

SPRING ACCUMULATION OF FAT BY GREATER SNOW GEESE IN TWO STAGING HABITATS

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ABSTRACT.—The influence of habitat on fat storage by Greater Snow Geese (*Chen caerulescens atlanticus*) on their St. Lawrence River estuary spring staging grounds was studied in 1979 and 1980. In all, 373 individuals (two-year old and older birds only) were collected in two types of marsh during the six-week staging halt: the traditionally-occupied fresh-water, *Scirpus*-dominated marshes of the upper estuary (SCI) and in the newly-invaded (after the early 1960s) salt-water, *Spartina*-dominated marshes (SPA) of the lower estuary. The birds reached SPA a few days later than SCI in early April, at which time their total fat reserves amounted to about 10% of their body weight. Fattening at SCI increased steadily throughout the staging period, while at SPA, it slowed markedly in females and stopped completely in males around the middle of the staging period. In birds departing for the arctic around 18–20 May, the total fat reserves amounted to 19–20% of the body weight. Males departing from SCI carried 23% more fat on the average than those of SPA ($P < 0.01$), while the difference amounted to 9% in females ($P > 0.05$). It appears unlikely that the geese could increase these reserves after leaving the St. Lawrence estuary and before reaching their high-arctic nesting grounds.

In arctic-nesting geese, energy reserves available to birds at the beginning of the breeding season constitute one of the major determinants of reproductive success (Hanson 1962; Ryder 1967, 1970; Newton 1977; Raveling 1978). This has been shown for Lesser Snow Geese (*Chen c. caerulescens*; Harvey 1971, Ankney 1977, Ankney and MacInnes 1978) and Canada Geese (*Branta canadensis*; Raveling and Lumsden 1977, Raveling 1979). However, until recently little attention had been paid to the process of fat accumulation in the spring (Wypkema and Ankney 1979, McLandress and Raveling 1981).

The Greater Snow Goose (*Chen caerulescens atlanticus*) is unique among arctic-nesting North American geese because it makes only a single known stop during spring migration. The spring population has increased in recent years from 25,400 in 1965 to 170,000 and 180,000 in 1979 and 1980, respectively (Anon. 1981), and the geese have also expanded their staging area. Traditionally, they used the bulrush-dominated (*Scirpus americanus*) tidal marshes of the upper St. Lawrence River estuary around Cap Tourmente and Montmagny, Quebec (Lemieux 1959; see Fig. 1). Since the 1960s the geese have progressively invaded the cordgrass (*Spartina* sp.)-dominated tidal

marshes of the lower estuary, and by 1980, approximately 20% of the spring population used this newly invaded habitat (J. Bédard, unpubl. observ.).

Preliminary observations in 1978 indicated that geese responded differently to the conditions prevailing in these two types of marshes. To investigate these responses, a comparative study of the birds' food habits, movements, time and energy budget was conducted in 1979 and 1980. In this article, we summarize one aspect of that larger investigation, the process of spring fat accumulation, together with a comparison of fattening rates in birds using either *Scirpus* or *Spartina* marshes. In this way, we hope to establish whether the recent range expansion into the *Spartina* habitat has affected the accumulation of fat reserves essential for these birds to reach their breeding grounds in peak condition.

STUDY AREA

Our study was conducted on the south shore of the St. Lawrence River between Montmagny and Isle Verte (Fig. 1). The pronounced salinity gradient in the estuary strongly influences the littoral plant communities. Upriver from St. Roch-des-Aulnaies (salinity $< 15\text{‰}$), the three-square bulrush dominates the tidal

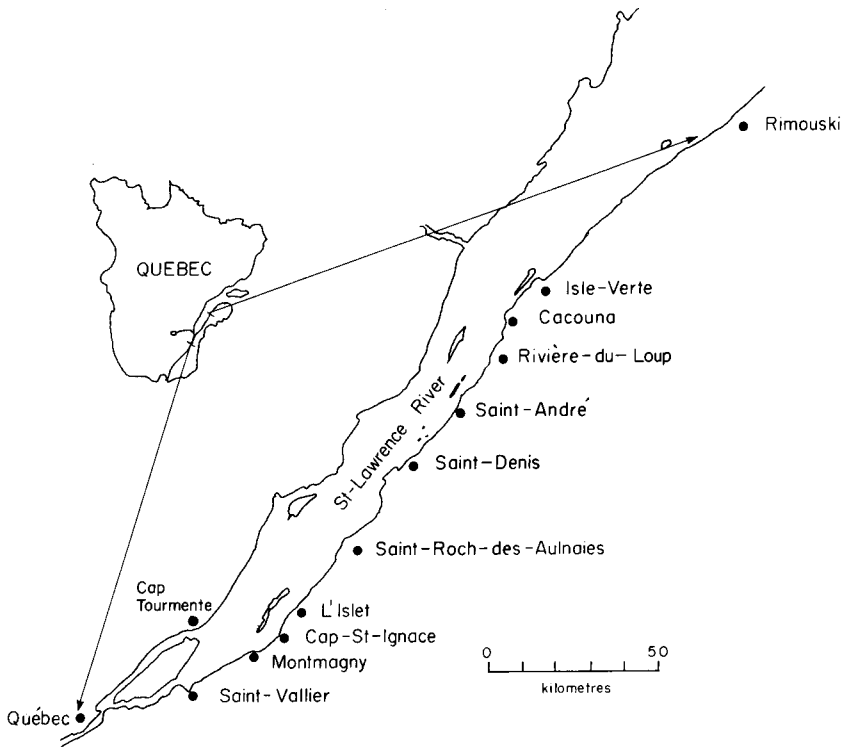


FIGURE 1. The St. Lawrence River estuary.

communities, along with arrowhead (*Sagittaria latifolia*), wild rice (*Zizania aquatica*), spikerushes (*Eleocharis* spp.) and prairie cordgrass (*Spartina pectinata*). Downriver, the salinity is greater than 15‰ and marshes are stratified altitudinally. Smooth cordgrass (*Spartina alterniflora*) and glasswort (*Salicornia europaea*) are the main vascular plants in the lower reaches; saltmeadow cordgrass (*Spartina patens*) occupies an intermediate position, while a complex community of various halophytes (*Glaux maritima*, *Limonium vulgare*, *Atriplex* sp., *Puccinellia* sp., etc.) characterizes the upper marsh. Agricultural fields adjacent to the marshes are also used by feeding geese. These fields are farmed intensively, normally undergoing a three- to five-year small grain-timothy grass (*Phleum pratense*) rotation. Observations and collection of geese in the fresh-water *Sicripus* marsh (SCI) were carried out mostly at Cap-Saint-Ignace and, in the salt-water *Spartina* marsh (SPA), mostly at Isle Verte. The size of the flocks was approximately 14,000 at SPA and 10,000 at SCI.

METHODS

We collected 226 geese in 1979 and 217 in 1980. Of these, 70 were juveniles (one-year old birds, excluded from the present analysis) while the remainder had adult plumage. It is known

that the Lesser Snow Goose rarely breeds before the third summer after hatching (Finney and Cooke 1978) but similar information is lacking for the Greater Snow Goose. Unfortunately, subadults (two-year old birds) could not be distinguished from breeding adults, since examining the cloacal bursa of thawed specimens produced unreliable results. Collections were made at approximately weekly intervals. Birds were shot and within a few hours were sealed in bags and frozen. Each specimen was weighed to the nearest gram before thawing and 11 external dimensions were measured. In 1979, rectrices were pulled out by hand on thawed specimens while remiges and contour feathers were cut with scissors and electric shears. The wings were disjointed at the elbow joint and the legs at the inter-tarsal joint. These structures were later included with the carcass (see below). The skin with the attached subcutaneous fat, and the abdominal fat mass were kept separately; the right half of the breast and the right leg (all those muscles originating either on the femur or the tibiotarsus) muscles were dissected out and the gizzard removed. The digestive tract was emptied and its contents weighed. Flesh was removed from the femur and tibiotarsus of the right leg and from the right side of the sternum and the pelvic girdle, and these bones were stored separately. "Car-

cass" here refers to the remaining organs including viscera plus both wings and the left leg. To hasten the autopsies in 1980, the breast muscle, sternum and pelvic girdle were not excised but were included with the carcass. All tissues and organs were chopped and/or ground while frozen, to minimize fat losses, before being freeze-dried to a constant weight. For the breast and leg muscles, the skin and the carcass, only an aliquot of the homogenate was dried. Water losses were monitored during the autopsies and necessary corrections made.

The leg bones were broken, immersed in a petroleum-ether solvent for 24 h and fat-extracted in the Soxhlet apparatus for 30 min (six fluxes). The freeze-dried soft tissues were powdered in a blender and a 1-g sample was weighed directly in a cellulose capsule before a 30-min extraction in the Rafatec apparatus (Randall 1974). The solvent was evaporated and the fat residue weighed in the flask. All analyses were done in duplicate, and in triplicate if differences exceeded 3%. The freeze-dried abdominal fat was assumed to contain 100% petroleum-ether extractable fat. The strong correlation between the fat and water content in the skin ($r = -0.97$, $P \ll 0.001$, $n = 223$) and leg muscles ($r = -0.92$, $P \ll 0.001$, $n = 223$) enabled us to use regression equations to estimate the fat content of these organs in 1980 (see Campbell and Leatherland 1980). Most of the analyses were made by regression procedures, but a few comparisons of paired samples were also made. In the latter case, geese collected within 10 days of the arrival of the first birds were called "arriving" whereas those collected during the four days preceding mass departure were called "departing."

Neter and Wasserman (1974) and Sokal and Rohlf (1969) were used as reference texts on statistical procedure while the data were analyzed using the Statistical Package for the Social Sciences (SPSS, Nie et al. 1975).

RESULTS

Geese began arriving on the staging grounds in late March and early April. In both years of the study, the number of birds increased gradually until 20 April. In 1980, the spring migration occurred approximately one week earlier than in 1979. In both years, geese arrived several days later at SPA than at SCI. Thus, the first flocks of staging geese were spotted on 7 April 1979 (30 March 1980) at SCI but on 14 April 1979 (4 April 1980) at SPA. Consequently, collection was delayed in both years at SPA.

Departure of the entire flock from the staging area spanned only one to two days and

coincided with propitious weather conditions. In 1979, the geese left SPA on 17 May and SCI on the following day. In 1980, departure dates were 16–17 May and 18–20 May, respectively.

Comparisons of external measurements showed no significant differences between individuals of the two representative flocks. Information collected during daily monitoring of these flocks revealed that no movement of geese occurred between sites, once established (around 20 April).

Ingesta-free body-weight (IFBW = fresh body weight – digestive tract content) was not an entirely reliable indicator of change in the body condition of the geese during staging. The IFBW was significantly correlated with date in SCI birds for both years ($r = 0.51$, $P < 0.001$, $n = 55$ in females and $r = 0.44$, $P < 0.01$, $n = 45$ in males in 1979; $r = 0.42$, $P < 0.01$, $n = 44$ in females and $r = 0.64$, $P < 0.001$, $n = 41$ in males in 1980). At SPA, correlations were absent in 1979 ($r = 0.20$, NS, $n = 42$ in females and $r = 0.02$, NS, $n = 49$ in males) and weak in 1980 ($r = 0.38$, $P < 0.05$, $n = 33$ in females and $r = 0.38$, $P < 0.05$, $n = 45$ in males).

We estimated the total fat reserves in geese collected in 1979 after summing the weight of fat extracted from seven different organs and tissues. The subcutaneous fat along with the abdominal fat mass accounted for 53% of this sum and these two tissues displayed the largest seasonal increase of all storage tissues examined. The carcass held 31% of total fat reserves while the remainder was located in the breast muscles, leg muscles, leg bones, and gizzard. In 1980, we estimated the total fat reserves of the birds from the 1979 regression equation relating total fat reserves on the one hand and subcutaneous plus abdominal fat on the other:

$$\text{TFR} = 1.325 (\text{SKF} + \text{ABF}) + 109.6$$

where TFR is the Total Fat Reserves (in g), SKF is the skin fat content (in g) and ABF the weight of the abdominal fat mass (in g). The relationship is very close since $r = 0.98$ ($P \ll 0.001$, $n = 171$).

We removed the last sample ($n = 3$) of SCI females in 1979 from the regression analysis because it was too small and because we could not obtain more specimens before the flock departed for the arctic (Fig. 2). Furthermore, we divided the 1980 fattening curve for SPA males into two segments because the curve levelled off at the end of April (Fig. 3). A similar procedure was not justified in the females from the same area for 1980 since a weak, positive trend remained in the data even after removing the 15 birds obtained before 20 April.

We were unable to pool the data from 1979

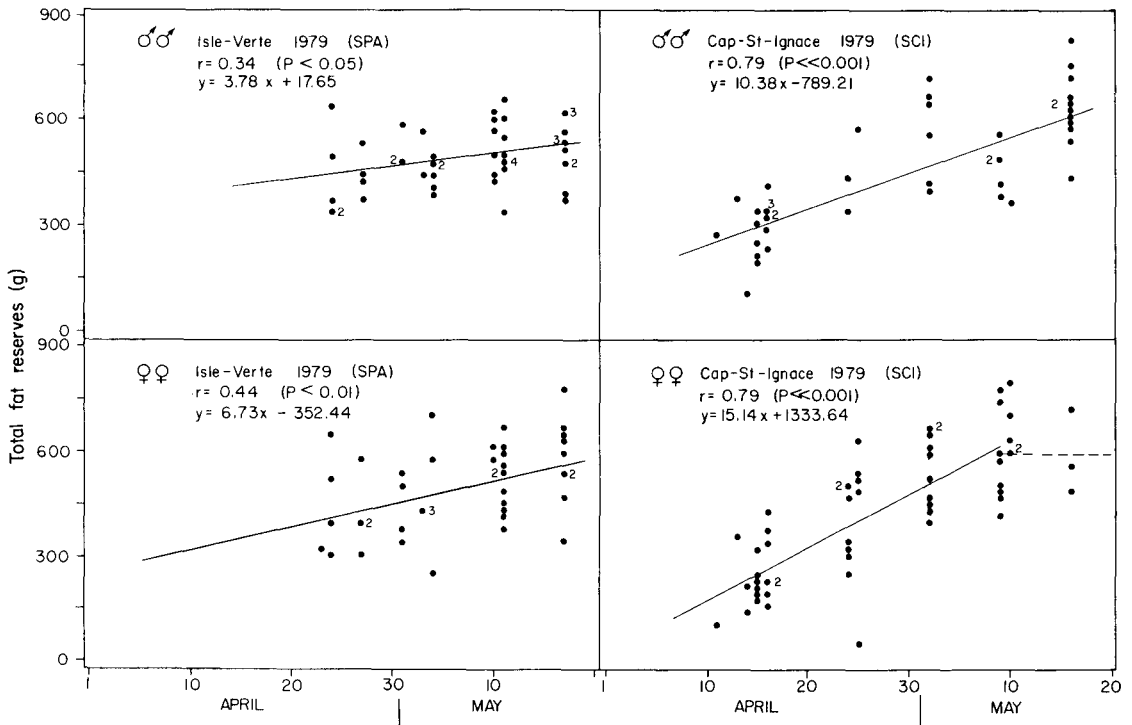


FIGURE 2. Changes (in g) in the Total Fat Reserves (TFR) of Greater Snow Geese during their spring staging halt of 1979. Groups were separated according to sex and habitat: *Scirpus* marsh (SCI) of the upper estuary with type locality at Cap Saint-Ignace vs. *Spartina* marsh (SPA) of the lower estuary with type locality at Isle Verte. Regressions were calculated using the Julian calendar.

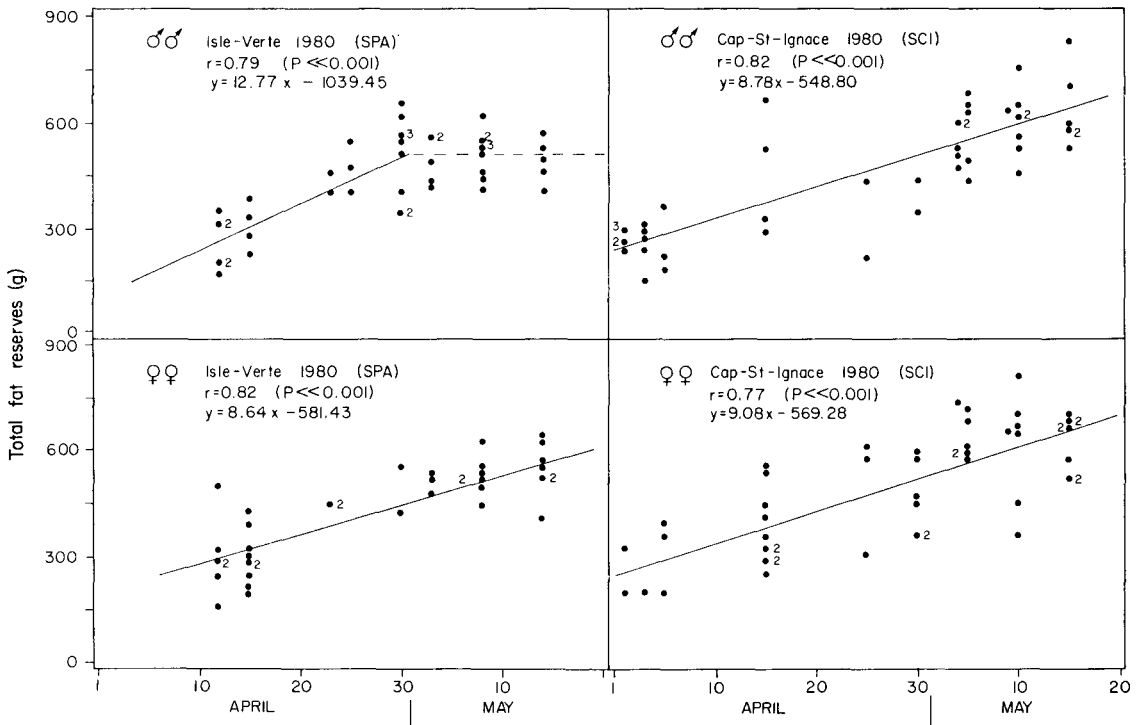


FIGURE 3. Changes (in g) in the Total Fat Reserves (TFR) of Greater Snow Geese during their spring staging halt of 1980. Details as in Figure 2.

TABLE 1. Total Fat Reserves (TFR in g) and Fat Index (FI in percent obtained from TFR/Ingesta-free body-weight \times 100) in the Greater Snow Goose upon arriving and leaving the St. Lawrence River staging grounds in two different types of tidal marshes (SCI for *Scirpus* and SPA for *Spartina* marshes). Differences between means are tested by Student's *t*-test, and homogeneity of the variances was respected.

		1979			1980			1979-1980		
		TFR (g)		FI	TFR (g)		FI	TFR (g)		FI
		$\bar{x} \pm SE$	(n)	%	$\bar{x} \pm SE$	(n)	%	$\bar{x} \pm SE$	(n)	%
Males										
Arriving	SCI	239 \pm 19 **	(16)	9.9	255 \pm 15 NS	(14)	9.1	a	a	
	SPA	433 \pm 34	(9)	14.3	270 \pm 24	(10)	9.2	a	a	
Leaving	SCI	638 \pm 30 *	(12)	19.7	635 \pm 46 *	(16)	18.9	637 \pm 25 **	(18)	19.4
	SPA	529 \pm 24	(12)	17.0	486 \pm 29	(5)	15.6	516 \pm 19	(17)	16.6
Females										
Arriving	SCI	246 \pm 22 **	(17)	9.3	275 \pm 38 NS	(16)	9.5	a	a	
	SPA	432 \pm 41	(9)	16.1	304 \pm 23	(15)	11.4	a	a	
Leaving	SCI	588 \pm 68 NS	(3)	19.3	626 \pm 28 NS	(8)	20.4	615 \pm 26 NS	(11)	20.0
	SPA	576 \pm 41	(9)	19.0	553 \pm 31	(7)	19.3	566 \pm 26	(16)	19.1

* The presence of differences in 1979 precludes pooling the data.

* $P < 0.05$; ** $P < 0.01$; NS, $P > 0.05$.

and 1980 since the statistical comparisons of the regression equations revealed that the rates of seasonal increase in TFR were significantly different in SCI females (15.1 vs. 9.1 g/day, $P < 0.01$) and in SPA males (3.8 vs. 12.8 g/day, $P < 0.01$) between the two years of study.

In females, the TFR was closely correlated with date at SCI. The gain was steady and rapid during both years. At SPA, a weaker correlation between these two variables in 1979 was due mainly to the shorter sampling period (Fig. 2); in 1980, when a more evenly spread and larger sample became available, the relationship improved ($r = 0.82$, $P \ll 0.001$ in 1980 vs. $r = 0.44$, $P < 0.01$ in 1979).

In males, TFR was closely related to date in both years of the study at SCI, but not at SPA. In 1979, TFR at the SPA site was only weakly correlated to date ($r = 0.34$, $P < 0.05$) and reflected a slight fattening. With samples obtained earlier in the season in 1980, we noted rapid fattening in the first half of the season, followed by a complete levelling off of the fat gains (Fig. 3).

In 1979, the fattening rate of both sexes was greater at SCI than at SPA (test for slope of the regression lines, $P < 0.01$ in males and in females). In 1980, the analysis revealed no difference in fattening rates between SCI and SPA birds for either of the sexes. However, comparison of years and study sites, by testing the slopes of the regression equations, was not always justified. For instance, a comparison of fattening rates between 1979 and 1980 in SPA males can be misleading because of the different fattening patterns. Therefore, we also re-

sorted to comparisons (by Student's *t*-test) of samples obtained during equivalent sampling intervals in both study areas. By this procedure, we found that "arriving" geese at SPA were significantly fatter than "arriving" ones at SCI (Table 1) in 1979 but not in 1980. This analysis also revealed that the males departing SCI carried significantly more fat than those departing SPA, both in 1979 and 1980 (Table 1). The difference became highly significant when both years were combined ($P < 0.01$; Table 1). The pooling of these two samples is justified since they did not differ significantly from each other between years ($P < 0.05$). "Departing" females from SCI were also fatter than "departing" females from SPA but the difference was not significant, even after pooling the data for the two years of the study ($P > 0.05$, Table 1). We believe that the small size of the 1979 sample ($n = 3$) before departure accounts, at least in part, for the absence of significant differences between "departing" females in the two localities.

We found no significant differences in the total fat reserves with respect to sex or year within a given marsh type (Table 1). However, in terms of percentage of total body weight, females were generally fatter than males from the same locality; the difference was significant for SPA birds when both years were combined (males vs. females, 516 ± 19 vs. 566 ± 26 g, $P < 0.01$; Table 1).

DISCUSSION

Records kept from 1977 to 1981 (Bédard, unpubl. observ.) reveal that the termination of

the staging halt in the St. Lawrence estuary is always abrupt and rather set in time, always occurring between 17 and 22 May. Regular censuses showed that flock size was maintained right up until departure. The arrival of geese, however, is somewhat less predictable and can be either very early (the first birds were seen on 30 March in 1980) or delayed by one or two weeks when the spring weather is unfavorable (1979 for instance). Considering the large size of the staging area, the birds do not spread instantly in all parts of it upon arrival. Thus, in 1979, the first geese were seen at SPA a full 10 days after they were first seen on the SCI marshes. In 1980, the milder spring conditions were related to a reduced interval of only four days. In the years since the study took place, we have seen the first geese come overland, presumably straight from the Atlantic coast, land first in the upper estuary region and then drift downriver over several days before settling in one of the salt-marshes of Saint-Denis, Saint André, Cacouna or Isle Verte (Fig. 1). That the first geese collected at SPA (both males and females) in 1979 were significantly fatter than the first ones collected at SCI (Table 1) suggests that the SPA birds had fattened while occupying or passing through the upper estuary in early April before moving to the lower estuary.

Geese can also fatten rapidly in the lower estuary, as is shown by the 1980 results. If the first samples collected between 10 and 20 April of that year are removed from the analysis, the correlation between TFR and date drops below significance level in males ($P > 0.05$) and loses much of its power in females ($r = 0.46$, $P < 0.05$ instead of $r = 0.82$, $P \ll 0.001$). These figures then resemble those of 1979 at SPA. These results further indicate that after 20 April, the fattening rate of SPA females in 1980 also levelled off considerably, although not as completely as in males (Fig. 3). Thus, our results show that the fresh-water, bulrush-feeding geese fatten steadily and rapidly throughout the staging period. The birds of the salt-water cordgrass marsh put on fat reserves just as rapidly as the others in the first half of the staging period (either by feeding for a while in the upper estuary, as in 1979, or in the lower estuary, as in 1980) but more or less completely cease their fattening for the second half of the staging period.

Individual variability in our results was considerable. For instance, some females from SPA carried more than twice as much fat as others (extremes of 325 and 750 g of fat) upon departure, and a similar situation prevailed among the SCI males in 1979. We must recall that our sample is "contaminated" by the pres-

ence of sub-adults of both sexes whose non-breeding program probably imposes much less pressure for fat accumulation by comparison with adult breeders. However, we found no indication that flock composition (age-wise) could differ so much between the two sites as to cause the observed differences in fattening. Thus, the proportion of juveniles and presumably that of subadults as well, was the same in the two flocks throughout the study. A part of the variation in our results could also stem from inherent structural differences among individuals. In the Lesser Snow Goose, for instance, Ankney and MacInnes (1978) noted that body weight (which they used as an indicator of body condition) was significantly related to culmen length upon arrival on the breeding grounds.

We attempted to correct for structural differences by dividing TFR by various morphometric measurements but without success. Following Wishart (1979), we then used the fat-free dry weight (FFDW) of the bird as an indicator of a structural difference in our samples (such an index can be used since there is no concurrent protein deposition). In 1979, we found a weak but significant correlation between TFR and FFDW in males ($r = 0.26$, $P < 0.01$, $n = 84$) and in females ($r = 0.27$, $P < 0.01$, $n = 90$). Therefore, the variability in the levels of lipid storage attained by different individuals can be partly accounted for by body size alone. In such instances, Gyug and Millar (1980) have suggested using the FFDW as a covariate but we were unable to use this approach because one or more organs in most birds had been damaged by the shot.

In 1980, we were able to collect 12 birds on the day of their arrival at the SCI site, and the fat reserves of these individuals amounted to 9% at the time (Table 1). Other samples obtained soon after arrival, but after a few days of local feeding, produced values of fat reserves around 10%. We consider that such a level is moderate and presume that fattening had begun before arrival in the St. Lawrence River estuary. Unfortunately, winter and early spring weights and fat contents are not available at this time. In Lesser Snow Geese, it is established (Ankney 1982) that body weight rises from a very low level in late winter (in Texas) just before departure for the continental staging grounds (Flickinger and Bolen 1979), to a very high value just after arrival on the breeding grounds at McConnell River. The body weight values in females increased from 1,800 g (probably equivalent to 5–6% fat index) to 2,900 g between these two moments of the yearly cycle.

An alternative explanation for the presence

of relatively high early-staging levels of fat reserves would be that the Greater Snow Geese have not undergone a mid-winter period of reserve depletion. Raveling (1979) noted the existence of marked differences in the late winter fat stores of two races of Canada Geese; the small, southerly-wintering Cackling Goose (*Branta canadensis minima*) had a fat content of 5% while in the bulky, northerly-wintering Giant race (*B. c. maxima*) this value was found to be 14%. This situation suggests a parallel with the two races of Snow Goose that occupy similarly divergent wintering ranges on the Gulf coast and the Atlantic coast.

When leaving the St. Lawrence staging area, both male and female Snow Geese had proportionately smaller amounts of fat than has been reported for other Anserinae at that time of the year. When we express our results in the units (Fat Reserve Index) used by Ankney (1977) and Ankney and MacInnes (1978) for the Lesser Snow Goose upon its arrival at its Hudson Bay breeding grounds, we find that fat reserves were proportionately smaller in our race. If we compare these values with those for *B. c. minima*, the difference is even greater. Raveling (1979) indicated that 21% of the body mass in males and 28% in females is made up of fat during the period just after spring staging. In the *maxima* race, the males have as much as 23% and the females 29% of their body mass in the form of fat (McLandress and Raveling 1981). Of course, in the Greater Snow Goose, there is a period of approximately three weeks following the departure of the birds from the staging grounds and their arrival upon the high-arctic nesting islands. It is possible that fattening could continue during this interval on other staging areas, perhaps in northern Québec or on Baffin Island. However, the prevailing conditions in late May and early June at these northern latitudes are so severe that we doubt if such a halt will be found, and whether fat accumulation could even occur there at that time. Wypkema and Ankney (1979) did not note any increase in fat content in *caerulescens* during the final phase of its spring staging along James Bay although protein reserves appeared to increase during this period.

We believe that differences in the time devoted to feeding and in the nutritional value of food items between the two sites led to the observed differences in the fat levels reached. In 1979 and 1980, the SCI females left with about 50 g more of extractable fat than those of SPA, while SCI males left with 120 g more. These quantities are equivalent to 1,880 and 4,515 kJ, respectively. Using the equation by Aschoff and Pohl (1970), we can calculate that

such reserves are equivalent to approximately three and seven days of energy expenditure at basal metabolic rate. In females, 50 g of fat is about the energetic equivalent of 2.5 eggs (see Ankney and Bisset 1976 for egg weight and Ricklefs 1974 for caloric content).

The existence of a greater difference between habitats in the post-staging condition of males as opposed to females is difficult to interpret at this time. The bioenergetic stresses of breeding are much smaller in males and therefore sizable differences such as those reported here can be tolerated without ill effects. In Lesser Snow Geese, however, males have apparently a crucial energy-demanding role in protecting females from sexual harassment by neighbors and from egg-dumping by other females in the dense colonies that are typical of this subspecies. Mineau and Cooke (1979) and Owen and Wells (1979) have commented on these problems. In Greater Snow Geese, the nesting colonies seem much looser (Lemieux 1959) and the importance of fat reserves stored during staging by males while on the breeding grounds is unknown.

Our results suggest that Greater Snow Geese have a diminished success in accumulating fat in this newly invaded spring staging habitat in salt marsh.

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