Effects of spring conditions on breeding propensity of Greater Snow Goose females

E. T. Reed, G. Gauthier & J.–F. Giroux

Abstract

Effects of spring conditions on breeding propensity of Greater Snow Goose females.— Breeding propensity, defined as the probability that a sexually mature adult will breed in a given year, is an important determinant of annual productivity. It is also one of the least known demographic parameters in vertebrates. We studied the relationship between breeding propensity and conditions on spring staging areas (a spring conservation hunt) and the breeding grounds (spring snow cover) in Greater Snow Geese (*Chen caerulescens atlantica*), a long distance migrant that breeds in the High Arctic. We combined information from mark–recapture, telemetry, and nest survey data to estimate breeding propensity over a 7–year period. True temporal variation in breeding propensity was considerable (mean: 0.574 [95% CI considering only process variation: 0.13 to 1.0]). Spring snow cover was negatively related to breeding propensity ($\beta_{snow} = -2.05 \pm 0.96$ SE) and tended to be reduced in years with a spring hunt ($\beta = -0.78 \pm 0.35$). Nest densities on the breeding colony and fall ratios of young:adults were good indices of annual variation in breeding propensity, with nest densities being slightly more precise. These results suggest that conditions encountered during the pre–breeding period can have a significant impact on productivity of Arctic–nesting birds.

Key words: Breeding propensity, Capture–recapture, *Chen caerulescens atlantica*, Environmental stochasticity, Greater Snow Goose, Reproduction.

Resumen

Efectos de las condiciones primaverales en la propensión reproductora de las hembras de ánsar nival.— La propensión reproductora, definida como la probabilidad de que un adulto sexualmente maduro se reproduzca en un determinado año, constituye un importante determinante de la productividad anual. También es uno de los parámetros demográficos menos conocidos de los vertebrados. Estudiamos la relación entre la propensión reproductora y las condiciones reproductoras en áreas de acumulación primaveral de nutrientes (cacería primaveral orientada a la conservación) y emplazamientos de reproducción (capa de nieve durante la primavera) en el ánsar nival (*Chen caerulescens atlántica*), un ave migratoria que recorre grandes distancias y que se reproduce en el Alto Ártico. Combinamos la información de marcaje–recaptura, telemetría y datos de supervivencia en el nido para estimar la propensión reproductora durante un período de siete años. La variación temporal verdadera en la propensión reproductora fue significativa [media: 0,574 (95% CI, considerando únicamente la variación en los procesos: de 0,13 a 1,0)]. La capa de nieve primaveral se relacionó negativamente con la propensión reproductora ($\beta_{snow} = -2,05 \pm 0,96$ EE), tendiendo a reducirse en los años en que se había producido una cacería primaveral ($\beta = -0,78 \pm 0,35$). Las densidades de los nidos de la colonia reproductora y la tasa de jóvenes:adultos en otoño constituyeron buenos índices de la variación anual en la propensión reproductora, siendo las densidades de los nidos ligeramente más precisas. Tales resultados sugieren que las condiciones presentes durante el período previo a la reproducción pueden tener un impacto significativo en la productividad de las aves que nidifican en el Ártico.

Palabras clave: Propensión reproductora, Captura–recaptura, *Chen caerulescens atlantica*, Estocasticidad medioambiental, Ánsar nival, Reproducción.

Eric T. Reed* & Gilles Gauthier, Dépt. de Biologie and Centre d'Études Nordiques, Univ. Laval, Sainte–Foy, QC G1K 7P4 Canada.– Jean–François Giroux, Dépt des Sciences Biologiques, Univ. du Québec à Montréal, Succursale Centre ville, C. P. 8888, Montréal, QC, H3C 3P8 Canada.

* Present address: Migratory Birds Population Analyst, Canadian Wildlife Service, Environment Canada, 351 St. Joseph Blvd, Gatineau, QC K1A 0H3 Canada. E–mail: eric.reed@ec.gc.ca

Introduction

Breeding propensity, defined as the probability that a sexually mature female breeds in a given year (i.e. lays at least one egg, whether it is successfully or not), has a strong impact on the number of young produced. This parameter is thus of considerable interest in population dynamics, especially in long–lived species that may be prone to skip a breeding year when conditions are not appropriate (Tickell & Pinder, 1967; Chastel, 1995; Nur & Sydeman, 1999). Unfortunately, breeding propensity is difficult to estimate in most species because non–breeders are often less conspicuous or simply absent from breeding colonies (Spendelow & Nichols, 1989; Chastel, 1995). Thus, it is probably one of the least known demographic parameters in vertebrates.

Absence of an individual from the breeding site due to breeding failure is a form of temporary emigration. However, other situations may also lead to temporary emigration, and can thus be easily confounded with breeding propensity: for instance, home range of some individuals may not be completely enclosed in the study area, so that that they are outside a sampling frame in some years; or the capture process itself may cause an individual to temporarily leave the study area (e.g. Pradel et al., 1995).

Breeding propensity may be especially variable for species in unpredictable and highly heterogeneous environments such as the Arctic. In arctic-nesting geese, it has been suggested that a large proportion of individuals may fail to breed in years of late snowmelt on the breeding grounds (Barry, 1962; Prop & de Vries, 1993; Reed et al., 1998). Delayed snowmelt prevents access to nesting sites and can impair the acquisition of some nutrients for egg–formation (Choinière & Gauthier, 1995; Ganter & Cooke, 1996). Recent estimates of breeding propensity in waterfowl indicate high values for this parameter (0.74–0.90 of mature adults breeding in a given year: Kendall & Nichols, 1995; Lindberg et al., 2001; Sedinger et al., 2001). In contrast to previous suggestions, these studies detected small annual variation in breeding propensity (see also Cooch et al., 2001).

In addition to late snowmelt on nesting areas, events during spring migration may also influence breeding propensity in long–distance migrants. Nutrient reserves accumulated during spring staging are used to meet energy costs of spring migration and reproduction (Ankney & MacInnes, 1978; Gauthier et al., 1992; Choinière & Gauthier, 1995; Gauthier et al., 2003). Factors such as reduced food availability due to drought, or high disturbance due to spring hunting that negatively affect spring fattening may thus result in reduced breeding effort (Davies & Cooke, 1985; Mainguy et al., 2002; Féret et al., 2003).

In open population mark–recapture models, detection probabilities confound the probability of being present in the sampled area and the probability of being detected given presence (Kendall & Nichols, 1995). When sampling is limited to a single site and provides one capture occasion per time period (e.g. Lebreton et al., 1992), separation of these two probabilities is not possible, as only their product is estimable. To circumvent this problem, *ad hoc* and maximum likelihood estimators of temporary emigration based on the robust design (Pollock, 1982) were developed by Kendall et al. (1997). In this design, multiple subsamples (secondary samples) within primary sampling periods are used to estimate probability of detection, conditional on animal presence; these detection probabilities are then used to adjust estimates from standard mark-recapture techniques, assuming a closed population during secondary samples (Pollock, 1982; Pollock et al., 1990). Recently, it was recognized that this approach could be used to estimate probability of breeding when presence is synonymous with breeding (Kendall & Nichols, 1995; Kendall et al., 1997; Lindberg et al., 2001). In geese, this condition is met when non-breeders undertake a molt migration away from breeding sites before banding (e.g Salomonsen, 1968; Abraham, 1980; Reed et al., 2003a).

We estimated annual variation in breeding propensity in Greater Snow Geese (*Chen caerulescens atlantica*), a long–lived migrant that breeds in the High Arctic, a highly variable environment. Building on a long–term capture–mark–recapture study at a major breeding site, we combined information from recaptures, radio–tracking, and nest monitoring to estimate breeding propensity of adult female Greater Snow Geese over a 7–year period. Our objective was to investigate temporal variation of breeding propensity of adult females and evaluate the influence of 1) snow cover at the onset of nesting in the Arctic, and 2) a conservation hunt recently implemented on the spring staging area (Mainguy et al., 2002). We hypothesized that breeding propensity would be lower in years of extensive spring snow cover in the Arctic and in years with a spring conservation hunt on the staging area. We also sought to find out if other variables easier to sample were correlated with breeding propensity in order to use them as an index.

Study area

Data were collected at the Bylot Island breeding colony, Sirmilik National Park, Nunavut Territory, Canada. This area supports the largest concentration of breeding Greater Snow Geese, representing ca. 15% (55,000 breeding adults in 1993) of the world breeding population (Reed et al., 1998). Field work was concentrated at two main study sites, separated by ~30 km: the Base–camp valley, an important brood–rearing area where weather data collection and banding occurred, and the Camp–2 area where most geese nest and where nesting data were collected (Bêty et al., 2001). Most families that use the Base–camp area

for brood–rearing moved from camp–2 within 6 days after hatching (Mainguy, 2003). We defined the superpopulation (*sensu* Kendall et al., 1997) as females that had nested on Bylot Island's south plain in at least one year of the study.

Methods

Capture and marking of geese

Flightless geese were captured in corral traps during molt with the help of a helicopter and by personnel on foot over a 5 to 8–day period in early August from 1994 to 2001 (Menu et al., 2001). Captured birds were mostly successful parents with their young since non–breeders and failed-nesters left the island for distant molting sites or had regained flight ability by the time of banding (Reed et al., 2003a). This is referred to as the main banding operation.

All birds captured for the first time were fitted with a metal U.S. Fish and Wildlife Service leg band and a sample of adult females was fitted with individually coded plastic neck bands. Recaptures were noted systematically. Because we had evidence that neck bands reduced female breeding propensity (Reed, 2003), we restricted our analysis to females marked only with leg bands. Females that had lost neck bands before recapture, however, were included, their first capture without the neck band being considered their initial capture. Similarly, leg–banded females that were subsequently fitted with a neck band were censored by considering their last capture as a leg–banded female as a loss on capture.

From 1995 to 1999, captures of individual families were also made at the same site to fit radio-transmitters on neck bands (all years) or harnesses (1995 only) to adult females (Demers et al., 2003). This normally was done shortly before the main banding operation but overlapped in some years. In 2000–2001, incubating females were captured on their nest using bow traps (Mainguy, 2003) and also marked with radio–transmitters on neck bands. Presence of these females on Bylot Island in late summer was ascertained through aerial radio–tracking (see Reed et al., 2003a) to determine the number of radio–marked females located in the banding area. Detection range of radios was approximately 3–5 km from the ground and 10–15 km from the air (Bêty, 2001).

Extent of banding area and brood–rearing site fidelity

The area covered by the main banding operation varied among years in response to goose densities. We always covered the Base–camp valley before moving onto the adjacent plateau and other valleys (see map in Lesage & Gauthier, 1998). The study area was bounded to the west by Navy Board Inlet and to the east by glaciers, so geese were constrained to a north–south corridor (ca.

10 km). Patches of suitable brood–rearing habitat extended ~65 km to the south of the base-camp valley and were limited to one valley ~5 km to the north because of high mountains. Banding area was thus calculated as the distance between the most southerly and northerly capture sites each year (in km). In 1999, a year of almost complete reproductive failure (Mainguy et al., 2002), we covered the entire south plain of Bylot Island for banding.

We used the distance between inter–annual recaptures to estimate of brood–rearing site fidelity (denoted as F_i). Mainguy (2003) found that 42.5 % of females were recaptured < 5 km, 17.5% 6–10 km, 10.0% 11–15 km, 15.0% 16–20 km, and 15.0% 21–30 km of their previous capture location ($n = 40$ females). We estimated the proportion of females on Bylot Island that were within our banding area (F_i) as the proportion of females recaptured in the 5 km distance class (described above) that included our median distance between extreme capture locations each year. For example, if the distance between our most northerly and most southerly capture during banding was 6 km (median = 3 km), we used the proportion of radio–marked females that were recaptured < 5 km from their previous capture location (i.e. the smallest class of Mainguy, 2003) as measure of site fidelity. Variance of site fidelity was estimated as:

$$\widehat{var}(\hat{F}_i) = \frac{\hat{F}_i(1-\hat{F})}{n}$$

where i refers to year and n is the sample size (40 females).

Nest survival

Greater Snow Goose nests were found by systematic searches during incubation in 1995, and egg laying or early incubation from 1996 to 2001 at the Camp–2 area (Bêty et al., 2001). Fate of nests was determined by revisiting them in the first half of incubation, during hatching and after goslings had left the nest. Nesting parameters are not biased by our visits (Bêty & Gauthier, 2001). We used the Mayfield method to calculate daily nest survival and the product method to evaluate nest survival probability for the whole nesting period (denoted as S_i^n Johnson, 1979). Nest survival for the years 1996–2000 were taken from Bêty et al. (2002).

Temporary emigration model

Background and notation

We estimated temporary emigration using the sampling design described by Kendall et al. (1997), i.e. individuals are captured during secondary samples (closed population) nested within primary periods (open population). Our model requires combination of different sources of information from Cormack–Jolly–Seber models to esti-

mate temporary emigration. Model notation follows Lebreton et al. (1992) and Kendall et al. (1997).

First we define the following terms: Φ_i. Probability that an individual survives and does not permanently emigrate from primary period i to $i+1$, $(i = 1,2,...,k-1)$; p_i^0. Probability that an individual is caught in primary period i, given that the animal is alive and present in the superpopulation at period i, $(i = 1,2,...,k)$; p_i^*. Probability that an individual is captured in at least one of the l_i secondary samples of primary period i, given that the individual is located in the sampled area during period i; p_{ij}. Probability that an individual is captured in secondary sample j of primary period i, given that it is alive and present in the sampled area during period i; γ_i. Probability that a marked individual could not be captured during primary period i (i.e. is a temporary emigrant), given that it is in the superpopulation, but outside of the sampled area.

Kendall et al. (1997) described an *ad hoc* estimator of temporary emigration from the sampling area (banding area in our case). Temporary emigration from our study area is mainly due to non-breeding and nest failure (Reed et al., 2003a), but also incomplete fidelity to brood–rearing areas that we sampled. Our goal was to estimate breeding propensity $(1 - \gamma_i)$ of females from the Bylot Island breeding population, so we modified Kendall et al.'s (1997) estimator to take into account temporary emigration of breeding females due to nest failure $(1 - S_i^n)$ and change in brood–rearing site $(1 - F_i)$:

$$\hat{\gamma}_i = 1 - \frac{\hat{p}_i^0}{\hat{p}_i^* \hat{S}_i^n \hat{F}_i}$$

An appropriate variance estimate based on the delta method (Seber, 1982: 7) would be:

$$\widehat{var}(\hat{\gamma}_i) = \left(\frac{1}{\hat{p}_i^* \hat{S}_i^n \hat{F}_i}\right)^2 \widehat{var}(\hat{p}_i^0) + \left(\frac{\hat{p}_i^0}{(\hat{p}_i^*)^2 \hat{S}_i^n \hat{F}_i}\right)^2 \widehat{var}(\hat{p}_i^*) +$$

$$+ \left(\frac{\hat{p}_i^0}{\hat{p}_i^* (\hat{S}_i^n)^2 \hat{F}_i}\right)^2 \widehat{var}(\hat{S}_i^n) + \left(\frac{\hat{p}_i^0}{\hat{p}_i^* \hat{S}_i^n (\hat{F}_i)^2}\right)^2 \widehat{var}(\hat{F}_i)$$

We could ignore covariance terms because our samples were independent.

Primary period capture probabilities–CJS modeling

We used as a base model the Cormack–Jolly–Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber 1965) where survival (Φ_i) and capture (p_i^0) probabilities are time–specific (model Φ_t, p_t). We first tested the fit of this model using the goodness–of–fit (GOF) tests of program RELEASE (Burnham et al., 1987). Once we had a general model that provided a good fit to data, we proceeded to assess the effect of time on survival and capture probabilities. We used Akaike's Information Criterion modified for small sample size (AICc) to select the best approximating model (low-

est AICc value; Burnham & Anderson, 1998). Other models were ranked relative to deviations from the best model (ΔAICc). We used program MARK v2.1 (White & Burnham, 1999) for model selection and parameter estimation. We also used AICc weights (ωAICc), which represent the weight of evidence in support of each model in the candidate set (Burnham & Anderson, 1998).

Secondary sample capture probabilities–radio–tracking

Capture probabilities for secondary sampling period (p_i^*) could not be estimated directly from the mark–recapture data because we avoided multiple recaptures of individuals in a given year. We used instead an independent sample of radio–marked females to estimate closed population capture probabilities. We assumed that radio–marked females, whose number was known, represented a random sample of the geese present in the study area. Even though we sampled the banding area systematically rather than randomly, we did not search for radio–marked females during the main banding operations and our selection of banding sites was thus independent from these birds being present or absent at the site. Few adults not marked with radios were captured more than once in the same year (3% of adult females between 1994 and 2001) so we can view our sampling as simple random sampling without replacement.

Mean daily capture probabilities over secondary samples ($\bar{p}_{ij}$) were estimated as the number of radio–marked females caught during the main banding operation over the sum of the number of radio–marked females present each day of capture over the entire banding period (i.e. radio–days). Once a female was captured, she was removed from the sample of birds available for capture (only one radio–marked female was caught twice in the same year) and new females could be added when radio–marking overlapped the main banding operation.

The variance was computed as:

$$\widehat{var}(\hat{\bar{p}}_{ij}) = \frac{\hat{\bar{p}}_{ij}(1 - \hat{\bar{p}}_{ij})}{n_{ij}}$$

The probability that a female was captured in at least one of the secondary periods (p_i^*) was calculated as:

$$\hat{p}_i^* = 1 - (1 - \hat{\bar{p}}_{ij})^k$$

where k was the number of days of banding in a given year. The variance was estimated as:

$$\widehat{var}(\hat{p}_i^*) = \left(k\left(1 - \hat{\bar{p}}_{ij}\right)^{k-1}\right)^2 \widehat{var}(\hat{\bar{p}}_{ij})$$

In 1999, breeding was a general failure and less than 2,000 geese were on Bylot Island during banding operations (Gauthier, personal observation). The main banding operation and marking of females with radios took place at the same time, which prevented us from using radio–marked fe-

males to estimate p_i^* in that year. Based on visual observations, we estimated that about 85% of geese present on Bylot Island were captured, but because of uncertainty on the exact number we added a SE of 0.05 to this estimate (thus assuming that between 0.75 and 0.95 of the geese were captured).

Covariates of breeding propensity

We tested whether breeding propensity varied among years using the sum of squares derived from estimates of breeding propensity probabilities inversely weighted by their total variance and the covariances of open population capture rates (p_i^0, other variables in the calculation of breeding propensity being independent). The statistic for the null hypothesis (homogeneity across years) follows a chi–square distribution with $n - 1$ degrees of freedom (where n is the number of breeding propensity rates) (Sauer & Williams, 1989). This analysis was performed with program CONTRAST (Hines & Sauer, 1989). Total variance of breeding propensity estimates is contaminated by sampling error, which can lead to an overestimation of temporal variation in this parameter. Using a variance–components approach, we partitioned the total variability of estimated breeding propensity and calculated the percentage of the total variation that was accounted for by the sampling variation and covariation (Gould & Nichols, 1998).

We then proceeded to test the effect of snow cover on the breeding grounds and the implementation of a spring conservation hunt on breeding propensity. Each year, a visual estimate of snow cover in the base–camp valley was made on 5 June (Lepage et al., 1996; Reed et al., 2003b). From 1997 to 2001, a simultaneous assessment of snow cover was made at Camp–2, which showed that data from our Base–camp valley was representative of the situation at Camp–2. Snow cover on 5 June averaged 71% but was variable among years (range: 40% to 85%). In Quebec, a spring conservation hunt (hereafter called spring hunt) on Greater Snow Geese was allowed in 1999–2001. We categorized years with a binary variable (with or without spring hunt). We used a weighted least squares approach to estimate regression coefficients (± SE) with the covariates (Lebreton, 1995; Link, 1999). Thus, variances of the annual estimates of breeding propensity, as well as covariances of p_i^0 were accounted for in the regression analysis. We fitted main effects only and tested for a negative effect of the covariates, i.e. $\beta < 0.0$ (β_{snow} = slope of the relationship between snow cover and breeding propensity; β_{hunt} = difference in breeding propensity between years without and with a spring hunt) with one–tailed z–tests.

The method used here to estimate breeding propensity is difficult and expensive in the field (e.g. requires large number of radio-marked birds),

so we looked for a simple, reliable index of breeding propensity that could be used for monitoring purposes. Two indices were examined: productivity surveys in fall and nest densities at the main breeding colony. Productivity surveys on the fall staging areas of this population have been conducted by the Canadian Wildlife Service (CWS) along the St. Lawrence River Estuary in Quebec, Canada since 1973. Proportion of young in the fall flight varied from 0.02 to 0.37 between 1995 and 2001 (Reed et al., 1998, A. Reed CWS unpublished data). Nest density (nests per 50 ha) was estimated as the number of nests found divided by the area of the search zone (data from Bêty et al., 2002). We transformed these estimates as nests per ha (1996: 1.0, 1997: 2.64, 1998: 6.52, 1999: 1.1, 2000: 1.64). We used the weighted least squares approach to test for positive relations between these indices and breeding propensity ($\beta > 0.0$) with one–tailed z–tests. We also computed the total sums of squares (SS_t) of the breeding propensity estimators as well as the residual sums of squares (SS_r) from each model. We then calculated a coefficient of correlation ($R^2 = (SS_t - SS_r) / SS_t$)) for both indices to determine which fitted best the pattern of temporal variation in breeding propensity. Years 1996 to 2000 were used due to lack of precision of point estimates for 1995 and 2001 (see below).

Results

From 1994 to 2001, we marked 1646 adult females with leg bands and subsequently recaptured 227 of these birds. The goodness of fit test of our general model indicated a good fit ($\chi^2_{32} = 26.82$, $P = 0.14$).

Our best model had constant apparent survival and time dependent capture probabilities ($\Phi \ p_t$) and this model was strongly supported by the data (ωAICc = 0.98). The second best model was $\Phi_t \ p_t$ (ΔAICc = 8.2). Apparent survival estimates from our best model were 0.87 ± 0.04 and capture probabilities conditional on presence in the superpopulation (p_i^0) ranged from 0.02 to 0.07 (table 1).

Between 1995 and 2001, 42 radio–marked females were recaptured during the main banding operations out of 1,147 radio–days and these data were used to calculate an annual $\bar{p}_{ij}$ (1995: 2/64; 1996: 20/328; 1997: 4/304; 1998: 13/390; 2000: 2/24; 2001: 1/37). Estimated capture probabilities given presence in the sampled area (p_i^*) was thus highly variable and ranged from 0.09 to 0.46 (table 1).

We estimated nest survival for between 179 and 326 nests each year. Nest survival was highly variable among years, being lowest in 1995 and 1999 and highest in 1997 and 2000 (table 1). Fidelity to the brood–rearing area was also variable and inversely related to the size of the sampled area. The extent of the banding area was 10.5 km in 1995, 12.3 in 1996, 17.2 in 1997, 6.1 in 1998, the entire south plain of 70 km in 1999,

Table 1. Estimate of capture probability, given presence in the superpopulation (p_i^0), from the open population CJS model ($\Phi\ p_t$); capture probabilities given presence in the sampling area (p_i^*) obtained from radio–marked females; Mayfield estimate of nest survival (S_i^n) for the entire nesting period; fidelity to brood–rearing sites (F_i) estimated as the proportion of individuals expected to be present in the banding area; and probability of temporary emigration from the superpopulation of Greater Snow Geese on Bylot Island (γ_i) and breeding propensity of adults ($1 - \gamma_i$). Values are mean ± SE. See methods for details of calculations: [a] No radio–marked females were present on Bylot Island during banding; we visually estimated that 85% (range 75–95%) of the geese present on Bylot Island were captured; [b] Data from Bêty et al. (2002).

Tabla 1. Estimación de la probabilidad de captura, dada una presencia en la suprapoblación (p_i^0), obtenida a partir del modelo CJS de población abierta ($\Phi\ p_t$); probabilidades de captura dada una presencia en el área de muestreo (p_i^*), obtenidas a partir de las hembras marcadas con radiotransmisores; la estimación de Mayfield de la supervivencia de los nidos (S_i^n) para la totalidad del período de nidificación; fidelidad a los emplazamientos de cría (F_i), estimada como la proporción de individuos que se espera que estén presentes en el área de anillamiento; y probabilidad de emigración transitoria a partir de la suprapoblación del ánsar nival en la isla de Bylot (γ_i) y propensión reproductora por parte de los adultos ($1 - \gamma_i$). Los valores son medias ± EE. Para detalles sobre los cálculos, consultar los métodos: [a] En la isla de Bylot se observaron hembras marcadas con radiotransmisores durante el anillamiento; se capturaron aproximadamente un 85% (variación 75–95%) de los ánsares de la isla de Bylot; [b] Datos de Bêty et al. (2002).

Year	p_i^0	p_i^*	S_i^n	F_i	γ_i	$1 - \gamma_i$
1995	0.05 ± 0.01	0.20 ± 0.13	0.18 ± 0.03	0.60 ± 0.08	−1.28 ± 1.62	2.28 ± 1.62
1996	0.05 ± 0.01	0.40 ± 0.07	0.62 ± 0.03[b]	0.60 ± 0.08	0.65 ± 0.11	0.35 ± 0.11
1997	0.04 ± 0.01	0.09 ± 0.04	0.85 ± 0.02[b]	0.60 ± 0.08	0.19 ± 0.45	0.81 ± 0.45
1998	0.07 ± 0.01	0.18 ± 0.05	0.83 ± 0.02[b]	0.43 ± 0.08	−0.09 ± 0.39	1.09 ± 0.39
1999	0.02 ± 0.01	0.85 ± 0.05[a]	0.15 ± 0.02[b]	1.00 ± 0.00	0.83 ± 0.06	0.17 ± 0.06
2000	0.07 ± 0.02	0.46 ± 0.23	0.83 ± 0.03[b]	0.43 ± 0.08	0.56 ± 0.26	0.44 ± 0.26
2001	0.05 ± 0.01	0.10 ± 0.10	0.52 ± 0.03	0.60 ± 0.08	−0.64 ± 1.63	1.64 ± 1.63

7.7 km in 2000, and 12.6 km in 2001. Thus, the probability that a female present on Bylot Island during banding was also present in our banding area varied from 0.43 in 1998 and 2000 to 1.00 in 1999 (table 1).

Estimated temporary emigration (γ_i) from Bylot Island's south plain varied considerably among years (table 1). The large negative values for 1995 and 2001 were associated with a very poor precision as shown by the large variance of these estimates and their confidence intervals, which included 0 (95% CI: [−4.45 to 1.89] and [−3.83 to 2.55] for 1995 and 2001 respectively). We thus excluded 1995 and 2001 from further analyses, although they did not have a large weight given their large variance.

Breeding propensity ($1 - \gamma_i$) varied across years ($\chi^2_4 = 9.56$, $P = 0.049$) ranging from 1 in 1998 to 0.17 in 1999 (table 1). We estimated total variance at 0.137 and true temporal variance at 0.051, indicating that sampling variation accounted for 62% of the total variation. Average breeding propensity for these 5 years was 0.574 [95% CI considering only process variation: 0.131 to 1.017]. Breeding propensity was negatively related to snow cover on 5 June (fig. 1; β_{snow}: −2.05 ± 0.96, $z = -4.14$, $P = 0.02$) and was reduced in years with a spring hunt ($\beta_{hunt} = -0.78 \pm 0.35$, $z = -2.19$, P = 0.01).

Both nest density and young/adult ratio in the fall flight provided good indices of breeding propensity for the 1996–2000 period (fig. 2). However, nest density (nest/ha) was a better predictor of breeding propensity ($\beta_{nest\ density}$: 0.59 ± 0.11, $R^2 = 0.97$) than was young/adult ratio in the fall flight ($\beta_{young/adult}$: 5.02 ± 1.06, $R^2 = 0.89$).

Discussion

Factors affecting breeding propensity

Breeding propensity of adult female Greater Snow Geese varied considerably between 1996 and 2000, ranging from 0.17 to 1. True temporal variation in breeding propensity was large (95% CI: 0.13–1.0), with an average of 57% of surviving adult females breeding (successfully or not) in any given year. These results confirm that intermit-
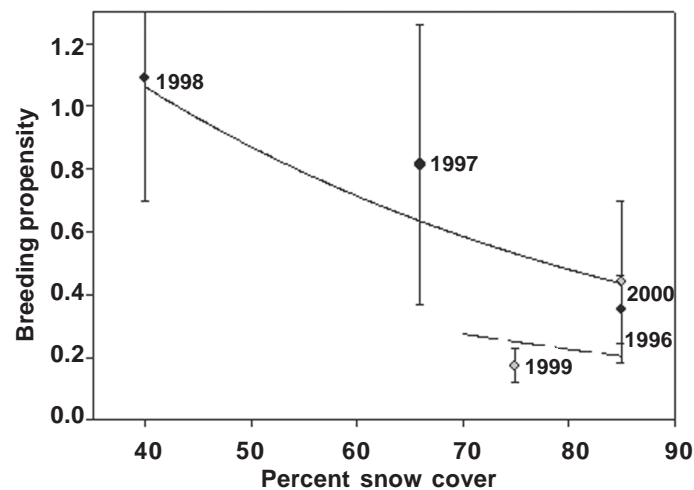
Fig. 1. Relationship between snow cover on 5 June on Bylot Island and estimated breeding propensity (± SE) of female Greater Snow Geese. The solid line and dark dots represents years without a spring hunt and the dashed line and grey dots represent years with a spring hunt. Lines are predicted values of breeding propensity from model: logit (breeding propensity) = 0.79 [± 0.67] − 2.05 [± 0.96] * snow cover −0.78 [± 0.35] * (0: no spring hunt; 1: spring hunt). Only estimates for years 1996–2000 are used due to imprecision of the 1995 and 2001 estimates.

*Fig. 1. Relación entre la capa de nieve observada en la isla de Bylot el 5 de junio y propensión reproductora estimada (± EE) del ánsar nival. La línea contínua y los puntos oscuros representan los años sin cacería primaveral, mientras que la línea discontinua y los puntos grises representan los años con cacería primaveral. Las líneas son valores previstos de la propensión reproductora a partir del modelo: logit (propensión reproductora) = 0,79 [± 0,67] − 2,05 [± 0,96] * capa de nieve − 0,78 [± 0,35] * (0: sin cacería primaveral; 1: con cacería primaveral). Sólo se emplean estimas para los años 1996–2000, debido a la imprecisión de las estimas correspondientes a los años 1995 y 2001.*

tent breeding is common in this population. High rates of temporary non-breeding are well documented in seabirds (Tickell & Pinder, 1967; Chastel, 1995; Nur & Sydeman, 1999) but results are more variable in waterfowl. Studies in Black Brant (*Branta bernicla nigricans*) and Lesser Snow Geese (*Chen caerulescens caerulescens*) found high breeding probabilities with no detectable temporal variation (Cooch et al., 2001; Sedinger et al., 2001), whereas studies in Canvasback (*Aythya valisineria*) and Barnacle Geese (*Branta leucopsis*) found important temporal variation in breeding probability (Anderson et al., 2001; Prop & De Vries, 1993).

Several studies in seabirds have suggested that temporal variation in breeding probability may be due to variations in prey availability (e.g. Chastel, 1995; Nur & Sydeman, 1999), whereas for prairie waterfowl habitat availability in relation to drought cycles may be a key determinant (Anderson et al., 2001). However, the mechanism governing the decision to initiate breeding in herbivores such as geese is less obvious. Our results indicate that spring snow cover is an important determinant of breeding propensity (see also Prop & De Vries, 1993). The other goose studies that showed no

variation in breeding propensity were conducted in low Arctic regions, where environmental stochasticity is presumably less than at higher latitudes. Our results suggest that, in the High Arctic where the summer is very short, climatic conditions in spring are a key determinant of breeding propensity, with most females (> 80%) breeding when snow cover is low and few (< 30%) breeding when snow cover is extensive. Our results thus support early suggestions that reproductive effort of geese can be quite variable in the high Arctic (Prop & De Vries, 1993), with widespread breeding failure in years of late snowmelt (Barry, 1962).

Snow cover at the time of nesting is governed by both winter snow accumulation and the speed of snow melt in spring. Thus, snow accumulation and air temperature, which influences the rate of snowmelt, may both influence breeding propensity. At our study site, we lacked an appropriate estimate of snow fall over the entire study area and spring air temperature was highly correlated to snow cover on 5 June, so we could not test these two variables separately (E. T. Reed, unpublished data). Climatic conditions could influence breeding propensity of herbivorous birds by limiting availability

of food or nest sites. Geese feed intensively during the interval between arrival on the breeding grounds and egg–laying (Gauthier & Tardif, 1991), and this nutrient intake contributes significantly to the energy invested in egg production (Bromley & Jarvis, 1993; Choinière & Gauthier, 1995; Ganter & Cooke, 1996; Gauthier et al., 2003). Snow cover can thus limit access to high quality foraging sites in lowlands, because primary production in the first snow–free areas (mountain and ridges) is low due to wind exposure and good soil drainage (Gauthier, 1993; Prop & De Vries, 1993). Early nesting is also important in seasonal environments because date at which young hatch strongly influences their growth rate (Larsson & Forslund, 1991; Lepage et al., 1998) and ultimately their survival and recruitment prospects (Spear & Nur, 1994; Lepage et al., 2000; Prévot–Julliard et al., 2001; Reed et al., 2003b). Although geese are flexible in the choice of their nest site when snowmelt is late (Lepage et al., 1996), a large proportion of adults may refrain from breeding if survival prospects of the young are too low at the date where nest sites become available.

In arctic–nesting geese, endogenous nutrient reserves acquired on the spring staging grounds are an important fuel source for the northward migration and contribute to breeding success (Ankney & MacInnes, 1978; Ebbinge,1989; Gauthier et al., 1992; Ebbinge & Spaans, 1995). Davies & Cooke (1983) and Alisauskas (2002) provided evidence that events occurring on spring staging areas influenced reproduction of arctic–nesting geese. In the first two years of the spring hunt (1999–2000), Féret et al. (2003) found a marked reduction in nutrient accumulation of Greater Snow Geese during spring staging due to heavy hunting disturbance (Béchet et al., 2003). This reduction of body condition was also detected in laying geese (Mainguy et al. 2002) and most reproductive parameters were negatively affected in years with spring hunt at our study site: geese laid later and had smaller clutch size than in previous years, and radio–marked females showed a marked reduction in breeding effort (Mainguy et al., 2002; Bêty et al., 2003). In this study, we found an overall reduction in breeding propensity during years with a spring hunt (1999 to 2001). Breeding propensity was at a record low value in 1999, although it was not especially low in 2000 when considering snow cover and it could not be satisfactorily estimated in 2001. Even though we only had two precise estimates, evidence suggests that the spring hunt negatively impacted breeding propensity in Greater Snow Geese.

Overall, our results suggest that spring climatic conditions in the Arctic and nutrient reserves acquired during spring staging may be important determinants of reproductive effort in Greater Snow Geese (see also Bêty et al., 2003). The effect of conditions encountered at arrival should increase as one moves from low to high Arctic, since environmental stochasticity should increase with latitude. Moreover, the amount of endogenous nutrients remaining upon arrival in the Arctic should be reduced as the length and cost of the spring migration increases with latitudinal range (Choinière & Gauthier, 1995).

Methodological considerations

Our results showed that temporary emigration could be used to estimate breeding propensity when only breeding individuals are subject to capture. In the case where some breeders are not at risk of capture, temporary emigration must be corrected as was done in this study using information from radio–marked birds. In our study population, most non–breeders and failed nesters undertake a molt migration from our sampling area (Reed et al., 2003a), and those that remain on the island have regained flight capacity and are thus not sampled at banding. We could not rule out the possibility that some geese considered as non–breeders actually nested outside the study area, but a large proportion of adult females (including non–breeders) are present on Bylot Island from the pre–laying to the incubation period before leaving the island for molting, too late for a breeding attempt (Reed et al. 2003a). Also, given the high level of breeding philopatry to Bylot Island previously found (Reed et al., 2003b), it seems unlikely that an important segment of the breeding population could temporarily settle elsewhere to breed.

Capture probabilities, given presence on the sampled area, varied considerably among years. Thus, estimates of capture probabilities from open population models (p_i^0) do not represent a valid index of breeding propensity. Because breeding propensity represents the probability that an adult will breed, irrespective of breeding success, we also had to correct our capture probability for individuals that leave Bylot Island following a nest failure. Furthermore, we did not sample all brood-rearing areas on Bylot Island but only specific ones, and the size of the sampling area varied in response to goose density. We therefore had to correct our estimates for incomplete fidelity of families to specific brood–rearing areas (Mainguy, 2003). However, biases may be associated with these correction factors, especially the brood–rearing site fidelity one which was rather crude.

The *ad hoc* method that we used was the best suited for estimation of breeding propensity and associated variance in our system. However, our first (1995) and last (2001) estimate of γ were $\ll 0$, because $p_i^0 \gg (p_i{}^* S_i^n F_i^{br})$. In 1995, this result may be due to a negative bias in nest survival estimation resulting from nests being found late during incubation and followed over a short period of time. We do not know which component(s) of the equation led to poor estimation of breeding propensity of the last encounter period (2001). However, negative estimates are not unusual when γ is close to 0.
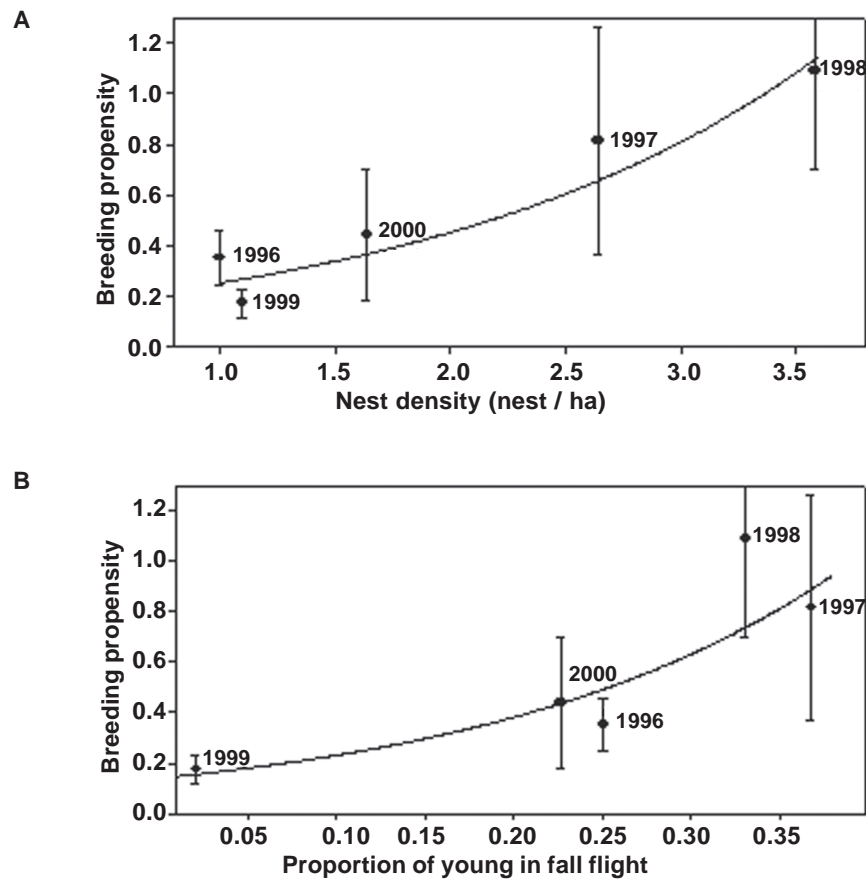
Fig. 2. Relationship between estimates of breeding propensity (± SE) of female Greater Snow Geese at Bylot Island between 1996 and 2000 and: A. Nest density (nest / ha) in the main nesting colony on Bylot Island (Bêty et al., 2002); B. Proportion of young in the fall flight in the St. Lawrence River estuary (Reed et al., 1998; unpublished data). Lines are predicted values of breeding propensity from model: A. Logit (breeding propensity) = 0.59 [± 0.33] * nest density, −1.95 [± 0.58], R^2 = 0.97; B. Logit (breeding propensity) = 5.03 [± 1.24] * young/adult ratio in the fall flight −1.97 [± 0.32], R^2 = 0.89.

Fig. 2. Relación entre estimas de propensión reproductora (± EE) en hembras del ánsar nival en la isla de Bylot entre 1996 y 2000, y: A. Densidad de los nidos (nidos / ha) en la principal colonia de nidificación en la isla de Bylot (Bêty et al., 2002); B. Proporción de jóvenes en el vuelo otoñal en el estuario del río San Lorenzo (Reed et al., 1998; datos no publicados). Las líneas representan los valores predichos de propensión reproductora extraídos del modelo: A. Logit (propensión reproductora) = 0,59 [± 0,33] *densidad de nidos, −1,95 [± 0,58], R^2 = 0,97; B. Logit (propensión reproductora) = 5,03 [± 1,24] * relación de jóvenes/adultos en el vuelo otoñal −1,97 [± 0,32], R^2 = 0,89.

Predictors of breeding propensity and consequences for population dynamics

Nest density at the main nesting colony and young/adult ratio in the fall flight were positively related to breeding propensity. Based on their respective coefficient of correlation, nest density provided a better index of breeding propensity than young/adult fall ratios. The former is less sensitive to variations in nest success (when nests are found in the early phases of nesting), and insensitive of

pre– and post fledging survival. Breeding effort of geese has often been inferred by fall or winter age ratios (e.g. Ebbinge, 1989; Ebbinge & Spaans, 1995). Our results indicate that fall age ratios can provide a reliable index of temporal variation in breeding propensity in this population. However, we believe that breeding ground indices should be preferred, as they are not influenced by factors occurring during the 3–month interval between the end of the egg–laying stage and arrival on the fall staging areas.

The proportion of young in the fall flight in 1999 (2.1%) was the lowest ever recorded since the inception of the productivity surveys in the St. Lawrence river estuary in 1973 (Reed et al., 1998). The combined occurrence of low breeding propensity and high predation pressure during the nesting period thus resulted in the near complete loss of this cohort. In contrast, most experienced females nested in 1998 and nest survival was high, resulting in a particularly strong cohort. Such variation across cohorts has been described for other species of waterfowl (Anderson et al., 2001). Other factors, such as gosling survival during their first year of life (Owen & Black, 1989; Francis et al., 1992a), also contribute significantly to variations in productivity of arctic–nesting geese.

The frequency of occurrence of 'bad' and 'good' years of reproduction has important consequences on the growth rate of this population (Gauthier & Brault, 1998). We showed that breeding propensity was negatively correlated to spring snow cover, and thus this variable could be considered in future population models of Greater Snow Geese, or other arctic–nesting birds that are likely to be affected by late snowmelt. The use of satellite imagery could be a useful monitoring tool for predicting breeding effort of arctic goose populations from information on snow–cover on the breeding grounds in spring (Reeves et al., 1976).

Acknowledgements

References

Abraham, K. F., 1980. Moult migration of Lesser Snow Geese. *Wildfowl*, 31: 89–93.

Alisauskas, R. T., 2002. Arctic climate, spring nutri-tion, and recruitment in mid–continent Lesser Snow Geese. *Journal of Wildlife Management,* 66: 181–193.

Anderson, M. G., Lindberg, M. S. & Emery, R. B. 2001. Probability of survival & breeding for juvenile female Canvasbacks. *Journal of Wildlife Management,* 65: 385–397.

Ankney, C. D., & MacInnes, C. D., 1978. Nutrient reserves & reproductive performance of female Lesser Snow Geese. *Auk,* 95: 459–471.

Barry, T. W., 1962. Effects of late seasons on Atlantic Brant reproduction. *Journal of Wildlife Management,* 26: 19–26.

Béchet, A., Giroux, J.–F., Gauthier, G., Nichols, J. D. & Hines, J. E., 2003. Spring hunting changes the regional movements of migrating greater snow geese. *Journal of Applied Ecology*, 40: 553–564.

Bêty, J., 2001. Interactions trophiques indirectes, prédation et stratégies de reproduction chez l'Oie des neiges nichant dans le Haut–Arctique. Ph. D. Thesis, Univ. Laval, Qc, Canada.

Bêty, J. & Gauthier, G., 2001. Effects of nest visits on predator activity and predation rate in a greater snow goose colony. *Journal of Field Ornithology,* 72: 573–586.

Bêty, J., Gauthier, G. & Giroux, J.–F., 2003. Body condition, migration and timing of reproduction in snow geese: a test of the condition–dependent model of optimal clutch size. *American Naturalist*, 162: 110–121.

Bêty, J., Gauthier, G., Giroux, J.–F. & Korpimäki, E., 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. *Oikos,* 93: 388–400.

Bêty, J., Gauthier, G., Korpimäki, E. & Giroux, J.–F., 2002. Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. *Journal of Animal Ecology,* 71: 88–98.

Bromley, R. G. & Jarvis, R. L., 1993. The energetics of migration and reproduction of dusky Canada geese. *Condor,* 95: 193–210.

Burnham, K. P. & Anderson, D. R., 1998. Model selection and inference: a practical information-theoretic approach. Springer–Verlag, New York, New York, USA.

Burnham, K. P., White, G. C., Brownie, C. & Pollock, K. H., 1987. Design and analysis methods for fish survival experiments based on release–recapture. *American Fisheries Society Monographs.*, 5.

Chastel, O., 1995. Influence of reproductive success on breeding frequency in four southern Petrels. *Ibis,* 137: 360–363.

Choinière, L., & Gauthier, G., 1995. Energetics of reproduction in female and male greater snow geese. *Oecologia,* 103: 379–389.

Cooch E. G., Rockwell, R. F. & Brault, S., 2001. Retrospective analysis of demographic responses to environmental change: a Lesser Snow Goose example. *Ecological Monographs,* 71: 377–400.

Cormack, R. M., 1964. Estimates of survival from

the sighting of marked animals. *Biometrika,* 51: 429–438.

Davies, J. C. & Cooke, F., 1983. Annual nesting productivity in snow geese: prairie drought and arctic springs. *Journal of Wildlife Management,* 47: 291–296.

Demers, F., Giroux, J.–F., Gauthier, G. & Bêty, J., 2003. Effects of collar–attached transmitters on behavior, pair bond, and breeding success of snow geese. *Wildlife Biology,* 9: 161–170.

Ebbinge, B. S., 1989. A multifactorial explanation for variation in breeding performance of Brent Geese *Branta bernicla. Ibis,* 131: 196–204.

Ebbinge, B. S. & Spaans, B., 1995. The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding dark–bellied Brent Geese *Brante b. bernicla* in the high Arctic. *Journal of Avian Biology,* 26: 105–113.

Féret, M., Gauthier, G., Béchet, A. & Hobson, K. A., 2003. Effect of a spring hunt on nutrient storage by Greater Snow Geese in Southern Quebec. *Journal of Wildlife Management,* 67: 796–807.

Francis C. M., Richards, M. H., Cooke, F. & Rockwell, R. F., 1992. Changes in survival rates of lesser snow geese with age and breeding status. *Auk,* 109: 731–747.

Ganter, B. & Cooke, F., 1996. Pre–incubation feeding activities and energy budgets of Snow Geese: can food on the breeding grounds influence fecundity? *Oecologia,* 106: 153–165.

Gauthier, G., 1993. Feeding ecology of nesting greater snow geese. *Journal of Wildlife Management,* 57: 216–223.

Gauthier, G., Bêty, J. & Hobson, K., 2003. Are greater snow geese capital breeders? new evidence from a stable isotope model. *Ecology,* 84: 3250–3264.

Gauthier, G. & Brault, S., 1998. Population model of the Greater Snow Goose: projected impacts of reduction in survival on population growth rate. In: *The Greater Snow Goose: report of the Arctic Goose Habitat Working Group*: 65–80 (B. D. J. Batt, Ed.). Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington, D.C. and Canadian Wildlife Service, Ottawa, Ontario.

Gauthier, G., Giroux, J.–F. & Bédard, J., 1992. Dynamics of fat and protein reserves during winter and spring migration in greater snow geese. *Canadian Journal of Zoology,* 70: 2077–2087.

Gauthier, G. & Tardif, J., 1991. Female feeding and male vigilance during nesting in Greater Snow Geese. *Condor,* 93: 701–711.

Gould, W. R. & Nichols, J. D., 1998. Estimation of temporal variability of survival in animal population. *Ecology,* 79: 2531–2538.

Hines, J. E. & Sauer, J. R., 1989. Program CONTRAST – A general program for the analysis of several survival or recovery rate estimates. Washington: *U.S. Fish and Wildlife Technical Report*, 24.

Johnson, D. H., 1979. Estimating nest success: the Mayfield method and an alternative. *Auk,* 96:

651–661.

Jolly, G. M., 1965. Explicit estimates from capture–recapture data with both dead and immigration–stochastic model. *Biometrika,* 52: 225–247.

Kendall, W. L. & Nichols, J. D., 1995. On the use of secondary capture–recapture samples to estimate temporary emigration and breeding proportions. *Journal of Applied Statistics,* 22: 751–762.

Kendall, W. L., Nichols, J. D. & Hines, J. E., 1997. Estimating temporary emigration using capture–recapture data with Pollock's robust design. *Ecology,* 78: 563–578.

Larsson, K. & Forslund, P., 1991. Environmentally induced morphological variation in the Barnacle Goose, *Branta leucopsis. Behavioral Ecology,* 2: 116–122.

Lebreton, J.–D., 1995. The future of population dynamic studies using marked individuals: a statistician's perspective. *Journal of Applied Statistics,* 22: 1009–1030.

Lebreton, J.–D., Burnham, K. P., Clobert, J. & Anderson, D. R., 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs,* 62: 67–118.

Lepage, D., Gauthier, G. & Menu, S., 2000. Reproductive consequences of egg–laying decisions in snow geese. *Journal of Animal Ecology,* 69: 414–427.

Lepage, D., Gauthier, G. & Reed, A., 1996. Breeding–site infidelity in Greater Snow geese: a consequence of constraints on laying date? *Canadian Journal of Zoology,* 74: 1866–1875.

– 1998. Seasonal variation in growth of greater snow goose goslings: the role of food supply. *Oecologia,* 114: 226–235.

Lesage, L., & Gauthier, G., 1998. Effect of hatching date on body and organ development in greater snow geese. *Condor,* 100: 316–325.

Lindberg, M. S., Kendall, W. L., Hines, J. E. & Anderson, M. G., 2001. Combining band recovery data and Pollock's Robust Design to model temporary and permanent emigration. *Biometrics,* 57: 273–281.

Lindberg, M. S., Sedinger, J. S., Derksen, D. V. & Rockwell, R. F., 1998. Natal and breeding philopatry in a Black Brant, *Branta bernicla nigricans*, metapopulation. *Ecology,* 79: 1893–1904.

Link, W. A., 1999. Modeling pattern in collections of parameters. *Journal of Wildlife Management,* 63: 1017–1027.

Mainguy, J., 2003. Déplacement des familles de la grande oie des neiges durant la période d'élevage, Ile Bylot, Nunavut. M. Sc. Dissertation, Université Laval.

Mainguy, J., Bêty, J., Gauthier, G. & Giroux, J.–F., 2002. Are body condition and reproductive effort of laying Greater Snow Geese affected by the spring hunt? *Condor,* 104: 156–162.

Menu, S., Gauthier, G. & Reed, A., 2001. Survival of juvenile Greater Snow Geese immediately after banding. *Journal of Field Ornithology,* 72:

282–290.

Nur, N. & Sydeman, W. J., 1999. Survival, breeding probability, and reproductive success in relation to population dynamics of Brandt's cormorants. *Bird Study,* 46S: 92–103.

Owen, M. & Black, J. M., 1989. Factors affecting the survival of barnacle geese on migration from the breeding grounds. *Journal of Animal Ecology,* 58: 603–617.

Pollock, K. H., 1982. A capture–recapture design robust to unequal probability of capture. *Journal of Wildlife Management,* 46: 757–760.

Pollock, K. H., Nichols, J. D., Brownie, C. & Hines, J. E., 1990. Statistical inference for capture–recapture experiments. *Wildlife Monographs,* 107: 1–97.

Pradel, R., Cooch, E. G. & Cooke, F., 1995. Transient animals in a resident population of snow geese: local emigration or heterogeneity? *Journal of Applied Statistics,* 22: 695–710.

Prévot–Julliard, A.–C., Pradel, R., Julliard, R., Grosbois, V. & Lebreton, J.–D., 2001. Hatching date influences age at first reproduction in the Black–headed gull. *Oecologia,* 127: 62–68.

Prop, J. & De Vries, J., 1993. Impact of snow and food conditions on the reproductive performance of barnacle geese Branta leucopsis. *Ornis Scandinavica,* 24: 110–121.

Reed, A., Giroux, J.–F. & Gauthier, G., 1998. Population size, productivity, harvest and distribution. In: *The Greater Snow Goose: report of the Arctic Goose Habitat Working Group*: 5–31 (B. D. J. Batt, Ed.). Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington, DC and Canadian Wildlife Service, Ottawa, Ontario.

Reed, A., Hughes, R. J. & Gauthier, G., 1995. Incubation behavior and body mass of female greater snow geese. *Condor,* 97: 993–1001.

Reed, E. T., 2003. Coûts des soins parentaux et effets des conditions environnementales sur la reproduction de la grande oie des neiges. Ph. D. Thesis, Université Laval.

Reed, E. T., Bêty, J., Mainguy, J., Giroux, J.–F. &

Gauthier, G., 2003a. Molt migration in relation to breeding success in Greater Snow Geese. *Arctic,* 56: 76–81.

Reed, E. T., Gauthier, G., Pradel, R. & Lebreton, J.–D., 2003b. Age and environmental conditions affect recruitment in greater snow geese. *Ecology,* 84: 219–230.

Reeves, H. M., Cooch, F. G. & Munro, D. E., 1976. Monitoring Arctic habitat and goose production by satellite imagery. *Journal of Wildlife Management,* 40: 532–541.

Rohwer F. C. & Anderson, M. G., 1988. Female-biased philopatry, monogamy, and the timing of pair formation in migratory waterfowl. *Current Ornithology,* 5: 187–221.

Salomonsen, F., 1968. The moult migration. *Wildfowl,* 19: 5–24.

Sauer, J. R. & Williams, B. K., 1989. Generalized procedures for testing hypotheses about survival or recovery rates. *Journal of Wildlife Management,* 53: 137–142.

Seber, G. A. F., 1965. A note on the multiple-recapture census. *Biometrika,* 52: 249–259.

– 1982. The estimation of animal abundance and related parameters. Second edition. MacMillan, New York, N.Y.

Sedinger, J. S., Lindberg, M. S. & Chelgren, N. D., 2001. Age–specific breeding probability in black brant: effects of population density. *Journal of Animal Ecology,* 70: 798–807.

Spear, L. & Nur, N., 1994. Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in western gulls. *Journal of Animal Ecology,* 63: 283–298.

Spendelow, J. A. & Nichols, J. D., 1989. Annual survival rates of breeding adult Roseate Terns (*Sterna dougalii*). *Auk,* 106: 367–374.

Tickell, W. L. N. & Pinder, R., 1967. Breeding frequency in the albatrosses *Diomeda melanophris* and *D. chrysostoma. Nature,* 213: 315–316.

White, G. C. & Burnham, K. P., 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study,* 46: S120–139.