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Nutrient Reserves of Premigratory Brant During Spring

LARRY D. VANGILDER,^{1,3} LOREN M. SMITH,^{1,4} AND RICHARD K. LAWRENCE²

¹Savannah River Ecology Laboratory, P.O. Drawer E, Aiken, South Carolina 29801 USA, and

²Department of Range and Wildlife Management, Texas Tech University, Lubbock, Texas 79409 USA

Brant (*Branta bernicla*), like other arctic-nesting geese, rely heavily on stored nutrient reserves during reproduction. Brant arrive on the nesting grounds with large lipid and protein reserves and metabolize substantial portions of these reserves during egg-laying and incubation (Ankney 1984). Because of their small body size, however, Brant must rely on exogenous sources of nutrients because they cannot store enough reserves to fast throughout incubation. Spring weather conditions on the arctic nesting grounds have substantial influence on Brant reproductive success. During late springs, when Brant arrive on snow-covered nesting grounds, they metabolize lipid reserves for maintenance until the snow disappears and nest sites and food become available. Consequently, nests are initiated later, clutch sizes are reduced, and the proportion of non-nesting Brant increases (Barry 1962).

Ebbinge et al. (1982) found that Brant that were heavier on the spring staging grounds on the Wadden Sea area in western Europe had a greater probability of returning the following fall accompanied

by young. They also found that during 1978 and 1979, when 35 and 33%, respectively, of fall populations were immatures, the rate of fattening and departure weights on the staging grounds were greater than in 1977, when no immatures were observed in the fall population. Although alternative explanations can be proposed, Ebbinge et al.'s (1982) results suggest that nutrient reserves acquired before arrival on nesting grounds may also influence reproductive success of Brant. Similar studies on North American populations of Brant have not been conducted on either the wintering or staging grounds.

Brant exhibit a rather protracted spring migration. Some Brant may begin the northward trek as early as late March to early April, while others do not leave wintering areas until mid-May (Palmer 1976). During aerial surveys of Brant conducted from 16 to 23 May 1977, 35,513 were counted. These Brant were distributed from New Jersey northward along the Atlantic coast (27% mostly on Long Island and in New Jersey), in the maritime provinces of Canada (14%), in the Gulf and estuaries of the St. Lawrence (36%), on Lake Ontario (12%), and on James Bay (10%) (Reed 1977). By comparing nutrient reserves of Brant that were collected on the most northerly of the major wintering areas during or immediately before spring migration with that of prelaying Brant collected by Ankney (1984) on the nesting grounds, we sought to determine whether Brant depart the wintering grounds with substantial nutrient reserves or

³ Present address: Missouri Department of Conservation, 1110 College Avenue, Columbia, Missouri 65201 USA.

⁴ Present address: Department of Range and Wildlife Management, Texas Tech University, Lubbock, Texas 79409 USA.

TABLE 1. Body weight and composition ($\bar{x} \pm \text{SE}$) of pre-migratory adult Brant during spring.

	Male	<i>P</i> ^a	Female
<i>n</i>	20		21
Fresh body weight (g)	1,514.6 ± 26.4	*	1,398.2 ± 17.2
Body weight ^b (g)	1,450.0 ± 22.5	*	1,331.7 ± 16.9
Body weight ^c (g)	1,449.3 ± 22.5	*	1,329.5 ± 17.0
Water (g)	760.8 ± 11.4	*	686.7 ± 10.1
Fat (g)	195.0 ± 10.5	NS	191.7 ± 8.1
Ash-free lean dry (g)	284.4 ± 6.3	*	261.2 ± 4.9
Ash (g)	52.9 ± 0.8	*	47.0 ± 1.0
Liver (g)	51.5 ± 1.5	*	46.2 ± 1.1

^a *P* = probability (from a *t*-test) that means in adjacent columns are different by chance; * = *P* < 0.05; NS = not significant, *P* > 0.05.

^b Body weight = fresh body weight - gastrointestinal contents.

^c Body weight = fresh body weight - [gastrointestinal contents + (ovary + oviduct) or testes].

possibly accumulate reserves later on spring staging areas.

During 7-9 May 1984, approximately 700 Brant were killed by diazinon (an organophosphate pesticide) in Nassau County, Long Island, New York. This kill occurred during early to mid-spring migration, and the Brant that died were probably from wintering areas all along the Atlantic coast (Vangilder and Smith 1985). For our purposes we called these Brant "pre-migratory," although some included in the sample probably wintered in New Jersey and had moved north to Long Island while others may have spent the entire winter on Long Island. These Brant were considered "pre-migratory" only in the sense that they had not yet departed from the most northerly of the 3 major wintering areas (Long Island, New York; Cape May to Barnegat Bay, New Jersey; and south of Hog Island Bay to Chincoteague Bay, Virginia; Kirby and Obrecht 1982). Wild birds that ingest diazinon die very rapidly (Grue et al. 1983); therefore, these Brant provided a unique and instantaneous sample of migrating birds. Forty-one Brant (20 adult males, 21 adult females) were obtained from the die-off and used for body composition analysis. Brant were sexed and aged according to the methods of Kirby et al. (1983) and Penkala (1977). Only males and females completely lacking a bursa were selected. In addition, the appearance of the oviduct and ovary of females was used to ensure that only adult females (and probably only females that had laid eggs in a previous breeding season) were selected.

The liver was excised, weighed, and returned to the body cavity. Testes or the ovary and oviduct were removed from the body cavity and weighed. Brant were then sheared and weighed. After shearing, the contents of the gastrointestinal tract were removed, and the carcass was reweighed. The carcass (minus feathers, testes or ovary plus oviduct, and the gastrointestinal contents) was refrozen, then ground in a commercial meat grinder.

The entire homogenate was dried to constant weight in a forced-air oven at 65°C to determine water

content. Lipids were extracted from duplicate 6-10-g samples of dried homogenate using a Soxhlet apparatus and petroleum ether. Ash was determined by placing duplicate 3-10-g samples of dried homogenate from each carcass into an oven whose temperature was gradually increased (over 2 days) to 600°C. Samples were held at this temperature for 24 h. The amount of ash-free lean dry mass (AFLDM), which we equated with protein reserves (Raveling 1979: 241), was determined by difference.

Male Brant were heavier, had larger livers, and contained absolutely more water, AFLDM, and ash than did females (*P* < 0.05; Table 1). However, the absolute amount of fat in female and male Brant did not differ. This indicates that female Brant had proportionately more lipid reserves than did males.

Gonadal recrudescence was not evident in either male or female Brant. The combined weight of both testes was 0.63 g (SE = 0.061, *n* = 20), and mean ovary mass was 1.36 g (SE = 0.074, *n* = 21). Oviducts had a mean mass of 0.97 g (SE = 0.047, *n* = 21).

A comparison of prelaying Brant collected on nesting areas on Southampton Island, N.W.T. (Ankney 1984) with pre-migratory birds from this study is shown in Table 2. Body weight of pre-migratory females was not different from prelaying females (*P* > 0.05). Pre-migratory females had smaller ovaries and oviducts but more lipid reserves and larger liver mass than did prelaying females (*P* < 0.05). Body weight, liver weight, and lipid reserves of pre-migratory males were larger than that of males collected during prelaying (*P* < 0.05).

Weights of pre-migratory Brant are also very close to those of Brant collected upon arrival on nesting areas. Barry (1962: fig. 5) reported that female and male Brant arriving on breeding areas weighed 1,395 and 1,575 g, respectively. By comparison, body weights of pre-migratory female and male Brant were 1,398 and 1,515 g, respectively. Body weights and lipid reserves of male prelaying Brant (Ankney 1984) were 11 and 50% lower, respectively, than those of male pre-migratory Brant. The similarity of weights

TABLE 2. Comparison of premigratory Brant from New York in the spring and prelaying Brant from East Bay, Southampton Island, N.W.T. (Ankney 1984). Values are presented as means (SE).

	Female			Male		
	Premigratory	P ^a	Prelaying ^b	Premigratory	P	Prelaying ^b
n	21		13	20		8
Body mass ^c (g)	1,331.7 (16.9)	NS	1,384.0 (33)	1,450.0 (22.5)	*	1,297.0 (25)
Body mass ^d (g)	1,329.5 (17.0)		1,250.0 ^e	1,449.3 (22.5)		ND ^f
Ovary or testes (g)	1.36 (0.074)	*	84.8 (7.6)	0.63 (0.061)		ND
Oviduct (g)	0.97 (0.047)	*	49.3 (3.0)			
Fat (g)	191.7 (8.1)	*	123.5 (11.0)	195.0 (10.5)	*	97.1 (7.5)
Liver	46.2 (1.1)	*	36.0 (1.7)	51.5 (1.5)	*	30.9 (2.4)

^a Probability (from a *t*-test) that means in adjacent columns are different by chance; * = $P < 0.05$; NS = not significant, $P > 0.05$.

^b Data from Ankney (1984).

^c Fresh body mass - gastrointestinal contents.

^d Fresh body mass - [gastrointestinal contents + (ovary + oviduct) or testes].

^e Standard error could not be calculated from data.

^f ND = no data.

of male Brant collected upon arrival (Barry 1962) to those of premigratory male Brant suggests that substantial amounts of lipid reserves are metabolized between arrival and the prelaying stage.

Estimates of protein levels (AFLDM) from this study were not directly comparable with those provided for prelaying Brant by Ankney (1984). It is possible that during spring migration Brant maintain lipid reserves acquired on wintering areas but increase protein reserves on spring staging areas, as is the case for Lesser Snow Geese (*Chen caerulescens caerulescens*; Wypkema and Ankney 1979).

Male Brant arrive on the breeding grounds with testes weighing 1.3 g (Barry 1962). The combined weight of both testes of male premigratory Brant was only 0.63 g. These results indicate that male Brant undergo testicular recrudescence at some time after leaving wintering areas but before arrival on nesting areas. Females arriving on nesting areas had ovary weights of 12 g, which rapidly increased to a peak at egg-laying of 44 g (Barry 1962: fig. 1). Ankney (1984) reported that ovaries weighed 84 g at the prelaying stage. The 40-g differences in ovary weights between prelaying (Ankney 1984) and egg-laying (Barry 1962) Brant probably reflects a reduction in the ovary weight of egg-laying Brant due to both egg-laying and follicular atresia. Barry (1962) reported that five females taken during egg-laying and incubation had ovaries with 17 atretic and 11 ruptured follicles. These Brant were collected during 1957, when spring was particularly late and the rate of follicular atresia was high. Ovaries of premigratory females weighed 1.36 g. Some ovarian recrudescence must occur during spring migration, with the rapid follicular growth phase occurring upon or shortly after arrival on nesting areas (Raveling 1978). Wypkema and Ankney (1979) found that the early phases of ovarian development did not begin in Lesser Snow Geese until

after they arrived on staging areas in James Bay. Gonadal recrudescence and the occurrence of courtship during spring migration has been demonstrated in other arctic-nesting geese (Cooch 1958, MacInnes 1966, Ryder 1967, Raveling and Lumsden 1977, Wypkema and Ankney 1979). Completion of the prenesting phase of breeding before arrival on nesting areas has been interpreted as an adaptation to the limited time available for arctic-nesting geese to complete egg-laying, incubation, hatching, and brood rearing (Ryder 1967, Newton 1977).

Accumulation of lipid reserves just before leaving wintering areas has been demonstrated in the Giant Canada Goose (*B. canadensis maxima*; McLandress and Raveling 1981). Many arctic-nesting geese, however, employ an alternative strategy whereby lipid reserves are accumulated after departure from wintering areas. Lesser Snow Geese leave wintering areas at a low body weight (Flickinger and Bolen 1979, Ankney 1982) and accumulate lipid reserves during migration, but before arrival at James Bay (Wypkema and Ankney 1979). Greater Snow Geese (*C. c. atlanticus*) and Canada Geese (*B. c. interior*) of the Mississippi Valley population accumulate lipid reserves on their last spring staging areas before departure for breeding areas (Hanson 1962, Raveling 1968, Raveling and Lumsden 1977, Gauthier et al. 1984).

The large fat reserves of Brant on wintering areas along the Atlantic coast of North America also contrasts with patterns of reserve accumulation suggested by weight data for Brant that winter in Europe and breed in Siberia. These Brant reach their lowest body weights just after winter is over and increase their weight from 1,250 to 1,600 g after they arrive on the spring staging area on the Wadden Sea in western Europe (cited in Ebbsing et al. 1982).

Brant that winter along the Atlantic coast of North America migrate along at least 2 different major routes

TABLE 3. Approximate distances (km) and estimated costs (g fat) of spring migration for Brant flying from Long Island, New York to Southampton Island, N.W.T. along different routes.

Route	Distance (km)	Cost (g fat) ^a
Inland route		
Long Island to Lake Ontario	483	55
Lake Ontario to James Bay	908	104
James Bay to Southampton Island	1,429	164
Total	2,820	323
Coastal route		
Short route		
Long Island to St. Lawrence Estuary	893	102
St. Lawrence Estuary to James Bay	834	96
James Bay to Southampton Island	1,429	164
Total	3,156	362
Long route		
Long Island to Bay of Fundy	748	86
Bay of Fundy to Prince Edward Island	303	35
Prince Edward Island to St. Lawrence Estuary	491	56
St. Lawrence Estuary to James Bay	834	96
James Bay to Southampton Island	1,429	164
Total	3,805	437

^a Calculated as cost (g fat) = $[(d/v)c]/k$ where $k = 9.0$ = yield in kcal from burning 1 g of fat (Ricklefs 1974); d = distance in kilometers; v = speed of flight in km/h = $(14.6 M^{0.20}) (3.6)$ (Tucker 1973), where M = body mass in kilograms; c = cost of migratory flight in kcal/h = $[(341.4 m^{0.73})/1,000] (0.86)$ (Calder 1974), where m = body mass in grams. For a 1.4-kg Brant these equations yield the following results: $v = 56.22$ km/h and $c = 58.13$ kcal/h. Calculations assume that a Brant uses only fat to supply energy needed for migratory flight.

when traveling from wintering to nesting grounds (Palmer 1976). Brant following the coastal route gradually move north along the coast of North America to the Bay of Fundy and into the Northumberland Strait around Prince Edward Island. They then fly around the Gaspé Peninsula to the St. Lawrence Estuary. From the St. Lawrence Estuary they proceed directly to James Bay. From James Bay Brant fly along the east coast of Hudson Bay to breeding areas around the Foxe Basin. A shorter variation of this route is to fly from the northern U.S. coast (e.g. Long Island, Cape Cod) directly to the St. Lawrence Estuary (A. Reed pers. comm.). Brant following the inland route depart Long Island and New Jersey wintering areas in mid-May and follow major water courses to Lake Ontario. From Lake Ontario they fly to James Bay and from James Bay to breeding areas around the Foxe Basin.

The approximate distances and estimated costs of spring migration for Brant flying along the inland route and the two versions of the coastal route are shown in Table 3. The inland route is shorter than either of the coastal routes, and therefore the costs are less. However, food is probably largely unavailable along this route until Brant reach James Bay. Brant leaving Long Island with 192 g fat (Table 1) and traveling the inland route would deplete most, but not all, of this energy reserve (159 g; Table 3) before arriving at James Bay. On the other hand, Brant leaving Long Island with 192 g fat and traveling either

of the coastal routes would not have enough stored reserves to reach James Bay without replenishing reserves along the way (Table 3). Brant foods are available along the coast and in the St. Lawrence Estuary (Reed 1977). Brant that travel north along the coastal route begin migration earlier (late March-early April) than do Brant migrating along the inland route (mid-May), yet both groups arrive at James Bay at about the same time (Palmer 1976). Thus, the Brant analyzed for this study may have included only those Brant that migrate along the inland route.

The magnitude of lipid reserves carried by pre-migratory Brant collected for this study can be further assessed by comparing pre-migrating reserve levels with the amount of reserves required for reproduction. For females, Ankney (1984) stated that ovaries of prelaying Brant contained 28 g of fat. Assuming a 75% conversion efficiency, a Brant leaving the wintering grounds with 191.7 g of fat and replenishing these reserves only on James Bay would have 154.4 g of fat $[191.7 - (28/0.75)]$ remaining after gonadal recrudescence if all the fat in the prelaying ovary was obtained from fat stores. The remaining fat stores (154.4 g) would still provide enough energy for a 3-day fast [based on Aschoff and Pohl's (1970) equation for BMR] before the prelaying fat level of 123.5 g (Ankney 1984) was reached. Therefore, during years when snow melt is not particularly late on arctic nesting grounds and some foods are available shortly after arrival, Brant could reproduce success-

fully if they were able to obtain enough food on James Bay to maintain the level of lipid reserves with which they left wintering areas.

Premigratory Brant have large lipid reserves when they leave wintering areas for spring staging and breeding areas. Although additional reserves must be accumulated during the northward migration, reserves accumulated before leaving the wintering grounds probably contribute to the energetic demands of migration and indirectly to reproduction.

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