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ORIGINAL ARTICLE

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Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*)

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Abstract Decisions made by birds during migration to breeding grounds can strongly affect the fitness of individuals. We investigated possible causes and reproductive consequences of inter-individual variation in the migratory behavior of an arctic-nesting species, the greater snow goose (*Anser caerulescens atlanticus*), by radio-tracking females at their staging area and on their breeding grounds. Females showed relatively high repeatability in the duration of migration (r_i=0.37) and arrival date on the breeding grounds (r_i=0.42) suggesting that these traits are characteristics of individuals. Conversely, no individual consistency in departure date from the staging area was detected (r_i=–0.02) indicating that environmental factors may have a large influence. Females paired with dominant males departed slightly earlier from the staging area than females accompanied by subordinate males. However, neither social status on the staging area (i.e. paired vs unpaired) nor dominance scores were associated with arrival time of individuals. Finally, the probability of breeding was positively related to arrival date indicating a reproductive cost of arriving too early on the breeding grounds. The combination of breeding probability and seasonal decline in breeding success nonetheless suggests that females arriving a few days earlier than the median arrival date attained highest reproductive success. Our results show that assessing the fitness consequences of early arrival by focusing solely on breeding females would lead to an overestimation of the genuine benefits. This study also indicates possible genetically based differences among individuals in migration duration and arrival time on the breeding grounds.

Keywords Arctic · Bird · Dominance · Migration · Repeatability

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Introduction

Although natural selection acts on individuals throughout their annual cycle, our understanding of the ecology and evolution of migrating organisms has been limited by our inability to follow individuals year round (Webster et al. 2002). In many bird species, migration is a major part of their life history and decisions made during migration from the wintering to the breeding grounds can have major effects on the reproductive success and survival, and hence the fitness of individuals (Møller 1994; Brown and Brown 2000; Berthold 2001).

Some theoretical models now integrate prebreeding migratory behavior as part of the overall reproductive strategy in birds (e.g., Rowe et al. 1994; Kokko 1999; Bêty et al. 2003). Optimization models of avian migration show that the shape of the relationship between arrival date on the breeding grounds and the expected reproductive success can strongly influence the migratory behavior of individuals (Weber et al. 1998, 1999). However, there is still little empirical data on the fitness costs and benefits of different migratory decisions in birds, especially in females (Brown and Brown 2000; Drent et al. 2003; Prop et al. 2003). Moreover, factors responsible for individual variation in the timing of migration are still poorly known.

Long-distance bird migration often consists of a series of long-distance flights separated by stopover periods during which nutrient reserves are accumulated. Environmental conditions (e.g., food supply, weather conditions) and intrinsic characteristics (e.g., body size, foraging efficiency) can influence the rate of nutrient acquisition at each staging site and migratory decisions of individuals (Weber et al. 1998; Drent et al. 2003; Prop et al. 2003). Pairing and dominance status of individuals affect foraging rate in several birds (McLandress and Raveling 1981; Ens and Goss-Custard 1984; Stahl et al. 2001) and, consequently, could affect the optimal timing of migration.

Climatic changes can influence the costs and benefits associated with the timing of migration (Both and Visser 2001). Predicting the consequences of climate changes for migratory birds is difficult as the environment can change at different speeds or in different directions along the migratory routes (Coppack and Both 2002; Strode 2003). In order to evaluate the potential for adaptive evolution of the timing of migration to recent and future climatic changes, it is crucial to examine whether genetically based differences exist among individuals (Berteaux et al. 2004).

We investigated intraspecific variation in the migratory behavior of a long-distance migrant, the greater snow goose (*Anser caerulescens atlanticus*), by radio-tracking females at their main spring staging area and on their breeding grounds, 3,000 km further north. Prior to their northward migration to the Arctic, greater snow geese accumulate large amounts of fat and protein on their staging area (Gauthier et al. 1984a, 1984b, 1992). Up to 50% of these reserves are used during migration and the rest used for egg production and incubation (Gauthier et al. 1992, 2003; Reed et al. 1995). The timing of breeding is crucial in this species due to a steep seasonal decline in reproductive success caused by environmental factors, mostly food supply (Lepage et al. 1998, 1999, 2000).

In previous analyses, we found no evidence that the timing of migration of female greater snow geese was related to their premigration body condition (fat reserves; Bêty et al. 2003). However, individuals arriving first on the breeding grounds initiated their nests earlier than late arriving ones and birds in better premigration condition nested earlier than those in poorer condition independently of their arrival date (Bêty et al. 2003). Females nesting early achieve a higher reproductive success than those nesting late (Lepage et al. 2000). In this paper, we first examined the repeatability in the migratory behavior of individuals. Then, we investigated the association among social status (i.e. paired or unpaired), dominance status, migratory pattern and probability of breeding (i.e. laying eggs). Finally, we estimated the reproductive consequences of arrival date. The originality of this study was our ability to follow the behavior of the same individuals on their staging area and distant breeding grounds for more than 1 year in order to investigate potential causes and fitness consequences of variation in migratory behavior.

Materials and methods

Study species

Greater snow geese winter along the Atlantic coast of the USA, stage along the St. Lawrence River in Quebec, Canada, during their spring and fall migration, and breed in the eastern high Arctic of Canada (Fig. 1). The whole population stops in Quebec in spring, the first birds arriving by mid-March and the last ones leaving by the end of May (Reed et al. 1998). Most geese reach their arctic breeding grounds in early June (Bêty et al. 2003).

Radio-tracking

We captured greater snow goose families on the breeding grounds during their molting period in August at the Bylot Island migratory bird sanctuary (73°08′N, 80°00′W; Fig. 1), Sirmilik National Park, Nunavut Territory, Canada (see Demers et al. 2003 for details on methods). Captures occurred after non- and failed-breeders had regained flight capabilities (Reed et al. 2003a). All adults captured were thus at least 2-year old or more, because snow geese do not breed as yearlings and few do so at two years of age (Reed et al. 2003b). From 1996 to 1998, we fitted 210 adult females with radio transmitters affixed to a neck collar engraved with 2-alphanumeric codes (total weight 60±7 g, 2.5±0.4% of bird body mass; mean±SD) (Demers et al. 2003). Longevity of radios was 16–24 months. We also recaptured 19 of the 210 birds and replaced their radio 1 or 2 years after the initial tagging allowing us to track

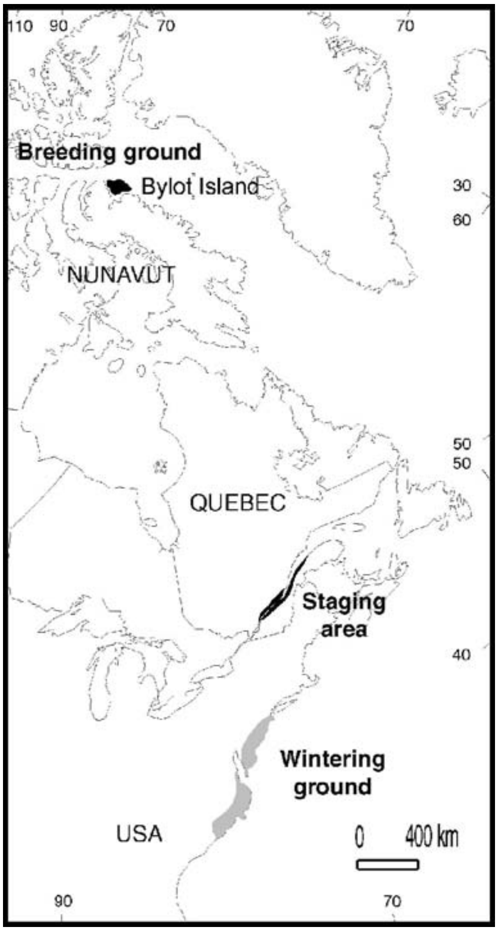

Fig. 1 Main wintering, staging and breeding areas of greater snow geese (*Anser caerulescens atlanticus*)

some individuals up to 3 years. Males associated with radio tagged females were marked with conventional yellow plastic neck collars (Demers et al. 2003). All captured birds were also banded with standard U.S. Fish and Wildlife Service metal leg bands.

From 1997 to 1999, we radio-tracked geese on their main spring staging area in Quebec and on their breeding ground on Bylot Island (Fig. 1). From the end of March to the departure of the last radio-marked birds at the end of May, five or six crews tracked birds on the staging area daily using vehicle-mounted receiving systems (Béchet et al. 2003). Aerial tracking by plane was also conducted every week. On the breeding grounds, we tracked birds during the prelaying, laying and early incubation periods (27 May to 20 June) at two nesting areas located 30 km apart on Bylot Island (see Bêty et al. 2001 for description of these areas). We conducted tracking sessions every 1 or 2 days 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; 27 May to 10 June). Finally, aerial tracking by helicopter was conducted every week over the south plain of Bylot Island (ca. 1,600 km^2) starting in early June. On the staging area, the range of transmitters 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.

Radio-collars modified the behavior of females (e.g. more time spent in comfort activities) during the first 2–3 months after marking and promoted separation from the original mate in some birds (Demers et al. 2003). However, transmitters had no significant effect on the behavior of females during the spring following marking (i.e. 8–9 months later), but nonetheless negatively affected some reproductive parameters probably due to a higher energetic cost of migration (slight delay in laying date and decrease in clutch size; Bêty et al. 2003; Demers et al. 2003). We assumed that these effects were similar across marked females and that transmitters did not bias comparisons among them or the repeatability of the spring migratory behavior at the individual level.

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 ground. The probability of missing an individual for two consecutive days was estimated at 4% on average on both the staging area and breeding ground (Bêty et al. 2003). Consequently, we are confident that our observations provided reliable estimates of individual departure and arrival dates. Migration duration of an individual was defined as the difference between its arrival and departure dates.

Social status, dominance score and breeding parameters

The social status (i.e. paired or unpaired) of marked females was determined each time they were observed during the spring staging period (see Demers et al. 2003 for details). We also recorded all aggressive interactions of marked females or their mate with unmarked individuals during observation bouts (mean duration ±SD: 45±40, 46±39 and 48±39 min, respectively in 1997, *n*=203, 1998, *n*=204, and 1999, *n*=96 bouts). Due to large flock size, no interaction among marked birds was observed. An interaction was defined as any direct confrontation between two birds, ranging from threats with lowered head and neck to active chases with flapping wings (Stahl et al. 2001). We considered an agonistic interaction as being won by an individual when the opponent turned and walked away. We calculated an individual dominance score as the number of interactions won by a focal bird divided by the total number of interactions in which the bird was involved multiplied by 100 to express it as a percentage (Lamprecht 1986). This approach has been successfully used in wild flocking birds such as oystercatchers (*Haematopus ostralegus*) (Ens and Goss-Custard 1984) and barnacle geese (*Branta leucopsis*) (Stahl et al. 2001). We calculated a dominance score for individuals involved in a minimum of ten interactions. This specific number was chosen because scores of individuals remained fairly constant above this threshold (J. Bêty, unpublished data).

Nests of radio-marked birds were found by extensive searches conducted mainly during the laying and early incubation periods on the breeding grounds. We categorized females as breeders (i.e. nest found) or non-breeders (i.e. no nest found). We are confident that we did not miss any nests of incubating females. However, we cannot exclude the possibility that some females classified as non-breeders may have initiated a nest, but lost it (due to predation) or abandoned it during the laying period. Snow geese are not known to renest after clutch failure (Lepage et al. 2000).

Radio-marked greater snow geese were faithful to their general spring staging and breeding areas (Mainguy et al. 2002). Females that nested successfully remained on Bylot Island throughout the summer, but virtually all non-breeding or failed-nesting females present in spring left the island after a few weeks for unknown molting areas (Reed et al. 2003a). Most females that did not complete their spring migration to the breeding ground were subsequently detected on the fall or spring staging area (Mainguy et al. 2002). These females apparently skipped breeding and migrated directly to their molting areas (Reed et al. 2003a).

Composite measures of reproductive success

In order to estimate the overall reproductive consequences of arrival date, we used the product of the average breeding probability associated to arrival time and the average breeding success associated to subsequent lay date (as predicted by the arrival date). The relationship between lay date and breeding success (number of young known to survive to the first winter) is based on large sample sizes of unmarked birds monitored over 7 years (1991–1997; Lepage et al. 2000). On the other hand, the relationship between arrival date and laying date was obtained by radio-tracking females on the breeding grounds (1997–1998; Bêty et al. 2003). We are confident that these relationships provide a good index of the average seasonal decline in breeding success and average laying date associated to arrival time of individuals.

Statistical analysis

Analyses were done with SAS version 8 (SAS Institute 1999). To correct for annual variations in the timing of migration due to environmental factors such as climatic conditions, all migratory parameters (i.e. departure date, migration duration and arrival date) were transformed as deviations from the yearly median for analyses.

Repeatability (i.e. the intra-individual correlation coefficient) in departure date, arrival date and migration duration was estimated using variance components calculated from mean square values obtained from one-way ANOVA (Lessells and Boag 1987). As some individuals were tracked for more than 1 year during the study, this may create lack of independence. We therefore used only one observation per individual (first time tracked on staging and breeding areas) to calculate the correlation matrix between dominance scores and migratory parameters (Spearman rank correlation).

To investigate the relationships between social status, dominance score, migratory behavior and breeding probability, we used generalized estimating equations (GEE) with the logit link function (procedure GENMOD of SAS using the statement REPEATED). These analyses consider each individual as statistically independent, but assume that multiple observations of the same individual are correlated (Horton and Lipsitz 1999). As the number of repeated observations per individual was low and unbalanced, we used an exchangeable structure to model the correlation matrix (i.e. matrix with one correlation coefficient for all individuals and repeated measures; Horton and Lipsitz 1999). Score statistics for Type 3 GEE analysis were used to test for the significance of a variable in models with other variables already included. Terms for which score statistics had p>0.05 were dropped sequentially from full models. All models included the variable year and interaction terms (first-order only due to restricted sample sizes). We used a

Table 1 Annual migratory parameters (median) in radio-marked female greater snow geese (*Anser caerulescens atlanticus*) tracked on their main spring staging area (southern Quebec) and breeding grounds (Bylot Island). Ranges are in parentheses

Year	n	Departure date (May)	Migration duration (days)	Arrival date (June)
1997	31	23 (18–26)	18 (9–25)	10 (28[a]–14)
1998	35	15 (12–19)	25 (11–32)	7 (30[a]–13)
1999	9	14 (5–18)	34 (25–45)	18 (10–25)

[a] May

model including departure date, social status and female dominance score to investigate the effect of these variables on the probability of being detected on the breeding ground. Because male and female dominance scores were well correlated (see Table 3 in Results), we pooled the aggressive interactions of marked females and their partners, and assigned a single dominance score to the pair in analyses with paired birds. We used a model including social status on the staging area as an independent factor to compare breeding probability (i.e. confirmed as breeder or not) of paired and unpaired females that completed migration. Finally, a model including departure date, dominance score of the pair and arrival date as independent factors was used to examine the effect of dominance status and migratory behavior on breeding probability of paired females.

Table 2 Repeatabilities (r_i) of departure dates from the main spring staging area, migration duration and arrival dates on the breeding grounds of radio-marked female greater snow geese, 1997–1999

Variable	ANOVA			r_i
	F	df	p	
Departure date	0.95	35.40	0.56	–0.02
Migration duration	2.23	19.21	0.04	0.37
Arrival date	2.52	19.21	0.02	0.42

Results

Repeatability

From 1997 to 1999, 75 individuals were successfully tracked on their main spring staging area and on their breeding ground for at least 1 year (Table 1). Departure date from the staging area was determined in more than 1 year for 36 females (2 years, n=32; 3 years, n=4). Of those females, 19 were tracked for 2 consecutive years on the breeding ground and 1 female over the 3 years of the study. We detected significant repeatability in migration duration and arrival date on the breeding ground, but no individual consistency in departure date from the main staging area (Table 2). Restricting the analysis of repeatability in departure date to females that were subsequently detected on the breeding ground each year gave similar results (r_i=–0.18, $F_{19,21}$=0.69, p=0.79).

Arrival time of individuals on the breeding grounds was strongly correlated with their migration duration but not with their departure date (Table 3). Individual consistency in migration duration indicates that birds that had relatively short migration in one year, and hence arrived relatively early on the breeding grounds, did so in the following years. On the other hand, departure was more synchronized among individuals than arrival time and was weakly correlated with migration duration (Table 2, Table 3). That explains why we can detect individual consistency in migration duration and arrival time but not in departure date.

Individual variations and reproductive consequences

Female snow geese paired with dominant males departed slightly earlier from the staging area than females accompanied by subordinate males (Table 3). However, neither male nor female dominance scores were associated with arrival date on the breeding grounds. Although most birds tracked on the staging areas in 1997 and 1998 successfully completed migration to the breeding ground (89%, n=35, and 77%, n=70, respectively), only 19% of the birds (n=58) succeeded in 1999 (χ^2=12.41, df=2, p=0.002). Mainguy et al (2002) argued that this low success resulted from a large-scale management action (i.e. a spring conservation harvest). Indeed, the new measure led to a considerable increase in the disturbance of geese (Béchet et al. 2003) and to a substantial reduction in the amount of nutrient reserves accumulated in 1999 on the staging area (Féret et al. 2003).

Table 3 Correlation matrix (Spearman correlations) of dominance scores and migratory parameters in radio-marked female greater snow geese (1997–1999). Sample sizes are shown in parentheses. Values of migratory parameters were standardized relative to yearly median. Top right half: paired females only; bottom left half: all females (paired, unpaired and unknown social status)

	Female dominance	Departure date	Migration duration	Arrival date
Male dominance	0.75 (27)***	–0.32 (37)*	0.19 (26)	–0.05 (26)
Female dominance	–	0.14 (35)	–0.10 (28)	–0.10 (28)
Departure date	–0.06 (52)	–	–0.25 (28)	0.20 (28)
Migration duration	–0.01 (40)	–0.35 (75)*	–	0.87 (28)***
Arrival date	–0.10 (40)	0.14 (75)	0.81 (75)***	–

* p<0.05; *** p<0.001

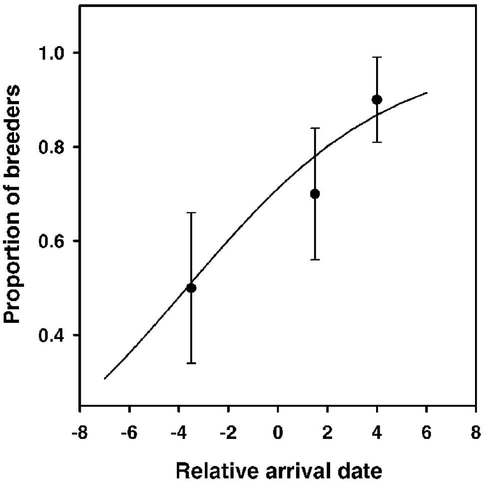

Fig. 2 Relationship between arrival date on the breeding ground and probability of breeding in female greater snow geese observed with a mate on the staging area. Arrival dates are standardized relative to the yearly median. To illustrate the adequacy of the model, each *point* represents the proportion of breeders grouped by arrival date (n=10 for each *dot*). GEE model: arrival date, β=0.23, 95% CI: 0.014–0.45, χ^2=4.2, df=1, p=0.04, n=30; Variables year, dominance score, departure date and interaction terms were dropped from the model (all p>0.16)

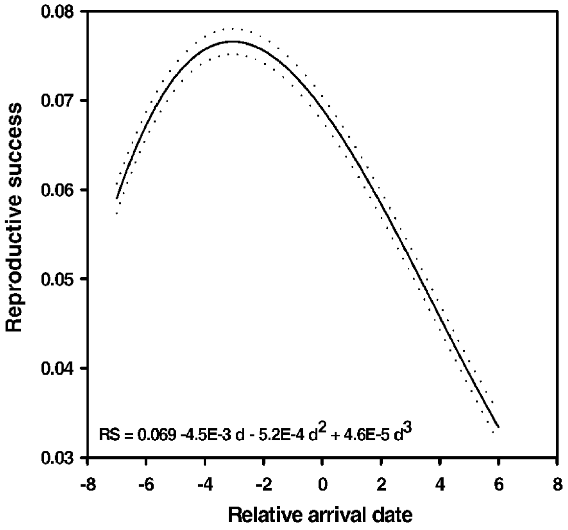

Fig. 3 Relationship between arrival date on the breeding ground and estimated reproductive success (*RS*: number of young surviving to the first winter) in female greater snow geese (calculated by combining average breeding probability and breeding success; see Materials and methods for details). The regression curve (*solid line*) corresponds to the equation given and the *dotted line* illustrates 95% prediction intervals for the regression (R^2=0.99, p<0.001)

The proportion of birds reaching the breeding ground was not associated with the social status on the staging area (59% of 27 unpaired birds vs 73% of 83 paired birds; χ^2=1.22, df=1, p=0.27), or with female dominance score or departure date (all p>0.34). Among paired females, the probability of reaching the breeding ground was not related to the dominance score of the pair either (β=–0.02, 95% CI: –0.050–0.01, χ^2=0.92, df=1, p=0.34).

No marked birds were confirmed as breeders in 1999. Thus, we excluded birds detected on the breeding ground in that year from the following analyses. Overall, the probability of breeding was much higher among females accompanied by a partner on the staging area compared to unpaired females (paired 67%, n=60 vs unpaired 38%, n=16: χ^2=3.99, p=0.045). Among paired birds, the probability of breeding was not related to the dominance score of the pair (β=–0.02, 95% CI: –0.06–0.02, χ^2=1.02, df=1, p=0.31) neither to departure date (β=0.29, 95% CI: –0.18–0.75, χ^2=1.60, df=1, p=0.21). On the other hand, the probability of breeding was higher among females arriving late on the breeding ground compared to those arriving early (Fig. 2) indicating a reproductive cost of arriving too early on the breeding grounds. However, late-arriving birds nested later (Bêty et al. 2003) and were thus subjected to a strong seasonal decline in breeding success due to environmental factors (Lepage et al. 2000). The combination of breeding propensity and breeding success associated to lay date indicates that the earliest and the latest arriving females were less successful on average than females arriving near the median arrival date (Fig. 3). Birds arriving about 3 days earlier than the median arrival date apparently attained the highest reproductive success.

Discussion

We examined potential causes and reproductive consequences of individual variation in bird migratory behavior by radio-tracking females on their staging and breeding grounds. Our main findings were: first, that female greater snow geese show individual consistency in the duration of the northward migration and arrival date on the breeding ground; and second, that arrival time is positively associated with the probability of breeding, indicating potential costs of arriving too early. To our knowledge, we provide the first estimate of repeatability in the duration of migration in wild birds by tracking the same individuals in successive years.

Repeatability of migratory behavior

Repeatability depends on genotypes and environments to which animals are exposed. Repeatability estimates can be considered an upper limit of heritability values (Falconer 1989; but see Dohm 2002 for assumptions and implications of violations). Empirical evidence suggests that repeatability values are often very similar to heritability derived from parent-offspring regressions (Boag and van Noordwijk 1987). However, in long-lived animals transient positive repeatability can arise during short-term studies when individuals are measured in consecutive years, and thus at relatively similar ages (Catry et al. 1999). In birds, age is generally a good predictor of dominance (e.g., Stahl et al. 2001; Lemel 1989; Brown et al. 1997). Therefore, the lack of association between female dominance score and migratory behavior found in this study suggests that individual variation in timing of migration is not strongly affected by age in greater snow geese. Madsen (2001) also reported that the migratory strategy in pink-footed geese (*Anser brachyrhynchus*) was not related to age. Migratory behavior could be in part culturally determined in species with extended parental care like geese (Sutherland 1998), and such transmission could affect individual consistency in migration strategy. In greater snow geese, some 10-month-old juveniles are seen with their parents on the nesting grounds indicating that they completed a first migration with them (J. Bêty, personal observation). Although cultural evolution could affect migration routes, no studies have yet shown that learning can affect the timing of migration of individuals (Sutherland 1998; Alerstam et al. 2003).

Although we cannot entirely rule out potential age and cultural effects, the relatively high repeatability estimates nonetheless suggest that genetically based differences among individuals in migration duration and arrival date are likely in greater snow geese. Selection experiments in birds indicate that some components of the migratory behavior such as timing and duration can indeed be genetically based (Berthold 2001). Møller (2001) recently provided evidence that spring arrival date of barn swallow (*Hirundo rustica*) has a large heritability while Rees (1989) found that arrival and departure dates of wintering Bewick's swans (*Cygnus columbianus bewickii*) had a slight heritability. However, lack of individual consistency or similarity between relatives (parents-sons, full-sibs) in spring arrival time has also been reported (e.g. pied flycatcher, *Ficedula hypoleuca*: Potti 1998). The lack of repeatability in departure date from the staging area indicates that environmental factors may govern departure time in greater snow geese. Moreover, departure is more synchronized among individuals than arrival on the breeding grounds and the effect of individual body condition on departure has already been discarded (Bêty et al. 2003). Therefore, weather conditions (especially wind speed and direction) and social stimuli are probably key factors determining departure of individuals (Berthold 2001; Schaub et al. 2004).

Causes and fitness consequences of variation in prebreeding migration

Environmental predictability at the current and future migratory stopover sites, and possible trade-offs between energy accumulation and mortality risk, cause uncertainty in the costs and benefits of different migratory decisions (Weber et al. 1998). Theoretical models suggest that high variance in body condition gain at a target staging site could generate a delayed departure from the preceding site in order to further increase condition before departure (Schaub and Jenni 2001). In geese, females paired with dominant males can experience reduced variance in foraging success (see Stahl et al. 2001). Thus, our results showing that female greater snow geese accompanied by dominant males departed slightly earlier from the main staging area than females paired with subordinate males are consistent with predictions of the theoretical model. However, early leaving females did not arrive earlier on the breeding grounds, as found by Tombre et al. (1996) for barnacle geese.

Recent studies show that body condition and energy accumulation rate on staging sites can affect the migratory pattern in geese (Drent et al. 2003; Prop et al 2003). We found no evidence that the timing of migration was influenced by the amount of nutrient reserves accumulated on the main staging area in greater snow geese (Bêty et al. 2003). The 2- to 3-week-long migration indicates that birds stopped at one or several other minor staging sites during their northward migration (see also Le Hénaff et al. 1995). Thus, foraging rate or energy accumulated between departure from the main staging site (Fig. 1) and the breeding grounds could affect arrival time of individuals and this would need further investigation. However, based on the isotopic composition of tissues of birds departing from the main staging area and arriving on the breeding grounds, accumulation of additional body reserves appears limited (Gauthier et al. 2003, unpublished data).

It has been reported for several species that individuals arriving early on the breeding grounds breed earlier than late arriving ones (e.g., Møller 1994; Tombre et al. 1996; Potti 1998; Bêty et al. 2003). As late-nesting birds perform more poorly than early ones in most components of reproductive success (Perrins 1970; Cooke et al. 1995), there is apparently a strong fitness benefit of arriving early. However, few empirical studies investigated the potential costs of early arrival, especially in capital breeders that rely partly on endogenous reserves for successful reproduction. Costs that could counteract the reproductive benefit of early arrival are: (1) harsh climatic conditions that could threaten adult survival and increase maintenance costs (Møller 1994; Brown and Brown 2000); (2) low food availability that could reduce energy reserves at the time of breeding (Prop and De Vries 1993); and (3) increased nest predation and parasitism rate (Palomino et al. 1998).

In greater snow geese, the positive relationship between arrival date and the probability of breeding could be linked to food availability. Low foraging success during the prelaying period may reduce nutrients available for egg production in birds arriving too early which in turn may have negatively affected their breeding probability. With respect to egg production, greater snow geese use a mixed capital-income strategy where nutrients are obtained from food ingested on the breeding grounds and from body reserves (Gauthier et al. 2003). There is some evidence that early breeders, which are those that arrive early (Bêty et al. 2003), use proportionally more of the nutrients acquired on the breeding grounds to produce their eggs relative to late breeders (Gauthier et al. 2003). Geese stopping during migration may save or even increase their endogenous reserves, especially birds arriving late and having the longest migration duration (Bêty et al. 2003). Consequently, some early arriving birds may have suffered from reduced food availability (e.g. due to snow cover), which in turn may have compromised egg formation and subsequent breeding attempt. Such effects could vary annually and thus affect the shape of the relationship between arrival time and breeding probability.

It is also possible that early arriving (and nesting) birds experience higher nest predation rate than late arriving ones, which would reduce our ability to find their nests and thus underestimates their genuine breeding probability. Lepage et al. (2000) found that early and late nesting females suffer high egg loss, but Cooke et al. (1995) showed that pre-incubation losses are more frequent in early nesting lesser snow geese (*Anser caerulescens caerulescens*) whereas incubation losses are more frequent in late nesters. Finally, because most nonbreeders leave Bylot Island during the incubation period to molt elsewhere (Reed et al. 2003a), we cannot exclude the possibility that some late migrants, non-breeding females may in fact have flown directly to their molting sites, thereby biasing upwards the probability of breeding among late arriving birds being detected on the island.

Unbiased measurements of the full reproductive costs and benefits of different migratory strategies are essential for models of optimal migration. We cannot clearly identify the proximate mechanisms that generate a positive relationship between arrival date and breeding probability in greater snow geese. Nevertheless, our results indicate that estimating the fitness consequences of arrival time by only studying breeding birds could lead to an overestimation of the genuine benefits of early arrival. On the other hand, the steep seasonal decline in breeding success more than offset the benefit of a high breeding probability observed in late arriving greater snow geese. Overall, our data suggest that the arrival date that maximizes reproductive success is a few days earlier than the arrival time of most birds in the population. Although the magnitude of this selection differential may be affected by some uncertainties in our calculations (see above), it nonetheless suggests that some factors may be preventing birds from arriving at the optimal date in this population. Alternatively, the migratory decisions may be optimized at the individual level (e.g. phenotypic- or condition-dependent).

Migration and adaptive adjustment

There are actually major concerns about the capacity of arctic species to evolve and adapt to rapidly changing climatic conditions (Berteaux et al. 2004). Long-distance migrants can be particularly vulnerable if the climate in breeding and wintering areas is changing at different speeds, thus preventing adequate adaptation (Both and Visser 2001). Phenotypic plasticity (i.e. changes within individuals) of the timing of migration and breeding date should allow migrating species to cope with short-term changes in climatic conditions (Coppack and Both 2002). However, microevolution (i.e. changes in gene frequencies between generations) is thought to be essential for the persistence of populations facing long-term directional changes in the environment (Lande and Shannon 1996; Berteaux et al. 2004).

Assuming that our repeatability estimate reflects the level of heritability, changes in migratory behavior across generations via microevolutionary changes would be expected in migration duration and arrival date on the breeding grounds, but not in departure date from the staging area in greater snow geese. Consequently, departure date might become maladaptive if the cues used for migration are independent of environmental changes occurring on the breeding grounds (see Both and Visser 2001). On the other hand, as breeding date is related to arrival time, some adaptive evolution of reproduction to climate changes would also be expected. Further investigations involving quantitative genetic analysis are needed to confirm the heritability of migration duration and arrival time in snow geese. Such information could significantly help predicting the response of migrating birds to rapid global change.

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