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GOSLING GROWTH AND SURVIVAL IN RELATION TO BROOD MOVEMENTS IN GREATER SNOW GEESE (*CHEN CAERULESCENS ATLANTICA*)

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Abstract.—Post-hatch brood movements to high-quality foraging sites are common in precocial birds but may entail costs for young. We assessed effects of overland movements of broods between the nesting and rearing areas in Greater Snow Geese (*Chen caerulescens atlantica*) breeding on Bylot Island, Nunavut, Canada, to determine whether these movements affected gosling survival and growth. We monitored 51 radiomarked females over five years to quantify movement distance, movement duration, and gosling survival. Gosling growth was compared over four years using a sample of web-tagged broods recaptured shortly before fledging among adults that (1) nested and reared their young in a dense colony, (2) left the colony and moved ~30 km to reach the main brood-rearing area, or (3) nested and reared their young in the main brood-rearing area. Brood movements by radiomarked birds were highly variable (2.6–52.5 km, depending on rearing areas used) and fairly rapid (≤6 days after hatch for 72% of the females). Gosling survival was not related to distance moved between nesting and brood-rearing areas. However, gosling growth was influenced by areas used and whether or not they had to move to reach their brood-rearing area. Geese nesting at the main brood-rearing area generally reared heavier and larger goslings than those that moved ~30 km from the main nesting colony to rear their brood at the main brood-rearing area. On the other hand, goslings leaving the nesting colony after hatch were heavier and larger than those that stayed there throughout brood rearing in one of two years. Although brood movements allow goslings access to high-quality habitats, they entail some costs. Thus, minimizing such movements through nest-site selection should provide a selective advantage by allowing goslings to maximize their growth. *Received 22 April 2005, accepted 3 January 2006.*

Key words: brood movements, Bylot Island, *Chen caerulescens atlantica*, goslings, Greater Snow Goose, growth, prefledging survival.

Croissance et Survie des Oisons en Relation avec les Déplacements des Familles chez *Chen caerulescens atlantica*

Résumé.—Le déplacement des familles vers les sites d'alimentation de haute qualité après l'éclosion est répandu chez les oiseaux nidifuges, mais peut comporter des coûts pour les jeunes. Nous avons évalué l'effet de ces déplacements entre les sites de nidification et d'élevage sur la survie et la croissance des oisons chez *Chen caerulescens atlantica* nichant à l'Île Bylot, Nunavut, Canada. Durant cinq ans, nous avons suivi le déplacement de 51 femelles munies de radio-émetteurs afin

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de quantifier la longueur et la durée de leurs déplacements, ainsi que la survie de leur couvée. La croissance des oisons a été évaluée durant quatre années à partir de recaptures effectuée peu avant la période d'envol de jeunes marqués à l'éclosion. Nous avons comparé la croissance des oisons entre des familles qui (1) ont niché et élevé leur couvée dans la colonie principale à densité élevée, (2) ont niché à la colonie principale et se sont déplacées sur ~30 km après l'éclosion vers le site d'élevage principal ou (3) ont niché et élevé leur couvée au site d'élevage principal. Les déplacements des familles suivies par télémétrie étaient hautement variables (2.6–52.5 km selon le site d'élevage utilisé) et rapides (≤6 jours après l'éclosion pour 72% des femelles). La survie des oisons n'était pas affectée par la distance parcourue entre les sites de nidification et d'élevage. Cependant, leur croissance était influencée par les sites utilisés et le fait de quitter ou non le site de nidification pour atteindre le site d'élevage. Les oisons des familles nichant au site d'élevage principal avaient généralement une masse et une taille corporelle plus élevées que ceux des familles nichant à la colonie principale et ayant parcouru ~30 km pour atteindre le site d'élevage principal. Par contre, pour une année sur deux où la comparaison était possible, les oisons des familles qui ont quitté la colonie principale ont connu une meilleure croissance que ceux qui y sont demeurés. Ainsi, bien que les déplacements des familles puissent permettre aux oisons d'avoir accès à des habitats de haute qualité, ils comportent également des coûts. Minimiser ces déplacements par le choix du site de nidification devrait donc procurer un avantage sélectif en permettant de maximiser la croissance des oisons.

Migration enables animals to maintain optimum conditions at all times when faced with changing vital requirements or environments (Dingle 1980). In birds, long-distance migratory movements between wintering and breeding areas are an example. Once on the breeding grounds, birds should select the best habitats to optimize their reproductive success (Cody 1985). Habitat selection theory (Fretwell 1972, Pyke 1983) predicts that individuals will move to habitat patches that maximize their fitness at different stages of the breeding cycle. Therefore, even within the breeding area, shorter but still significant movements may be required in response to changing vital needs.

In ground-nesting birds such as geese and ducks (Anatidae), selection of a nest site that minimizes the risk of predation on eggs and incubating females is essential. For instance, some species nest on islands to avoid mammalian predation (e.g., Petersen 1990, Tombre et al. 1998, Ebbinge and Spaans 2002). However, new requirements arise after hatching, as parents of precocial young must lead them to suitable feeding areas. This is especially critical in geese, because goslings require high-quality food plants to successfully complete growth. Timing of snowmelt in Arctic-nesting geese also influences choice of nesting sites (Lepage et al. 1996) and, thus, areas used for nesting are often located far from those used for brood rearing. Access to best feeding sites results in larger and heavier goslings at fledging (Larsson and Forslund 1991, Lepage et al. 1998, Sedinger et al. 2001), which may result in higher survival rates during the fall migration (Owen and Black 1989, Schmutz 1993, van der Jeugd and Larsson 1998, Cooch 2002, Menu et al. 2005) and larger final adult body size (Larsson and Forslund 1991). Presence of predator-escape habitat may also affect juvenile survival and thus influence the choice of rearing sites (Laing and Raveling 1993, Stahl and Loonen 1998). Parents selecting the best feeding sites with adequate refuges from predators should thus increase their chance of producing offspring.

Geese commonly make overland movements between nesting and brood-rearing areas to gain access to high-quality resources (Cooch et al. 1993, Sedinger et al. 2001). An increased predation risk has been associated with such movements (Duncan 1983), and a negative relationship between distance and brood survival has often been reported for ducks (Ball et al. 1975, Ringelman and Longcore 1982, Leonard et al. 1996) and other precocial birds (Erikstad 1985, Blomqvist and Johansson 1995). Increased mortality during brood movements may occur because individuals must cross unfamiliar areas or use habitats that lack escape cover against predator attacks. However, Eriksson (1978) suggested that benefits of selecting the best feeding areas for juveniles should outweigh mortality risks associated with movements. Although geese are probably less vulnerable to predation than ducks on land because of their greater adaptations to terrestrial life (Bellrose 1980), little information is available on gosling survival in relation to brood movements.

We examined the influence of movements between nesting and brood-rearing areas on gosling survival and growth in Greater Snow Geese (*Chen caerulescens atlantica*) breeding on Bylot Island in the Canadian High Arctic. At this site, the main brood-rearing area (MBR) lies ~30 km from the main nesting colony (MNC) and many parents move there to rear their brood shortly after hatch, primarily because of the availability of high-quality foraging plants (Massé et al. 2001). High brood-rearing site fidelity of females may further contribute to the high density of broods using the MBR (Mainguy 2003). Small numbers of Greater Snow Geese also nest at low density in the MBR and stay there to rear their brood (Hughes et al. 1994b, Lepage et al. 1996). This situation provided an opportunity to assess the potential costs of long-distance movements by comparing birds using different nesting and brood-rearing areas.

Our specific objectives were (1) to describe movements of radiomarked females that used areas distant from their nest site to rear their brood and (2) to examine whether distance moved was negatively associated with gosling survival. Finally, we tested whether movements to distant brood-rearing areas influenced growth by comparing this parameter among goslings that (1) hatched at MNC and stayed there, (2) hatched at MNC and moved a long distance to MBR, or (3) hatched at MBR and stayed there.

METHODS

Study area.—We conducted our study on the southwest plain of Bylot Island, Sirmilik National Park, Nunavut, Canada (73°N, 80°W), the most important breeding site for Greater Snow Geese (>20,000 pairs, ~15% of the world breeding population; Reed et al. 2002). Data were collected at three sites (Fig. 1). The MBR was a large glacial valley (2–5 km wide, ~50 km^2) bordered by steep hills to the north and southeast. This site was a good brood-rearing area because of the high density of wetlands (Hughes et al. 1994a). Some pairs (up to a few hundred) also nested there in most years (Lepage et al. 1996). Several thousand birds nested every year at the MNC (average annual nest density: 4–7 nests ha^{-1}), which was located ~30 km south of the MBR (Bêty et al. 2001). The MNC covered ~38 km^2 around a narrow valley (0.5 km wide) with some wetlands surrounded by low hills with gentle slopes. Some broods also used this site during the rearing period. Finally, a transit area (TA) covered ~10 km^2 and was used by Greater Snow Geese moving from the MNC to the MBR. The TA was centered on a narrow valley (0.3 km wide) with wetlands to the south, bordered by hills from the northeast to the southeast and by the seashore to the west. Very few birds nested in this area, though some reared their brood there throughout the whole brood-rearing period (see Fig. 1). Upland habitat dominated by mesic tundra and with very few, widely scattered wetlands and predator-safe areas such as lakes or ponds (Hughes et al. 1994b, Duclos 2002) was the most common habitat found between the three study sites (Massé et al. 2001).

Brood movements.—Females were marked with radiotransmitters affixed to neck collars (two-year life expectancy; total weight: 59 ± 9 g, <3% of bird's body mass) as part of a larger investigation on Greater Snow Goose migration in 1996–1999. These birds were caught in small banding drives of a few families at a time at the MBR in August (see Demers et al. 2003). In 1997–2001, we searched for nests of these females through radiotracking by helicopter and on the ground between late May and early July (see Mainguy et al. 2002). In 2000–2001, we also captured nesting females already marked with conventional neck bands just before hatching, using bow traps at the MNC, and changed their neck band for a radiotransmitter affixed to a new neck collar (see Reed et al. 2003). Because we were interested in females' movements from their nest to distant brood-rearing areas, we targeted females that had been marked in previous years at the MBR (see below). Goslings of radiomarked females were web-tagged at hatch.

To describe brood movements, we radiotracked females by helicopter every 1–3 days from 16 to 20 July 2000 and from 11 to 23 July 2001 during their movements to rearing areas.

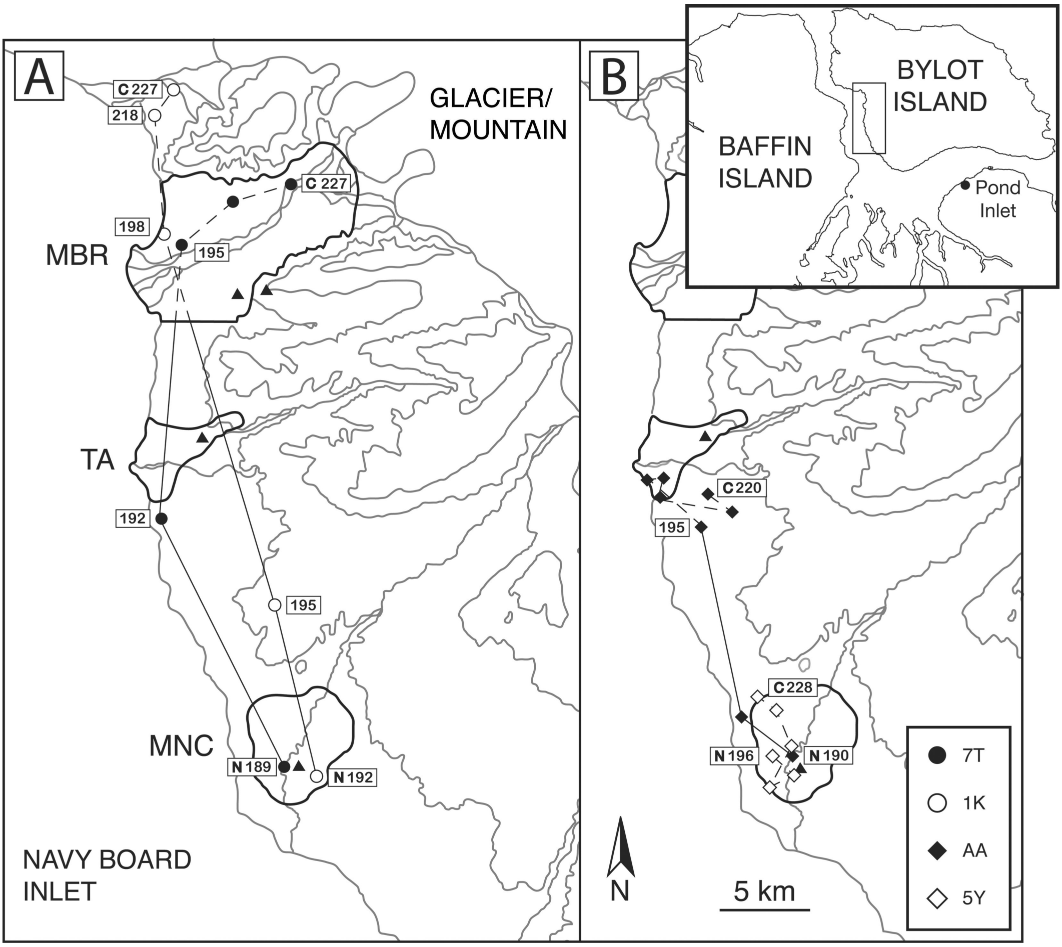

FIG. 1. Location of the three study sites (thick solid lines) on Bylot Island, Nunavut, Canada, with examples of radiotracked Greater Snow Goose females (neck-collar codes are shown in legend) moving from the main nesting colony (MNC) to the main brood-rearing area (MBR; map A), the transit area (TA; map B), or staying at the MNC (map B). Successive positions determined from aerial tracking between the nest (N) and capture-site near fledging (C) are linked. Numbers indicate Julian dates (1 = 1 January) associated with nest departure, capture, and some intermediate positions. Thin solid lines represent between-area movements (i.e., movement between nest and brood-rearing sites), whereas dashed lines represent within-area movements (i.e., movements within the brood-rearing area; see text). Ground receiving stations (triangles) are shown for each study site.

Females were spotted with binoculars from the air, and their brood size was determined when possible. We recorded their positions with a global positioning system (GPS) receiver, though the helicopter sometimes caused displacement of broods (≤200 m). Ground radiotracking was done from elevated blinds every 1–3 days until banding in August at the MNC and daily at the MBR during hatch and shortly after (1997–2001). This allowed us to determine departure date from the MNC and arrival date at the MBR. We individually recaptured radiomarked females still accompanied by young in mid-August 2000–2001 if they were not caught during banding (see below). All radiomarked females monitored in 1997–1999 were also recaptured in August, but presence of their young was not always determined; thus, those years were excluded from survival analyses, but were used in movement and growth analyses.

We determined distance moved between successive aerial locations (including the nest site and capture site during banding in August) in 2000–2001. We divided brood movements into two categories: (1) movements from the nest to the rearing area (i.e., "between-area") for those that changed area (Fig. 1) and (2) those within the brood-rearing area (i.e., "within-area"). This was established by plotting individual travel routes and determining when broods switched from clearly directional movements between successive locations to local movements without clear orientation or when families stayed in the same brood-rearing area (regardless of the site selected) for >10 days, judging from ground-tracking (Fig. 1). For females moving to the MBR, the southern limit of that study area was used to determine the end of the between-area movement. This limit corresponded approximately to the detection range of the ground-receiving stations. The length of between-area movement was the straight-line distance between the nest site and the first location in the brood-rearing area; the length of within-area movement was the longest distance between any pairs of locations once birds were settled on a brood-rearing area. We calculated minimum travel speed (m h^{-1}) between successive locations spaced in time by ≤72 h. Travel speed underestimates the walking speed, because the actual route followed by broods is not necessarily linear and broods do not walk all the time (Mainguy 2003). We also calculated total movement (i.e., distance moved in a straight line between the nest and capture sites) for all radiomarked females in 1997–2001.

Gosling survival.—We first compared gosling survival between years 2000 and 2001 in radiotracked families following the procedure of Rockwell et al. (1993). Briefly, the proportion (*P*) of hatched young surviving until recapture in August was calculated for each female by the ratio of brood size near fledging to goslings leaving the nest (BSF:GLN), and then averaged across all females. This calculation included females that lost all their young. We then calculated the expected value (*E*) of BSF for each individual *i* as

$$E(\mathrm{BSF})_i = \mathrm{GLN}_i \times \overline{P} \qquad (1)$$

and

$$DevP_i = \mathrm{BSF}_i - E(\mathrm{BSF})_i \qquad (2)$$

We used the deviation in *P* (*DevP*) when comparing years, because this metric is not brood-size dependent like *P* (see Rockwell et al. 1993). We then tested, in a second analysis, for a possible correlation of total movement on gosling survival (*DevP*). A significant relationship between *DevP* and total movement would indicate rejection of the hypothesis that survival (i.e., *P*) does not depend on distance moved between nesting and brood-rearing areas.

Gosling growth.—We searched for Greater Snow Goose nests (marked and unmarked birds) during laying and early incubation at the MBR and MNC in 1992–2001 (see Bêty et al. [2001] for details) and marked newly hatched goslings with uniquely numbered web-tags (Lepage et al. 1998). About five weeks later, families were captured in mass banding drives during a seven-day period in mid-August when adults were molting and before the young could fly. Captures occurred at the MBR in all years, but only in 1992 and 2001 at the MNC. All captured birds were sexed by cloacal examination and leg-banded. A sample of adult females also received neck collars each year (see Menu et al. [2000] for details). Goslings were measured (culmen, head, tarsus) with a caliper (to within 0.1 mm), weighed to the nearest 25 g (nearest gram in 1995–2001), and checked for the presence of web-tags.

We compared growth of goslings that stayed near their nesting area and those that moved to a distant rearing area using web-tagged goslings recaptured at banding. Unfortunately, we were unable to conduct all possible comparisons in the same years, because of variations in sampling effort and nesting goose density (i.e., reproductive effort) at both sites. The comparison between goslings that hatched at the MNC and moved to the MBR with those that hatched and stayed at the MNC could be made in 1992 and 2001 only. Similarly, the comparison between goslings that hatched and stayed at the MBR and those that hatched at the MNC and moved to the MBR could be made only in 1996 and 2000. Web-tagged goslings of radiomarked females were also used in growth analyses.

Statistical analyses.—All statistical tests were performed with SAS, version 8.0 (SAS Institute 1999). We used one-way analysis of variance (ANOVA) to compare distance traveled, speed, duration, and gosling survival (*DevP*) of individual broods among years or brood-rearing areas.

We used a paired *t*-test to compare travel speed according to type of movements (between- or within-area) using females for which we had both measures. We used Pearson's correlation test to assess whether *DevP* was related to total movement. For all analyses, radiomarked females nesting in more than one year were included only in their first year of successful nesting to avoid pseudoreplication.

We analyzed gosling growth for each year separately because of large annual variation (Lepage et al. 1998). Our sampling unit was brood mean (range: 1–5 goslings per brood) to ensure independence of our data. We used an index of body size derived from a principal component analysis (PCA) of head, culmen, and tarsus length based on all recaptured goslings (Lepage et al. 1998). The first principal component (PC1) explained >74% of the total variance, and weightings were similar for the three morphometric measurements. We compared body size (i.e., PC1 scores) and body mass of goslings hatched or captured in different areas (depending on year) with analyses of covariance (ANCOVAs) using gosling age as covariate. Because hatch date is known to affect gosling growth (Sedinger and Flint 1991, Lindholm et al. 1994, Lepage et al. 1998), we included it as a second covariate expressed as Julian date (1 = 1 January). However, because hatch date was negatively correlated with gosling age at capture ($-0.72 < r < -0.54$; all $P < 0.001$), we used the residuals of the regression of hatch date on age in our models as an age-independent measure of hatch date (hereafter called simply "hatch date") to avoid multicollinearity problems. Because we used brood means, we could not include the variable "sex" in our analyses. However, sex ratio did not differ from unity in all years and sites. Furthermore, Lepage et al. (1998) found little effect of sex on growth at our study area in goslings 35 days old. For model selection, a saturated model including second-order interactions and main effects was explored. Using a backward procedure, fitted variables and their interactions were dropped manually at $P > 0.10$. Finally, distance moved (i.e., total movement) by web-tagged goslings was compared between sites or years using one-way ANOVA.

Statistical tests were two-tailed, and inspection of residuals indicated no violation of the assumptions of normality and homogeneity of variance (except for minimal travel speeds, which were ln-transformed prior to analyses to meet assumptions). Results are presented as means ± SE.

Results

Brood movements.—Among 305 females radiomarked in 1996–1999, 52 were subsequently found nesting in 1997–2001. In most years, the low number of radiomarked females found nesting was attributable to the implementation of a spring conservation harvest, which negatively affected accumulation of body reserves on the staging areas (Féret et al. 2003) and significantly reduced breeding propensity (Mainguy et al. 2002, Reed et al. 2004). All these females but one nested at the MNC. In addition, 12 females were radiomarked on nests at the MNC in 2000, and 21 in 2001. After excluding the second attempt of females that we found nesting in more than one year ($n = 6$), the total sample was reduced to 79, of which 51 produced broods.

Forty-one radiomarked females were recaptured or resighted at the end of the summer. Females not found at banding either had left Bylot Island to molt following an early brood loss ($n = 4$; Reed et al. 2003), died during brood rearing ($n = 4$), or had a known radio failure ($n = 2$). At recapture, 27 females (66%) were located in or around the MBR; 8 (19%) were between the MNC and MBR, including 5 at or near the TA; 4 (10%) stayed at or near the MNC; and 2 (5%) moved elsewhere on the island (inland toward the glaciers or south of the MNC).

All measures of brood movements (length, speed, and duration) did not differ among years (all $P > 0.19$) and were thus pooled. Total movement by females tracked in 1997–2001 averaged 25.6 ± 1.7 km ($n = 41$) and varied considerably among individuals (range: 2.6–52.5 km), depending on the area selected by females to rear their brood (Table 1). The bulk of total movement by females was accounted for by the distance traveled during between-area movements shortly after hatch (in 2000–2001, 22.8 ± 1.5 km out of a total movement of 24.9 ± 2.2; $n = 22$). Once broods had settled on a rearing site, within-area movements (i.e., the longest distance between any pair of locations) were smaller than between-area movements (6.6 ± 0.8 vs. 24.7 ± 1.3 km, respectively; $n = 20$ birds for which we had both measures) and did not differ among birds that

TABLE 1. Characteristics of movements of radiomarked Greater Snow Goose females between the main nesting colony and different brood-rearing areas on Bylot Island, Nunavut, Canada, 2000–2001 (means ± SE; sample sizes in parentheses).

	Brood-rearing area		
	Main brood-rearing area (MBR)	Transit area (TA)	Main nesting colony (MNC)
Total movement (km) [a]	32.3 ± 1.2 (27)	15.2 ± 1.4 (8)	5.5 ± 1.0 (4)
Between-area movements [b]			
Distance (km)	27.9 ± 0.7 (13)	17.1 ± 1.2 (6)	NA [c]
Travel speed (m h^{-1})	218.0 ± 13.0 (14)	164.0 ± 30.0 (6)	NA [c]
Within-area movements [d]			
Distance (km)	7.0 ± 1.0 (14)	5.5 ± 1.0 (6)	2.8 (1)
Travel speed (m h^{-1})	37.0 ± 7.0 (7)	23.0 ± 7.0 (5)	20 ± 7.0 (2)

[a] Distance in a straight line between the nest and capture sites in August. Also includes data from 1997–1999.

[b] Distance in a straight line between the nest and first location in the brood-rearing area.

[c] These birds stayed in the same area to rear their brood; hence, there are no between-area movements.

[d] Longest distance in a straight line between any pairs of locations once settled on a brood-rearing area.

used different brood-rearing areas (*F* = 0.77, df = 1 and 17, *P* = 0.39; Table 1). Minimal travel speed during between-area movements was greatest for Greater Snow Geese that moved the farthest (MBR; *F* = 5.96, df = 1 and 19, *P* = 0.025; Table 1). Minimal travel speed during within-area movements was much slower than that during between-area movements (30 ± 5 vs. 191 ± 13 m h^{-1}, respectively; paired *t* = –8.23, df = 12, *P* < 0.001) and did not differ among areas (*F* = 2.74, df = 1 and 11, *P* = 0.13; Table 1). Duration of between-area movements was available only for individuals that moved to the MBR and was fairly short (5.8 ± 0.5 days; *n* = 32). Total movement was not correlated with hatch date (*r* = –0.14, *P* = 0.37, *n* = 41).

Gosling survival.—Gosling survival of radiomarked females was higher in 2000 than in 2001 (BSF/GLN pooled across females: 83% [*n* = 18 goslings leaving the nest] vs. 45% [*n* = 49], respectively) according to a comparison based on *DevP* (*F* = 6.47, df = 1 and 19, *P* = 0.02). Gosling survival was not correlated with total movement in 2000–2001 (*n* = 21 broods; Fig. 2).

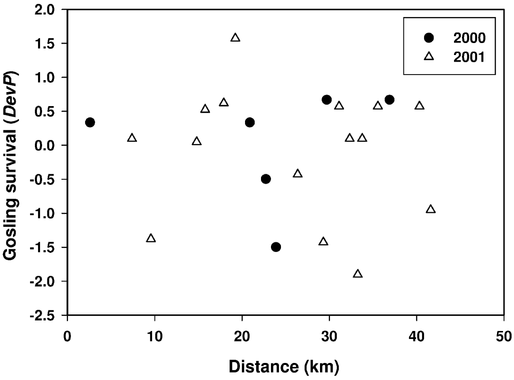

FIG. 2. Relationship between gosling survival (*DevP*, expressed as deviations from expected value; see text) and total movement (i.e., distance moved between the nest and brood-rearing areas) for radiomarked females in 2000–2001 (*r* = –0.06, *P* = 0.78, *n* = 21).

Gosling growth.—In 1992, 1996, 2000, and 2001, a total of 5,801 goslings was web-tagged (annual range: 289–1,860) and 427 goslings from 211 broods were recaptured near fledging (annual range: 44–155 goslings from 28–74 broods). Goslings recaptured in 1996 and 2000 were of the same age (31.1 ± 0.2 days old), whereas those recaptured in 1992 were slightly younger (29.2 ± 0.6 days old) and those in 2001 were older (35.1 ± 0.3 days old). In all analyses, two-way interactions between site, age, and hatch date were not present (all *P* > 0.11) and were thus deleted from the models, except for an interaction between age and hatch date (*P* = 0.004) for body mass in 1996. The covariate age always contributed to the model (all *P* < 0.001), whereas the covariate hatch date was retained in models for 1996 and 2000 (all *P* < 0.06) but deleted for 1992 and 2001 (all *P* > 0.29).

In 1992, goslings that hatched at the MNC and recaptured at the MBR were heavier and larger than those that stayed at the MNC (mass: *F* = 15.3, df = 1 and 25, *P* < 0.001; size: *F* = 3.86, df = 1 and 25, *P* = 0.06) but not in 2001 (mass: *F* = 0.00, df = 1 and 56, *P* = 0.98; size: *F* = 0.50, df = 1 and 56, *P* = 0.48; Fig. 3). However, the total movement of goslings differed between 1992 and 2001 according to rearing area used (*F* = 4.53, df = 1 and 41, *P* = 0.04). Although broods hatched at the MNC had moved a similar distance to reach the MBR in both years (1992: 32.1 ± 0.8 km, *n* = 9 broods; 2001: 32.4 ± 0.8 km, *n* = 17), those that stayed near the MNC after hatch had moved a greater distance in 2001 than in 1992 (11.7 ± 2.2 km [*n* = 3] vs. 4.9 ± 0.5 km [*n* = 15], respectively).

Goslings that hatched and were reared at the MBR were heavier (in 1996 only; 1996: *F* = 4.61, df = 1 and 45, *P* = 0.04; 2000: *F* = 1.72, df = 1 and 71, *P* = 0.19) and larger (1996: *F* = 5.86, df = 1 and 46, *P* = 0.02; 2000: *F* = 4.37, df = 1 and 70, *P* = 0.04) than those that hatched at the MNC and moved to the MBR (Fig. 4). Total movement by goslings was similar between 1996 and 2000 according to nesting area used (*F* = 0.23, df = 1 and 55, *P* = 0.64). Those that hatched and were reared at the MBR had moved a distance of 2.9 ± 0.3 km (*n* = 34 broods), whereas those that hatched at the MNC and were reared at the MBR had moved a far greater distance (29.8 ± 0.6 km, *n* = 24).

DISCUSSION

Brood movements to foraging sites are common in precocial birds and can entail fitness costs and benefits. In Greater Snow Geese, we found that most birds using the MNC on Bylot Island moved to distant areas (e.g., MBR) to rear their brood. These movements could reach ≥30 km, occurred shortly after hatch, and were generally completed within a week. Despite the young age of goslings, our results show that families can move a considerable distance to reach specific feeding areas very early during the brood-rearing period. Similar post-hatch movements have been reported in other geese (Cooch et al. 1993, Sedinger et al. 2001). However, we found considerable variation among individuals; some females reared their young very close

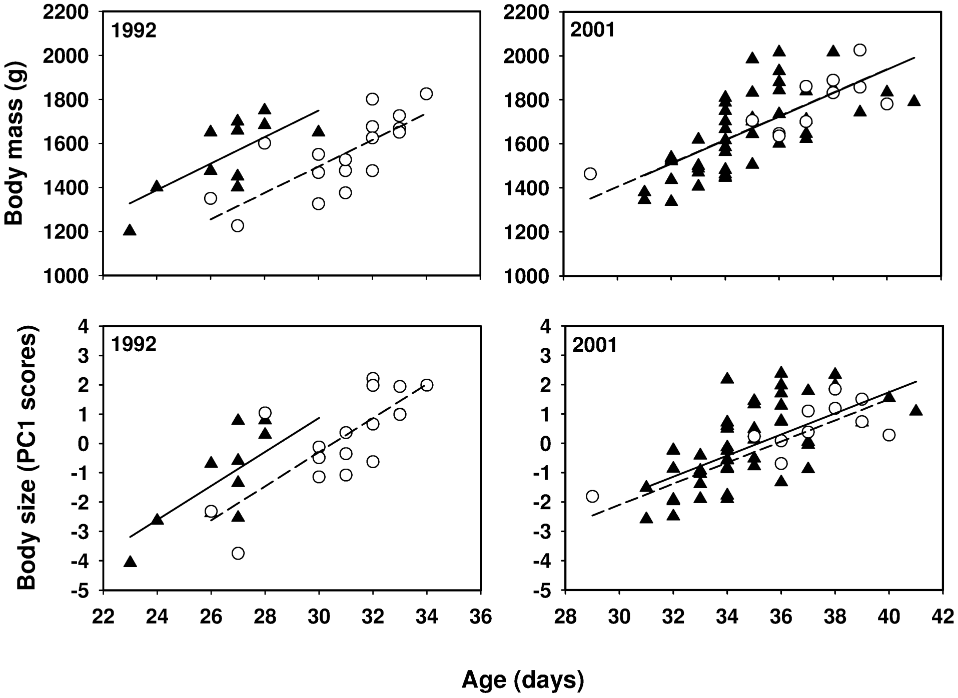

FIG. 3. Relationship between body mass (g) or body size (PC1 scores; see text) and age of goslings according to the brood-rearing area used, main brood-rearing area (MBR; filled triangles, solid line) or main nesting colony (MNC; open circles, dashed line), in 1992 and 2001. All goslings hatched at the MNC.

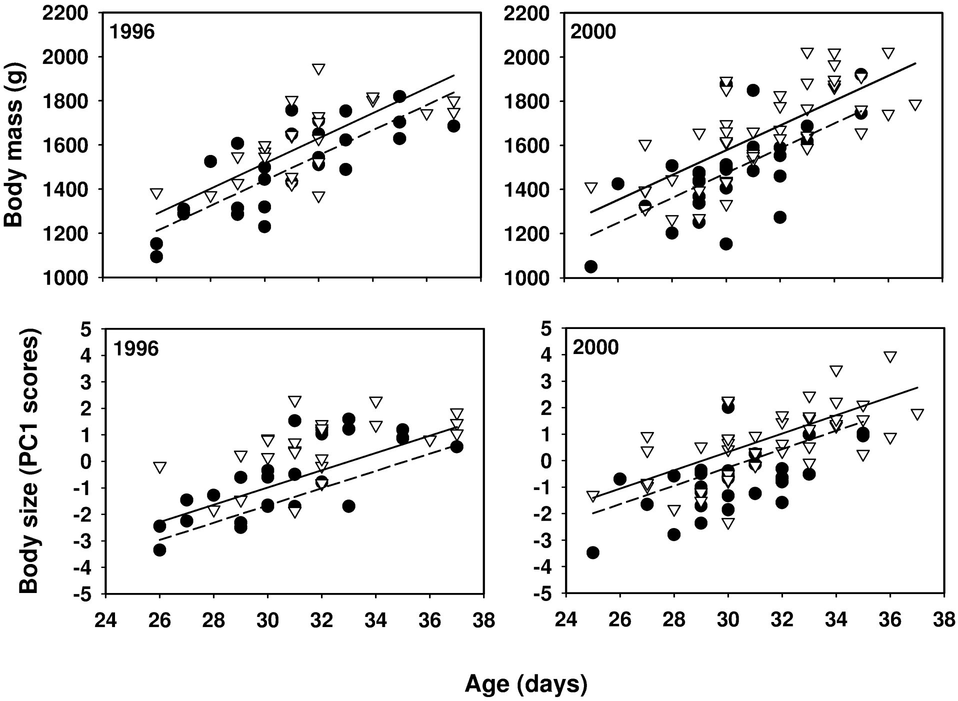

FIG. 4. Relationship between body mass (g) or body size (PC1 scores; see text) and age of gosling reared at the main brood-rearing area (MBR) according to the nesting area used, the MBR (open triangles, solid line) or the main nesting colony (MNC; filled circles, dashed line), in 1996 and 2000.

to their nesting area. Once settled on a rearing site, Greater Snow Goose broods tended to stay within a restricted area, as reported in Lesser Snow Geese (*C. c. caerulescens*; Healey et al. 1980), Barnacle Geese (*Branta leucopsis*; Larsson and Forslund 1991), and Black Brant (*B. bernicla nigricans*; Lindberg et al. 1998). Overall brood movements within the rearing area (i.e., maximal distance between any pairs of locations) were of the same magnitude (~5 km) as those described by Hughes et al. (1994b) for this population, and the length and speed of these movements were independent of the distance traveled before settling. One should remember that within-area movement length does not take into account all the distance covered by broods but rather provides an index of their home-range size once on their rearing area.

Mortality observed in 2000–2001 during brood rearing was relatively high and variable between years, but nonetheless comparable to that found in other goose species (Flint et al. 1995, Schmutz et al. 2001). We found no evidence for survival costs associated with distance moved shortly after hatch as found in other precocial species, especially ducks (Ball et al. 1975, Blomqvist and Johansson 1995, Leonard et al. 1996). It is likely that geese are less vulnerable to predation during overland movements when compared to ducks because of their greater adaptation to terrestrial environment, biparental care, large body size, and strong defense behavior when broods are attacked by predators. However, movements between the nest and brood-rearing areas occurred during the first week after hatch, whereas our recaptures were made five weeks later. Thus, other factors than distance moved may have influenced gosling survival during the subsequent four-week period, and this may have masked any potential effect of early long-distance movement on survival. Exclusion of three females in 2000–2001 that either left the island after experiencing an early brood loss or died during brood rearing may also have limited our capacity to fully evaluate the costs associated with brood movements.

In contrast to survival, the rearing area used and whether or not families had to travel a long distance to reach this area influenced gosling growth. Parents that left the MNC to settle at the distant MBR reared heavier goslings than those that stayed at the colony after hatch in one out of two years. The MBR has the highest density of wetlands on the island, and thus provides high-quality habitat for broods (Hughes et al. 1994a, Massé et al. 2001). In Ross's Geese (*C. rossii*), Slattery (2000) showed that goslings from broods that moved the farthest from a dense nesting colony were the largest and heaviest. Similarly, Lesser Snow Goose goslings that dispersed to alternate rearing areas showed better growth than those remaining on the traditional feeding areas, which had been severely degraded by overgrazing (Cooch et al. 1993, Williams et al. 1993). Greater Snow Goose density on Bylot Island is relatively high (Massé et al. 2001), and grazing by Greater Snow Geese reduces standing crop and plant production (Gauthier et al. 1995, 2004). Therefore, broods staying at or near the nesting colony may be at a disadvantage compared with those moving out to rear their brood because of the high density of geese nesting there (several thousand; Bêty et al. 2001) in relation to the biomass of forage plants available (Massé et al. 2001). In many goose species, including Greater Snow Geese, there is a direct link between feeding conditions encountered by growing goslings and body mass at fledging (Aubin et al. 1993, Cooch et al. 1993, Lindholm et al. 1994, Lepage et al. 1998, Sedinger et al. 2001, Hill et al. 2003). The absence of difference in growth between goslings recaptured at the MBR or at the MNC in 2001 may be a consequence of the higher goose density at the MNC in that year as compared with 1992 (G. Gauthier unpubl. data), which may explain why families moved farther from the center of the MNC in 2001. Such movements may have allowed goslings access to feeding sites of quality comparable to those fed on by goslings that moved to the distant MBR.

Although goslings accrued some benefits by leaving the nesting colony, we nonetheless found that they had reduced growth in terms of body mass and size compared with those hatched directly at the distant brood-rearing area. This indicates that long-distance movements may entail some costs. Goslings hatched at the MBR had immediate access to high-quality forage plants in the extensive wetlands present there (Hughes et al. 1994a), whereas those hatched at the MNC had to make long overland movements to reach the site. In addition to the potential energetic cost of walking ≥30 km, they had to cross extensive areas of upland habitat where food abundance and quality are lower than in wetland habitat, particularly at this time of year (Hughes et al. 1994a, Massé et al. 2001, Duclos 2002, Mainguy 2003). In turn, this would lower the quality of their food intake during part of their between-area movements, though these movements occurred in the first days of life, when yolk reserves still provide part of the energy required by young (Ankney 1980). Furthermore, by settling first in the best habitats, birds nesting at or near the MBR may have reduced access to these habitats for birds arriving later from distant nesting areas (Prop et al. 1984, Hughes et al. 1994b, Stahl et al. 2001). Thus, improved access to high-quality food may explain the improved growth of goslings hatched at the MBR compared with those moving from distant nesting areas. However, a limitation of our study is that we were unable to compare the three scenarios (i.e., hatching at the colony and staying there, hatching at the colony and moving to a distant brood-rearing area, or hatching at a good brood-rearing area and staying there) in the same years.

Rapid growth and large body mass at fledging are important for goslings growing in the Arctic. Indeed, survival of goslings during fall migration is often related to body mass at fledging (Owen and Black 1989, Schmutz 1993, van der Jeugd and Larsson 1998, Cooch 2002, Menu et al. 2005). Therefore, variations in growth related to the selection of different nesting and brood-rearing areas may have significant fitness consequences for goslings.

In conclusion, we showed that long-distance brood movements are common in Greater Snow Geese. Movements had no negative effects on gosling prefledging survival, but, along with the area used for brood rearing, they apparently affected their growth. Goslings moving to distant, high-quality brood-rearing areas tended to have a better growth rate than those that stayed at the main nesting colony, but they nonetheless had reduced growth compared with broods that hatched directly at the high-quality brood-rearing areas and avoided long-distance movements. Although brood movements allowed goslings access to good foraging sites, they entailed some costs.

Thus, it is advantageous to locate nest sites as close as possible to good brood-rearing areas to minimize such movements and, ultimately, maximize gosling growth.

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