

Population models for Greater Snow Geese: a comparison of different approaches to assess potential impacts of harvest

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Abstract

Population models for Greater Snow Geese: a comparison of different approaches to assess potential impacts of harvest.— Demographic models, which are a natural extension of capture–recapture (CR) methodology, are a powerful tool to guide decisions when managing wildlife populations. We compare three different modelling approaches to evaluate the effect of increased harvest on the population growth of Greater Snow Geese (*Chen caerulescens atlantica*). Our first approach is a traditional matrix model where survival was reduced to simulate increased harvest. We included environmental stochasticity in the matrix projection model by simulating good, average, and bad years to account for the large inter–annual variation in fecundity and first–year survival, a common feature of birds nesting in the Arctic. Our second approach is based on the elasticity (or relative sensitivity) of population growth rate (λ) to changes in survival as simple functions of generation time. Generation time was obtained from the mean transition matrix based on the observed proportion of good, average and bad years between 1985 and 1998. If we assume that hunting mortality is additive to natural mortality, then a simple formula predicts changes in λ as a function of changes in harvest rate. This second approach can be viewed as a simplification of the matrix model because it uses formal sensitivity results derived from population projection. Our third, and potentially more powerful approach, uses the Kalman Filter to combine information on demographic parameters, i.e. the population mechanisms summarized in a transition matrix model, and the census information (i.e. annual survey) within an overall Gaussian likelihood. The advantage of this approach is that it minimizes process and measured uncertainties associated with both the census and demographic parameters based on the variance of each estimate. This third approach, in contrast to the second, can be viewed as an extension of the matrix model, by combining its results with the independent census information.

Key words: Greater Snow Geese, Population model, Transition matrix, Generation time, Hunting mortality, Kalman Filter.

Resumen

Modelos poblacionales del gran ánsar nival: comparación entre distintos enfoques empleados para evaluar los impactos potenciales de la cosecha.— Los modelos demográficos, que son una ampliación natural de la metodología de captura–recaptura (CR), constituyen un excelente instrumento orientativo a la hora de decidir cómo gestionar las poblaciones de flora y fauna. Comparamos tres enfoques de modelos distintos para evaluar los efectos de una mayor cosecha en el crecimiento poblacional del ánsar nival (*Chen caerulescens atlantica*). Nuestro primer enfoque consiste en un modelo de matrices tradicional en el que se redujo la supervivencia a efectos de simular una mayor cosecha. Incluimos estocasticidad medioambiental en el modelo de proyección matricial simulando años buenos, medios y malos a efectos justificar la significativa variación interanual en la fecundidad y en la supervivencia durante el primer año, dado que constituyen una característica común de las aves que nidifican en el Ártico. Nuestro segundo enfoque se basa en la elasticidad (o sensibilidad relativa) de la tasa de crecimiento poblacional (λ) con respecto a los cambios en la supervivencia como funciones simples del tiempo generacional. El tiempo generacional se obtuvo a partir de la matriz de transición

media basada en la proporción observada de años buenos, medios y malos entre 1985 y 1998. Si suponemos que la mortalidad por caza se suma a la mortalidad natural, una fórmula simple predice cambios en la λ como una función de cambios en la tasa de cosechas. El segundo enfoque puede considerarse como una simplificación del modelo de matrices, puesto que emplea resultados de sensibilidad formal derivados de la proyección poblacional. Nuestro tercer enfoque, de mayor alcance potencial, utiliza el filtro de Kalman para combinar información sobre parámetros demográficos; es decir, los mecanismos poblacionales resumidos en un modelo de matrices de transición, y la información censal (es decir, la inspección anual) en una probabilidad gaussiana general. La ventaja de este enfoque es que minimiza los procesos y las incertidumbres medidas que se asocian, tanto con el censo como con los parámetros demográficos basados en la varianza de cada estimación. El tercer enfoque, a diferencia del segundo, puede considerarse como una ampliación del modelo de matrices, combinando sus resultados con la información censal independiente.

Palabras clave: Ánsar nival, Modelo poblacional, Matriz de transición, Tiempo generacional, Mortalidad por caza, Filtro de Kalman.

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Introduction

Demographic models based on transition matrices are a natural extension of standard capture–recapture (CR) methodology because age or stage–specific survival and fecundity parameters essential to build transition matrices are often estimated using standard CR analyses. More sophisticated CR analyses (e.g. multi–state models) are also well suited for estimating parameters such as dispersal, which are required for more complex transition matrix models like those built for metapopulations (Caswell, 2001; Lebreton & Pradel, 2002; Lebreton et al., 2003). In an applied context, population models are especially useful for the conservation of endangered species or the management of exploited species, and they can be instrumental in recommending sustainable harvest levels. In structured populations, transition matrices are widely used to model growth rate (Caswell, 2001).

In this paper, we focus on a harvested species through a case study, the Greater Snow Goose (*Chen caerulescens atlantica*) population. The Greater Snow Goose is a long–distant migrant that breeds in the eastern high Arctic of Canada and winters in temperate areas of eastern North America (Reed et al., 1998). Even though the species is hunted, its population has increased considerably over the past three decades (Menu et al., 2002). The high population growth rate (9%/yr) and the apparent lack of density–dependence have generated great concerns over the potential negative impact of overgrazing from high densities of geese on their breeding and staging habitats. Even though density–dependence may be locally important in some goose populations (Cooch & Cooke, 1991; Pettifor et al., 1998), Menu et al. (2002) failed to find any evidence for it at the population level in Greater Snow Geese. Use of food subsidy in farmlands in winter and spring may be an important factor to explain the absence of population–wide density–dependence effect in this population. This situation led to recommendations to take actions to stop the population growth as soon as possible (Giroux et al., 1998). Population models were thus developed to determine the harvest levels required to achieve management goals.

Our objective was to compare three different modelling approaches that were applied to the case of the Greater Snow Goose, and discuss their advantages and disadvantages. We show how models incorporating a functional relationship between survival and hunting mortality can be built and used to explore various harvest scenarios. Finally, we will show how the Kalman Filter, a technique rarely used in wildlife biology, can be used to improve parameter estimates of the model, and thus model projections.

Data set

Data for the Greater Snow Goose population were available from several sources. First, fecundity and survival data come from a long–term capture–recap-

ture study conducted since 1990 at the breeding colony of Bylot Island in the Canadian Arctic (see Lepage et al., 2000; Reed et al., 2003 for details). Adult survival came from a detailed mark–resight studies conducted on both the breeding and southern staging grounds, and young survival came from band recovery analyses (Gauthier et al., 2001; Menu et al., 2002). Thus, our survival estimates were not confounded by permanent emigration. Second, fall age–ratio counts have been conducted by the Canadian Wildlife Service since the early 1970s in southern Quebec. Third, accurate estimates of population size came from a spring photo inventory conducted annually since 1970 in southern Quebec by the Canadian Wildlife Service (Reed et al., 1998). Finally, harvest data was obtained from the annual National Hunter Surveys conducted by the Canadian Wildlife Service and the US Fish and Wildlife Service. We divided the total number of young or adults harvested by the fall population size to obtain an index of harvest rate in this population as explained by Menu et al. (2002). The alternative method of using band recovery rates to estimate harvest rates was not possible because band reporting rate was confounded by several factors in this population. These factors include the occurrence of band solicitation at some periods, the introduction of toll–free number bands in the course of the study, and language difference between Quebec and the US which likely affected reporting rate. Recently, however, Calvert (2004) showed a very good correlation between our harvest rate estimates and adult band recovery rates in this population, which suggests that our harvest rate index tracked fairly well annual changes in harvest.

Annual reproductive output of Greater Snow Geese is highly variable and is characterized by boom and bust years because of the short nesting season and strong environmental variability of the high Arctic. Late onset of spring is associated with a reduced probability of breeding, delayed nest initiation, and poor gosling growth and survival rates. Annual production, as indexed by fall age:ratio count, can vary by more than one order of magnitude (Gauthier et al., 1996). Environmental stochasticity is thus an important aspect of the demography of this population.

Transition matrix model

Transition matrices are relatively easy to use when assessing the effects of various harvest scenarios on population growth rates. For instance, one can empirically modify survival rates to evaluate the effects of changes in harvest rates on population growth rates (e.g. Rockwell et al., 1997). Gauthier & Brault (1998) developed a first population model for Greater Snow Geese based on a four age–class transition matrix because the age when all females have started to breed is four years in this species. They used a post–breeding census formulation (sensu Caswell, 2001) because survival rates were estimated with birds banded in late summer, shortly

before the fledging of young (i.e. the time interval is from summer to summer). The four age-classes were thus fledging young and adults 1, 2 and 3+ year old:

$$\mathbf{A} = \begin{bmatrix} 0 & S_A F_2 & S_A F_3 & S_A F_4 \\ S_Y & 0 & 0 & 0 \\ 0 & S_A & 0 & 0 \\ 0 & 0 & S_A & S_A \end{bmatrix} \quad (1)$$

where F = fecundity, S_A = adult survival and S_Y = young (i.e. first-year) survival. Fecundity was obtained as follows:

$$F = BP \cdot (TCL/2) \cdot P_1 \cdot NS \cdot P_2 \cdot P_3 \quad (2)$$

where BP = breeding propensity, TCL = total clutch size, NS = nesting success, P_1 = egg survival in successful nests, P_2 = hatching success, and P_3 = gosling survival from leaving the nest to fledging (Lepage et al., 2000).

Instead of using a single transition matrix, Gauthier & Brault (1998) used three transition matrices to characterize three different states: good (G), average (A) and bad (B) years of reproduction (hereafter called quality of reproduction). Although this categorization is an oversimplification of reality, it recognizes the large environmental stochasticity encountered on the breeding ground. The annual quality of reproduction was categorized as bad (B) when the proportion of young in the fall age-ratio counts was < 10%, average (A) when it was 10–30%, and good (G) when it was \geq 30%. Parameters that differed between the three matrices were fecundity and young survival in their first-year, S_Y (most fecundity components in equation 2 and young survival were moderately or considerably reduced in average or bad years, respectively), but not adult survival, S_A (see Gauthier & Brault, 1998 for details).

The three matrices yielded different asymptotic growth rate ($\lambda = 1.17$ for G years, 1.01 for A years and 0.84 for B years). Gauthier & Brault (1998) used Monte Carlo simulations to combine the three transition matrices in various proportions. At each yearly iteration, one matrix was randomly selected based on probabilities equal to a chosen ratio of good:average:bad years. A ratio of 6G:3A:1B years yielded a growth rate similar to the rate observed from the spring population survey over a 16-year period when the observed ratio of G:A:B years was 5:3:2. To evaluate the impact of increased harvest on population growth, they reduced the survival of adults, young, or both in each matrix by various proportions. They also explored the effect of reduced survival under various combinations of good, average or bad years. For instance, under the scenario of 6:3:1, adult survival had to be reduced from 0.83 to 0.76 to stop population growth ($\lambda = 1$) if only the harvest of adults was increased; in contrast, if only the harvest of young was increased, their survival had to be reduced from 0.42 to 0.24 to stop population growth. Using an ad hoc procedure, Gauthier & Brault (1998) estimated that stability could be achieved if harvest rates were in-

creased 1.6 times in both adults and young, 2.0 times if the harvest was increased in young only, and 2.3 times if it was in adults only (fig. 1A).

A model based on the relationship between generation time and elasticity

The approach of Gauthier & Brault (1998) implicitly assumed a direct, inverse relationship between survival and hunting mortality, i.e. that hunting mortality is additive to natural mortality. However, hunting mortality can be compensatory or additive to natural mortality, or somewhere in between (Nichols et al., 1984). Hunting mortality is compensatory to natural mortality when the risk of dying from natural causes decreases in response to increase in hunting mortality (Boyce et al., 1999). In contrast, hunting mortality is additive when the risk of dying from natural causes is independent from hunting mortality. Although these two concepts are quite simple, their analytical treatment becomes complex when both forms of mortality (i.e. natural and hunting) occur simultaneously, as it is commonly the case. Analysis of the relationship between hunting mortality and survival then involves the theory of competing risk (Anderson & Burnham, 1976; Lebreton, 2005). However, for high values of survival and moderate value of harvest, Burnham & Anderson (1984) showed that the interaction between survival (S) and harvest (H) can be approximated by the relationship:

$$S = S_0(1 - bH) \quad (3)$$

where S_0 = survival in absence of hunting (this is analogous to the equation for discrete time scale, i.e. when harvest and natural mortality do not overlap in time; Lebreton, 2005). When hunting mortality is fully compensatory, $b = 0$ and thus $S = S_0$. In contrast, when hunting mortality is fully additive, $b = 1$ and thus can be ignored.

The assumption of additive mortality provides a starting point for modelling the impact of harvest on population growth in age-structured populations. The variation in survival (ΔS) that is induced by a variation in harvest rate (ΔH) can be expressed as:

$$\Delta S = S_0(1 - (H + \Delta H)) - S_0(1 - H) = -S_0\Delta H \quad (4)$$

The relative change in survival can be expressed as:

$$\frac{\Delta S}{S} = -\frac{S_0\Delta H}{S_0(1 - H)} = -\frac{\Delta H}{(1 - H)} \quad (5)$$

Ultimately, we want to determine the impact of a change in survival ΔS induced by a change in harvest ΔH on the growth rate of the population (λ). In a transition matrix population model, the sensitivity (s) of λ to a change in the value of element a of the matrix is given by the formula (Caswell, 2001):

$$s_a = \frac{d\lambda}{da} \quad (6)$$

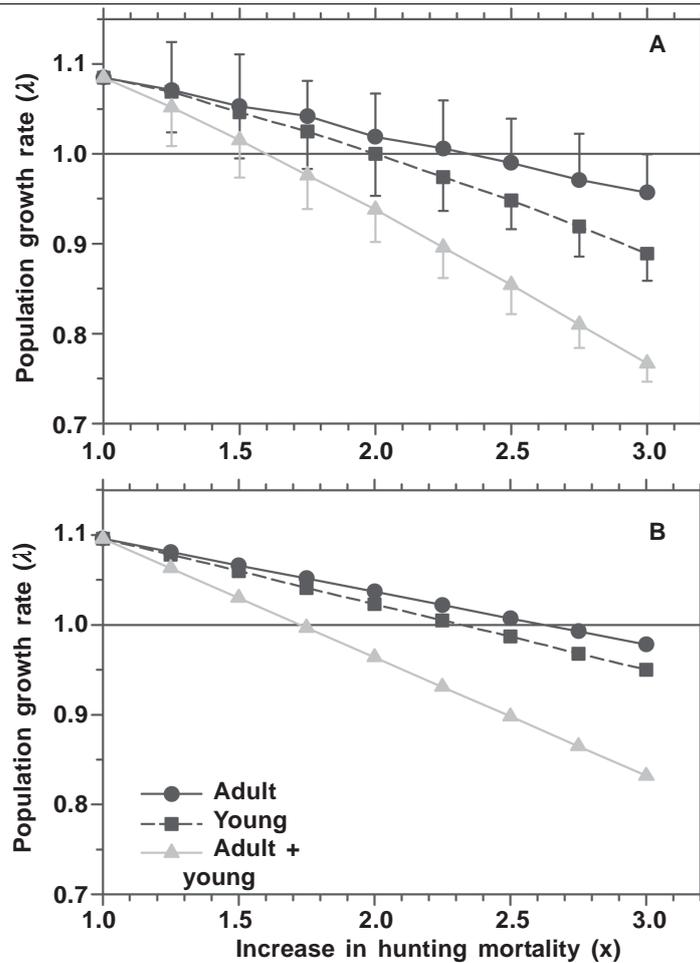


Fig. 1. Change in Greater Snow Goose population growth rate as function of various proportional increases in harvest (hunting mortality) of adults only, young only, or both: A. Model based on stochastic simulations using three different transition matrices for good (G), average (A) and bad (B) year of reproduction combined in a ratio 6G:3A:1B (approach 1; mean with 1 SE); B. Model based on the relationship between generation time of the mean transition matrix and elasticity (from fig. 2; approach 2).

Fig. 1. Cambio en la tasa de crecimiento poblacional del ánsar nival como función de varios aumentos proporcionales en la cosecha (mortalidad por caza) de adultos, jóvenes o ambos: A. Modelo basado en simulaciones estocásticas utilizando tres matrices de transición distintas para un año de reproducción bueno (G), medio (A) y malo (B) combinadas en una ratio de 6G:3A:1B (enfoque 1; media con 1 EE). B. Modelo basado en la relación entre el tiempo generacional de la matriz de transición media y la elasticidad (de la fig. 2; enfoque 2).

The change in λ induced by a change in the element a of the matrix (say, survival) is thus the product of the change in survival and the sensitivity of λ to this parameter (Caswell, 2001). Given that we have an age-structured population, we further want to separate the effects of harvesting young (i.e. first-year birds) or adults on the population. We are thus interested in changes induced by harvest on the survival of adults (S_A) and young (S_Y). We can write:

$$\Delta\lambda = s_{S_Y} \Delta S_Y + s_{S_A} \Delta S_A$$

$$\Delta\lambda = \frac{d\lambda}{dS_Y} \Delta S_Y + \frac{d\lambda}{dS_A} \Delta S_A \tag{7}$$

The relative change in λ is given by:

$$\frac{\Delta\lambda}{\lambda} = \frac{S_Y}{\lambda} \frac{d\lambda}{dS_Y} \frac{\Delta S_Y}{S_Y} + \frac{S_A}{\lambda} \frac{d\lambda}{dS_A} \frac{\Delta S_A}{S_A} \tag{8}$$

in the last equation, we note that $S/\lambda \cdot d\lambda/dS$ is the

elasticity (e), i.e. the proportional change in λ induced by a proportional change in survival (Caswell, 2001). Lebreton & Clobert (1991) showed that there is a simple and direct link between generation time (T) and the elasticity of λ with respect to fecundity and adult survival. Several definitions of generation time exist but the most meaningful one here is the *mean generation time* (\bar{T}), which can be defined as the mean age of the parents of all offspring produced at the stable age distribution. This statistic can be easily calculated from a transition matrix model. The elasticity of λ with respect to fecundity and first-year survival is equal to $1/\bar{T}$ and the one of adult (i.e. after-first year) survival is equal to $1 - 1/\bar{T}$ (fig. 2). Finally, we can substitute the expression $\Delta S/S$ by its equivalent in term of harvest (equation 5) and thus obtain:

$$\frac{\Delta\lambda}{\lambda} = \frac{1}{\bar{T}} \left(-\frac{\Delta H_y}{1-H_y} \right) + \left(1 - \frac{1}{\bar{T}} \right) \left(-\frac{\Delta H_A}{1-H_A} \right)$$

$$\Delta\lambda = - \left[\frac{1}{\bar{T}} \left(\frac{\Delta H_y}{1-H_y} \right) + \left(1 - \frac{1}{\bar{T}} \right) \frac{\Delta H_A}{1-H_A} \right] \lambda \quad (9)$$

Equation (9) provides a simple and straightforward way to assess the impact of harvest rates on population growth. The equation can be generalized by including a term for fecundity (F). This generalization can be useful when harvest affects fecundity in addition to survival (e.g. due to egg harvesting). Equation (9) then becomes:

$$\Delta\lambda = - \left[\frac{1}{\bar{T}} \left(\frac{\Delta H_y}{1-H_y} \right) + \left(1 - \frac{1}{\bar{T}} \right) \frac{\Delta H_A}{1-H_A} + \frac{1}{\bar{T}} \frac{\Delta F}{F} \right] \lambda \quad (10)$$

If F varies across age classes, one can use a mean fecundity weighed by the stable age distribution.

To apply this approach to Greater Snow Geese, we first calculated a mean transition matrix for the period 1985–1998 to account for the annual environmental stochasticity. For each year, we had a known Q_i quality of reproduction (Q_p , good, average or bad) and the realized harvest rate (H_p , from Menu et al., 2002). Each value of Q_i had a corresponding set of age-specific fecundity parameters. Adult survival was defined as a function of annual harvest rate, i.e. $S_A = f(H_p)$. We thus generated 14 different matrices for the period 1985–1998, filling up the elements of each matrix with the elements of vectors Q_i and H_p . The mean transition matrix was:

$$\bar{\mathbf{A}} = \begin{bmatrix} 0 & 0.129 & 0.284 & 0.350 \\ 0.865 & 0 & 0 & 0 \\ 0 & 0.865 & 0 & 0 \\ 0 & 0 & 0.865 & 0.865 \end{bmatrix}$$

$$= \begin{bmatrix} 0 & F_2 S_y & F_3 S_y & F_4 S_y \\ S_A & 0 & 0 & 0 \\ 0 & S_A & 0 & 0 \\ 0 & 0 & S_A & S_A \end{bmatrix} \quad (11)$$

A pre-breeding formulation is here preferred

over a post-breeding one (e.g. see equation 1) in order to have all "first-year" elements (i.e. fecundity and young survival) in the first line of the matrix as it is the elasticity of λ to those elements that is related to $1/\bar{T}$ (fig. 2). This mean matrix yielded an asymptotic λ of 1.096, which was similar to the realized growth rate of the population over the same period based on the spring census (1.094), and a mean generation time of 6.446. Using the mean harvest rate observed on adults (0.06) and young (0.30) during 1985–1998, we increased the harvest of young and adult by various factors (fig. 1B). According to this model, population growth could be stopped if the current harvest level was increased by 1.75 times on both adults and young, 2.3 times on young only, and 2.7 times on adults only.

Improving the parameter estimates: integrated modelling using the Kalman Filter

In the two previous approaches, models were validated by comparing the projected growth rates with the realized rates estimated by the annual spring survey. Although this is a standard procedure in the literature, it is an *ad hoc* one that has no formal basis (Lebreton & Clobert, 1991). This procedure also ignores the variance associated with both the demographic parameters and the survey. An alternative is the Kalman Filter (Kalman, 1960; Kalman & Bucy, 1961), a more robust approach that combines both sources of information, that is demographic data (i.e. transition matrix) and census data (i.e. annual survey).

For each time step, the filter calculates the best estimate using both the prediction generated by the model (called a state equation) and the actual population measure (Harvey, 1989). Thus, when model prediction differs from the survey estimate, the filter updates the model parameters to find the best likelihood-based compromise between the prediction and the survey estimate based on the measurement errors of model parameters and survey estimates. The overall likelihood is the product of the Kalman Filter likelihood, as a function of the parameter values, and the capture-recapture likelihood. The former contains the information on parameters brought by the census, the second that brought by capture-recapture data. In that sense, the Kalman Filter does not privilege one source of information over the others and gives them weights directly linked to the amount of information they contain. This approach was proposed by Besbeas et al. (2002) for integrating matrix-based population model and census information. Besbeas et al. (2003) further described a normal approximation that maximized the likelihood of the Kalman Filter (see also Morgan et al., in prep.).

In our case, the state equation was the transition matrix model:

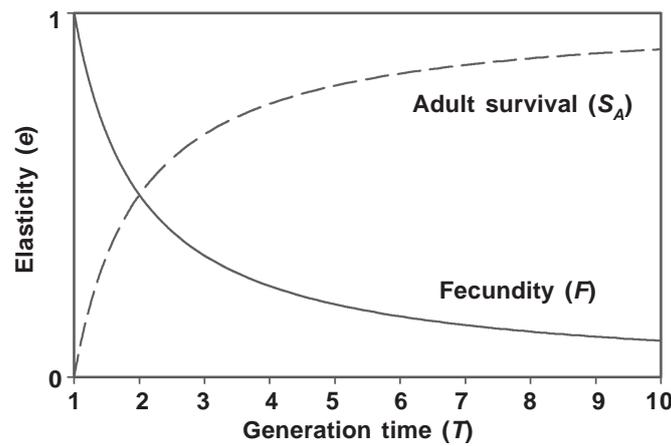


Fig. 2. Elasticity of the asymptotic growth rate (λ) with respect to adult (i.e. after–first year) survival and fecundity as a function of generation time (Lebreton & Clobert, 1991).

Fig. 2. Elasticidad de la tasa de crecimiento asintótico (λ) respecto a la supervivencia de los adultos (i.e. despues del primer año) y fecundidad como función del tiempo de generación (Lebreton & Clobert, 1991).

$$N_{t+1} = \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & F_2 S_Y & F_3 S_Y & F_4 S_Y \\ S_A & 0 & 0 & 0 \\ 0 & S_A & 0 & 0 \\ 0 & 0 & S_A & S_A \end{bmatrix}_t \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix}_t + \varepsilon_t$$

$$= G_t(\theta)N_t + \varepsilon_t \tag{12}$$

where ε_t is a random term for departure from the model, incorporating in particular demographic stochasticity (see Besbeas et al., 2002), distinct form uncertainty in parameters. The observation equation was the census of the total population, $y_{(t)}$ (i.e. spring inventory of the population, from Reed et al., 1998 and unpublished data):

$$y_{(t)} = \sum N_{i(t)} + \eta_{(t)} = (1111)N_{(t)} + \eta_{(t)} \tag{13}$$

where $\eta_{(t)}$ is a random variable for census uncertainty. We assumed a constant coefficient of variation for the census, i.e. $\text{Var}(\eta_{(t)}) = y_{(t)}^2 c^2$ where c is the coefficient of variation of the census.

The key relationship in the state equation relates adult survival to harvest rate. Gauthier et al. (2001) empirically estimated the parameters of this relationship using a complex CR analysis of live recaptures of adult Greater Snow Geese throughout the year. In their analysis, they modeled the relationship

$$S = (a - bH)/r$$

where r is a parameter to account for band loss (in this equation, b has a slightly different meaning than

in the equation $S = S_0(1 - bH)$ as here it is the product bS_0). We used this equation to define adult survival in the state equation, i.e. we substituted S_A by $(a - bH)/r$ in the transition matrix. The other elements of the matrix (fecundity and young survival) were similar to those used in the previous modelling approach (equation 11) and considered to be constant (i.e. we assumed no measurement error as a first approximation). The measurement error associated with the census information, $y_{(t)}$, was the coefficient of variation (c) associated with the population survey, which is a further parameter to be estimated, brought into the overall likelihood by the combination of the state and census equations inherent in the Kalman Filter. We used the approach described by Besbeas et al. (2003) to maximize a combined likelihood function with four parameters, $L(a, b, r, c)$. Complete results are developed in Gauthier, Besbeas, Lebreton and Morgan (in prep.). In particular, the results were quite insensitive to various reasonable choices for the initial population size and structure and its standard error.

When we applied the Kalman Filter to the data for the period 1985–2002, the ML estimates of r , a , and b only changed slightly compared to the initial values taken from Gauthier et al. (2001), with a slight improvement in precision (table 1). The similarity between the updated estimates and the initial values indicates that the census information was compatible with the demographic information as built into the transition matrix model. The estimated CV of the censused population size, which is a further parameter estimated by the Kalman Filter besides the CR parameters, was equal to 0.199.

This value was larger than the estimated CV of the survey (~0.10, Béchet et al., 2004) but compatible with it because of its large standard error. The model predictions generally tracked the observed changes in population size much better than the transition matrix model alone based on the initial parameter values (fig. 3).

The change in survival estimates, although small, has nevertheless a strong effect on the quality of population projections. The weakness of the increase in precision is not surprising for two reasons. First, the overall good compatibility between the census and the capture–recapture information on survival induces only a slight change in estimates within their capture–recapture based confidence interval. Second, the estimated CV of the survey clearly limits the amount of information on survival processes brought in by the census data.

Discussion

The modelling approaches we described are prospective, i.e. they attempt to evaluate the impact of changes in survival rate induced by variations in harvest rates on population growth rate (Caswell, 2000). The standard approach of empirically varying survival rates in a transition matrix is simple and straightforward. In this case, the impact on λ is directly related to the elasticity of the parameter (as shown above) and thus can easily be derived analytically. The model of Gauthier & Brault (1998) also attempted to capture in the model the very high variance in annual fecundity and survival of young typical of species living in highly unpredictable environments like the Arctic. Their model recognized three environmental states and at each time t a state was randomly chosen, assuming independence between each state. More complex models with dependence between environmental states (i.e. state at time $t+1$ depends of state at time t) are possible (Caswell, 2001) but were not considered for Greater Snow Geese given the low correlation found between environmental states (Gauthier, unpubl. data).

In stochastic models, the effect of changes in survival on λ can not be obtained directly from the elasticity values but must be evaluated through simulations using the stochastic growth rate estimator (Tuljapurkar, 1990; Caswell, 2001). However, care must be used when calculating the growth rate in stochastic simulations. For instance, we later found that the stochastic simulations of Gauthier & Brault (1998) were slightly biased. This bias was uncovered when the three matrices were recast into a pre–breeding census using the same demographic parameters. The asymptotic growth rate of each matrix remained the same (as it should be), but we obtained a different stochastic growth rate. For instance, when running 10,000 simulations of 10,000 time steps with a 6:3:1 ratio of G, A and B years, the stochastic growth rate for a pre–breeding formulation was 1.094 (1.092–1.096, 95% CI) compared to 1.071 (1.068–1.074) for a post–breeding formulation (calculated with ULM, Legendre & Clobert, 1995;

Table 1. Initial parameter values for the relationship $S = (a - bH)/r$ estimated by Gauthier et al. (2001) and Kalman Filter values obtained from the approximate combined likelihood analysis (Mean \pm SE): P. Parameter; I. Initial values; KF. Kalman Filter values.

Tabla 1. Valores de parámetros iniciales para la relación $S = (a - bH)/r$ estimada por Gauthier et al. (2001) y valores del filtro de Kalman obtenidos a partir del análisis aproximado de probabilidades combinadas (Media \pm EE): P. Parametro; I. Valores iniciales; KF. Valores del filtro de Kalman.

P	I	KF
r	0.950 \pm 0.008	0.943 \pm 0.007
a	0.926 \pm 0.022	0.935 \pm 0.018
b	1.207 \pm 0.560	1.100 \pm 0.524
c		0.199 \pm 0.190

Gauthier, unpubl. data). Cooch et al. (2003) showed that this difference was due to significant covariation among matrix elements, i.e. that years of low fecundity also have low survival of young. In a typical post–breeding formulation, this covariation is broken because the survival of young born in year i is found in the matrix selected for the next time step. Seasonal matrices must then be used to solve this problem (Cooch et al., 2003).

Our modelling based on the relationship between generation time and elasticity conveniently summarized the link between harvest rate and λ in a simple equation. This is advantageous because, for managers who want to set harvest levels to reach specific management goals, harvest is the variable of primary interest, not survival. Our model assumes that hunting mortality is additive to natural mortality. In adult Greater Snow Geese, Gauthier et al. (2001) provided evidence, based on live recaptures of marked birds throughout the year, that hunting mortality is additive. This is probably a robust result for long–lived species like geese because their low natural mortality rate ($\leq 10\%$, Gauthier et al., 2001) does not allow much room to compensate for additional mortality due to harvest (see also Francis et al., 1992; Rexstad, 1992). In cases where some compensation in hunting mortality occurs (i.e. $b < 1$ in the equation $S = S_0(1 - bH)$), the model can be modified to accommodate a different value of b (see Lebreton, 2005). However, this assumes that a precise estimate of b is available, which is rarely the case. Hence, in many circumstances, one may be forced to assume the default value of 1 for b and use the equation presented here as an approximation. The model based on generation time cannot account for

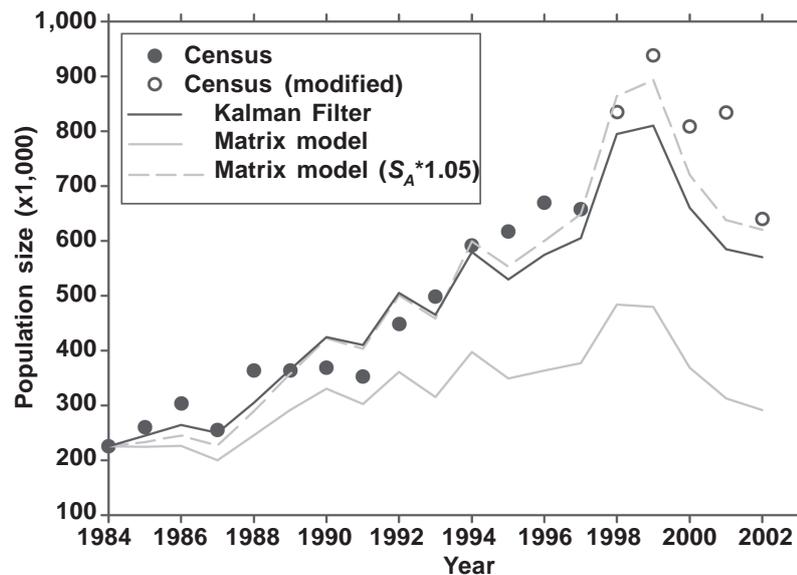


Fig. 3. Trajectory of population size over time predicted by the Kalman Filter, the matrix model alone, the matrix model when adult survival has been increased by 1.05x, and measured by the spring photographic inventory (census). From 1998 onward, the census method changed (see text).

Fig. 3. Trayectoria del tamaño poblacional a lo largo del tiempo, prevista por el filtro de Kalman, por sólo el modelo de matrices, y por el modelo de matrices cuando la supervivencia de los adultos se ha visto incrementada en 1,05x y cuando ha sido medida por el inventario fotográfico primaveral (censo). A partir de 1998, el método censal cambió (véase el texto).

environmental stochasticity in the same way that Gauthier & Brault (1998) did in their model. As an alternative, we used a mean matrix for Greater Snow Geese, which provided a good approximation of the observed growth rate for the population over the period considered.

One counterintuitive result that came out from this modelling approach and the previous one is that the same proportional increase in the harvest rates of young has slightly greater impact on population growth rate than when applied to adults. This result is surprising because adult survival has the highest elasticity (0.84). The reason is that the actual harvest rate is much higher in young than in adults. For the period of reference (1985–1998), the mean harvest rate of adults was only 0.06 compared to 0.33 in young, more than a five-fold difference (Menu et al., 2002). This reflects the fact that young are much more vulnerable to hunting than adults in geese due to their inexperience (Menu et al., 2002; Calvert, 2004). Hence, a doubling of harvest in young means a far greater increase in absolute number of birds killed than in adults.

Our approach based on generation time can be viewed as a simplification of the matrix model approach because it uses formal sensitivity results derived from population projection. In contrast, the approach based on the Kalman Filter can be viewed as an extension of the matrix model that combined

model results with the independent census information. The greatest advantage of the Kalman Filter is that it attempts to incorporate uncertainties associated with both the census and demographic parameters based on the variance of each estimate. Our application of the Kalman Filter was centered on the parameters of the equation relating adult survival to harvest, $S = (a - bH)/r$, with an additional parameter (r) accounting for marker loss. The parameter values updated by the filter differed only slightly compared to the initial values estimated by Gauthier et al. (2001) and the difference was greatest for b , as expected given that this parameter had the lowest precision. The updated value of b (1.10) in the relation $S = (a - bH)/r$ is closer to the theoretical slope of 0.93 (i.e. the value of parameter a) expected for complete additivity of hunting mortality than the initial value of 1.21. This reaffirms the original conclusion of Gauthier et al. (2001). The Kalman Filter may be especially useful in situations where the slope parameter (b) is poorly known or in situations where hunting mortality can be partly compensatory (i.e. $0 < b < 1$). The updated parameter values generated by the filter can thus provide information on the extent of compensatory mortality occurring in the population.

The Kalman Filter dramatically improved the prediction of the model compared to the transition matrix alone as judged by the correspondence be-

tween the prediction and the observed population size. Although the fit appears poorer for the most recent years, part of the discrepancy results from a change in the survey method starting in 1998. A telemetry study conducted in 1998–2000 showed that the survey underestimated the true population (Béchet et al., 2004) because it increasingly missed some flocks as the population expanded. The survey method was thus definitively modified in 2001 to reduce this negative bias. The reduction of the value of parameter b by the Kalman Filter indicates that the impact of hunting on survival may have been slightly overestimated, and thus adult survival underestimated. Even though this underestimation was slight, and quite within the confidence interval of the parameter estimated by the CR analysis, it nonetheless had a large impact on the model prediction. This is not surprising given the very high sensitivity of λ to adult survival. An *ad-hoc* increase of 5% in adult survival in the transition matrix model alone yielded a prediction almost identical to the one obtained by the Kalman Filter (fig. 3), further suggesting that the impact of hunting on survival was slightly overestimated.

In our application of the Kalman Filter, we ignored the error associated with the fecundity and young survival rates for simplicity. We expected that the bias would be slight given the very low elasticity of these parameters compared to adult survival (the combined elasticity of fecundity and young survival is only 0.16 compared to 0.84 for adult survival). Subsequent analyses suggested that inclusion of the error associated with fecundity had a negligible effect on the model results (Gauthier et al, in prep.).

Concluding remarks

We believe that our second modelling approach based on the relationship between generation time and elasticity provides a simple mean to directly model the impact of harvest rate on population growth rate and we recommend its use. This minimally requires some demographic parameters and harvest rate data. Projections from the model can easily be used by managers to evaluate the effect of various harvest scenarios on population growth rate. In the case of the Greater Snow Goose where the initial goal was to stop population growth, one can directly estimate the harvest rate of adults, young, or both needed to reach this goal (fig. 1). Even though we used a mean matrix and thus ignored the stochastic component of fecundity modeled by Gauthier & Brault (1998), predictions from this model were similar to those of their more complex stochastic model. Implementation of changes in harvest regulations will of course result in perturbations that will affect generation time and thus model predictions; hence, updated parameter values will eventually be required in the transition matrix. However, this is inherent to any prospective analyses based on elasticity (Caswell, 2001).

When census information is available, the Kalman

Filter allows a formal integration of independent information from the survey into the model, and this improved model predictions. The updated parameter values of the relationship between survival and harvest (a , b and r) generated by the filter could, in turn, be used to improve projections of the impact of variations in harvest rate on population growth rate using our second approach. For the case of the Greater Snow Goose, doing that did not change markedly the projections shown in fig. 2B, probably because parameter values were relatively well estimated to start with. However, in an adaptive management framework (Walters, 1986), a more sensible way to use the Kalman Filter would be to generate projections one-step at a time; e.g., based on the current year production and the latest survey figure, one can project the next year population for various harvest scenarios and choose the scenario that matches most closely the population goal. By doing that on an annual basis, the model constantly updates its parameters, and hence should improve the quality of predictions over time (see Fonnesebeck & Conroy, 2004 for a similar approach). We are currently implementing this predictive component in the Greater Snow Goose model.

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