SHORT COMMUNICATIONS

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ARE BODY CONDITION AND REPRODUCTIVE EFFORT OF LAYING GREATER SNOW GEESE AFFECTED BY THE SPRING HUNT?

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Abstract. A spring hunt was implemented on the staging areas of Greater Snow Geese (*Chen caerulescens atlantica*) in Quebec in 1999 and 2000. We evaluated whether this activity, which occurred during the period of spring nutrient storage, may have affected the body condition and reproductive effort of laying geese. We collected laying females in years with a spring hunt (1999–2000, $n = 34$) and compared them with birds collected in years without a hunt (1989–1990, $n = 10$). All indices of body condition and clutch size were significantly lower in years with a hunt than in years without, and laying dates were delayed. Tracking of radio-marked females on the staging and breeding areas showed that a lower proportion of females reached the nesting areas in years with a hunt (28% in 1999–2000, $n = 80$) than in years without (85% in 1997–1998, $n = 80$) and that fewer females nested (9% vs. 56%, respectively). Our results suggest that the spring hunt negatively affected nesting geese.

Key words: body condition, breeding effort, clutch size, Greater Snow Goose, laying date, nutrient reserve, spring hunt.

¿Son Afectadas por la Cacería de Primavera la Condición Física y el Esfuerzo Reproductivo de *Chen caerulescens atlantica*?

Resumen. La cacería de primavera fue implementada en áreas de escala de *Chen caerulescens atlantica* en Quebec en 1999 y 2000. Evaluamos si la cacería, que se llevó a cabo durante el período primaveral de acumulación de nutrientes, pudo haber afectado la condición fisica y el esfuerzo reproductivo de los gansos. Colectamos hembras que estuvieran poniendo huevos en años con cacería de primavera (1999–2000, $n = 34$) y las comparamos con aves colectadas en años sin cacería (1989–1990, $n = 10$). Todos los índices de la condición física y del tamaño de la nidada fueron significativamente menores en años con cacería que en años sin cacería, y se retrasaron las fechas de puesta. El seguimiento de hembras marcadas con radio en áreas de escala y cría mostró que una menor proporción llegó a las áreas de nidificación en años con cacería (28% en 1999–2000, $n = 80$) que en años sin cacería (85% en 1997–1998, $n = 80$), y que menos hembras nidificaron (9% vs. 56%, respectivamente). Nuestros resultados sugieren que la cacería de primavera afecta negativamente a los gansos nidificantes.

Waterfowl use stored fat and protein to meet the high energy and nutrient costs of laying and incubating eggs (Ankney and MacInnes 1978, Thomas 1983, Alisauskas and Ankney 1992). In arctic-nesting geese, accumulation of fat in spring is also essential to complete the long migration (Gauthier et al. 1992) and is a major determinant of reproductive success (Ankney and MacInnes 1978, Ebbinge 1989, Ebbinge and Spaans 1995).

In Greater Snow Geese (*Chen caerulescens atlantica*), a period of intense fat and protein accumulation takes place in spring along the St. Lawrence River in Quebec (Gauthier et al. 1984, 1992). About half of the fat stored in spring is used to complete the 3000-km flight to their breeding grounds in the High Arctic (Gauthier et al. 1992). Even though exogenous nutrients acquired through feeding on the breeding grounds make a significant contribution to the formation of the eggs (Gauthier and Tardif 1991, Choinière and Gauthier 1995), endogenous reserves are still important during laying and especially incubation (Boismenu et al. 1992, Reed et al. 1995).

Like many other white goose populations in North America, the Greater Snow Goose population has increased considerably over the past 30 years (Reed et al. 1998), increasing crop depredation on farmlands (Filion et al. 1998) and threat of damage to natural breeding, staging, and wintering habitats due to overgrazing (Giroux et al. 1998). In order to limit the rapid growth of this population, the Canadian Wildlife Service implemented a spring conservation hunt (hereafter

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called the spring hunt) during the staging period in southern Quebec. This is the first time since the enactment of the Migratory Bird Treaty in 1917 that a spring hunt has been allowed. Disturbance of birds in spring, whether caused by hunting or other human-related activities, may increase the time spent in flight, reduce feeding time (Bélanger and Bédard 1989, Mosbech and Glahner 1991, Madsen and Fox 1995, Madsen 1998), and thus compromise the accumulation of nutrients at a critical period of their life cycle. In this paper, we examine whether the spring hunt of Greater Snow Geese may have affected the body condition of laying females, their reproductive investment, and their breeding effort.

METHODS

STUDY AREA

The study was conducted on Bylot Island (73°08′N, 80°00′W), Nunavut, Canada, which is a major breeding colony of Greater Snow Geese (Reed et al. 1998). To evaluate nesting conditions, we visually estimated the percentage of snow cover in various parts of the Base-camp Valley each spring (Lepage et al. 1996). We also calculated the mean daily temperature between 25 May and 15 June, corresponding to the time between arrival of geese and the beginning of laying. Weather data were obtained from the Pond Inlet meteorological station, which is 65 km southeast of the study area (see Lepage et al. 1996 for details).

EVALUATION OF BODY CONDITION AND REPRODUCTIVE INVESTMENT

Females were collected with a rifle during the laying period in 1989 and 1990 (Choinière and Gauthier 1995, years without a spring hunt) and in 1999 and 2000 (years with a spring hunt). Geese were shot near their nest and their eggs were removed. Additional eggs were collected from other nests during the same period. Shortly after collection, geese were weighed (to the nearest 25 g) and five measurements were taken following Dzubin and Cooch (1993): culmen and tarsus length were measured with a caliper (to within 0.1 mm); wing, total body, and tail length were measured with a meter stick (to within 1 mm). Birds were then necropsied in the field. Right breast muscles, gonads, and oviduct were dissected and stored frozen. Dry mass of these tissues was later obtained by freeze-drying in the laboratory. Abdominal fat (excluding mesenteric fat attached to the intestine loops) was also dissected and weighed fresh (to within 0.1 g). Gonads were examined to determine the breeding status of females. Females were classified as laying if they had at least one postovulatory follicle and developing follicles (or an egg in the oviduct). Laying date of the first egg was back-calculated according to the number of postovulatory follicles present, assuming a laying interval of 33 hr (Poussart et al. 2000). Potential clutch size was defined as the sum of developing and postovulatory follicles (Choinière and Gauthier 1995). Atretic follicles were also counted.

Eggs (from the nest or oviduct) were weighed fresh (to the nearest 0.1 g) and measured (width and length) with a caliper (to within 0.1 mm). Eggs were heated at 85°C in water for 90 min and then separated into shell (with membranes), albumen, and yolk in the field. These constituents were stored frozen and dry mass was later determined by freeze-drying in the laboratory.

The following components were considered as body condition indices: whole body mass, dry breast muscles (an index of protein), and abdominal fat (a reliable index of total body fat, Gauthier and Bédard 1985). Dry oviduct, potential clutch size, fresh egg mass (laid egg only), dry yolk mass, dry albumen mass, and number of atretic follicles were used as indices of reproductive investment. For egg, albumen, and yolk mass, means of all eggs in a clutch were used as independent values in the statistical analyses.

EVALUATION OF BREEDING EFFORT

As part of a larger investigation on Greater Snow Goose movements, 305 females (60 in 1996, 73 in 1997, 79 in 1998, and 93 in 1999) were marked with radio-transmitters affixed to neck collars (Demers 2000). Birds were caught in August on Bylot Island during their molting period (see Blouin et al. 1999 for details). From 1997 to 2000, 6 crews using 4-element Yagi antennas mounted on vehicles conducted ground tracking of the entire staging area of southern Quebec daily. In addition, aerial surveys were carried out weekly to search for missing birds. Because of our extensive coverage of the spring staging area, we are confident that all birds alive in spring and with a functioning radio were detected. We subsequently determined the number of birds that reached the breeding grounds through intensive tracking during the pre-laying, laying, and early incubation periods (end of May to end of June). Aerial tracking by helicopter was conducted weekly over the south plain of Bylot Island (complete coverage of ca. 1600 km^2). We also conducted ground tracking every one or two days with an antenna mounted on a snowmobile and from fixed towers located on high ground near the two main nesting areas. We searched for nests of radio-marked females by foot in areas where we detected signals.

STATISTICAL ANALYSIS

All statistical tests were performed with SAS statistical software version 8.0 (SAS Institute 1999). We compared the condition of geese in years with a spring hunt (1999 and 2000) with years without a hunt (1989 and 1990; Choinière and Gauthier 1995). Because body size of Greater Snow Geese has declined over time (Reed and Plante 1997), we standardized the body condition of geese to account for potential differences in size over the 10-year span. We estimated body size by performing a principal components analysis on the five morphological measurements for the whole dataset. We used the scores along the first principal component (PC1) as an overall measure of body size (Gauthier et al. 1992). The PC1 was related to all body condition indices and oviduct mass (all $r^2 > 0.17$, all $P < 0.01$) and thus residuals from these regressions were used to correct for body size. We use the term *adjusted values* to refer to these variables.

Goose nesting parameters (laying date and clutch size) were collected annually at our study site (see Lepage et al. 2000 for details). Kruskal-Wallis one-way ANOVA was used to compare laying dates of collected birds with those of the population. To control for

TABLE 1. Nestling conditions and laying dates of Greater Snow Geese on Bylot Island, Nunavut, Canada.

	1989	1990	1997	1998	1999	2000
Snow-free area on 5 June (%)	20	15	35	60	20	15
Daily temperature (°C)[a]	−1.1 ± 3.2	−1.2 ± 3.2	−1.9 ± 5.3	1.8 ± 3.4	−2.3 ± 2.8	−3.8 ± 4.3
Laying date of collected bird[b]	9	12	—[c]	—[c]	16	14
Laying date of the colony[b,d]	11	13	10	7	17	17

[a] From 25 May to 15 June (mean ± SD).

[b] Median laying date in June.

[c] No birds collected.

[d] From Lepage et al. (1996), Bêty et al. (2001), and Gauthier, unpubl. data.

possible long-term decline in egg or clutch size, we also examined the relationships between these variables and year with linear regressions. For egg size, we used an index of volume (length × width^2) for the first egg laid in a clutch (i.e., one egg per clutch was used in the analysis). Geese collected in 1999–2000 (spring hunt) were pooled as an experimental group and those collected in 1989–1990 (no spring hunt) were pooled as the control group. No significant between-year difference was found for any variable within each group (ANOVA, $P > 0.1$), except for potential clutch size (3.1 ± 0.2 in 1999 vs. 3.9 ± 0.3 in 2000, $P < 0.02$) and dry egg albumen (7.5 ± 0.2 g in 1999 vs. 8.1 ± 0.1 g in 2000, $P < 0.01$). Comparisons of body condition and reproductive investment indices between groups were made using one-way ANOVA. For body condition indices and dry oviduct mass, the number of postovulatory follicles was used as a covariate to control for the exact laying stage (ANCOVA).

Telemetry data were pooled into two groups for 1997–1998 (no spring hunt) and 1999–2000 (spring hunt). Generalized linear models were used to examine the proportion of geese detected on the breeding grounds and, among detected geese, the proportion that nested. Binary response variables were used for both parameters in logistic regressions.

Statistical tests were two-tailed and significance levels were set at 0.05. Inspection of residuals indicated no violation of the assumptions of normality and homogeneity of variance. All means are presented ±SE, unless otherwise indicated.

RESULTS

WEATHER DATA

Spring weather conditions (i.e., snowmelt and air temperature), were generally comparable across years, with two exceptions (Table 1). In 1998, spring temperatures were especially warm and the snowmelt early, and in 2000 temperatures were cool.

BODY CONDITION AND REPRODUCTIVE INVESTMENT

We collected four laying females in 1989 and six in 1990, compared to 18 females in 1999 and 16 in 2000. In all years, the collected birds tended to be early nesters relative to the colony as a whole ($\chi^2_1 = 22.3$, $P < 0.001$ for 1999–2000; $\chi^2_1 = 4.9$, $P < 0.03$ for 1989–1990; Table 1). During the two years with a hunt (1999–2000), geese started laying 2–7 days later than in years without a hunt (1989–1990, $\chi^2_1 = 22.8$, $P < 0.001$ for collected birds; $\chi^2_1 = 311.5$, $P < 0.001$ for the colony; Table 1).

Body condition indices and dry oviduct mass were slightly related to the laying stage of the birds (ANCOVA: number of postovulatory follicles, $F_{1,37} < 3.5$, $P > 0.07$ except dry oviduct mass, $F_{1,36} = 6.9$, $P < 0.02$; the interactions between the covariate and the dependent variables were not significant, all $P > 0.1$, and were deleted from the models). All indices of body condition were significantly lower in years with a spring hunt than in years without a hunt (Table 2). Adjusted body mass and breast-muscle mass of birds sampled in 1999–2000 were 10% lower than in 1989–1990, whereas adjusted abdominal fat was 29% lower.

Average potential clutch size in years with a spring hunt was considerably reduced (by almost 1.5 eggs, a 29% reduction) compared to years without a hunt (Table 2). This comparison was not confounded by a long-term decline in clutch size because there was, on the contrary, a very slight increase in clutch size over time (1989 to 2000, $F_{1,3284} = 7.2$, $P < 0.01$, $\beta = 0.0208 \pm 0.0078$ egg year^{-1}). The average number of atretic follicles was much higher in 1999–2000 than in 1989–1990 (3 vs. 1, respectively), suggesting a high frequency of follicular atresia during years with a spring hunt. There was no difference in the egg, yolk, albumen, or oviduct mass between years with and without a hunt (Table 2). Although there was a trend for lighter eggs with less albumen in years with a hunt, this was confounded by a long term decline in egg size that was present even when excluding the years with a hunt ($F_{1,1015} = 7.3$, $P < 0.01$, $\beta = -0.8517 \pm 0.3157$ cm^3 year^{-1}).

BREEDING EFFORT

All radio-marked birds identified on the breeding grounds ($n = 90$) had been previously detected on the spring staging areas, confirming that our coverage was adequate. Fewer individuals were detected on Bylot Island during the two years with a spring hunt than in those without (Table 3). During the two years without a hunt, we found the nests of about half of the radio-marked geese detected on the breeding grounds. Even though the spring was much earlier in 1998 than in 1997, the proportion of radio-marked geese found nesting was similar during these two years (20 out of 34 in 1997 vs. 18 out of 34 in 1998, $\chi^2_1 = 2.3$, $P > 0.1$).

TABLE 2. Body condition and reproductive investment indices of laying female Greater Snow Geese on Bylot Island, Nunavut, Canada, in 1989–1990 (no spring hunt) and 1999–2000 (spring hunt). Mean ± SE (*n*); indices were tested with one-way ANOVAs except where indicated. All effects had one degree of freedom.

Indices	1989–1990	1999–2000	Error df	*F*	*P*
Body condition					
Body mass (g)[a,b]	2942 ± 67 (10)	2665 ± 38 (30)	37	12.7	0.001
Abdominal fat (g)[a,b]	52.8 ± 5.2 (10)	37.8 ± 3.2 (27)	34	6.1	0.02
Dry breast muscles (g)[a,b]	65.6 ± 1.7 (10)	58.7 ± 1.0 (29)	36	12.3	0.001
Reproductive investment					
Dry oviduct (g)[a,b]	17.1 ± 1.6 (10)	15.0 ± 0.6 (29)	36	2.9	0.09
Potential clutch size (*n*)	4.8 ± 0.3 (10)	3.4 ± 0.2 (29)	37	14.5	<0.001
Atretic follicle (*n*)	1.0 ± 0.3 (10)	3.2 ± 0.3 (28)	36	17.0	<0.001
Egg mass (g)[c]	123.8 ± 2.0 (13)	119.5 ± 1.1 (42)	53	3.4	0.07
Dry egg albumen (g)[c,d]	8.2 ± 0.2 (22)	7.8 ± 0.1 (42)	62	3.6	0.06
Dry egg yolk (g)[c,d]	23.0 ± 0.4 (22)	23.1 ± 0.3 (48)	68	0.07	0.8

[a] Values were standardized from the residuals of the relationship between the dependent variable and body size (the overall mean sample value was added to each individual residual).

[b] Analyzed using ANCOVA, with postovulatory follicles as covariate.

[c] Means of all the eggs collected within a clutch were used as independent values (range 1–6 eggs per clutch).

[d] Oviducal eggs were included.

This contrasted sharply with the situation during the two years with the spring hunt (1999–2000), when almost no radio-marked geese were found nesting (Table 3). Most birds that did not reach the breeding grounds or were not found nesting had survived, as 81% (n = 42) of those birds were subsequently detected on the fall staging area in 1997–1998, and 66% (n = 35) in 1999 (radio-tracking coverage was only partial during fall 2000; hence no comparative figure is available).

DISCUSSION

Our results show that, in years when geese were hunted in spring, their body condition at laying, their clutch size, and their breeding effort were reduced, and their nesting delayed. Although our control sample was collected 10 years earlier than our sample of geese in years with a spring hunt, we do not think that this biased the comparison. Despite the continuous population increase over this period, these birds have not yet damaged their breeding habitats and their spring condition may, on the contrary, have improved due to increased use of farmlands and corn in spring (Gauthier et al. 1992, Filion et al. 1998). Even though body size of geese has declined over time (Reed and Plante 1997), we controlled for that in our analysis. Furthermore, we showed that there was no evidence for a density-dependent decrease in clutch size over this period as found in Lesser Snow Geese (*Chen caerulescens caerulescens*; Cooch et al. 1989).

Low reproductive investment in arctic-nesting geese may be caused by late snowmelt, which deprives them of food and nesting sites (Newton 1977). Our weather data showed that snowmelt was similar between 1989–1990 and 1999–2000, although air temperature was lower in one of the two years with a spring hunt. However, any possible delay in spring phenology in years with a spring hunt was slight when compared to very late years (e.g., 1992, see Lepage et al. 1996). For the telemetry data, one of the two years without a spring hunt (1998) was characterized by a very early spring. Yet, the breeding effort of radio-marked geese was similar between these two years, which argues against the hypothesis that weather was responsible for the differences observed across the four years (1997 to 2000). Therefore, although we cannot entirely rule out the influence of weather, it seems unlikely that this was the primary factor causing differences between years with and without a spring hunt.

We suggest that poor body condition upon arrival in the Arctic was a major reason for the reduced breeding

TABLE 3. Number (%) of radio-marked female Greater Snow Geese tracked on the spring staging areas along the St. Lawrence River, Quebec, and on the breeding grounds on Bylot Island, Nunavut, Canada.

	1997–1998	1999–2000	χ^2_1
n leaving staging areas[a]	80	80	—
Breeding grounds			
n females detected (%)	68 (85)	22 (28)	57.6***
n nests detected (%)	38 (56)	2 (9)	16.9***

[a] 36 in 1997, 44 in 1998, 35 in 1999 and 45 in 2000.

*** $P < 0.001$.

effort, late nesting, and reduced clutch size of Greater Snow Geese in 1999 and 2000. Birds arriving with reduced fat and protein reserves would have to feed more on or near the breeding grounds in order to acquire the nutrients needed to produce eggs (Choinière and Gauthier 1995). This would have delayed the onset of laying, and thus reduced the average clutch size (Lepage et al. 2000). For many birds, body condition may have been so poor that they simply skipped breeding. Detection in fall of most radio-marked birds that were not found nesting confirmed that they were still alive (Olson 2001).

It is interesting that the sum of developing, postovulatory, and atretic follicles of laying females was similar in 1989–1990 and 1999–2000 (5.8 ± 0.2 vs. 6.7 ± 0.3, respectively). This value agrees with the maximum clutch size of six eggs for Greater Snow Geese (GG, unpubl. data). Thus, females initiated the development of about the same number of follicles in 1999–2000 as in 1989–1990, but they apparently resorbed two more follicles in the former years in response to their poor body condition or late nest initiation date. In Lesser Snow Geese, Hamann et al. (1986) suggested that follicular atresia allowed females to adjust their final clutch size to the state of their endogenous reserves during laying in order to optimize energy allocation between reproductive output and individual survival. Alternatively, follicular atresia could be a mechanism used by late-nesting females to reduce their clutch size due to the seasonal decline in offspring reproductive value (Lepage et al. 2000). Although females delaying nesting can improve their body condition through feeding on the breeding grounds (Gauthier and Tardif 1991), late nesting will result in a reduction in offspring reproductive value.

During the two years with a spring hunt, the accumulation of fat and protein reserves of females was significantly reduced on the spring staging areas in Quebec (Féret and Gauthier, unpubl. data). A reduction in body condition upon departure for the arctic migration was thus likely responsible for the reduced condition of laying birds in those years. The smaller number of radio-marked females detected on Bylot Island in 1999–2000 compared to 1997–1998 even suggests that the fat reserves of many birds were too low to successfully reach the nesting areas. Gauthier et al. (1992) showed that, in a normal year, almost half of the fat reserves accumulated in spring are required to complete the 3000-km spring migration. Although most birds were still alive (they were detected later, Olson 2001), the proportion of subsequent resightings tended to be lower in the year with a spring hunt. Thus, we cannot exclude the possibility that some birds may have died of exhaustion or from injuries in years with a spring hunt. Even though radio-transmitters may affect the migration and reproduction of females (Demers 2000), this effect was present in all years and thus cannot explain the differences observed in years with and without a spring hunt.

In conclusion, body condition and most reproductive parameters of laying Greater Snow Geese were reduced in years with a spring hunt. Several factors other than hunting could also affect nutrient accumulation in spring (e.g., food availability, Davies and Cooke 1983, Féret and Gauthier, unpubl. data). However, Béchet and Giroux (unpubl. data) showed that increased disturbance caused by hunters was the most likely factor explaining the low pre-migratory body condition of geese in years with a spring hunt. We therefore suggest that the spring hunt may not only increase mortality but may also reduce fecundity of geese. This additional impact of the spring hunt should be considered in management programs aimed at controlling Snow Goose populations in North America.

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