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Body Condition, Migration, and Timing of Reproduction in Snow Geese: A Test of the Condition-Dependent Model of Optimal Clutch Size

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ABSTRACT: The seasonal decline of avian clutch size may result from the conflict between the advantage of early breeding (greater offspring value) and the advantage of a delay in lay date (improved body condition and hence clutch size). We tested predictions of a condition-dependent individual optimization model based on this trade-off (Rowe et al. 1994) in a long-distance migrant, the greater snow goose (*Chen caerulescens atlantica*), using data on condition, migration, and reproductive decisions of individuals. We closely tracked radio-marked females at their main spring staging area and on their breeding grounds. Our results were consistent with predictions of the model. Early-arriving females had a longer prelaying period and initiated their nests earlier than late arrivals. After controlling statistically for arrival date, we determined that females with high premigration condition had an earlier lay date than those in low condition. After controlling for the seasonal decline (i.e., lay date), we observed that clutch size was not related to premigration condition. Moreover, we took advantage of an unplanned manipulation of the prebreeding condition that occurred during our long-term study. We found that a reduction in condition caused a delay in lay date. However, after controlling for the seasonal decline, it did not affect clutch size. Our study indicates that geese simultaneously adjust their lay date and clutch size according to their premigration condition and migratory behavior as predicted by the condition-dependent optimization model.

Keywords: clutch size, individual optimization, breeding date, migration, seasonal decline, phenotypic plasticity.

The timing of reproduction is critical for successful reproduction in seasonal environments (Schultz 1991; Einum and Fleming 2000; Thomas et al. 2001). In most bird species, individuals that reproduce early in the breeding season lay a larger clutch size and reach a higher reproductive success than those that breed late (e.g., Klomp 1970; Perrins 1970; Daan et al. 1988). Theories of life-history strategy predict that reproductive decisions of an individual should be adapted to environmental conditions (e.g., food availability, predation risk, or weather condition) and intrinsic properties (e.g., body size and foraging efficiency). If individuals are able to perceive these differences, then their life-history traits are expected to follow an optimal reaction norm with respect to the specific conditions encountered (Stearns 1992; Kisdi et al. 1998).

The seasonal decline in avian clutch size is generally associated with a seasonal decline in offspring survival prospects (e.g., Perrins 1966; Daan et al. 1990; Hochachka 1990; but see Christians et al. 2001). The relationship between timing of breeding and clutch size may be the outcome of a conflict between the advantage of breeding early (greater offspring value) and the advantage of a delay in breeding (improved body condition leading to higher potential clutch size). This idea, referred to as the cost-of-delay hypothesis (Drent and Daan 1980), predicts that birds in poor condition have more to gain from a delay in breeding than birds in good condition. Rowe et al. (1994) formalized this hypothesis into a dynamic model of condition-dependent individual optimal strategy. Their model predicts optimal combinations of clutch size and timing of breeding based on the initial condition of individuals and the onset of condition gain (determined by their arrival date on the breeding grounds; fig. 1).

There are three major assumptions to the model as outlined by Rowe et al. (1994). First, the relative cost of delay increases as lay date increases. Thus, the rate of decline in

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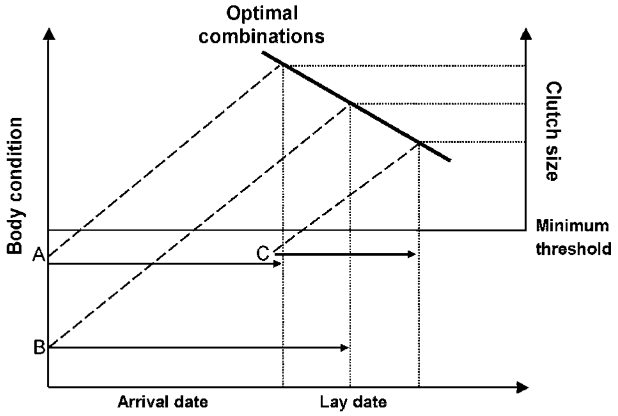

Figure 1: Graphical representation of the condition-dependent optimization model of clutch size versus lay date (modified from Rowe et al. 1994). The thick line shows the optimal combinations of clutch size and lay date assuming a trade-off between the cost (decreasing offspring value) and the benefit (increasing condition and hence clutch size) of a delay in lay date (see Rowe et al. 1994 for details of calculations). Letters represent individuals with different initial condition or arrival date on the breeding grounds. Dashed lines illustrate the increase in condition. Individuals must first reach the minimum threshold condition before producing a clutch and then delay laying until the optimal curve is crossed. Dotted lines connect the resulting lay date and clutch size for individuals reaching the optimal curve at different times. Arrows indicate the prelaying duration (lay date − arrival date).

offspring value, as a proportion of existing value, must increase with lay date. Second, the relative benefit of delay decreases as condition increases. This means that gain in clutch size (with accumulated condition) resulting from delay, as a proportion of existing clutch size, must decrease with increasing condition. Most functions will satisfy these assumptions except in unusual cases, such as an exponentially decreasing rate of offspring value or an exponentially increasing rate of condition gain. Third, the rate of condition gain is positive. If these three criteria are met, at least in the vicinity of an optimal combination of lay date and clutch size, then the model predicts that individual differences in initial condition or in the onset of condition gain will lead to a seasonal decline in clutch size.

There is growing evidence that energetic constraints during laying play an important role in determining optimal breeding decisions in birds (Monaghan and Nager 1997; Stevenson and Bryant 2000). In precocial species, it is generally recognized that clutch size limitation can operate at the egg-laying stage (e.g., Lack 1967; Rohwer 1992; Cooke et al. 1995). In many arctic-nesting birds, endogenous reserves acquired before arrival on the breeding grounds were traditionally considered the primary source of nutrients for egg formation (Ryder 1970; Ankney and MacInnes 1978; Drent and Daan 1980). However, recent studies have shown that exogenous nutrients acquired on the breeding grounds can be as important for egg formation as endogenous reserves acquired on staging areas (e.g., Choinière and Gauthier 1995; Ganter and Cooke 1996; Klaassen et al. 2001). As a result, the nutrient reallocation hypothesis, originally proposed to explain the seasonal decline in clutch size in arctic-nesting geese (Ryder 1970), was rejected, and the condition-dependent individual optimization model has been invoked to explain why late-nesting geese lay fewer eggs (Ganter and Cooke 1996; Lepage et al. 2000).

Our goal was to test predictions of the condition-dependent optimization model in the greater snow goose (*Chen caerulescens atlantica*), a long-distance migrant that breeds in a highly seasonal environment, the High Arctic. This species exhibits a strong seasonal decline in clutch size (intra-annual decline, 0.20 egg/d; Lepage et al. 2000) and a very steep seasonal decline in offspring fitness (number of young surviving to winter declines by 90% over the span of laying dates, ∼10 d; Lepage et al. 2000). These seasonal effects are due to environmental factors (mostly food supply) and are not related to parental quality (Lepage et al. 1998, 1999). Greater snow geese accumulate large amounts of fat and protein on their main staging area in southern Quebec before their 3,000-km migration to the Arctic (Gauthier et al. 1984, 1992). However, up to 50% of these reserves are depleted during migration (Gauthier et al. 1992), and exogenous nutrients acquired through feeding on the breeding grounds make a significant contribution to egg formation (Choinière and Gauthier 1995). The delay between arrival on the breeding grounds and egg laying can be up to 2 wk (Gauthier and Tardif 1991). Food intake by prelaying females is high (Gauthier 1993) and enables them to gain body condition (average rate of gain: 5.9 g fat/d and 5.3 g protein/d, calculated from Choinière and Gauthier [1995]). Because the main assumptions of the optimization model are well supported by field data in the greater snow goose, it is a good candidate to test predictions of the model.

We tested three predictions of the individual optimization model with respect to the migratory behavior and body condition of individuals. First, after controlling for their initial condition, we expect that early-arriving birds should experience a longer delay on the breeding grounds but still lay earlier than late-arriving ones (individual *A* vs. *C* in fig. 1). Second, after controlling for their arrival date, we expect birds in better condition to have a shorter delay on the breeding grounds and thus lay earlier than those in poor condition (individual *A* vs. *B* in fig. 1). Third, after controlling for the effect of lay date, we expect no residual effect of initial condition on clutch size. To test these predictions, we radio-tracked individual females at their main spring staging area and on their breeding

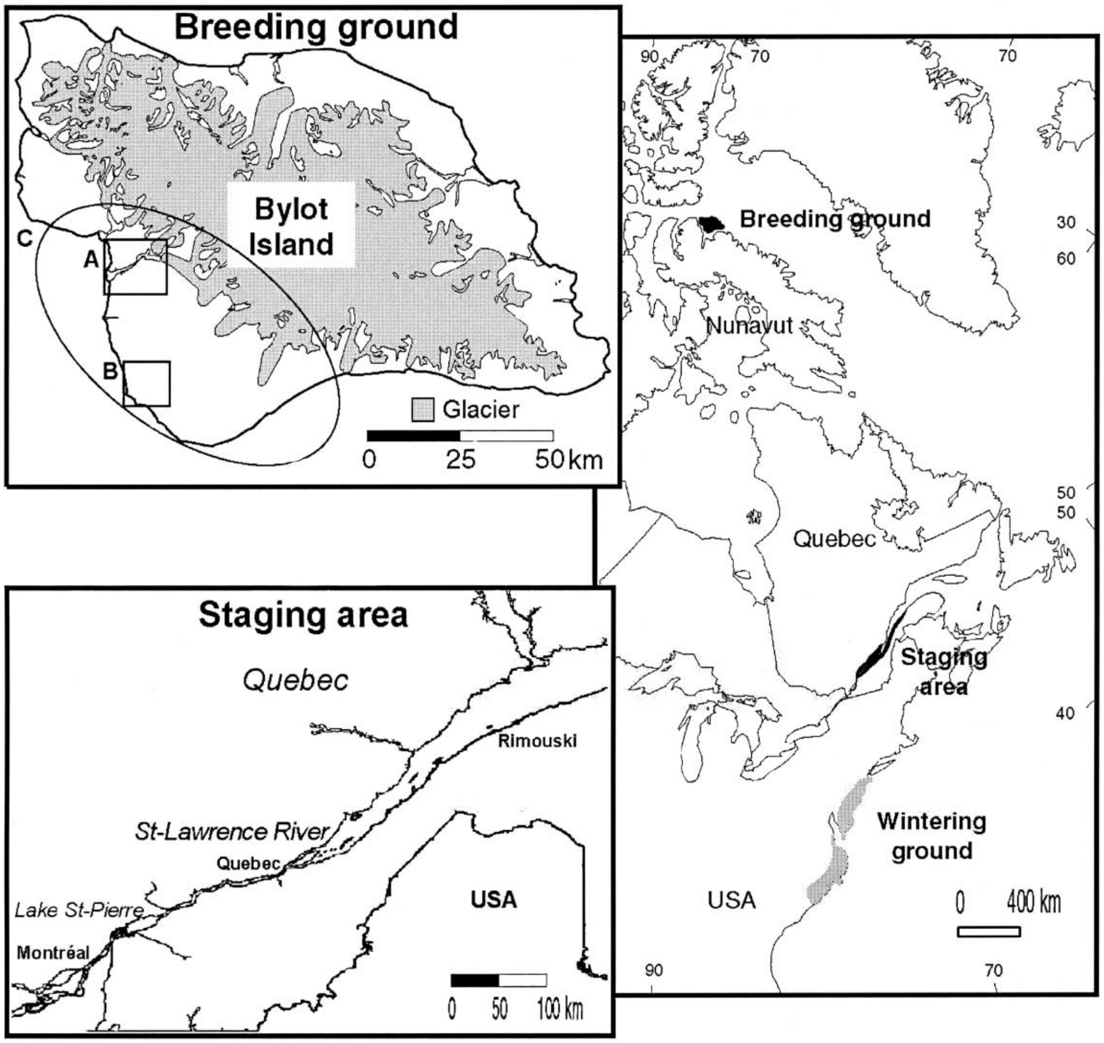

Figure 2: Study areas and detailed map of the main staging area and breeding ground of greater snow geese. Birds were radio-tracked along the Saint Lawrence River, southern Quebec (mostly from Lake Saint-Pierre to Rimouski), and on Bylot Island, Nunavut, at two nesting areas (*A* and *B*) and over the south plain of the island (*C*).

grounds. Moreover, we took advantage of an unplanned manipulation (i.e., management actions) to investigate the effect of a reduction in prebreeding condition on lay date and clutch size. The originality of this study is due to our ability to relate events occurring during the spring migration to the subsequent reproductive decisions of birds in order to test key predictions of the condition-dependent model of optimal clutch size.

Material and Methods

Radio-Marked Individuals

We captured female greater snow geese breeding at the Bylot Island migratory bird sanctuary (73°08′N, 80°00′W; fig. 2) during their molting period in August (see Blouin et al. 1999 for details). In 1996 and 1997, we fitted 131 adult females with a radio transmitter affixed to a neck collar engraved with two alphanumeric codes (total weight 59 ± 9 g, 2.5% ± 0.5% of bird body mass, mean ± 1 SD; Demers et al., in press). Only family groups were captured, and thus all birds were at least 2 yr old or more because snow geese do not breed as yearlings and few do so at 2 yr of age (Reed et al. 2003). Longevity of radios was 16 to 24 mo. On the staging area, the range was generally 1–3 km on the ground and 4–5 km in the air but reached 5–10 km and 10–20 km in the open Arctic habitat, respectively (see also Hughes et al. 1994). Transmitters had no effect on the activity budget of individuals during the spring following marking but negatively affected some reproductive parameters (slight delay in lay date and decrease in clutch size; Demers et al., in press). We assumed that these effects were similar across marked females and that transmitters did not bias comparisons among them (see also "Discussion").

In 1997 and 1998, we radio-tracked geese on their spring staging area along the Saint Lawrence River in southern Quebec and on their breeding grounds in Nunavut (fig. 2). From the end of March to the departure of the last radio-marked birds at the end of May, five to six crews tracked birds on the staging area daily using vehicle-mounted receiving systems. Aerial tracking by plane was also conducted every week. On the breeding grounds, we tracked birds during the prelaying, laying, and early incubation periods (May 27–June 20) in two main nesting areas located 30 km apart on Bylot Island (fig. 2; see Bêty et al. 2001 for description of the goose colonies). We conducted tracking sessions (1–4 h) every 1 or 2 d from towers located on elevated ground at each area. We also used a receiving system mounted on a snowmobile to track birds in the surroundings of these nesting areas (<15 km; May 26–June 10). Finally, aerial tracking by helicopter was conducted every week over the south plain of Bylot Island (~1,600 km^2; fig. 2) starting in early June. During laying and early incubation, we searched by foot for nests of females whose signal had been detected.

We defined departure date as the last date that a radio was detected on the staging area and arrival date as the first date that it was detected on the breeding grounds. Average daily detection probability was 79% ± 21% (mean ± 1 SD) after May 10 on the staging area (e.g., daily detection probability = 100 × number of days that an individual was detected from May 10 to its departure date/total number of days from May 10 to departure date of the individual) and 81% ± 24% on the breeding grounds during the prelaying period. The probability of missing an individual for 2 d was thus on average 4% on both the staging area and the breeding grounds. Consequently, we are confident that our observations provided reliable estimates of departure and arrival dates of individuals relative to each other's departure and arrival dates. Migration duration was defined as the difference between arrival and departure dates. For birds whose nests were found, we determined lay date (date of first egg laid; Lepage et al. 1999) and clutch size (maximum number of eggs found in a nest after the start of incubation). Snow geese do not renest after a clutch failure (Lepage et al. 2000). The prelaying duration was the difference between the lay and arrival dates. Prelaying durations are minimum estimates because daily detection probability of nesting birds was 87% ± 23% during prelaying.

To estimate body condition of geese on the spring staging area, we used the abdominal profile index, which provides an estimate of stored energy by scoring the roundness of the abdominal region (Owen 1981; Brown 1996). In geese, the abdominal cavity is a site of fat deposition, and abdominal fat is a good indicator of overall body fat (Gauthier and Bédard 1985). Profiles were scored subjectively from a distance using a scope (20–60 ×) and a six-category scale with an intermediate level between categories. In greater snow geese, abdominal profile indices are linearly related to body mass corrected for body size (first principal component derived from culmen, tarsus, and head length measurements), although the variance is high for individuals assigned to the same profile score ($R^2 = 0.15$, $n = 141$, before spring migration; Féret 2002). On average, an increase of one profile score corresponds to an increase of 100 g in body mass, and the repeatability of profiles attributed to the same bird is high within and among observers (≤0.5 score for >90% of observations; Féret 2002). Variability in abdominal profile score (Brown 1996) was reduced for radio-marked birds by having four experienced and well-trained observers for most observations (>75%).

The premigration condition of marked females was defined as the latest condition index observed <10 d before the annual median departure date from the staging area. At that time, geese had reached about 75% of their premigration body condition. Marked birds not observed during this time interval were excluded from analyses involving body condition. We standardized body condition scores using the seasonal changes in abdominal profile of the population. Seasonal change was characterized over the staging period by determining the abdominal profile of random samples of adults. We made observations in four regions located throughout the staging area. In each region, we scored the profile of about 50 randomly selected, unmarked adults every 5 d. Although we could not distinguish sexes in those birds, males and females store similar amounts of fat during the staging period (Gauthier et al. 1992). We used the difference between the abdominal profile measured in radio-marked females and the value predicted from the year-specific linear relationship between date and abdominal profile for the whole population as a relative index of body condition for radio-marked females.

Reduction in Body Condition due to Hunting Disturbance

In order to limit the growth of the greater snow goose population (Menu et al. 2002), the Canadian Wildlife Service implemented a spring conservation hunt from 1999 to 2002 throughout southern Quebec from early April to the end of May. This new hunting activity led to a substantial increase in the disturbance of the geese. Although this had little effect on overall stopover length and departure date from the staging area (Béchet et al., 2003), body condition of geese at departure was considerably reduced (reduction in abdominal fat mass ranging from 29% to 48% in birds collected in 1999 and 2000 depending on the site; Féret et al., 2003). Furthermore, Mainguy et al. (2002) found evidence that body condition of laying females on the breeding grounds was also reduced in those years. The reduction in condition was not a density-dependent effect due to the population increase, since the premigration condition of geese remained stable during the two decades preceding the hunt years because of the high food supply that geese can find in farmlands (Gauthier et al. 1992; Féret et al., 2003). Although this was not a controlled experiment, this large-scale management action represented a unique opportunity to test predictions of the condition-dependent optimization model of clutch size and lay date.

Nests of unmarked geese were monitored from 1988 to 2002 at the Bylot Island snow goose colony. Nests were found by systematic searches mostly during the laying or early incubation period (see Bêty and Gauthier 2001 for details). Clutch sizes of one or more than six eggs were removed from the sample (3% of total) because most of them result from partial predation and intraspecific nest parasitism, respectively (Lepage et al. 2000; G. Gauthier, personal observation). Lay dates in arctic-nesting geese are strongly influenced by weather conditions on breeding grounds (e.g., Skinner et al. 1998). We used the percentage of snow-free area in the study area on June 5 as an index of climatic condition (Lepage et al. 1996). This index is well correlated with the average spring temperature (May 25–June 15) obtained from a meteorological station located 65 km southeast of the study area ($r = 0.70$, $n = 12$; G. Gauthier, unpublished data).

Data Analysis

Analyses were done in SAS version 8 (SAS Institute 1999). Medians were compared between years using Mann-Whitney tests (Siegel and Castellan 1988). Multiple linear regressions were performed with the GLM procedure of SAS. We visually inspected residuals to detect violation of the assumptions required for analysis. We used Type III SS to test the significance of a variable in models with other variables already included. Terms for which SS had $P > .05$ were dropped sequentially from full regression models. We used a model including the variables' date and year to examine the seasonal change in body condition of geese on the staging area.

We performed multiple linear regressions to relate the migratory behavior to subsequent reproductive decisions of radio-marked females. In these analyses, values were transformed as deviations from the yearly median. A linear regression was used to relate arrival date and prelaying duration. We used a model including arrival date and premigration body condition to relate the migratory pattern and the condition of marked females to their lay date. Finally, to examine the relationship between condition and clutch size, a model including lay date and premigration body condition as independent variables was used. All these regression models also included the variable year and interactions terms in order to test for interannual variation in the slope of the relationships between standardized life-history traits. Because some radio-marked females were followed in more than one year, we retained only the first breeding season in which a female was successfully tracked on staging and breeding grounds to avoid pseudoreplication.

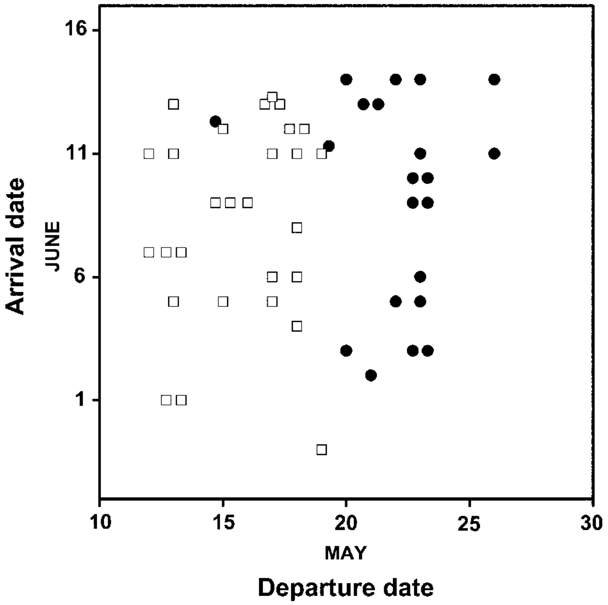

Figure 3: Relationship between departure date from the main spring staging area and arrival date on the breeding grounds of radio-marked female greater snow geese in 1997 (*closed circles*) and 1998 (*open squares*). Points were offset to display full sample size.

We tested the effect of the reduction in prebreeding condition in hunting years on lay date using a multiple regression model, which included the variables climatic condition in the Arctic and hunting on the staging area (yes = 1, no = 0) as independent variables. A model including variables lay date and hunting was used to test for the effect of a reduction in condition on clutch size. Unless otherwise indicated, values provided are means ± 1 SE.

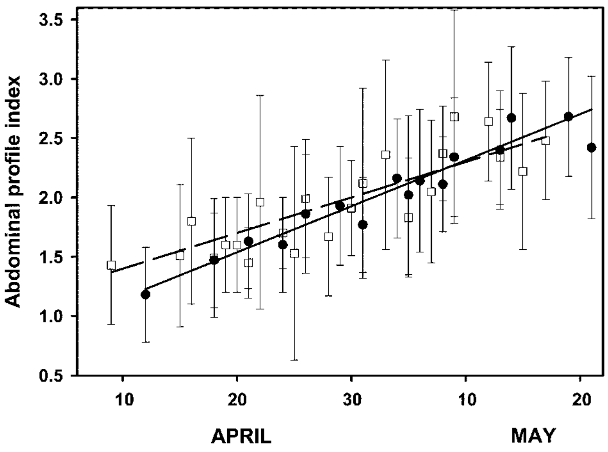

Figure 4: Seasonal change in abdominal profile index (API) of greater snow geese during the spring staging period in 1997 (*closed circles, solid line*) and 1998 (*open squares, dashed line*). Values are mean ± 1 SD (each dot represents 49–189 individuals). Multiple linear model: API $= -1.6 + 0.030 \times \text{date} - 1.10 \times \text{year} + 0.008 \times (\text{date} \times \text{year})$; $F = 406.1$, df $= 3, 3, 195$, $P < .001$, $R^2 = 0.27$. Julian date, January 1 = 1; year: 1997 = 1, 1998 = 0.

Results

Radio-Marked Individuals

In 1997 and 1998, a total of 49 radio-marked females with known premigration body condition were subsequently tracked on the breeding grounds, and 30 of them were found nesting. Departure from the staging area was relatively synchronized within a year, with virtually all birds leaving over an 8-d period (fig. 3). The median departure date was 6.5 d earlier in 1998 than in 1997 (May 16.5 and May 23, respectively; Mann-Whitney test, $Z = 5.61$, $P < .001$). Migration duration varied considerably among individuals and was longer in 1998 (median = 25 d, range 11–31) than in 1997 (median = 18 d, range 11–28; $Z = -3.68$, $P < .001$). Arrival on the breeding grounds was less synchronized than departure because it was spread over a 13–15-d period each year. However, the median arrival date was similar in both years (June 10 and June 9 in 1997 and 1998, respectively; $Z = 0.80$, $P = .42$; fig. 3). Median lay date was earlier in 1998 than 1997 (June 11, $n = 18$, and June 14, $n = 12$, respectively; $Z = 2.27$, $P = .02$). The delay between arrival and lay date (prelaying) was highly variable among birds but did not differ between years (1997, median = 2.5 d, $n = 12$, range 0–9; 1998, median = 2.0 d, $n = 18$, range 0–10; $Z = -0.13$, $P = .89$).

Seasonal change in body condition of geese on the staging area was similar over the 2 yr of the study, although daily rate of condition increase was 21% lower in 1998 than in 1997 ($\beta = 0.030 \pm 0.001$ and 0.038 ± 0.001 abdominal profile index/d, respectively; $t = 4.13$, $P < .001$, $n = 3{,}199$; fig. 4). Premigration condition index varied considerably among marked birds and was spread over 2.5 abdominal profile scores. Departure date of individuals from the staging area was not correlated with their premigration body condition (table 1). Similarly, arrival date of individuals on the breeding grounds was not correlated with their departure date or premigration body condition (fig. 3; table 1).

Since departure was synchronized, migration length of individuals was highly correlated with their arrival date (table 1). Thus, assuming that the energetic balance of migration is similar for birds with the same migration duration, the postmigration body condition of individuals arriving at the same time on the breeding grounds should be related to their premigration body condition. Therefore, after we controlled statistically for the effect of arrival date (i.e., energetic balance of migration), relative premigration body condition should reflect the relative postmigration condition. Based on this assumption, we then tested our three predictions of the condition-dependent optimization

Table 1: Correlation matrix (Pearson correlations) of the studied life-history characteristics

	Departure date	Arrival date	Migration duration	Prelaying duration[a]	Lay date	Clutch size
Body condition[b]	−.04	−.13	−.11	−.16	−.35*	.15
Departure date		.05	−.46***	.13	.17	−.10
Arrival date			.85***	−.74***	.70***	−.26
Migration duration				−.61***	.41*	−.09
Prelaying duration[a]					−.04	−.19
Lay date						−.51**

Note: Values were standardized relative to yearly median. Sample sizes are 49 females except for correlations involving lay dates ($n = 30$) or clutch sizes ($n = 27$).

[a] Prelaying duration = lay date − arrival date.

[b] Premigration body condition.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

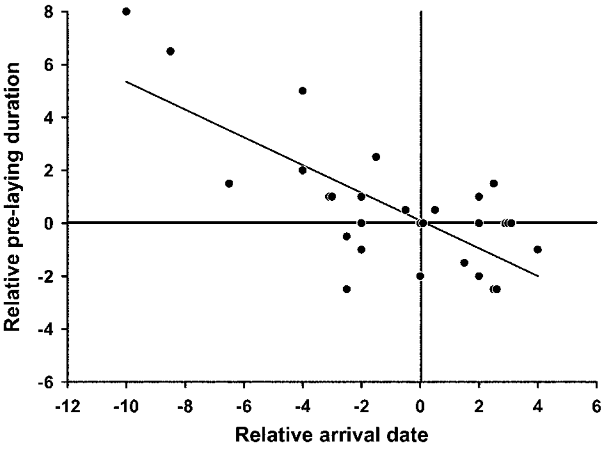

Figure 5: Relationship between prelaying duration (lay date − arrival date) and arrival date on the breeding grounds of radio-marked greater snow geese. Values are standardized relative to the yearly median. Linear regression: prelaying = 0.099 − 0.53 × arrival date; $F = 33.7$, df = 1, 28, $P < .001$, $R^2 = 0.55$. Variable year and interaction terms were removed from the model (all $P > .24$). Points were offset to display full sample size.

model. First, early-arriving females had a longer prelaying period than late ones (fig. 5) but nonetheless initiated their nests earlier than late-arriving ones after we controlled statistically for their premigration body condition (table 2). This supports the first prediction. Second, lay date was negatively related to the premigration body condition of females after we controlled statistically for arrival date (table 2), thus supporting the second prediction. Finally, clutch size of marked females declined with lay date but was not related with premigration body condition after we controlled statistically for lay date (table 2), thus supporting our third prediction.

Reduction of Body Condition by Hunting

From 1988 to 2002, lay date was determined for 3,677 nests monitored on Bylot Island (ranging from 32 to 359/yr). Lay dates were strongly associated with climatic conditions (i.e., snow-free area) on the breeding grounds and were later in years with late snowmelt (fig. 6). This covariate was thus retained in the analysis. In the 4 yr with hunting on the staging area (i.e., reduction in prebreeding condition), birds laid significantly later than in years without hunting (fig. 6). After controlling for the overall seasonal decline in clutch size, we did not detect any significant effect of hunting on clutch size (fig. 7). We conclude that birds that left the staging area in lower body condition in hunting years delayed laying but laid a similar number of eggs compared with birds that laid at similar dates in years without hunting.

Discussion

Our results support three key predictions of the condition-dependent optimization model of reproductive decisions in an arctic-nesting species. Geese appeared to simultaneously adjust their lay date and clutch size according to their premigration body condition and migratory behavior in order to optimize their expected reproductive success. To our knowledge, this is the first field study that integrates body condition, migration, and reproductive decisions to simultaneously test several predictions of the condition-dependent model. By incorporating both proximate and ultimate mechanisms, the dynamic optimization model based on the cost-of-delay hypothesis (Drent and Daan 1980) can explain the seasonal decline in clutch size. According to this model, the seasonal decline in avian clutch size reflects adaptive phenotypic plasticity of individuals. Thus, variations among individuals in initial condition and onset of condition gain on breeding grounds combined with the seasonal decline in offspring value can explain the breeding delay of some individuals and their subsequent reduced clutches (Rowe et al. 1994).

The energetic cost of migration may be higher in radio-marked birds than in unmarked ones. The condition-dependent model predicts that females in lower condition should lay later and smaller clutches than females in higher condition (fig. 1). The delay in lay date and decrease in clutch size observed in radio-marked greater snow geese relative to unmarked birds (Demers et al., in press) are in accordance with this prediction.

Our observations indicate that geese breeding on Bylot Island did not migrate directly from their main staging area to their breeding grounds. The 2–3-wk-long migration indicates that most birds spent some time at one or several other staging areas in between (Le Hénaff et al.

Table 2: Results of general linear models of lay date and clutch size

Dependent variable and effect	df	*b*	SE	*F*	*P*
Lay date:					
Arrival date	1, 27	.45	.09	27.6	<.001
Body condition[a]	1, 27	−1.18	.56	4.5	.04
Clutch size:					
Lay date	1, 24	−.22	.08	7.95	.009
Body condition[a]	1, 24	−.08	.33	.06	.82

Note: Variable year and interaction terms were dropped from the models (all $P > .19$). Multiple $R^2 = 0.57$ and 0.26 for lay date and clutch size model, respectively.

[a] Premigration body condition.

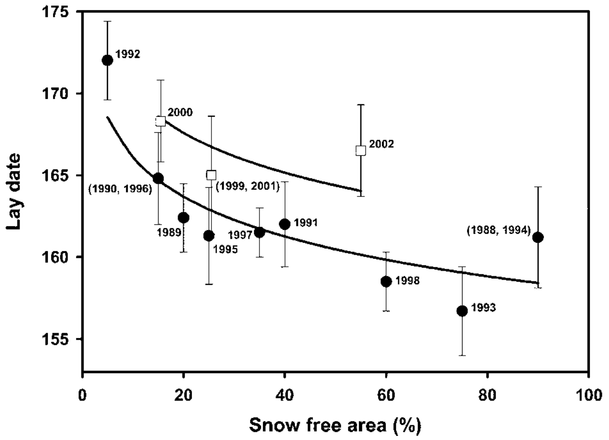

Figure 6: Relationship between lay date of greater snow geese and climatic condition (% snow-free area on June 5) in years with hunting on the spring staging area (*open squares*, 1999–2002) and without (*closed circles*, 1988–1998). Corresponding years are near each data point. Values are mean ± 1 SD (each dot represents 52–522 nests). Lay dates are expressed in Julian date, January 1 = 1. Multiple linear model: climatic condition (log-transformed), $F = 2{,}220$, $df = 1, 3{,}674$, $P < .001$; hunting (on staging area: yes = 1, no = 0), $F = 1{,}086$, $df = 1, 3{,}674$, $P < .001$; lay date = 174.2 − 3.5 × climatic condition + 3.9 × hunting. The use of log-transformed snow-free area improved the fit of the model (untransformed, $R^2 = 0.40$; transformed, $R^2 = 0.51$).

1995). It is possible that geese stopping during the migration were able to feed and thus spare or even increase their endogenous reserves, especially for birds with the longest migration duration. Consequently, late-arriving birds may have arrived in better condition than early-arriving ones that had similar premigration condition (see also Tombre et al. 1996). This does not affect our conclusions about the relationship between premigration condition and reproductive decisions because we controlled statistically for arrival date (and thus migration duration). However, arrival date of individuals could be associated with body condition on arrival at breeding grounds. Our data do not allow us to independently evaluate the effects of arrival date and postmigration condition on individual breeding strategy, and this needs further investigation. However, the relative cost of migration could be higher in heavier individuals than in lighter ones. Although this could reduce the absolute difference in condition on arrival between heavy and light departing birds, it does not affect our finding that relative premigration body condition affects optimal lay date and clutch size.

The rate of condition gain before breeding (i.e., the slope of dashed lines in fig. 1) should influence the trade-off between lay date and clutch size (Rowe et al. 1994). Variation in foraging efficiency or environmental conditions encountered by individuals can affect the time at which birds reach the minimum threshold condition required to invest in egg production and also the rate of nutrient acquisition on the breeding grounds. An increase in the rate of condition gain will always increase the optimal clutch size. For instance, birds in lower condition may accumulate nutrient reserves at a higher rate than birds in better condition and consequently have a different optimal combination of lay date and clutch size (Rowe et al. 1994). We did not find evidence for that in our data, since there was no effect of premigration condition on clutch size after we controlled for the seasonal decline.

A controlled experiment involving manipulation of the premigration condition or the migratory pattern of individuals would have strengthened our conclusions. However, manipulating these variables on the staging areas (e.g., by feeding birds to improve condition or holding birds to delay departure without affecting their condition) and measuring the effects on the breeding grounds pose a formidable challenge. In this study, we nonetheless showed that a reduction in prebreeding condition generated by a large-scale, unplanned experiment on the main staging area (i.e., implementation of a spring hunt) caused a consistent delay in the timing of breeding over 4 yr. This provides additional support for the condition-dependent optimization model. However, we cannot identify the exact mechanism involved because this delay might result from delayed arrival date on the breeding grounds and/or a

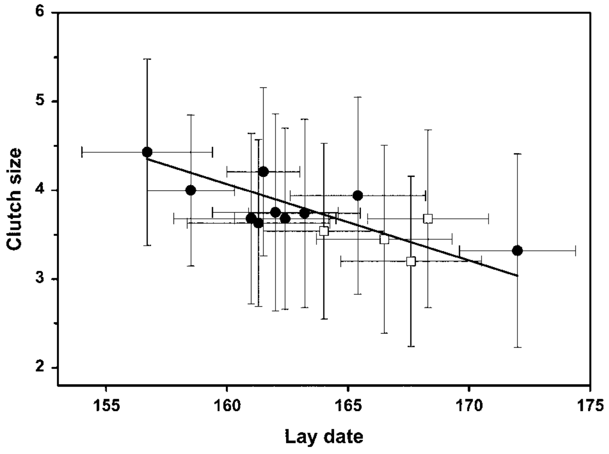

Figure 7: Relationship between clutch size and lay date of greater snow geese in years with hunting on the spring staging area (*open squares*, 1999–2002) and without (*closed circles*, 1989–1998). Values are mean ± 1 SD (each dot represents 72–316 nests). Lay dates are expressed in Julian date, January 1 = 1. Linear regression: clutch size = 17.83 − 0.09 × lay date; $F = 503.3$, $df = 1, 3{,}073$, $P < .001$, $R^2 = 0.14$; hunting on staging area, $\beta = 0.05$ egg, 95% confidence interval = −0.03 to 0.14, $F = 1.5$, $df = 1, 3{,}072$, $P = .22$, and interaction term, $P = .89$, were removed from the model.

lengthening of the prelaying period on the breeding grounds (see fig. 1). The absence of association between premigration body condition and arrival date of radiomarked birds may suggest that the migratory pattern is not strongly dependent on premigration condition. However, Mainguy et al. (2002) found evidence that a lower proportion of marked birds successfully completed the migration in years with hunting on the staging area.

Our study indicates that the migratory behavior may play a major role in the overall breeding strategy of individuals. Both and Visser (2001) recently showed that adjustment of breeding date to environmental conditions on the breeding grounds can be constrained by the timing of spring migration in long-distance migrants. The predictability of the environment (e.g., social environment, food supply, and climatic factors) at the current and future stopover sites may cause uncertainty in the costs and benefits of different migratory decisions (Weber et al. 1998). High variance in condition gain at a target staging site may result in a delayed departure from the preceding site in order to further increase body condition before departure (Schaub and Jenni 2001). Accordingly, individual characteristics such as high social status and experience may reduce the variance in foraging success and explain the rapid migration of some individuals.

Recent models of optimal avian migration assume that reproductive success is determined by arrival date and nutrient reserves at arrival (e.g., Alerstam and Hedenstrom 1998; Farmer and Wiens 1998). This is consistent with our observations for greater snow geese. However, factors that determine the arrival date of individuals on the breeding grounds remain unknown, since we detected no association with premigration body condition or departure date. Few empirical studies have linked the migratory behavior and subsequent reproductive decision of individuals in long-distance migrants (but see Sandberg and Moore 1996; Marra et al. 1998), and most observations are limited to arrival dates without information on body condition of individuals. In this study, we showed that early-arriving birds lay earlier and thus achieve higher reproductive success than late-arriving birds (Lepage et al. 2000), which is consistent with other studies (Petersen 1992; Nilsson and Persson 1994; Dalhaug et al. 1996). Nevertheless, there is still little empirical data on the fitness costs and benefits of different migratory decisions in birds (Møller 1994; Palomino et al. 1998; Brown and Brown 2000; Madsen 2001). Early-arriving birds may encounter extreme weather conditions that could threaten their survival, increase maintenance costs, and restrict nutrient accumulation (Farmer and Wiens 1998). Birds may thus face a trade-off between arrival date, survival, and energy reserves at the onset of breeding.

In nesting geese, previous studies showed that body reserves accumulated on spring staging areas influenced subsequent reproductive success (Teunissen et al. 1985; Ebbinge and Spaans 1995). However, the early suggestion that this was largely because endogenous reserves at arrival on the breeding grounds was a direct determinant of clutch size (Ryder 1970; Ankney and MacInnes 1978) needs to be revised. First, the strong covariation between lay date and clutch size indicates that both traits should always be considered together. Second, with respect to egg production, snow geese use a mixed capital-income strategy (i.e., egg nutrients come from both food ingested on site and body reserves; Choinière and Gauthier 1995; Ganter and Cooke 1996; Gauthier et al., in press). As in many other species, late-nesting snow geese perform more poorly than early ones in most components of reproductive success (Cooke et al. 1995; Lepage et al. 2000). Our results indicate that birds in better prebreeding condition reach optimal combinations of lay date and clutch size earlier than birds in poor condition and consequently achieve higher reproductive success. Birds would appear to be under persistent directional selection; that is, individuals in good condition lay earliest, have the largest clutches, and achieve the highest fitness. However, phenotypic variation in clutch size and lay date may be maintained by environmentally induced variation in nutritional condition and the onset of condition gain on the breeding grounds independently from the genetic component (Price et al. 1988; Price and Liou 1989; Rowe et al. 1994). Females may also vary in their timing of reproduction and clutch size for reasons other than body condition and arrival date (e.g., habitat quality and availability of mates or nest sites; Winkler and Allen 1996; Kelly and VanHorne 1997).

Conclusion

Our study indicates that greater snow geese adjust their reproductive decisions according to their body condition and migratory behavior, as predicted by the condition-dependent optimization model. Despite the significance of this model for understanding reproductive patterns, our knowledge of the numerous factors involved, such as those causing intraspecific variations in the timing of migration, is still limited. To be fully understood, life-history traits related to migration and reproduction (e.g., timing of breeding and clutch size) should not be looked at in isolation but within a single framework.

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