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COMPARATIVE SPRING HABITAT AND FOOD USE BY TWO ARCTIC NESTING GEESE

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ABSTRACT.—The timing of egg laying is generally constrained by female condition, which is partly determined by the food available to her before laying. Although it was generally believed that geese rely exclusively on internal nutrient reserves for egg production, spring feeding is intensive in many populations of geese, significantly adding nutrients necessary for egg production and incubation. We compared the spring feeding ecology of Greater White-fronted Geese (*Anser albifrons frontalis*) and Canada Geese (*Branta canadensis hutchinsii*) on a shared nesting ground on the Kent Peninsula, NWT (68° N, 108° W), where pairs feed intensively from arrival until incubation. Live plant biomass did not significantly increase within specific habitats during preincubation, but the total available biomass was greater after snow melt because habitats with higher biomass became available. Live plant biomass available in pond margins (30–60 g/m^2) was 4–15 times higher than in habitats that were available earlier, i.e., mud-flats and hummocks (4–8 g/m^2). Before snow melt, both species shared the 1–20% of the study area that was snow free (max. density 600 pairs/km^2), opportunistically used the only two available habitats, mud-flats and hummocks, and primarily ate (50–70%) tillers of *Puccinellia* spp. During snow melt, pairs dispersed, pair density decreased (max. of 40 pairs/km^2), and interspecific differences in habitat and food use appeared. White-fronted Geese used pond margins and ponds more often than Canada Geese. After snow melt, White-fronted Geese predominantly fed in ponds on *Carex* spp. and *Dupontia fisheri* rhizomes and basal stems; Canada Geese continued feeding opportunistically, pecking leaves in all habitats and grubbing rhizomes in pond margins and ponds. White-fronted Geese used the grubbing technique more often than Canada Geese in all habitats and periods. *Received 13 Feb. 1998, accepted 17 Nov. 1998.*

Energy investment by females in reproduction is highest during the period of egg formation in birds with precocial young, such as geese (King 1973). Clutch size and timing of laying are potentially constrained by female condition, which is partly determined by the amount of energy and nutrients available to her before egg formation (Drent and Daan 1980, Winkler and Walters 1983).

Early nesting is critical for Arctic nesting geese because of the short summer and the rapid seasonal decline in components of reproductive success such as gosling growth and probability of producing recruits (Barry 1962, Cooke et al. 1984, Cooch et al. 1991, Sedinger and Flint 1991, Lindholm et al. 1994). One strategy to facilitate early nesting is to carry nutrient reserves accumulated during migration to the breeding grounds (Ankney and MacInnes 1978, Wypkema and Ankney 1979, Ankney 1984, Budeau et al. 1991, Bromley and Jarvis 1993, Choinière and Gauthier 1995). There is, however, an upper limit to the amount of reserves that can be economically carried during migration (Lindstrom and Alerstam 1992).

In migratory birds, the timing of rapid follicular development (RFD) initiation with respect to spring migration may affect the relative contribution to egg production of nutrients acquired en route versus those acquired on nesting grounds. Timing of RFD initiation directly determines laying date of the first egg (reviewed by Rohwer 1992). Because some female geese in some locations typically nest soon (3–6 days) after their arrival on the nesting ground (*Anser rossii*: Ryder 1970; *Anser caerulescens caerulescens*: Ankney 1977, Ankney and MacInnes 1978; *Anser canagica*: Thompson and Raveling 1987; *Branta bernicla bernicla*: Spaans et al. 1993), RFD is initiated before arrival, hence the date of nest initiation is independent of food availability on the nesting ground (Raveling 1978, Ankney 1984, Newton 1977; but see Prop and de Vries 1993).

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In other populations most female geese lay at least 12 days after arrival on the nesting grounds, long enough for the completion of RFD of the first egg [*Branta bernicla nigricans*: Raveling 1978; *B. canadensis*: MacInnes et al. 1974, Bromley 1984; *A. albifrons*: Fox and Madsen 1981, Budeau et al. 1991; *A. caerulescens caerulescens* (at La Pérouse Bay): Findlay and Cooke 1982; *A. c. atlantica*: Gauthier and Tardif 1991]. In this case, food availability on the nesting ground can affect the date of RFD initiation, the date of nest initiation, and potentially clutch size and constancy of incubation. Most of the energy necessary for egg formation and laying was met by food on the nesting grounds for *A. albifrons frontalis* (Budeau et al. 1991), *B. canadensis occidentalis* (Bromley and Jarvis 1993), and *A. caerulescens atlantica* (Choinière and Gauthier 1995). Intermediate cases may occur where the time available for feeding between arrival on the nesting ground and laying varies greatly among females and/or among years within populations (Raveling 1978).

Food availability in the Arctic in spring was traditionally thought to be so low that, although female geese could feed, they could not meet their energy requirements for daily maintenance or egg production (Barry 1962, Ryder 1970; reviewed by Rohwer 1992). For some species, body mass of females generally increases before or during egg production (Wypkema and Ankney 1979, Budeau et al. 1991, Bromley and Jarvis 1993, Choinière and Gauthier 1995) indicating that energy intake during these periods could at least meet requirements for daily maintenance (Ganter and Cooke 1996, Carrière 1996). Further, variation in timing of nesting can be related to variation in food availability prior to egg formation (Prop and de Vries 1993). Thus, food availability and use in the Arctic in spring clearly is significant.

In the Arctic, food availability during preincubation is highly variable. This variation hinders interspecific comparisons of feeding ecology during preincubation because we cannot differentiate between factors that are site specific (e.g., weather, snow melt patterns, plant phenology) and species specific (e.g., body size, bill morphology; Prevett et al. 1985, Fox et al. 1992).

We compared the feeding ecology of Greater White-fronted Geese (*Anser albifrons frontalis*) and Canada Geese (*Branta canadensis hutchinsii*) during preincubation. These species have similar body mass (White-fronted Goose 8% > Canada Goose; R.G.B., unpubl. data), reproductive chronology, and share the same Arctic spring feeding and nesting grounds on the Kent Peninsula, NWT, Canada.

Our objectives were to determine (1) how snow melt affected the availability of feeding habitats and plant biomass, (2) whether White-fronted and Canada geese differed in their use of habitat and food during preincubation on a shared nesting ground, and (3) how changes in habitat and food availability resulting from snow melt affected dispersal, habitat and food use, and the timing of nesting in these two species of geese.

STUDY AREA AND METHODS

The study was conducted on the Walker Bay Study Area (68° 22′ N, 108° 04′ W), southwest Kent Peninsula, Northwest Territories (Fig. 1), as part of longterm studies on the breeding ecology of White-fronted and Canada geese (see Bromley et al. 1995). The shallow plain of the river valley is a high density nesting area for both species of geese (Bromley et al. 1995).

Studies of the feeding ecology during preincubation were made on an intensive study area positioned to permit semicontinuous observation of geese in spring while minimizing disturbance caused by human movements (Fig. 1). The area was further divided into two sites: site A (0.72 km^2) was representative of the habitats found all along the river and typical of areas in which arriving geese concentrated until snow melt; site B (4.33 km^2) was representative of the rest of the general study area where nesting typically occurred. Site A, a raised levee paralleling the river, was drier than site B. Habitats available to geese were classified from dry to wet: hummock, mud-flat, pond margin, and pond (see plant list per habitat in Carrière 1996). Mud-flat habitats were sparsely vegetated flats of exposed glacial marine sediments (ca 3000 yrs ago; Dyke and Dredge 1989), largely saline clays and silts. Hummock habitats were formed by frost heaves (5–30 cm high) and covered by thin soil where *Salix* spp. dominated. Pond margins were the edges of depressions that were wet from snow melt to early June, had low salinity, and formed meadows dominated by graminoids and forbs. Pond habitats were depressions 0.10–1.00 m deep, inundated at least until early July, and dominated by hydrophilic forbs. All habitats formed a fine grained mosaic with patches (i.e., continuous areas of same habitat) of various shapes. Most patches covered 50–900 m^2, with some mud-flats outside sites A and B extending more than 1 km^2.

General phenology.—We recorded the phenology of

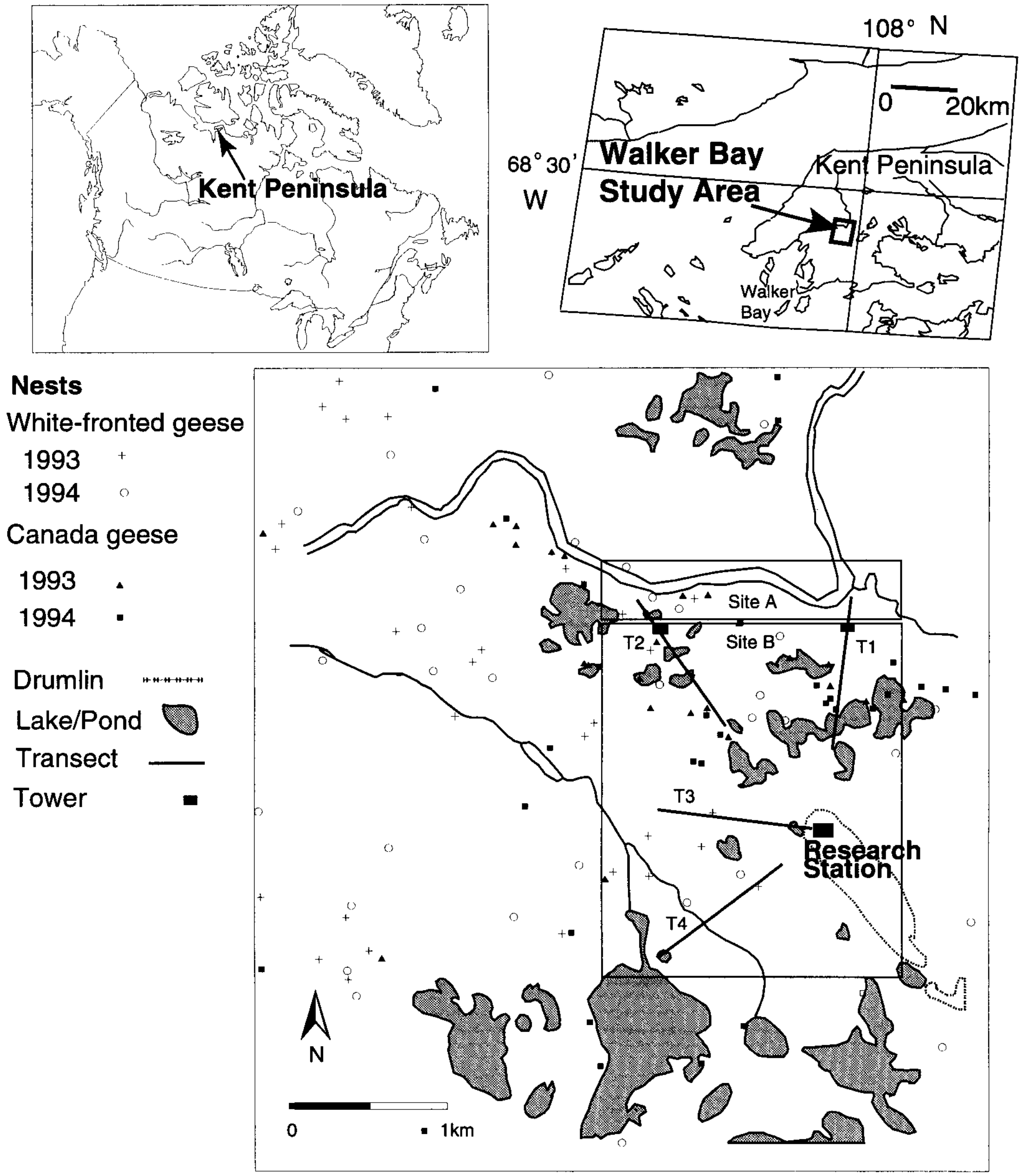

FIG. 1. Walker Bay Study Area is situated in a valley near Walker Bay on the Kent Peninsula, NWT, Canada. A section selected for detailed study was divided into 2 sites: site A was snow-free first in spring and was typical of habitats available along the river banks. Snow melt phenology in site B was typical of the rest of the study area.

snow melt, goose arrival, and goose dispersal along four 1 km transects (Fig. 1). At 2–3 day intervals we visually estimated snow cover (±5%) in 200 × 200 m areas, situated in pairs, one on each side of the transect at each of five stations 200 m apart. Thus, we covered 11% of site A (2 stations) and 7% of site B (18 stations). At each station, we used binoculars to count and locate all geese that could be identified to species.

Preincubation was divided into three periods defined by snow melt phenology on site A: (1) before snow melt (snow cover >80%), (2) during snow melt (snow cover = 20–80%)—a period of rapid change, and (3) after snow melt (snow cover <20%).

Nesting phenology.—Nests were located by observing nest building behavior from towers. Date of the first egg laid (i.e., date of nest initiation) was estimated only for nests found during laying by subtracting 1.3 d per egg (R.G.B., unpubl. data) already laid. Nests outside site A and B were located during ground surveys of randomly selected 1 km^2 plots (Bromley et al. 1995). We compared median laying dates for combinations of years and species using Kruskal-Wallis ANOVA on Ranks tests, followed by non-parametric multiple comparison tests using Excel 97 following Daniel (1978).

Habitat availability.—We measured habitat availability in the areas at two towers (see below) by mapping habitat patches with a 20 × 20 m grid in the field and using aerial photographs. Availability of a habitat was defined by the cumulative area of all patches of that habitat as a proportion of the total snow-free area. Only snow-free areas were considered accessible to feeding geese (Hall et al. 1997).

Use and selection of habitats.—We observed goose pairs throughout preincubation from two towers in 1993 and one tower in 1994. Daily observations were conducted from one tower at a time depending on the distribution of geese in the study area. We used the scan sampling method (Altman 1974), with scans conducted every 2–6 hr during the 24 hr cycle. During a scan, we observed all pairs present within 400 m of the observation tower. Sections of sites A and B were visible from both towers (Fig. 1). For each pair, we noted sex, behavior, and habitat used by each pair member. Sex was determined using relative neck size (larger in males), abdominal profile (larger in females with developing follicles; Owen 1981, Fox et al. 1995), and alert position (male usually standing higher). Pairs were recorded as feeding when either the female or both members were grubbing (on below-ground plant parts), pecking (on above-ground plant parts), searching for food (moving with head down), or drinking.

We calculated habitat use for each scan as the proportion of observed feeding pairs using each available habitat. Pond and pond margin use data were pooled as wet habitats to obtain sufficiently large samples for a *G*-test (Sokal and Rohlf 1981). For analysis, we pooled habitat use data within snow melt period and tower. Habitat use data were assumed to be independent within and between scans. This seemed reasonable for two reasons. First, preliminary observations on focal individuals indicated that pairs showed little synchronization in movements between habitat patches (i.e., no group behavior). Second, because of the extreme patchiness of habitats, pairs could use all available habitats within 2 hr (minimum time interval between scans); 58% of Canada Geese (n = 96) and 43% of White-fronted Geese (n = 69) individuals observed in focals used more than 1 habitat patch within 10 min (S.C., unpubl. data). The constant movement of pairs between the observed and unobserved areas during preincubation minimized pseudoreplication. For example, no individual with a coded neck collar (from 1987–1994 banding operations; Bromley et al. 1995) was observed in more than six different scans (only 30% of collared individuals were observed more than twice).

For each year and period, interspecific differences in habitat use were analyzed without reference to habitat availability using *G*-tests of independence, followed, when significant differences were detected, by pairwise unplanned comparison tests (Sokal and Rohlf 1981; using Excel 97).

Habitat use was compared to availability before and after snow melt, but not during melting, because availability changed too rapidly, i.e., from 20% to 80% snow-free area in <7 d. We used χ^2 goodness-of-fit tests, followed by Bonferroni simultaneous confidence interval tests (Sokal and Rohlf 1981, Neu et al. 1974; using Excel 97) to detect sources of significant differences (design 1 in Thomas and Taylor 1990).

Plant availability within habitats.—We estimated food plant availability in snow-free habitats by sampling randomly 20 × 20 cm quadrats within habitat patches in site A and B, 4 times between 17 May–14 June throughout preincubation (1993: n = 120; 1994: n = 218). We collected all above and below ground vegetation 0.1–3 cm deep then froze each sample for transportation. Ground vegetation below 3 cm was never thawed and was considered unavailable to geese. In the laboratory, live above and below ground vegetation was sorted by species, dried at 45° C to constant mass, and weighed. We pooled plant species according to food plant categories used in the analysis of feces (see below). Availability of each food plant category in each habitat was defined as the average proportion of total dry biomass represented by that category in each habitat during each snow melt period (Fig. 2).

We analyzed total (pooled species) above and below ground biomass separately. We first analyzed differences in total biomass among habitats and sampling dates for each year separately using Kruskal-Wallis ANOVA on Ranks tests, followed by multiple comparison tests to detect pairwise differences (Daniel 1978). We then pooled sampling dates and analyzed differences in biomass among habitats and years with Two Way ANOVA using square-root transformed data (Sokal and Rohlf 1981).

Diet.—We determined diet using two complementary methods: (1) microhistological analyses of feces and (2) detailed observations of feeding techniques. Additional data were available from the esophageal content of 16 female Canada Geese collected in 1994.

Throughout preincubation, we collected all feces that we could assign to an individual bird (i.e., a bird that was observed defecating). Feces were individually frozen for transportation, dried in the laboratory, and analyzed using microhistological techniques (see Johnson 1982). We sampled four slides per feces, with 20 observation fields per slide. We identified most plant fragments (80–100% per feces) to genus. We grouped

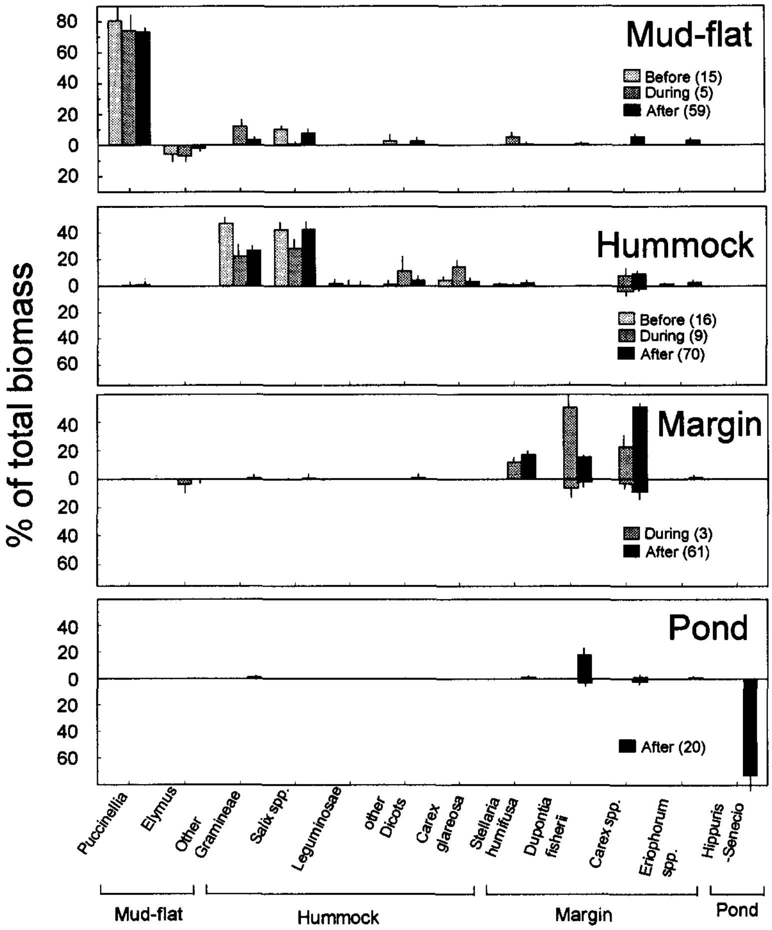

FIG. 2. Relative availability of plants in each snow-free habitat before, during, and after snow melt, measured as the average percent food in dry biomass on the Walker Bay Study Area, NWT, May–June 1993–1994. Sample sizes are given in parentheses, years pooled. Availability of aboveground plant parts is given above the zero line and of below ground plant parts below the zero line.

some rare food plants of the same genus or family that were growing in the same habitat (Table 1, Fig. 2). The validity of the identification of plant fragments in feces was assessed by analyzing plant mixtures of known composition (Holechek and Gross 1982) and by comparing fecal results to esophageal contents of female Canada Geese (Carrière 1996). We could not easily differentiate *Salix arctica* from *Potentilla nivea,* nor discriminate *Dupontia fisheri* and *Eriophorum* spp. from some fragments of other Gramineae and Cyperaceae, respectively. *Potentilla* spp. and *Eriophorum* spp., however, were relatively rare on the study area (Fig. 2, see other Dicots and *Eriophorum* spp.). Some below ground plant parts could not be identified reliably (Carrière 1996). Feces analyses consequently provided only an estimate of use of common above ground food plants on our study area. Coefficients of variation of the proportion of food plants among slides within feces ranged from less than 5% for graminoids to 10–20% for dicots. We defined diet as the average percent of each food plant (% of fragments) present in the feces (frequency of occurrence method; Johnson 1982). Diet was determined for each goose species and snow melt period by pooling years, with individual feces representing sampling units.

We compared use of each food plant among all possible combinations of goose species and snow melt periods using Kruskall-Wallis ANOVA on Ranks tests followed, if significant, by multiple comparison tests (Daniel 1978) using Excel 97.

Feeding techniques.—Use of below ground plant parts was indexed by the proportion of feeding pairs grubbing in each habitat during scans. Conversely, pairs were assumed to eat above ground plant parts while pecking.

We used a Paired *t*-test to determine if the propor-

TABLE 1. Diet of White-fronted and Canada geese before, during, and after snow-melt, from arrival on the nesting grounds to incubation, Walker Bay Study Area, Kent Peninsula, NWT, 1993–94. "Arriving" females were collected before snow-melt, "pre-laying" females during and after snow-melt, and the incubating female after snow-melt.

	Fecal content (% of fragments)														Esophagal content (% dry mass)				
	White-fronted Geese						Canada Geese								Canada Geese (females)				
	Before		During		After		Before		During		After				Arrival		Prelaying		Early inc.
Food plant	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	H^a	P	$\bar{x}$	SE	$\bar{x}$	SE	
Number of feces or geese	27		13		14		15		43		19				6		9		1
Puccinellia tillers[b]	52	4 C	18	6 AB	5	2 A	73	5 C	24	3 B	9	2 AB	63	<0.001	96	5	27	16	
Elymus arenarius rhizomes	3	1	10	7	tr		tr		1	1	tr		11	0.05					
Other Gramineaes[c]	26	3 BC	29	6 C	17	5 ABC	13	3 A	14	2 AB	29	5 C	20	0.001					
Salix buds[d]	2	0	3	1	2	1	5	1	4	1	5	4	9	>0.05					18
Other dicots[e]	9	2 C	1	1 A	11	5 BC	2	1 AB	4	1 BC	7	3 BC	19	0.002	1	0	5	11	
Stellaria humifusa	tr[i]	A	2	1 AB	2	1 AB	tr	A	12	3 C	5	3 AB	36	<0.001	tr		61	11	
Dupontia Fisheri tillers	tr	A	tr	ABC	11	6 BC			1	1 AB	13	5 C	41	<0.002	3	4			64
Carex spp. tillers[f]	tr	A	23	7 B	20	5 B	tr	A	20	3 B	13	4 B	56	<0.003			1	2	18
Hippuris-Senecio[g]					5	4					3	3							
Carex seeds[f]			tr		1	1			tr		tr						6	7	
Unidentified[h]	7		13		25		6		20		15								

[a] Kruskal-Wallis tests of differences of food use for each goose species-period combination. Results from unplanned multiple comparisons tests are given using capital letters near food use values. Values with different letters differ within each row.

[b] *Puccinellia* spp.: *P. phryganodes*, *P. arctica*.

[c] Other Gramineae: *Festuca* spp., *Poa* spp., *Calamogrostis* spp., *Arctophila fulva*.

[d] *Salix* spp.: *S. arcticaor S. lanata* closed buds before snow-melt, closed-open buds after snow-melt, open buds-leaves in esophagus.

[e] Other dicots: *Potentilla* spp., *Draba* spp., *Sueda calceoliformis*, *Astragalus* spp., *Hedysarum* spp., *Oxytropis* spp.

[f] *Carex* spp.: *C. bigelowii*, *C. salina*, *C. subspathacea*.

[g] *Hippuris* sp.: *H. vulgaris* or *H. tetraphylla*. *Senecio* sp.: *S. congestus*, includes rhizomes, young shoots, and leaves.

[h] Unidentified includes fragments of dicots, of *Eriophorum* spp., and all rhizomes except those of *Elymus* sp., and *Hippuris* spp.

[i] tr = trace.

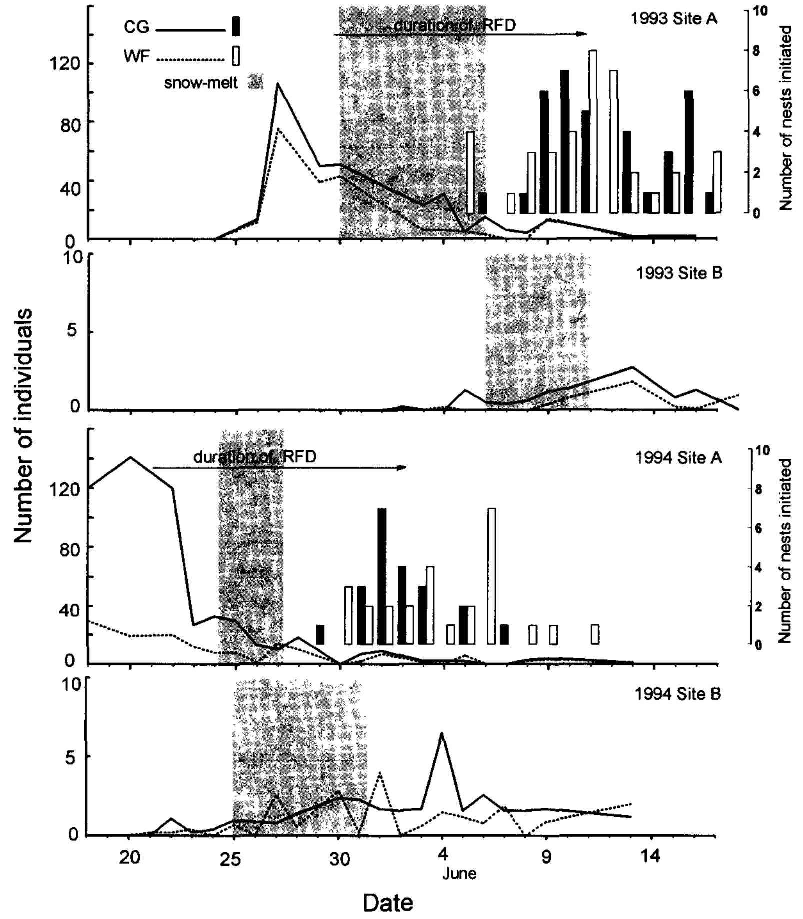

FIG. 3. Number of individual White-fronted Geese (WF) and Canada Geese (CG) counted daily at each station on sites A (n = 2) and B (n = 18; see Fig. 1), from arrival to early incubation, and number of nests initiated daily by each species on the Walker Bay Study Area, NWT, 1993–1994. Arrows indicate duration of rapid follicular development (RFD) for a first egg layed at the median laying date each year. Shaded areas indicate periods of snow melt, defined as 80–20% snow cover. Snow melt pattern on site A was used to define periods for all analyses.

tion of time spent grubbing differed between goose species, pairing observations within habitat-period-year combinations. For each species, we used linear regression to analyze how the proportion (arcsine square-root transformed in degrees; Sokal and Rohlf 1981) of time spent grubbing changed with the proportion of below ground biomass available in different habitats, snow melt periods, and years. The short, rapid melting period in 1994 was combined with the after-melt period.

Unless otherwise stated, statistical analyses were performed using SigmaStat™ (version 1.0; Jandel Scientific Software 1993) in the PC DOS and Microsoft® Windows™ operating system. Statistical significance was established at $P \leq 0.05$.

RESULTS

Annual phenology.—Upon our arrival on 20 May 1993 and 17 May 1994, sites A and B were 95% and 99% snow covered, respectively. Hummock and mud-flat habitats located along the river were the only habitats available. Relative to 1987–1996 (R.G.B., unpubl. data), snow melt was early in 1994 and average in 1993 (Fig. 3). In general, snow melted first on dry habitats (mud-flat, hummock), then on wet ones (pond margin, pond), and earlier on site A than on site B (Fig. 3). The periods before snow melt were 10 days (1993) and 7 days (1994); melting periods were 7 days (1993) and 3 days (1994), and periods after snow melt [end of melting to onset of incubation (median laying date + 4 days)] were 9 days (1993) and 13 days (1994). The total length of the preincubation periods on the nesting ground were thus 26 d in 1993 and 23 d in 1994.

Geese were present along the river (on site A or outside the intensive study area) upon our arrival in 1993 ($n = 50$–80 pairs) and 1994 ($n = 140$–150 pairs), but major arrivals occurred around 27 May 1993 and on or prior to 20 May 1994 (see transect surveys: Fig. 3, site A). During snow melt, goose numbers decreased on site A (and from other areas along the river) and increased slightly on site B as geese dispersed from areas along the river to the rest of the study area (Figs. 1, 3).

We are confident that the pairs observed during this study were part of the locally nesting population because about ⅓ of the collared individuals we found nesting in the study area ($n > 11$ of each species per year) were observed on site A and other areas along the river. Individuals collared in other study areas were never observed on Walker Bay Study Area (R.G.B., pers. obs.).

The first nests were found on 5 June 1993 and on 28 May 1994. Median laying dates were 11 June 1993 (White-fronted Goose: $n = 38$, Canada Goose: $n = 35$) and 2 June 1994 (White-fronted Goose: $n = 26$, Canada Goose: $n = 21$) for both species (Kruskal-Wallis ANOVA on Ranks: $H = 77.4$, $P < 0.001$; medians were different between years only; Fig. 3). The minimum intervals between goose arrival and median laying date were 14 days in 1993 and 13 days in 1994.

Use and selection of habitats.—White-fronted and Canada geese did not differ in their use of habitats before snow melt in either year (G-tests of independence: 1993: $G_{\text{adj}} = 0.083$, 1 df, $P > 0.05$; 1994: $G_{\text{adj}} = 0.031$, 1 df, $P > 0.05$; Fig. 4A, B). Both species also used habitats according to their availability during that period (χ^2 Goodness-of-fit: all $\chi^2 \leq 3.08$, $P > 0.05$).

Habitat use differed between species during snow melt in both years (G-tests of independence: 1993: $G_{\text{adj}} = 18.14$, $P < 0.001$; 1994: $G_{\text{adj}} = 39.26$, $P < 0.001$). Both species fed in newly available wet habitats (pond margin and pond) during snow-melt, but White-fronted Geese used them more often than did Canada Geese.

Pairwise comparison tests showed that in both years Canada Geese used hummock and mud-flat habitats significantly more often than White-fronted Geese and that White-fronted Geese used wet habitats significantly more often than Canada Geese (Fig. 4C, D).

Similar interspecific differences in habitat use were observed after snow melt in both years (G-test of independence: 1993: $G_{\text{adj}} = 23.03$, $P < 0.001$; 1994 sites pooled: $G = 69.44$, $P < 0.001$). Pairwise comparison tests showed that White-fronted Geese used ponds (1993 and 1994) and pond margins (1994) significantly more often than Canada Geese (Fig. 4E, F, G).

In 1993, habitat selection (i.e., use vs availability) by both species differed after snow melt (χ^2 Goodness-of-fit: Canada Goose: $\chi^2 = 94.8$, $P < 0.001$; White-fronted Goose: $\chi^2 = 117.9$, $P < 0.001$). Canada Geese preferred (i.e., use > available) mud-flat, pond margin, and pond, and avoided hummock habitats (Fig. 4E). White-fronted Geese preferred pond and avoided hummock habitat (Fig. 4E). In 1994, most geese fed near tower 1 after snow melt (Fig. 1), where the relative availability of habitats differed greatly between site A and B (Fig. 4). Consequently, we analyzed habitat use in each site separately. Data in dry (mud-flat/hummock) and wet (pond margin/pond) habitats were pooled at site B to obtain sufficient sample sizes for χ^2 tests. Near the river (site A), Canada Geese used habitats according to their availability (χ^2 Goodness-of-fit: $\chi^2 = 0.92$, $P > 0.05$; Fig. 4F), while White-fronted Geese preferred pond margin and pond habitats and avoided mud-flat habitats ($\chi^2 = 49.8$, $P < 0.001$). On site B, Canada Geese again used habitats according to their availability ($\chi^2 = 0.22$, $P > 0.05$; Fig. 4G) and White-fronted Geese still preferred wet habitats (pond margin/pond) and avoided dry ones (mud-flat/hummock; $\chi^2 = 23.4$, $P < 0.001$).

Diet.—Nine food types were recognized in feces (Table 1). The number of different food types detected increased as snow melted, as expected because of the increase in available habitats. A major food before snow melt was *Puccinellia* spp. tillers, which accounted for 52% and 73% of White-fronted and Canada

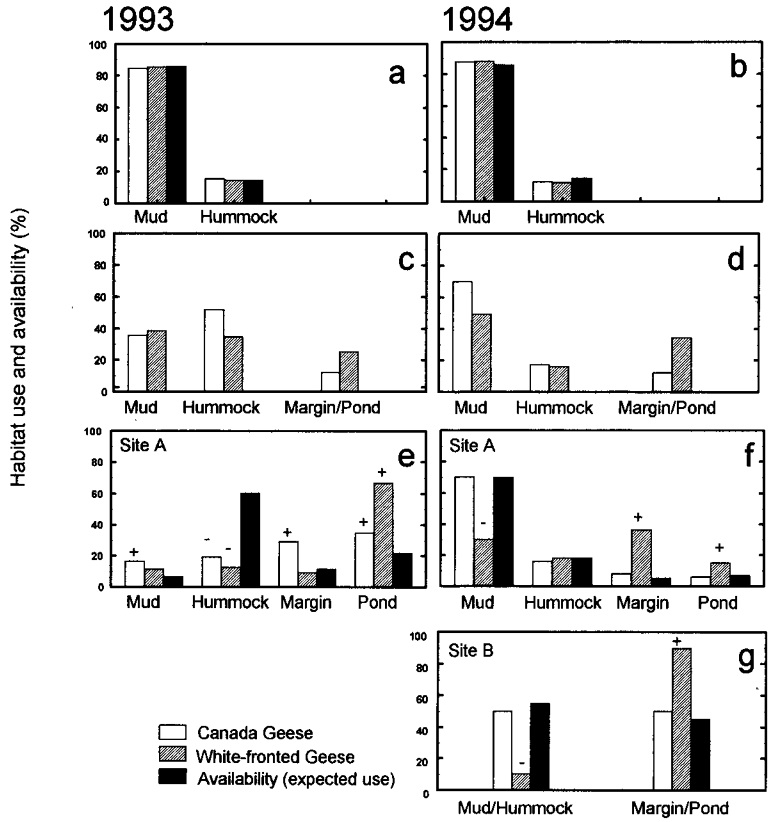

FIG. 4. Use (% of feeding pairs) of mud-flat, hummock, pond margin, and pond habitats by White-fronted (WF) and Canada geese (CG), and availability of these habitats during preincubation on the Walker Bay Study Area, NWT, 1993–1994. (a–b) Before snow melt 1993 (CG: n = 332; WF: n = 228) and 1994 (CG: n = 1265; WF: n = 383). (c–d) During snow melt 1993 (CG: n = 532; WF: n = 137) and 1994 (CG: n = 637; WF: n = 168); habitat availability could not be estimated. (e) After snow melt at site A in 1993 (CG: n = 120; WF: n = 87). (f–g) After snow melt in 1994, site A (CG: n = 50; WF: n = 33) and site B (CG: n = 22; WF: n = 29). A "+" indicates use > availability, "−" indicates use < availability and no symbol indicates use = availability ($P > 0.05$).

goose diet respectively. After snow melt, more than 50% of the diets of White-fronted and Canada geese were composed of *Carex* spp. and *Dupontia fisheri.* For both species, most (85%) feces contained food plants representative of at least 2 habitats. Consequently, changes in diet reflected changes in both habitat use and food use within habitats.

The greater diversity of the diet found in the feces of Canada Geese relative to esophagi (Table 1) is probably caused by the accumulation of food fragments in the digestive system. Nevertheless, analyses of esophageal content indicated that some Gramineae (fragments not identified at the genus level) could be overestimated in fecal analyses, whereas *Stellaria humifusa, Dupontia fisheri,* and *Carex* seeds could be underestimated (see methods, Carrière 1996). Young leaves and open buds of *Salix* spp. were found only in female Canada Geese collected during incubation.

Available biomass.—Plant biomass varied among combinations of habitats and sampling dates for both above ground (Kruskal-Wallis ANOVA on ranks: 1993: H = 46.0, $P <$ 0.001; 1994: H = 152.1, $P <$ 0.001) and below ground plant parts (1993: H = 25.7, P = 0.012; 1994: H = 58.7, $P <$ 0.001; Fig. 5). There was little seasonal increase in total dry biomass within each habitat, except after the median laying date for above ground biomass in pond margins (1994 only) and below

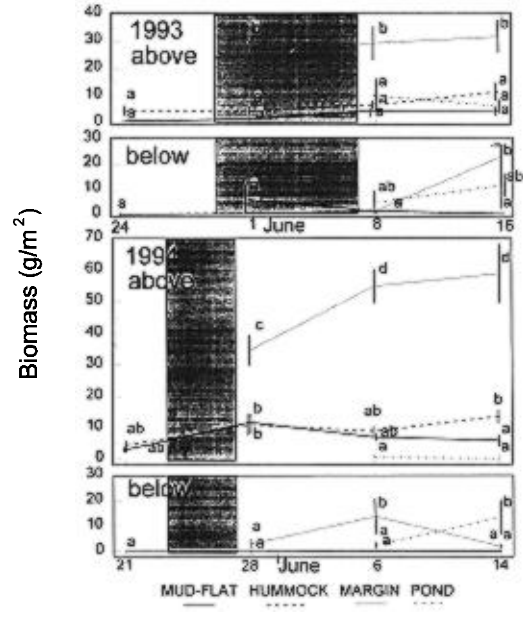

FIG. 5. Live above and below ground dry biomass (mean ± SE) available to geese in 4 habitats during preincubation on the Walker Bay Study Area, NWT, 1993–1994. Values with same letter within graphs do not significantly differ (multiple comparison tests after a Kruskall-Wallis ANOVA on Ranks test for each year, above and below ground biomass tested separately, all tests $P < 0.02$). Grey areas indicate periods of snow melt (80–20% snow cover on site A). Number of sampled 20 × 20 cm quadrats per sampling date were: (1993) mud-flat = 3, 5, 17, 14; hummock = 6, 9, 11, 11; pond margin = NA, 3, 6, 6; pond = NA, NA, 3, 26 and (1994) mud-flat = 12, 16, 24, 23; hummock = 10, 16, 16, 16; pond margin = NA, 17, 16, 16; pond = NA, NA, 16, 20. NA = datum was not available, under snow.

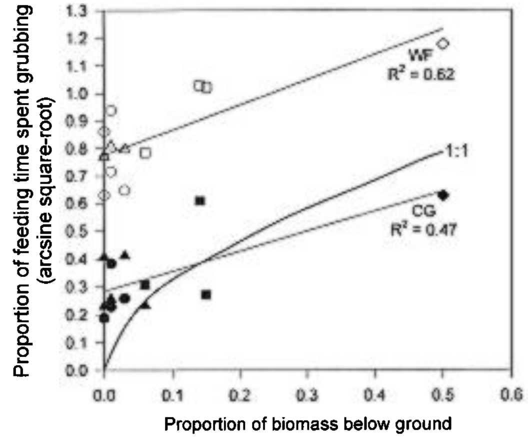

FIG. 6. Relationship between below ground biomass available and proportion of feeding time spent grubbing by female White-fronted (WF) and Canada geese (CG) during preincubation on the Walker Bay Study Area, NWT, 1993–1994. Each point is the proportion of scanned pairs observed grubbing (arcsine square-root transformed) in a habitat during a specific period and year. Closed symbols are Canada Geese, open symbols are White-fronted Geese. Habitats are mud-flat (circles), hummock (squares), pond margin (triangles), and pond (diamonds). Linear regressions: for WF: $y = 0.78 + 0.91x$ [0.50–1.32; ß(95%CI)], $F = 18.0$, $P = 0.001$; for CG: $y = 0.28 + 0.72x$ [0.27–1.17; ß(95%CI)], $F = 9.9$, $P = 0.009$.

ground biomass in pond margins (1993) and pond (1994). Seasonal changes in below ground biomass were mostly the result of a gradual deepening of the active layer. We pooled sampling dates and found differences in above ground biomass among habitats (Two Way ANOVA: $F = 112.1$, $P < 0.001$) and years ($F = 4.25$, $P = 0.04$; habitat-year interaction, $F = 7.25$, $P < 0.001$). Above ground biomass in pond margins was higher than in any other habitat, particularly in 1994. We found a tendency for below ground biomass to be lower in dry (0–1.08 g/m^2) than in wet habitats (1.33–24.4 g/m^2; Two Way ANOVA: $F = 2.61$, $P = 0.05$), but no difference between years ($F = 1.53$, $P > 0.05$; habitat-year interaction, $F = 4.09$, $P = 0.007$).

Use of below ground food plants.—Canada Goose pairs grubbed less often than White-fronted Geese (Canada Goose: 12.4%, White-fronted Goose: 56.9%; Paired *t*-test: $t = -14.2$, $P < 0.001$; Fig. 6), which grubbed extensively even in habitats where below-ground biomass was very low (i.e., in mud-flat/hummock), before widespread snow melt and thawing of the ground surface. Spatial distribution of below ground vegetation (mostly *Elymus* sp. rhizomes) was clumped in these habitats and available below ground biomass may have effectively been much higher in some patches used by foraging individuals. In all habitats, before and during snow melt, most of the below ground biomass was frozen under the active layer and hence was not available to geese.

There was a significant positive relationship between the proportion of below ground biomass in different habitat-year-period combinations and the proportion of feeding time geese spent grubbing in these habitats (linear regression: White-fronted Geese: $F = 18.0$, $P = 0.001$; Canada Geese: $F = 9.9$, $P = 0.009$; Fig. 6). This indicates that both White-fronted and Canada geese modified their feeding behavior with changes in below ground food availability.

DISCUSSION

Arrival, phenology, and timing of laying.—The minimum interval between peak arrival and laying was 1–4 day longer than necessary for rapid follicular development (Alisauskas and Ankney 1992a), which is typical in most goose populations during early and average years (Raveling 1978, Fox and Madsen 1981, Budeau et al. 1991, Gauthier and Tardif 1991, Bromley and Jarvis 1993). Arrival and laying initation were both earlier in 1994 than in 1993 and peak initiation of laying occurred about 15 days after peak arrival in 1993, but apparently only 12–13 days after arrival in 1994. The longer interval in 1993 likely was due to later snow melt that year; nest initiation closely followed snow melt in site B. In contrast, during the early snow melt of 1994, nesting sites became available (i.e., when snow cover <50% in site B) 5–8 days before peak nest initiation, indicating that completion of RFD, rather than snow melt, constrained nesting that year. These relationships were remarkably similar in White-fronted and Canada geese.

The close proximity of prenesting feeding sites to nesting sites conveys benefits to geese arriving on the Arctic nesting grounds before RFD. During both years, pairs of both species dispersed from early exposed locations near the river to additional areas exposed late during snow melt. This resulted in their using feeding areas that were increasingly distant from the river. Such short distance movement by breeding pairs from feeding areas to nearby nesting areas has been observed in other goose populations (Gauthier 1993, Prop and de Vries 1993). This local dispersal is similar to the final migratory flight from staging areas to the breeding grounds in populations where most females nest soon after arrival in the Arctic (Ankney and MacInnes 1978, Wypkema and Ankney 1979). For the latter case, however, the flight occurs late in RFD (Wypkema and Ankney 1979). Unlike geese nesting adjacent to feeding sites, this flight necessarily draws largely upon body reserves during RFD because long migratory flights would use more energy than local dispersal. Furthermore, earlier arrival on the breeding ground enables pairs to directly assess nesting conditions (Wypkema and Ankney 1979, Peterson 1992, Rohwer 1992, Ganter and Cooke 1996).

Although little plant growth occurred, food availability rapidly and greatly increased during preincubation. The change in total available biomass was due to the rapid exposure of habitats with large plant biomasses during snow melt, a common phenomenon in tundra ecosystems (Wielgolaski et al. 1981). This may play an important role in determining individual reproductive decisions in many Arctic nesting geese (Gauthier 1993, Prop and de Vries 1993) because increasing food availability before and during egg-production could improve individual condition (as indexed by body mass; Bromley and Jarvis 1993, Choinière and Gauthier 1995, Ganter and Cooke 1996). Which components of reproductive success (laying date, clutch size, nest attentiveness, condition at hatching, or a combination of these) may be affected by a female's improved body condition depends on the timing of changes in food availability with respect to RFD initiation in individual females (e.g., Bolton et al. 1993, Dalhaug et al. 1996).

Interspecific differences in feeding ecology.—Snow melt, and the concomitant changes in habitat and food availability, enabled us to detect similarities and differences in resource use and selection between White-fronted and Canada geese during preincubation. In both years, both species shared feeding sites and had the same average date of nest initiation (i.e., RFD initiation), hence they could experience the same changes in the availability of resources at similar times relative to their reproductive process.

Both species used habitats opportunistically before snow melt when pair density was highest (up to 600 pairs/km^2 in snow-free areas) and habitat availability lowest (1–20% of study area was snow free). With onset of snow melt, both species dispersed and overall pair density decreased (<40 pairs/km^2).

After snow melt, Canada Geese generally used habitats more opportunistically than White-fronted Geese, which consistently selected wet habitats with high plant biomass. Below ground food plants were used more extensively by White-fronted Geese than by Canada Geese in all habitats. These differences are similar to those reported between *Branta canadensis interior* and *Anser caerulescens caerulescens* on a common staging area on James Bay (Prevett et al. 1985), but unlike our study those differences could be explained in part by segregation of feeding areas.

Although we could not test for density dependent habitat selection because of synchronous changes in habitat availability and in pair density with snow melt, the evidence indicates that interspecific differences in the relative suitability of habitats for feeding exists. Consistent with a release from population density effects in a constant environment (Rosenzweig 1985, Morse 1990), White-fronted Geese changed from opportunistic to selective use of habitats with the highest plant biomass. In contrast, Canada Geese exhibited a relatively weak shift.

We suggest three possible non-exclusive explanations for the interspecific differences in habitat use and diet we observed.

1. Pond margin and pond habitats may be more profitable to White-fronted Geese than to Canada Geese because of the longer and apparently more robust bill morphology of the former (WF culmen is 35.3% and skull is 15.4% longer than CG's; Bolen and Rylander 1978, Gawlik and Slack 1996, R.G.B., unpubl. data). A longer bill may enable White-fronted Geese to be more efficient at grubbing in the ground, presumably giving them easier access to resources buried in a frozen and dry substrate. There is a spectrum of feeding techniques used by geese to obtain food (Bolen and Rylander 1978, Bellrose 1980, Prevett et al. 1985, Ganter and Cooke 1996) but we still know little of how morphology affects the relative efficiency of these techniques among species.

2. White-fronted and Canada geese may differ in their food use because their nutrient requirements for reproduction differ. Protein, fat, and calcium are the most important nutrients required for egg formation (Robbins 1993, Alisauskas and Ankney 1992a). Geese generally switch from a simple, carbohydrate-rich diet before spring migration to a protein-rich one during spring migration and egg production (Mainguy and Thomas 1985, Prevett et al. 1985, Budeau et al. 1991, Alisauskas and Ankney 1992b, Bromley and Jarvis 1993, Gauthier 1993), suggesting that protein is a limiting nutrient to egg formation in geese (Krapu and Reinecke 1992). Incubating females mainly require large fat reserves for maintenance (Raveling 1979, Le Maho et al. 1981, Boismenu et al. 1992). Nutrient requirements for egg formation and incubation therefore differ, and whether a female should select for protein or energy rich food during egg production will depend on her initial nutrient reserves, and on how requirements are met through food intake and reserve reallocation.

How females allot nutrients ingested during preincubation to short (egg production) and long term (incubation) requirements may be reflected in their incubation behavior (Bromley 1984, Thompson and Raveling 1987). White-fronted Geese have cryptic nesting behavior, and like Emperor and Giant Canada (*B. c. maxima*) geese, rely mostly on stored nutrients for incubation (mean feeding time per day = 1–8 min; Thompson and Raveling 1987; R.G.B., unpubl. data). In the central Canadian Arctic, Canada Geese nest openly, defend their nests, and take frequent recesses to feed (mean: 40 min per day; Jarvis and Bromley, in press; R.G.B., unpubl. data). Little feeding during incubation by White-fronted Geese suggests a greater requirement for energy rich food prior to incubation. Longer incubation recesses by Canada Geese imply a greater reliance on foraging to meet nutrient requirements during incubation, allowing for more nutrients (e.g., protein) ingested prior to incubation for egg production (see Thompson and Raveling 1987). Thompson and Raveling (1987) suggested that greater incubation attentiveness may be related to larger body size in geese, because they are vulnerable to different types of predators and have a greater fasting endurance (Calder 1974, Boismenu et al. 1992).

3. For Canada Geese, feeding pair density may not entirely reflect the suitability of the habitat for feeding during laying (Van Horne 1983). Canada Geese typically nest on pond margins (R.G.B., unpubl. data), and as laying time approaches pairs may show increasing territorial behavior in some patches of this habitat. Intraspecific aggressive behavior was

observed, and could exclude conspecifics from some patches of pond margins. In contrast, White-fronted Geese prefer hummock habitat to nest in, and their territorial behavior appears much weaker (R.G.B. and S.C., pers. obs.).

Potential for competition.—Interspecific competition for habitat and food in spring is believed to be minimal in geese because species usually segregate either spatially (different ranges: Bellrose 1980, Ebbinge et al. 1982, Owen and Black 1990; different feeding habitats: Fox et al. 1992) or temporally (different timing of breeding: Fox et al. 1992). We documented differences in the feeding ecology of two sympatric goose species that nest in synchrony and differ mostly in bill morphology, slightly in body mass, and in incubation behavior. We did not examine niche shifts with changes in the relative densities of each species during spring (Madsen and Mortensen 1987) because both species experienced similar decreases in pair densities with snow melt. Nonetheless, we showed that both species overlapped in habitat use but each differed in its preferred feeding technique and hence in its selection of plant parts ("niche complementarity"; see Nudds 1992). On our study area, potential for both intra- and interspecific competition for food is highest before snow melt, when food availability and diversity are low, and pair density is high.

Interactions between nutrient requirements, foraging ability and food profitabilities (hence habitat selection: Stephens and Krebs 1986) in goose species with similar body sizes but with different bill morphologies warrant further study.

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