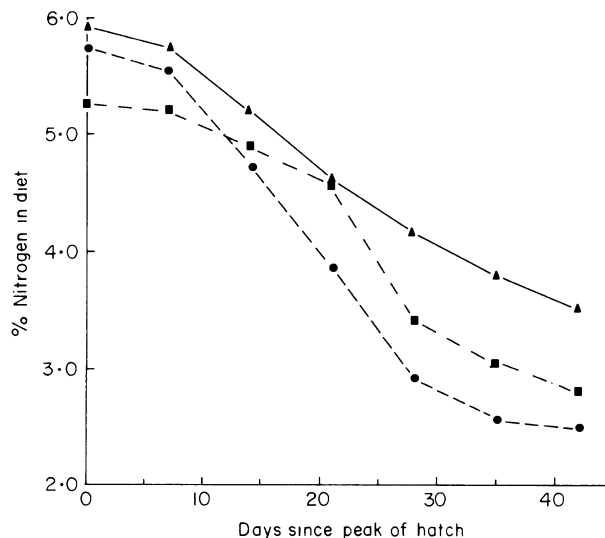


FIG. 11. Seasonal variation in calculated nitrogen content of the diet (percentage of dry weight) of cackling goose goslings: (●) 1977, (■) 1978, (▲) 1979. See text for description of calculations.

from Sedinger & Raveling 1984), per cent time spent feeding in mudflats *v.* meadows and per cent nitrogen content of foods. We calculated per cent time feeding on mudflats from Fig. 8. Nitrogen concentrations were measured directly in oesophageal samples of arrowgrass from goslings which had fed on mudflats ( $n = 3$ ), meadows ( $n = 4$ ) and on *Carex mackenziei* ( $n = 5$ ). Nitrogen concentrations averaged 11, 41 and 51% higher in oesophageal samples than in clipped samples of these three foods, respectively (which we believe to be the result of foraging in areas with higher protein content plants, see above). Because of this difference, we increased our estimates of nitrogen concentrations in clipped samples (data from Figs 3, 4) by the appropriate correction factors (e.g. 11% for arrowgrass from mudflats) to estimate the nitrogen concentrations in foods consumed by geese. We used the correction calculated from *C. mackenziei* for other sedges and grasses. There were no significant seasonal trends in the correction factors. Our estimates of nitrogen concentrations in foods were probably overestimates because some of the differences between oesophageal and clipped samples were the result of contamination of oesophageal samples by saliva (Moss 1972). Composition of the diet was estimated from linear regressions relating per cent contribution to the diet by a food to the number of days following peak of hatch (J. S. Sedinger & D. G. Raveling, unpublished). Calculated dietary nitrogen levels varied from between 5.3% (1978) and 5.9% (1979) at the peak of hatch to between 2.5% (1977) and 3.5% (1979) at the beginning of fledging (Fig. 11).

Calculated seasonal changes in dietary nitrogen were influenced primarily by reduced use of mudflats, where arrowgrass had the highest nitrogen content, and decreased consumption of arrowgrasses. Nitrogen would have declined from 5.6 to 3.9% of the diet (average of declines in 1977–79, a 31% decline) as a result of the observed changes in habitat use and diet alone, even if plant nitrogen levels had been constant (compare with the average 48% decline in Fig. 11). Thus, seasonal patterns in dietary nitrogen were not principally dependent on declining plant nitrogen levels. However, declines in dietary nitrogen late in brood-rearing, due to shifts in diet and habitat use, were exacerbated by lower nitrogen levels in previously ungrazed plants (Hardwood 1977; Cargill 1981, see above).

Scott (1973) recommended between 20% and 22% protein in the diet for maximum growth rates of waterfowl. About 55% of the nitrogen in artificially prepared diets is incorporated into tissue by poultry (Scott, Nesheim & Young 1976). Geese incorporate between 11% and 50% of the nitrogen in their plant foods into tissue (Marriot & Forbes 1970; Sedinger 1984). If we assume that 30% (J. S. Sedinger & D. G. Raveling, unpublished) of dietary nitrogen is incorporated into tissue by geese, maximum growth rates would require overall dietary protein levels of about 40% ( $55/30 \times 22\%$ ) or 6.45% nitrogen when feeding on green plants alone. Calculated levels of dietary nitrogen were below this level even under the best foraging conditions (Fig. 11). Thus, even early in brood-rearing, grazing conditions were suboptimal and goslings hatching 1 week after the peak of hatching had between 19% (1979) and 32% (1977) less protein in their diet during the third through to the fifth weeks of age (period of rapid growth) than goslings hatching 1 week prior to the peak (Fig. 11).

Early hatching broods thus experienced a superior nutritional environment at any given age compared with later hatching goslings. The reduction in dietary nitrogen levels was primarily due to shifts in habitat use and diet (see above) in response to reduced availability of high quality foods, which was the result of grazing by the geese themselves. Seasonal patterns in dietary nitrogen thus represented a case of intraspecific competition favouring those broods that hatched early (see below).

*Natural selection for hatch date*

Nutrition during the growing period may ultimately influence the ability of animals to deposit fat (March & Hansen 1977) and protein (Moss, Simmonds & McNary 1964; Swatland 1977) as adults. Poor early nutrition may result in a permanent reduction in adult body size (Wilson & Osbourn 1960). The ability to accumulate fat and protein reserves is especially important in geese because the size of the clutch laid by a female is directly related to the size of such reserves (Ankney & MacInnes 1978; Raveling 1979). Final adult body size may also influence the ability of males to attract mates (Ankney 1977b). Improved early nutrition may also reduce the age of first reproduction as indicated by a higher proportion of geese nesting as 2 year olds when they had hatched in a year with early as opposed to late nesting (Finney & Cooke 1978). Finally, early hatching lesser snow geese, *Anser caerulescens caerulescens*, were recruited into the breeding population at a higher rate than those hatching later in a season (Cooke, Findlay & Rockwell 1984). Both Lieff (1973) and Wurdinger (1975) demonstrated that nutrient levels in plants limit growth rates in geese. Thus, poorer nutrition later in brood-rearing, due to intraspecific competition and plant phenology, should provide strong selection pressure favouring early nesting.

Mortality of incompletely developed goslings due to early autumn freeze-up in some years (Barry 1962, 1967) has also been proposed as an important factor favouring early arrival and nesting in arctic geese (Cooch 1958; Ryder 1967). However, such gosling mortality was reported only for years when the brood-rearing period was significantly shorter than 'normal' due to both delayed nest initiation and early autumn freeze-up. The best documented case occurred in 1959, when nesting was delayed 10 days and autumn freeze-up occurred 14 days earlier than the average for the other 8 years of the study (Barry 1967). Despite the abbreviated brood-rearing period in 1959, 55 days separated the hatching of the first clutch and autumn freeze-up. This was 5–15 days longer than the 40–50 days required for brant young to fledge (Barry 1962; Mickelson 1975). Thus, even during a short brood-rearing period, only the very latest hatching goslings were probably prevented from fledging and strengthening flight muscles prior to autumn freeze-up. Furthermore, the failure to fledge in late hatching goslings was probably also the result of slowed growth due to poor diet and so was a result of nutritional factors rather than strictly the shortness of the brood-rearing period.

Early arrival may be disadvantageous in some years because weather delays the availability of nest sites causing females to use stored lipid reserves for maintenance and consequently to lay smaller clutches (Cooch 1958; Barry 1962; Mickelson 1975; MacInnes *et al.* 1974; Raveling & Lumsden 1977). Early nesters may also suffer egg loss due to inclement weather (Raveling & Lumsden 1977), flooding (Cooch 1958; Barry 1962) or predation (Findlay & Cooke 1982). The disadvantages of early arrival and nesting act in opposition to the nutritional advantages of early nesting to produce stabilizing selection favouring dates of arrival on nesting areas that, on average, allow geese to begin nesting as soon as secure nest sites become available. The intensity of these opposing selection pressures has apparently been strong enough to produce the striking synchrony in nest initiation dates observed in arctic geese (Cooch 1958; Barry 1962; MacInnes 1962; Ryder 1972; Mickelson 1975; Raveling & Lumsden 1977).

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