

**Hugh Boyd  
(editor)**

# **Population modelling and management of Snow Geese**

**Occasional Paper  
Number 102  
Canadian Wildlife Service**



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## Foreword

This Occasional Paper is unusual in consisting of three separate but related papers. The analysis by Dr. Charles Francis of the relative impact of hunting in the spring, compared with the conventional hunting seasons in fall and winter, was originally commissioned for the purpose of improving managerial understanding of the impact of spring hunting by indigenous peoples in northern Canada. This updated version is immediately relevant to the questions addressed in the other two papers.

The paper by Cooke et al. is a greatly revised and expanded version of one read by Professor Cooke at an international meeting on goose management held in Zwolle, Netherlands, in November 1997. In it, Cooke commented on the model and the choice of parameters that had been used by Rockwell et al. (1997) in a paper published in *Arctic ecosystems in peril* (Batt 1997), which provided the underpinning for the argument in that report that a great increase in the hunting kill of mid-continent Lesser Snow Geese *Anser caerulescens caerulescens* (hereafter referred to as Snow Geese) was required first to slow down and then to reverse the rapid and sustained increase in the numbers of those geese. The chief purpose of such a reduction was to end the locally severe damage being inflicted by the geese on the vegetation of coastal wetlands along the west side of Hudson Bay.

Cooke argued that, although the model used by Rockwell et al. (1997) was basically sound, they had used obsolete or erroneous values for some of the key parameters. He showed that if updated values were used, the estimated numbers of adult geese that it would be necessary to remove from the population in order to end its growth might be much larger than Rockwell et al. (1997) had suggested.

Having heard Cooke's paper, I thought it would be of value to publish it, after peer review, so that administrators and biologists in the relevant regions of Canada and the United States could consider the practical implications of the widely different alternative projections being put forward. I also encouraged further debate between Rockwell and Cooke and their associates, in the belief that it might help to clarify the issues.

Meanwhile, the recommendations by Batt (1997) have been adopted, after extensive consultations, by the Canadian and U.S. regulatory agencies, have survived a

Canadian court challenge, and began to be given effect in the spring of 1999. (Scientific peer review and administrative processes rarely work in synchrony.) In addition to asking Professor Ankney to act as a referee, I offered Dr. Rockwell the opportunity to counter Cooke's claims. It is unorthodox to see an author and a referee collaborating in writing a response to criticisms of the paper that started this controversy. But I believe that it may be useful, to regulators and managers, as well as to scientists, to set out the alternative views. The debate here hinges on biologists' judgments about the merits of different values of key parameters in a population model. Their choices cannot be strictly "objective," because everyone brings different biases with them, depending on their experiences and beliefs. This is why it is necessary to canvass a wide variety of scientists, as well as other "interested parties," before making major decisions.

The importance of this particular case is that a major change in regulations — the authorization of spring shooting by nonnative hunters — was reintroduced, after more than 80 years, on the basis of results from a population model that contained some unreliable estimates. Rockwell and Ankney now claim that their revised target number of geese that must be shot in order to end the population increase is well within reach, after the changes in regulations that have already been put in place in the United States, where there has been a resurgence of interest in waterfowl in the last five years, quite apart from the special case of Snow Geese. However, Cooke et al., without commenting on the feasibility of achieving the goal, caution that, because of uncertainties in the best available estimates of population parameters for Snow Geese, the required harvest could still be up to twice as high as the revised numbers now accepted by Rockwell and Ankney. It must be several years before the outcomes of the general and the specific changes in regulations can be assessed with confidence.

This is a most unusual case, involving a decision to reduce the size of an animal population, not because of any detrimental effects on human economic interests,<sup>1</sup> but in order to protect an Arctic ecosystem, in which there had hitherto been no wide public interest. Far more often, the concern of conservation agencies and groups, within and outside governments, is to ensure the preservation of

<sup>1</sup> But note that attempts to increase the kill of Greater Snow Geese *Anser caerulescens atlanticus* in Quebec are intended to reduce their damage to agricultural crops in spring, not their damage to Arctic ecosystems.

threatened species or populations of animals or plants, especially those of which many people happen to have become aware. In that context, the technique called “population viability analysis” has become fashionable in several countries. That approach, like the one dealt with here, asks regulators to make decisions based on the use of population models. What emerges from the papers presented here is that there are considerable risks in making any management decision that relies on a single choice among many possible numerical solutions derived from such models. The decision-making process should always involve careful peer review of recommendations derived from the products of modelling before any important decisions are made. If this collection of papers increases awareness of the need for caution, it will have been useful.

Many other considerations in addition to scientific ones are involved in environmental policy making and decision making. Scientists can play their parts by providing the best available information and advice. That will rarely be as complete and reliable as they would wish, but making a “best guess” is much better than remaining aloof because perfection has not been achieved.

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Hugh Boyd  
Ottawa, Ontario  
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# The relative impact of a spring hunt on Snow Goose population dynamics

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## Abstract

Interest in the effect of spring hunting on goose population dynamics has arisen recently in two quite different contexts: measuring the impact of spring harvests by aboriginal hunters, and predicting the potential for using spring harvest to control populations. I developed a matrix-based population model to quantify the relative impact of spring versus autumn harvests on the population dynamics of Lesser Snow Geese *Anser caerulescens caerulescens* nesting around the Hudson Bay lowlands. Key parameters affecting the conclusions of the model were the relative vulnerability of young and adults in each season and the proportion of adults losing mates in spring that subsequently fail to breed or have reduced breeding success. With a range of assumptions about these parameters, the estimated impact of a spring harvest was between 1.1 and 1.5 times the impact of shooting the same number of birds in early autumn. The relative impact would be greater if the spring harvest were directed at breeding adults and reduced if it were directed at young geese. If it becomes necessary to set quotas for aboriginal hunters, these results can be used to apportion the harvest between spring and autumn. These results can also be used, in conjunction with estimates of the likely success rates of hunters, to predict the value of spring harvest as a tool to control goose populations. If such a harvest is planned, additional research is needed to determine the relative vulnerability of young and adults in spring, as well as the effects of mate loss in spring on breeding success.

## 1. Introduction

The nonaboriginal hunting season for waterfowl in North America is currently restricted to autumn and early winter by the Migratory Birds Convention, 1916. This timing was selected because the numbers of full-grown birds, assuming a successful breeding season, are at a maximum then, with many young birds available for harvest. Some birds harvested in autumn would otherwise have died of natural causes before the next breeding season. In addition, some species of waterfowl appear to show compensatory mortality, such that nonhunting mortality rates are reduced as a result of hunting mortality (Nichols 1991b). Finally, the likelihood of disrupting future breeding through breaking up pair bonds or disturbing feeding birds will be minimal at this time.

Recently, interest in a spring hunt for certain populations of Arctic-nesting geese has arisen in two quite different contexts. The first involves subsistence harvest in spring by aboriginal peoples in Canada. In this case, there is concern that spring harvest could have adverse impacts on some populations of geese, such as Canada Geese *Branta canadensis* nesting in northern Quebec, which appear to have declined recently (Canadian Wildlife Service Waterfowl Committee 1998).

The second involves a spring hunt as part of an effort to reduce the size of certain populations of geese, particularly the mid-continent population of Lesser Snow Geese *Anser caerulescens caerulescens* (hereafter called Snow Geese). This population has grown severalfold over the past few decades and is now severely damaging areas of the Arctic salt-marsh ecosystem (Abraham and Jefferies 1997). Recent calculations indicate that a large increase in the harvest would be required to reduce the population to acceptable levels within a reasonable time period (Cooke et al., this volume). Because it is unlikely that such an increase could be achieved within current regulatory frameworks, several measures have been suggested to increase the harvest. These include allowing a spring harvest. If spring hunting has a proportionately greater impact on population growth, then fewer birds would need to be harvested in spring than in fall to achieve the same reduction in population growth.

It is important to estimate quantitatively the effect of spring hunting on goose population dynamics, in order to make wise decisions about the use of a spring hunt as a management tool. For example, a spring hunt of Snow Geese to reduce population size may be more readily justified if it, in conjunction with other planned control measures, has a high likelihood of reducing the number of geese to the point that habitats are no longer being damaged. With respect to aboriginal harvest, if it became necessary to set quotas, differences in the impact of harvests in different seasons could be used to apportion the harvest between seasons.

Most analyses of the impact of hunting on waterfowl populations have been based on the relatively well monitored nonaboriginal hunt in autumn and winter. Thus, one way to estimate the impact of a spring harvest is to compare its impact with that of an autumn harvest. This can be done by using population models to estimate the impact of shooting one bird in spring relative to that of shooting one bird in autumn. If there were no difference between a spring and an autumn hunt, then models could be based on total numbers of



birds harvested, without consideration of when they were harvested. If shooting a bird in spring had twice the impact of shooting a bird in autumn, then twice as many birds could be harvested in autumn than in spring for a given impact on population growth rate.

There are several factors that could influence the relative impact of spring and autumn hunting. As noted above, some waterfowl species appear to show compensatory mortality, in that natural mortality is lower in years of higher hunting mortality (Nichols 1991b). If this occurs because of density-dependent mechanisms on the wintering grounds, or if most natural mortality occurs during winter, then a spring hunt would lead to less compensatory reduction in natural mortality than an autumn hunt. Quantifying this effect would require detailed knowledge of mechanisms and timing of compensatory mortality. These are currently not understood for any waterfowl species (Nichols 1991b). For most populations of geese that have been studied, however, hunting mortality appears to be largely additive to other forms of mortality, with no evidence of compensatory mortality (Francis et al. 1992a; Rexstad 1992). Thus, in this paper, I shall assume strictly additive mortality.

A second factor that differs between spring and autumn is population size, which is lower in spring because of mortality, both hunting and natural, during winter. Thus, one goose in spring is a greater proportion of the population than a goose in autumn, and killing a fixed number of geese in spring represents a higher kill rate than killing the same number in autumn. With respect to mortality due to hunting, the last bird shot in a particular season is a greater proportion of the remaining population than the first, but this is not a seasonal effect (it would apply equally if all the harvest was on the same day). To evaluate seasonal effects, per se, it is only appropriate to consider seasonal declines in numbers associated with natural mortality.

A third factor that could differ between the seasons is the relative vulnerability of age classes. In autumn, at least in the nonnative hunt, young geese are killed disproportionately. This is presumably because they are less wary and less skilled at avoiding hunters, although selection by hunters of young birds (which may be preferred for eating) could be involved. By spring, surviving young birds may have become more wary, reducing their vulnerability relative to adults. Alternatively, if young birds have become independent from their parents, they may again become more vulnerable, but probably less so than in autumn. For long-lived species such as geese, which do not breed until they are two or more years old, shooting a young bird has substantially less impact on population growth than shooting a breeding adult, regardless of time of year.

Finally, hunting has indirect consequences, such as disruption of social groups and feeding, which could have a greater impact in spring than in autumn. Geese pair for life, with most pair formation apparently occurring in winter and early on spring migration (Cooke et al. 1975). Females losing mates in spring may fail to breed or may have reduced nesting success that year, because of failure to find a new mate or nesting with an inexperienced partner. Disturbances associated with hunting could affect the ability of birds to feed and store nutrient reserves. Insufficient nutrient reserves could increase vulnerability to other forms of mortality at any time of year. In spring, reduced nutrient reserves could affect reproductive output, especially because geese may be

dependent on stored nutrients for breeding (Ankney and MacInnes 1978).

The most conclusive way to evaluate different harvest regimes would be to alter experimentally the harvest patterns and measure the response of the population. Such an approach would simultaneously integrate all factors and lead to rigorous testing of hypotheses about population dynamics (Nichols 1991a). However, such an approach has several disadvantages. First, it would be highly disruptive to the current harvest and may be socially unacceptable. Second, production of young by Arctic-nesting waterfowl varies considerably from year to year owing to weather and other variables, so that any experiment would need to be run for several years to evaluate different conditions. Finally, it is difficult to measure either population size or survival rates with much precision, so, again, many years would be required to detect the effects of an experiment. Over a period of several years, many uncontrolled factors may change, obscuring the results of the experiment. Furthermore, if the effects were detrimental, much damage might be done before it was detected.

For these reasons, it is both necessary and appropriate to use models to estimate the effects of different harvest regimes on population growth. Even if an experiment were contemplated, it would be wise to use models to predict the potential impact, as an aid to experimental design. In this paper, I develop a general method for estimating the relative impact of harvests at different times of year on populations, using stage-based matrix population modelling techniques (Caswell 1989). I then use this approach to model harvests based on data from the population of Snow Geese nesting around the Hudson Bay lowlands. This species was chosen for three reasons. First, it is the species for which there is a particular concern about overpopulation. Second, it forms a substantial proportion of the waterfowl harvest for many aboriginal people in northern Quebec and Ontario, particularly Cree living along the shores of James Bay (Boyd 1977; Prevett et al. 1983; Wesley 1993). Finally, relatively good data are available on demographic parameters such as production rate and survival rate, particularly from the pioneering studies of Graham Cooch (1958, 1961) at colonies on Baffin and Southampton islands and the long-term studies of Fred Cooke and his associates at La Pérouse Bay (LPB) in Manitoba (Cooch et al. 1989, 1991; Francis et al. 1992a,b; Rockwell et al. 1993; Cooke et al. 1995).

Before developing a model, it is important to consider the definitions of a spring hunt and an autumn hunt. With respect to aboriginal hunting on northern staging areas, these differences are clear, because autumn is limited to August to mid-October, and spring to April to June. For the non-aboriginal hunt, the "autumn" season actually extends through winter, with dates ranging from September through 10 March, although the precise dates of the season vary among localities. For modelling purposes, I have contrasted a hunt that takes place on 1 September with a hunt that takes place on 1 May. This approximates differences between the autumn and spring hunts by aboriginal peoples and estimates the maximum seasonal differences. The difference between a spring hunt in April and a hunt in early March at the end of the current nonaboriginal season would be substantially less. I consider this more in the discussion.

In this paper, I highlight parameters that have a strong effect on the model and indicate areas for which more data are required to refine the models. To the extent that

demographic parameters are similar, the results are likely to be directly relevant to Canada Geese, the other species that is particularly important in the harvest by aboriginal people around James Bay and Hudson Bay. The models could readily be adapted to accommodate differences in demography for other species of geese, although developing similar models for ducks would require addressing the issue of compensatory mortality.

## 2. Methods

Population dynamics were modelled using stage-classified matrix methods (Caswell 1989), with a one-year projection interval, reflecting the annual breeding cycle of geese. Birds were grouped into five classes based on their age on 1 September, with the final stage representing birds four years or older. The census date was chosen to reflect the population available for harvest at the beginning of the season, but the same results would have been obtained with any other projection date, provided the parameters were adjusted accordingly. Survival rates differ for goslings, yearlings, and older birds, but do not differ measurably with age beyond the second year (Francis et al. 1992b). Snow Geese do not breed until they are at least two years old, and the proportion of female geese breeding and the mean number of young they raise to fledging increase until their fifth summer (Rockwell et al. 1993). For geese at LPB, productivity declined for older birds, but it is unclear whether this was due to physiological factors or was a consequence of use of traditional nesting areas that have been degraded as a result of rapid colony growth and consequent overgrazing (Rockwell et al. 1993). Because it may not be valid to generalize the results to other colonies, I have simplified the model by assuming that productivity remains constant after the fifth summer and used a mean value for older birds.

To estimate the impact of spring and autumn harvests, I set up a model in which a harvest took place either in early September or in early May. Assuming that hunting mortality is largely additive to other forms of mortality in geese (Francis et al. 1992a; Rexstad 1992), I modelled annual survival ( $S$ ) for age class  $i$  with the equations

$$S^i = (1 - H_{\text{autumn}}^i) \times (1 - M_{\text{winter}}^i) \times (1 - M_{\text{summer}}^i)$$

for the autumn harvest and

$$S^i = [(1 - M_{\text{winter}}^i) - H_{\text{spring}}^i] \times (1 - M_{\text{summer}}^i)$$

for the spring harvest, where  $M_{\text{winter}}^i$  represents natural mortality from 1 September to 30 April,  $M_{\text{summer}}^i$  represents natural mortality from 1 May through 31 August, and  $H_{\text{autumn}}^i$  and  $H_{\text{spring}}^i$  represent the harvest rate in autumn and the following spring, respectively. Both harvest rates are expressed as a proportion of the starting population at the end of August, so that they can be compared directly in terms of number of birds harvested. The difference between the two harvests is that, by the time the spring hunt takes place, the population has already been reduced by overwinter mortality.

The total harvest at each time of year was apportioned among age classes based on estimates of the relative vulnerability and abundance of each age class at the time of harvest. Band recovery data (mainly from nonaboriginal hunters) from various colonies around Hudson Bay indicate that

young birds are 2–3 times more vulnerable than adults in early autumn, although the difference is lower later in the season (Francis et al. 1992b). Anecdotal data suggest that the difference between age classes may be less in the aboriginal hunt (Cooch 1953). To evaluate the consequences of this type of variation, I modelled vulnerability of young as ranging from one to three times that of adults in autumn.

Few data are available on the relative vulnerability of young birds in spring, because the aboriginal hunt has not been closely monitored, and a nonaboriginal hunt has not been allowed. Thus, it was necessary to simulate various possibilities. First-year birds are likely to be less vulnerable than in autumn, having survived exposure to extensive hunting through one season. Francis et al. (1992b) found that harvest rates of young and older birds banded in late winter in Louisiana were similar. However, if young birds are no longer accompanying their parents, they may become more vulnerable by late spring. If young birds differ from adults in staging areas, migration timing, or migration routes, then their vulnerability may differ among hunting areas. To cover the range of possibilities, I modelled vulnerability of young as ranging from one to three times that of adults in spring. Finally, for comparison, I considered the cases where only young, or only adults, were harvested in either season. I assumed that there was no variation in relative vulnerability to hunters with age after the first year.

Age-specific survival rates were derived from the analyses of Francis et al. (1992a,b). Mean annual adult survival between 1970 and 1988 at LPB was about 0.83, but it increased significantly from 0.78 to 0.88 during this period (Francis et al. 1992a). This change was due to a large increase in the Snow Goose population, without a corresponding increase in the number of geese being shot, which led to a decrease in the proportion shot (Francis et al. 1992a; Cooke et al., this volume). Adult survival rates in the absence of nonaboriginal hunting were estimated at about 0.92 from the intercept of a regression of recovery rates on survival, which corresponds to a mortality rate of 0.08. Because most geese from this colony do not migrate south through James Bay (Francis and Cooke 1992a), where a substantial aboriginal hunt takes place, this 8% mortality represents mostly natural mortality. The extent of annual variation in non-hunting mortality is unknown, because high sampling errors of the adult survival estimates obscured any underlying variation beyond the long-term increase.

Mean annual survival of young from LPB banded in late July, shortly before fledging, was about 0.42 over the period 1970–1988, with a long-term decline from 0.57 to 0.35 (Francis et al. 1992a). Yearly variation in first-year survival was large relative to sampling variation. Independent estimates of first-year survival based on recaptures and recoveries showed close similarities (Francis and Cooke 1993), confirming that the variation was well measured and not due to sampling error. Variation in first-year survival at other colonies, particularly northern colonies, was even greater, with survival postfledging ranging from 0.07 to 0.70 (Francis et al. 1992b). The proportion of mortality due to nonaboriginal hunting was estimated from the recovery rate, on the assumption that recoveries represented about one-third of geese killed by hunters (Martinson and McCann 1966; Cooke et al., this volume).

The seasonal distribution of natural mortality is an important component of the model. Little is known about the

timing of natural mortality in geese. Potential causes of natural mortality include stress during migration (Owen and Black 1991), winter and early spring die-offs as a result of disease (e.g., cholera), and starvation on the breeding grounds or elsewhere (Ankney 1975). Mortality of young was greatest in years when nesting was late and growth rates were slow and was inversely related to hunting kill (Francis et al. 1992a,b). This suggests that most mortality occurred after the geese were banded, but before the start of the hunting season, presumably on the breeding grounds or early in the autumn migration. For modelling purposes, I assumed that this pre-season mortality occurred in August and averaged 25%. Because this mortality occurs before the model anniversary date (31 August), it becomes a component of productivity. Varying this parameter has the same effect as varying other productivity parameters in the model. Natural mortality of adults and of young after August was assumed to be uniformly distributed throughout the year, resulting in two-thirds of mortality taking place between 1 September and 1 May. I assumed that natural mortality of young after August averaged 25% and that of adults averaged 8%, based on long-term averages at LPB. However, I also tested the consequences of varying these parameters over a range of values.

Recovery rates (an index of mortality due to hunting) and overall mortality rates of yearlings were both slightly higher than those of adults, but the difference could not be measured with precision (Francis et al. 1992b). As an approximation to observed values, I assumed that survival rates of yearlings were about 5% lower than those of adults.

Mean age-specific reproductive rates of Snow Geese were based on the expected brood size at fledging for each age class estimated by Rockwell et al. (1993: Fig. 5), multiplied by 0.5 to allow for the fact that only females produce young. Their analyses did not include geese that do not breed or that fail very early in breeding. These parameters vary with age, because younger birds are less likely to breed than adults. The relative breeding propensity of different age classes can be estimated from the age-specific capture probabilities of geese at banding in late July or early August. Non-breeders usually leave the colony on a moult migration before banding, so that most birds captured are likely to have bred. I used program SURGE4 (Lebreton et al. 1992) to estimate mean age-specific capture probabilities for two-year-old, three-year-old, and older females at 0.13, 0.26, and 0.30, respectively (unpubl. data). Yearlings were almost never captured, as they do not breed. The difference between capture probabilities of younger and older birds can be assumed proportional to their breeding probabilities (Clobert et al. 1994). Thus, the breeding probability for two-year-old geese, relative to adults, is  $0.13/0.30 = 0.43$ , and for three-year-old geese,  $0.26/0.30 = 0.87$ . Determining the absolute proportion of breeders requires an estimate of the proportion of older birds that breed. I assumed this to be about 0.90, although the precise figure is not known. Varying this parameter affects the total number of young produced in exactly the same manner as varying the proportion of young birds that survive postfledging (i.e., through to the beginning of September), so it was not tested separately.

Snow Geese select mates in wintering areas or in early spring, when populations from many different colonies are mixed (Cooke et al. 1975). If early pair formation is important to successful breeding, some birds losing mates

during a spring harvest may fail to breed. To model this, I adjusted the total production of young for age class  $i$  by  $(1 - P_{\text{fail}} \times H_{\text{spring}}^i)$ , where  $P_{\text{fail}}$  represents the proportion of birds that fail to breed as a result of mate loss. I varied  $P_{\text{fail}}$  from 0 to 1 to cover all possibilities. This equation assumes that fates of pair members are independent and will overestimate the impact of mate loss if there is a tendency for both birds to be shot together.

Within the model, total production of young by individuals in a particular age class was calculated as the product of their survival rate to the following summer, the probability that they breed (remembering that they will have graduated to the next age class), the number of young produced per breeding attempt, and the survival rate of those young to the end of August.

For most analyses, I used deterministic models, for which the asymptotic growth rate was measured by the dominant eigenvalue ( $\lambda$ ) of the projection matrix. This is a measure of what the growth rate would be if the population were at a stable age distribution. Because the equations were nonlinear (harvest rates of each age class depend upon the age distribution at that time because of differences in vulnerability), growth rates were calculated iteratively by repeated matrix multiplication. The relationship between the spring and autumn harvest was evaluated by determining the population growth rate, assuming that all of the harvest occurred in autumn, and then iteratively finding the harvest rate that would allow the same population growth rate if all harvest occurred in spring. I simulated autumn harvest rates ranging from 1% to 20%, but the model proved not to be very sensitive to this parameter, so it was not considered further.

Extreme variability in reproductive and survival rates of Snow Geese (Cooch et al. 1989; Francis et al. 1992a) prevents them from reaching a stable age distribution. To test whether models that incorporate this variation would affect the conclusions, I also used stochastic models, in which survival rates were randomly selected from a range of values with a fixed mean. The same set of random values was used to estimate first the effect of the autumn harvest, then the effect of the spring harvest. This was repeated 10 000 times for each combination of variables. I also used this approach to determine how productivity of young influenced the relative impact of spring and autumn harvests.

For all models, the relative impact of the spring harvest was defined as the ratio of autumn to spring harvest that produced the same growth rate. Because these rates are measured relative to the same starting point (the population on 31 August), this ratio represents the number of birds that could have been harvested in autumn for the same average impact on population dynamics as harvesting one bird in spring. I measured effects in terms of numbers of birds, because that is the variable most readily measured by monitoring programs and also most relevant to a hunter. All models were implemented with a C++ program developed for this purpose.

### 3. Results

#### 3.1 Model validation

Estimated population growth rate using mean parameters, including mean harvest rates, from LPB was about 7.4% per year ( $\lambda = 1.074$ ). This represents a 4.5-fold increase in

population size over 20 years, which is consistent with the observed increase in the colony at LPB from about 2000 to 8000–9000 pairs between 1968 and 1988 (Cooch and Cooke 1991). This provides some reassurance that the basic population model is reasonable, despite uncertainties in several parameters. Both adult and first-year survival rates changed dramatically between 1970 and 1988, with an increase in the former and a decrease in the latter (Francis et al. 1992a). I simulated the effects of these changes, assuming the changes were strictly linear, with slopes as determined by Francis et al. (1992a) and found that changes in adult and first-year survival have roughly balanced each other and had little effect on population growth rates.

Rockwell et al. (1997) developed a similar model, also using data from LPB, and calculated a value for  $\lambda$  of 1.11. The parameter estimates they used differed in several respects from the ones I used; the most important difference was that they used reproductive values from the 1970s, when they were high, and adult survival rates from the mid-1980s, when they were high. In my models, I used the mid-value for each. In any case, both estimates of growth rate are higher than estimates for the mid-continent population of Snow Geese, which suggest a  $\lambda$  of 1.05–1.06 (Cooke et al., this volume). Differences among colonies are expected because of differences in productivity (e.g., northern colonies have more variable productivity [Francis et al. 1992b] and likely have lower mean values), as well as different hunting mortality owing to different migration routes (Francis and Cooke 1992b). Because LPB is a relatively small colony, its dynamics will have less influence on the mean for the mid-continent population than will those of other colonies.

Fortunately, population growth rate has little effect on estimates of the relative impact of spring harvest. For example, altering mean reproductive parameters or harvest rates to change the population growth rate from +6% per year to –1.3% per year has less than a 1% effect on the difference between spring and autumn harvests. This suggests that, despite differences in growth rate among colonies, population parameters from LPB should provide a reasonable basis for estimating the effects of a spring harvest on Snow Geese in general.

### 3.2 Relative impact of a spring harvest

Differences in the impact of spring and autumn harvests arise for three main reasons. First, the population has been reduced by natural mortality, so that a bird shot in spring represents a higher proportion of the remaining population and hence a higher harvest rate. Second, the relative vulnerability of young may differ in spring and autumn, which affects the age ratio in the harvest. Because shooting adults has a greater effect on population dynamics than shooting young, changes in the age ratio between seasons influence the impact of hunting in each season. Third, birds losing mates in spring may be less likely to nest successfully, either because they fail to mate or because of reduced productivity with a new mate.

Because some of these parameters either are likely to vary with circumstances or are unknown, I modelled a range of possible values for each. In the Discussion, I consider values of these parameters that are likely to be relevant with respect to both the aboriginal and a nonaboriginal spring hunt.

To estimate effects due to natural mortality during winter, I first considered a scenario in which the harvest is restricted to a single age class (adults or young). For adults, if natural mortality varies from 4% to 14%, the relative impact of a spring harvest changes from about 1.04 to 1.12. Assuming a natural mortality rate of 8% per year, as was estimated for LPB, the spring harvest has a relative impact of 1.067. In other words, for a given impact on population dynamics, 6.7% more geese could be shot if all harvest occurred in early autumn than if all harvest took place in spring. For young geese, if natural mortality (after 1 September) varies from 0.10 to 0.40, the relative impact of a spring harvest ranges from 1.07 to 1.40. Assuming a natural mortality rate of 25% per year, the relative impact is 1.21. The natural mortality rate for young geese during this period is difficult to estimate, because no data are available on the proportion of natural mortality occurring after the start of the hunting season. Francis et al. (1992a,b) inferred that most natural mortality occurred before hunting begins, so 25% mortality afterwards may be a high estimate. Nevertheless, in this paper, I assume that natural mortality is 8% per year for adults and 25% per year (after immediate postfledging mortality) for young. If natural mortality, especially of young, is lower, the relative impact of a spring harvest will be less than estimated.

With these values, if harvest were evenly distributed between age classes relative to their abundance in each season (i.e., young and adults were equally likely to be shot), the relative impact of a spring harvest is 1.09. This is close to the effect of shooting only adults, because the overall impact of harvesting adults on population dynamics is much greater than the impact of harvesting young.

### 3.3 Effect of changing age ratio in the harvest

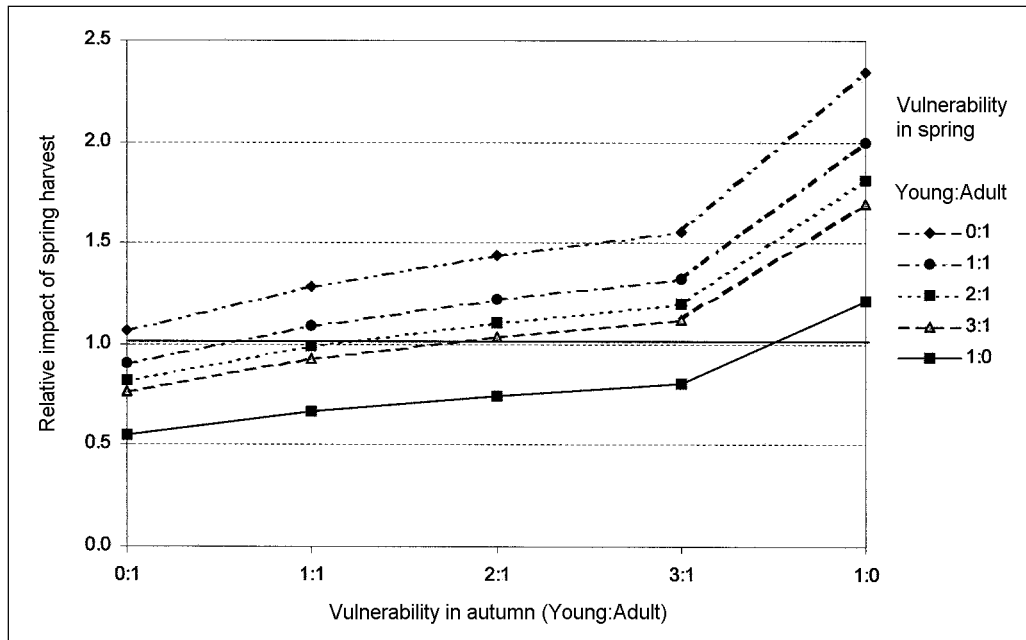
Although the difference between a spring and an autumn harvest is intrinsically small, differences between seasons in the relative vulnerability of young and adults can have a bigger effect on the impact of each harvest (Fig. 1). At one extreme, if the spring harvest is entirely of young (Fig. 1, bottom line), it will always have less impact than an autumn harvest (values less than 1.0), unless the autumn harvest is also mainly young. For this model, shooting a young bird in spring has about 0.6 times the impact of shooting an adult in autumn, but 1.2 times the impact of shooting a young bird in autumn. At the other extreme, if only adults are harvested in spring (Fig. 1, top line), the spring harvest will always have a greater impact. The impact of shooting an adult in spring is about 2.3 times that of shooting a young bird in autumn, but only 1.07 times the impact of shooting an adult in autumn. If the autumn harvest were all adults, it would have a greater impact than a spring harvest that includes even a moderate number of young. If young are 2–3 times more vulnerable than adults in autumn (consistent with data for the autumn nonaboriginal hunt) but are as vulnerable as adults in spring, the relative impact would be between 1.22 and 1.32.

### 3.4 Effect of mate loss

The estimated impact of a spring harvest is substantially increased if geese that lose mates in spring do not nest successfully that year (Fig. 2). If young and adults were

**Figure 1**

Impact of harvesting Snow Geese in spring relative to harvesting an equivalent number of birds in autumn in relation to the relative vulnerability of young and adults in each season. The ratio of 0:1 represents harvesting only adults in spring (top line) or in autumn (left edge). The ratio of 1:0 represents harvesting only young in spring (bottom line) or in autumn (right edge).



equally vulnerable in autumn and in spring, the relative impact of a spring harvest would be increased from 1.09 to 1.26 if all geese that lost mates during the spring hunt failed to breed. If young are twice as vulnerable in autumn but equally vulnerable in spring, the impact ranges from 1.22 to 1.41 (Fig. 2). Few data are available on which to base an estimate of this proportion. Martin et al. (1985) found that female Snow Geese widowed just before nesting were unable to acquire nest sites or initiate nesting. This indicates that unpaired birds, even if they could potentially obtain copulations, are unlikely to nest. Although Snow Geese are believed to mate mainly during winter or in early spring (Cooke et al. 1975), three-bird chases, which are usually associated with pair formation, have been observed throughout the spring, including shortly after arrival on the breeding grounds (F.G. Cooch, pers. commun.). If similar numbers of females and males lose mates in a spring hunt, it is probable that many could pair again. Also, females losing mates on spring migration could potentially pair with younger males that might not otherwise have bred. Because Snow Goose pairs travel together on spring migration and are vulnerable to being shot together, the models may overestimate the proportion of widowed birds. Thus, although a spring hunt, especially late in spring, is likely to have some effect on nesting success, it may not cause greater than a 50% reduction in breeding success of widowed birds. In this case, the relative impact of a spring hunt, assuming young are 2–3 times more vulnerable than adults in autumn, but not in spring, becomes 1.32–1.42.

### 3.5 Effect of annual variation in productivity

The preceding estimates were based upon deterministic models that assumed that demographic parameters do not change over time. I also estimated the impact of a spring

harvest using stochastic models, with similar mean values, but considerable yearly variation in the actual parameters. The basic conclusions were the same as just presented, with the relative impact of a spring harvest little affected by the variance, so I have not presented details of the simulations.

I also used stochastic models to examine the effect of annual variation in production of young on the relative impact of the spring harvest. I ran 10 000 simulations, with mortality of young over August averaging 25%, but ranging from 0% (representing high breeding success) to 100% (representing total nesting failure). The age structure of the population varied with production of young. I then compared the average impact of spring harvest each year relative to breeding success in the preceding and following nesting seasons.

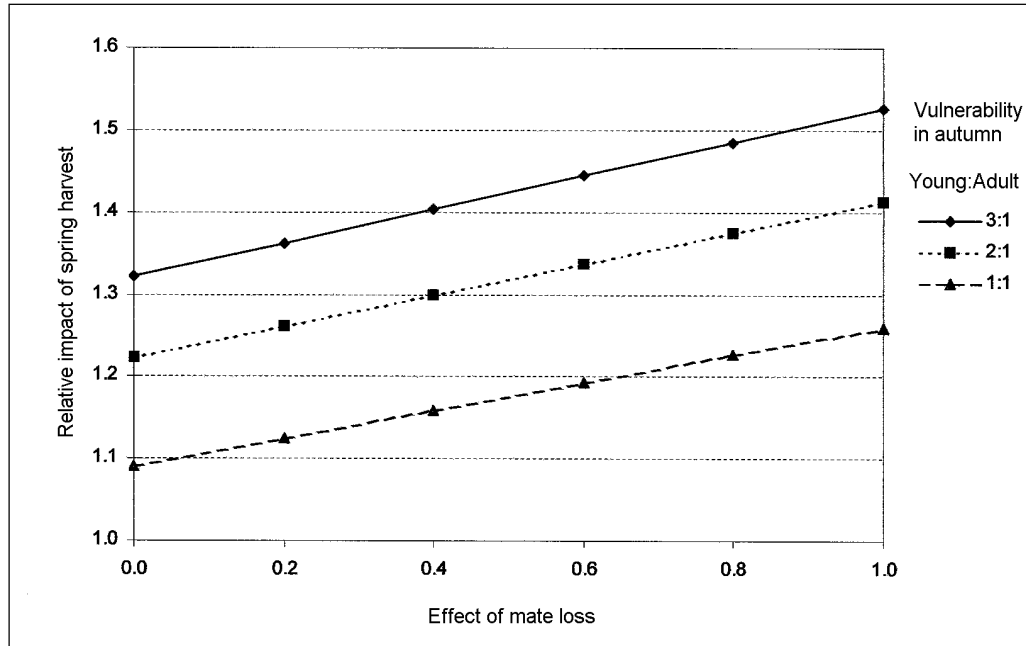
The effect of spring harvest was more similar to that of autumn harvest after seasons of poor productivity. This was because there were few young in the population, so that most birds shot in either season were adults. Similarly, the difference between a spring and an autumn harvest was reduced if there was poor productivity in the following season. This was because the relative difference between adults and young was reduced if most birds failed to breed in the following season. Of course, the impact of hunting on the population, regardless of season, is more significant preceding or following a poor breeding season, because few young are produced to replace birds that are shot.

## 4. Discussion

These models indicate that seasonal effects alone lead to relatively little difference in the impact of killing a bird in spring (1 May) versus early autumn (1 September). For adults, assuming 8% annual mortality from natural causes, the difference was 7%, indicating that 7% more adults can be

**Figure 2**

Impact of harvesting Snow Geese in spring relative to harvesting an equivalent number of birds in autumn in relation to the effect of mate loss on subsequent breeding success, where an effect of 0.0 indicates no effect (i.e., all females that lose mates pair again, with no loss of breeding success), whereas an effect of 1.0 means that all females that lose mates fail to breed that year. The top line assumes that young are three times as vulnerable, the middle twice as vulnerable, and the bottom equally vulnerable as adults in autumn. All lines assume that young and adults are equally vulnerable in spring.



harvested in autumn for the same impact on population growth. For young, the difference was larger, 20%, because of higher natural mortality after 1 September. These estimated differences represent extremes, because they assume an eight-month interval between the autumn and spring harvest. In fact, the current nonaboriginal hunt extends until 10 March, and an extension of that hunt into spring could start on 11 March. The intrinsic difference between a hunt in March and a hunt in April, owing to natural mortality alone, would be almost negligible.

Of much greater importance were changes in the relative vulnerability of adults and young over the year. Ignoring for the moment potential effects of mate loss, if adults and young were equally vulnerable throughout the year, the average impact of a spring harvest would be only about 9% greater than that of an autumn harvest. If young were 2–3 times more vulnerable than adults in autumn but of similar vulnerability in spring, the impact of a spring harvest would be 20–30% greater than that of an autumn harvest.

From the perspective of the nonaboriginal harvest, relatively high vulnerability of young in autumn is indicated by band recovery data. Francis et al. (1992b) showed that the mean recovery rate of young birds banded before the hunting season was about double that of adults. Assuming no difference in reporting rate by age class, this indicates a harvest rate at least twice that of adults. If there is moderate post-fledging mortality prior to the start of the hunting season, recovery rates of young birds banded on the breeding grounds, just before fledging, will underestimate their harvest rates. Thus, vulnerability of young probably averages more than twice that of adults.

Direct recoveries from banding at staging areas during the hunting season indicate that harvest rates for

young are about double those of adults throughout most of the season (Francis et al. 1992b). Recoveries of birds banded on wintering areas in Texas suggest continued higher vulnerability of young, but recoveries of birds banded in Louisiana indicate no difference in recoveries by age class. The Louisiana sample was generally banded slightly later in winter, although other factors are probably involved in differences between these areas. In any case, results from Louisiana are consistent with the suggestion that relative vulnerability of young is reduced by the end of the season.

Reductions in the relative vulnerability of young are also suggested by analyses of age ratio data from waterfowl harvest surveys. As part of these surveys, hunters are asked to submit tails for each goose that they have shot, which are then used to determine the age of the goose (Geissler 1990). I examined age ratios by month throughout the hunting season for all Snow Goose tails returned between 1962 and 1997 in the Central and Mississippi flyways ( $n = 67\ 000$ ). The estimated proportion of young in the harvest declined from 55% to 50% from September through November and then dropped to 42% in December, 32% in January, and 25% in February. The decline is substantially greater than expected based on reductions in the proportion of young available to be harvested (owing to both hunting and natural mortality). Some of the decline could be due to bias, if some young geese had completed a tail moult by February and were thus confounded with adults. The extent of this moult in young Snow Geese has not been studied, but it is unlikely to be sufficiently extensive to explain all of the seasonal change. The proportion of young in the harvest in February approaches the proportion that might be expected in the population at that time, although a more complex analysis, considering variation in productivity among colonies and among years, is

needed to confirm this. If this were the case, it would suggest that the vulnerabilities of young and adults were similar in spring.

A confounding factor in the analysis could be changes in the behaviour of birds in spring. During autumn and winter, young birds usually accompany their parents. If they become more independent in spring, their vulnerability may increase slightly. Furthermore, if they tend to flock or migrate separately from adults, this could also affect their vulnerability. For example, Francis et al. (1992b) found lower recovery rates of nonbreeding adults than of breeding adults and suggested that this could be due to differential migration (i.e., being harvested in different areas) or to the effects of accompanying young on the vulnerability of breeding adults. If young birds in spring migrate at different times than adults, the relative impact of a spring harvest could vary depending upon whether it coincided with passage of more young or more adult birds. Dave Ankney (pers. commun.) suggested that adult females, because of their need to gather sufficient nutrient reserves for feeding, could be less wary and hence more vulnerable.

Age ratios, and hence relative vulnerabilities, in the aboriginal harvest are not known. Cooch (1953) suggested that aboriginal hunters in autumn may selectively shoot adults. Although this may be a strategy to keep the young in the area, so that the whole family can be shot (J.C. Davies, pers. commun.), it would nevertheless increase the kill rate of adults. Limited data from check stations at Moose River, Ontario, indicate that the proportion of adults in the kill may be greater for aboriginal than for nonaboriginal hunters (K. Abraham, pers. commun.). If the effect of attempting to shoot all birds in a family is such that aboriginal hunters shoot age classes roughly in proportion to their abundance in the population, this could result in similar vulnerabilities for young and adults in the autumn harvest. Assuming similar ratios in the spring harvest, the difference between the spring and autumn harvest could be as low as 9%. If young birds happened to be shot more often in spring, the difference would be even less. In spring, young birds are more difficult to distinguish from adults at a distance, so deliberate selection for ages would be more difficult. Further data on age ratios in the spring (and autumn) harvest by aboriginal peoples are required to refine these estimates.

The models are strongly influenced by the effect of mate loss, but data are not available to quantify by how much, or whether, mate loss reduces breeding success. Intuitively, it seems likely that the probability of a widowed Snow Goose finding a new mate would decrease later in the season. If so, this suggests that a hunt in late March or April would have less effect on breeding success of females losing mates than a hunt in May on staging areas in James Bay or nearer their breeding areas.

One factor that was not considered in these models was the effect of disturbance associated with hunting on the energetics of geese. Ward and Stehn (1989) estimated the energetic cost of aircraft disturbances to Brant *Branta bernicla* in terms of lost feeding time and energetic expenditure. They calculated that extensive aircraft disturbance could potentially prevent Brant from putting on sufficient reserves for migration, but the model depended on the assumption that geese could not increase their rate of nutrient intake. A 10% increase in food intake would have largely offset the impact of disturbance. The impact of disturbance associated

with hunting depends on the number of hunters, their behaviour, the number of locations where geese encounter hunters, and the number and distribution of refuges where geese can feed undisturbed. These factors are not necessarily correlated with the number of geese shot and are thus difficult to model. Because Snow Geese use stored nutrients for egg production (Ankney and MacInnes 1978), disturbance in spring could reduce productivity as well as increase mortality from starvation. However, this may be relevant only if disturbance is so great that geese are unable to compensate by increased foraging. Unless there is a deliberate effort to harass geese, it seems unlikely that disturbance could be sufficient to have a measurable impact on population dynamics.

Models used in this paper, although built for Snow Geese, could also be used to evaluate the impact of spring harvest on other waterfowl. For species such as Canada Geese, which also have high adult survival, largely additive hunting and natural mortality, long-term pair bonds, delayed maturation, and highly variable first-year survival, results will be similar to those for Snow Geese. Quite different results might be expected for ducks such as Mallards *Anas platyrhynchos*, which have much lower survival rates, produce large numbers of young, breed at one year of age, and appear to exhibit some compensatory mortality, whereby natural mortality rates are reduced in relation to increased hunting mortality (Nichols 1991b). Information on timing and mechanisms of compensation would be required to develop a model for such species.

## 5. Management implications

### 5.1 Harvest by aboriginal peoples

Harvesting of waterfowl by aboriginal peoples in Canada takes place during autumn and spring migration. The spring harvest, particularly of geese, was traditionally very important, because waterfowl returning in spring often represented the first fresh food available after the long northern winter. Although alternative food sources are now available, they may be relatively expensive or limited in quantity and are considered less desirable or less nutritious. Thus, wild game continues to be important for many aboriginal peoples in Canada (Coad and Richardson 1994). The spring harvest is also important socially for retaining the cultural traditions of many aboriginal people.

My models suggest that the relative impact of spring harvest by aboriginal peoples is unlikely to be more than 40%, and possibly as little as 10%, greater than that of an autumn harvest. The impact cannot be quantified more precisely, because several key parameters are not known. These include the age ratio in the spring harvest relative to autumn and the effect of mate loss near the breeding grounds on breeding success. At one extreme, assuming that young are three times as vulnerable as adults in autumn but equally vulnerable in spring and that geese widowed in spring all fail to breed, the spring harvest could have a 52% greater impact than an autumn harvest. Alternatively, given that aboriginal hunters may selectively shoot adults in autumn and that many geese losing mates in spring may find new mates and breed with moderate success, the relative impact of a spring harvest is likely to be less than 20% greater than that of an autumn harvest.

Some goose populations harvested by aboriginal peoples are declining or at relatively low levels, such as the northern Quebec Canada Geese (Canadian Wildlife Service Waterfowl Committee 1998). If it ever became necessary to set quotas on aboriginal harvest, then models in this paper could be used to apportion the harvest among seasons (provided that information can be obtained on missing parameters, such as age ratios in the harvest). For example, if an autumn harvest of 50 000 geese could be supported and the impact of a spring harvest was 25% higher than that of an autumn harvest, then a harvest allocation of 25 000 geese in autumn and 20 000 in spring or an allocation of none in autumn and 40 000 in spring would have an equivalent impact on the goose population. Decisions on allocation between seasons, using this type of sliding scale, could be made by the local people based on their own desires.

Of course, for those people with access to species that have been increasing, such as Snow Geese, the relative impact of harvests at different times of year is unimportant. In fact, from the perspective of population control, it may be appropriate to encourage harvesting by aboriginal people in spring, with a preference for shooting adults. The total harvest of Snow Geese around James Bay and Hudson Bay was estimated by harvest surveys in the mid-1970s at about 31 000 birds in Quebec (Boyd 1977) and 45 000 in Ontario (Prevett et al. 1983). About 25% of the Ontario harvest (Prevett et al. 1983) and 13% of the Quebec harvest (Reed 1991) took place in spring. A more recent survey in 1991 (Berkes et al. 1992) suggested that the Ontario harvest had increased to 55 000 geese, but that is a much smaller increase than the growth rate of the population (Cooke et al., this volume). A substantial further increase would be required to reach the same harvest rates as in the early 1970s.

## 5.2 Harvest to control large populations

A “spring” harvest by nonaboriginal hunters would presumably take place mainly in more southerly staging areas, where most hunters are living, from 11 March through early May. Although the effect of mate loss from an early spring harvest is unknown, there would still be 1–2 months in which birds losing mates could find a new one. Thus, most of the difference between spring and autumn would probably be due to seasonal effects and changes in relative vulnerability.

The relative impact of harvest in March and April will be little different from that of harvest during the regular season in February or early March. However, a spring harvest will have about a 20% greater impact than the average for the rest of the season, assuming that young are, on average, about twice as vulnerable as adults over the regular season but similar in vulnerability in spring, and allowing for the fact that the mean harvest date in the regular season is about two months later than the date used in the model (1 September).

To obtain a preliminary estimate of the potential gain of adding a spring harvest, as part of a strategy to increase the overall harvest, I examined the monthly distribution of harvest using U.S. harvest statistics. For the Mississippi and Central flyways in the United States, on average during the hunting seasons from 1990 to 1997, approximately 21–22% of the harvest occurred in each month from October to January, with a reduction to about 12% in February. Only

about 1% took place in each of September and March. Clearly, this distribution of harvest is influenced strongly by the distribution of geese in each month and existing season limits within these periods (e.g., until a few years ago, few states had seasons beyond mid-February). If these factors are ignored and a change in regulations led to harvests in March and April similar to current harvests in October–January, this could increase the total harvest by about 45%. Allowing for a 20% greater impact of a spring harvest, this would be equivalent to a 54% increase in the regular season harvest. Similar increases would also be required in Canada to achieve a 54% increase in the total harvest.

Based on these estimates, adding a spring harvest alone would not be sufficient to control goose populations. Cooke et al. (this volume) predict that a further increase of 2.1- to 4.7-fold in the harvest, relative to the harvest estimate for 1997, would be required in 1999 to reduce the population growth rate sufficiently to cause the Snow Goose population to decline. Particularly if the true value is in the middle or upper part of that range, other measures, in addition to adding a spring harvest, would be required to achieve the recommended reductions in population growth rate.

Given these results, it would seem appropriate to estimate the projected impact of all proposed measures to increase harvest, so as to determine which measures might be required. To do this would require estimates of the availability of geese in different areas at different times of year (i.e., the number of potential hunter-days in each region of the Snow Goose migration route), the numbers of hunters likely to participate in each hunting season period, and the probable success rate of those hunters. The latter would be influenced by other changes in measures such as allowing electronic calls or baiting. These data could be used, in conjunction with the results from the models presented in this paper, to obtain a better estimate of the likely impact of any proposed changes in regulations and to determine whether they are likely to be sufficient to control the population.

## 6. Research needs

These models highlight key factors that need to be better understood to estimate the impact of a spring harvest with more precision. Particularly if regulations are changed to allow such a harvest by nonaboriginal hunters, research programs are needed to measure these factors.

The first factor is the relative vulnerability of each age class to hunters at different times of year. This requires information on the age ratio in the harvest, as well as information on the age ratio in the population at the time of harvest. Some information on the harvest age ratio in the nonaboriginal hunt is already available, at least through February, based on tail fan surveys. Additional surveys involving inspection of whole birds would be desirable, because aging birds based solely on tail fans may become less reliable later in the season as a result of replacement of the juvenile tail feathers during the winter (Palmer 1976). Additional surveys are also required to estimate age ratios in the aboriginal hunt. The population age ratio could be estimated through visual surveys of the population to estimate age ratios in flocks, because young birds can usually still be distinguished by their darker necks, even in spring. An appropriate sampling scheme would be needed to ensure that the samples were representative of the population in



different areas at different times. Models can also be used to estimate changes in the population age ratio through the season, but they are dependent upon accurate estimates of the population size and age ratio at the beginning of the season and of total harvests by age class throughout the season.

The second factor is the breeding success of females widowed at different times during the season, especially at different times in spring. This would require marking females in winter or in spring in such a way that they can be followed to the breeding grounds, probably with satellite radio transmitters. The breeding success of females experimentally widowed at different times could then be contrasted with that of controls. This would be a difficult and expensive research project, but the results are essential to accurately measure the effects of spring harvest on goose population dynamics.

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# Impact of hunting on population growth of mid-continent Lesser Snow Geese

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## Abstract

Populations of Lesser Snow Geese *Anser caerulescens caerulescens* in the mid-continent of North America have increased to the point where they are causing serious damage to some Arctic coastal ecosystems. A recent modelling exercise by R.F. Rockwell and colleagues (referred to as the Original Model) suggested that increasing harvest rates of adults to approximately twice the average level in recent years would lead to negative population growth and hence (under certain assumptions) be sufficient to control the population. However, some of the parameters in their models appear to have been inappropriate. Based on revised parameters, which are consistent with analyses of recent data, we suggest that an increase of 3.0- to 7.3-fold in the harvest, relative to the same period analyzed in the Original Model, would have been required to reduce populations at the desired rate in 1994. Despite recent increases in harvest, we predict that a further increase of 2.1- to 4.7-fold, relative to the estimated harvest for 1997, would be needed in 1999 to achieve this population reduction. Wildlife managers need to be aware of these larger targets when considering appropriate measures to control the population. Given the uncertainties in many parameter estimates, further modelling, combined with ongoing monitoring of population size and demographic parameters, will be required to evaluate and refine any management actions.

## 1. Introduction

Populations of Arctic-nesting geese in many parts of the world are increasing rapidly (Ebbinge et al. 1984; Madsen 1991; Ankney 1996; Madsen et al. 1996; Abraham and Jefferies 1997, and references therein). These increases have been attributed largely to greater availability of agricultural crops for food in winter (Cooch and Cooke 1991; Ankney 1996; Abraham and Jefferies 1997). In many places, geese have moved from traditional feeding areas, such as coastal marshes, into agricultural crops, such as winter wheat, rice, and corn (Bateman et al. 1988), which provide a higher nutrient value and are more widely available than traditional foods (Alisauskas et al. 1988).

This abundance of nutritious food may have led to increased overwinter survival or to higher productivity, owing to increased nutrient reserves for breeding, allowing populations to grow. These population increases have often

been welcomed, as they provide increased opportunities for bird-watching and hunting. Some farmers may welcome the geese insofar as the birds remove surplus plant material, such as weeds. Other farmers consider the geese to be a nuisance because of increased losses to crops.

Whereas many concerns about increasing goose populations relate to negative interactions between geese and agriculture in the winter, a major management concern in the case of Lesser Snow Geese *Anser caerulescens caerulescens* (hereafter referred to as Snow Geese) in the mid-continent of North America is the negative impact that these geese are having on parts of the Arctic ecosystem. Snow Geese concentrate in large flocks at staging areas and on their breeding grounds and sometimes feed by uprooting below-ground vegetation. This has contributed to significant habitat destruction on the coastal salt marshes of the Hudson Bay lowlands (Abraham and Jefferies 1997, and references therein) as well as on inland habitats, such as around Queen Maud Gulf (QMG) in Nunavut (Alisauskas 1998). These Canadian Arctic ecosystems are being degraded by increasing numbers of Snow Geese, and this problem has become a focus for agencies responsible for waterfowl management. A multinational task force was convened to focus on potential solutions to this problem, culminating in a special publication of the Arctic Goose Joint Venture of the North American Waterfowl Management Plan entitled *Arctic ecosystems in peril* (Batt 1997). That report outlined the fundamental problems of overabundance of Snow Geese and discussed related issues of their population biology and management, from which we summarize the following key points:

1. There have been very large increases in all mid-continent Snow Goose populations (Abraham and Jefferies 1997). Estimates of growth rates for the overall population range from 5% to 9% annually over the last 25 years, resulting in population levels in the mid-1990s that were perhaps four times what they were in the early 1970s. During this time, harvest declined (Abraham and Jefferies 1997: 27).
2. There is ample evidence indicating that Snow Geese are causing widespread destruction of Arctic salt-marsh vegetation, with as much as 30% of the total area of salt marsh along the coasts of James Bay and Hudson Bay heavily damaged by geese (Abraham and Jefferies 1997).

3. Some of these geese have thus far avoided density-dependent population regulation by colonizing nesting areas not known to have been used by Snow Geese within historic record.
4. A modelling exercise (Rockwell et al. 1997) involving analysis of a time-invariant age-classified projection matrix was presented, concluding that the most effective management option for regulation of the population would be to increase adult mortality rates.
5. It was recommended that, because annual adult mortality is composed of both natural and hunting mortality, apparently in an additive way, the most effective way to increase adult mortality would be to increase hunting kill. From the modelling exercise, it was suggested that the population could be decreased within a reasonable period if the population growth rate could be reduced to 0.95, and that this could be achieved if the current harvest rate of adults were doubled (Rockwell et al. 1997: 99).
6. It was recommended that this doubling of harvest rate should be brought about by a variety of changes in the current hunting regulations, including removing bag limits, allowing baiting and electronic calls, and legalizing spring hunting (i.e., hunting later than the current 10 March closing date).

There is little doubt that increased numbers of Snow Geese have created problems, most acutely in the Arctic ecosystems where they typically breed. However, we challenge some assumptions underlying the suggestion in the report by Batt (1997) that doubling the kill rate would be sufficient to reduce the mid-continent population of Snow Geese. Some parameter estimates in the model of Rockwell et al. (1997; hereafter called the Original Model) appear to have been inappropriate. Use of more appropriate assumptions changes estimates of the extent to which the kill rate must be increased to reduce the mid-continent population of Snow Geese. Rather than a twofold increase in harvest, relative to the values used in the Original Model, we estimate that a 3.0- to 7.3-fold increase would have been needed to reduce population size adequately in 1994.

In this paper, we first present an argument, based on harvest statistics and estimated population growth rates, as outlined in the report (item 1 above; Batt 1997), that suggests that anything less than a fourfold increase in harvest, relative to the period considered in the Original Model, is unlikely to stop population growth. We then review the assumptions used to derive some of the key parameters in the Original Model. Revised estimates for these rates based on currently available data lead to much higher estimates of the extent to which harvest needs to be increased to reduce the population.

## 2. A check of the model based on harvest data and population growth

Based on their model, Rockwell et al. (1997) estimated that doubling the adult harvest rate would increase mortality sufficiently to reduce the population. They assumed that the total harvest, at the time of their analysis, was equivalent to the mean value from 1985 to 1994, which was 305 000, considering only the U.S. portion of the harvest (Rockwell et al. 1997: 99). Including the Canadian harvest

brings this total to about 400 000 geese (Table 1). This implies that a reported harvest of 800 000 geese per year should be sufficient to cause the population to decline, a value that was approached by the estimated harvest in 1997 (Fig. 1, Appendix 1). However, simple calculations of estimated changes in harvest rates, based on the estimated harvest and population growth rates, suggest that this increase would not be nearly sufficient.

As noted by Abraham and Jefferies (1997), the mid-continent population of Snow Geese ( $n$ ) increased at least three- to fourfold from the early 1970s to the mid-1990s. At the same time, the estimated total harvest ( $g$ ) actually decreased from 1970 to 1994 (the last year of data used in their analysis) (Fig. 1, Table 1). From this, it follows that the average harvest rate ( $g/n$ ), which is assumed to be proportional to the mortality rate due to hunting, must have decreased during this period. Allowing for the three- to fourfold increase in population size and about a 20% decrease in the average harvest between 1970 and 1994, the harvest rate by 1994 must have been between one-quarter and one-fifth of its value in the early 1970s.

Thus, a total harvest 3–4 times larger than its mean value in the early 1970s, equivalent to 4–5 times larger than its mean during the early 1990s, would have been required to bring harvest rates to the equivalent of 1970s levels. However, the population of Snow Geese was already growing in the 1970s (Fig. 2). If reproductive output and recruitment rates have not been changing over time (as was assumed in the Original Model, based on the tendency for colonies to move to new nesting grounds if they deplete an old one), then this four- to fivefold increase in the harvest will not even be sufficient to stop the population from growing, let alone cause it to decline at the intended rate. Although the estimated harvest has increased in the past few years (Fig. 1), the U.S. mean from 1995 to 1997 was only 35% higher than the mean during the early 1970s (Table 1).

The preceding arguments suggest that increasing the harvest to twice its level in the mid-1990s, as recommended by Rockwell et al. (1997), would not be sufficient to control the population, and a much larger harvest would be required. Thus, some of the assumptions in the Original Model must have been inappropriate.

## 3. Review of key assumptions in the Original Model

### 3.1 Original derivation of change in kill rate required to reduce Snow Goose abundance

Population size can be reduced only if the growth rate  $\lambda$  (defined as the asymptotic growth rate expected when neither survival nor fecundity changes over time) is reduced to a value of less than 1.0. This can be achieved by decreasing reproductive output, by increasing mortality, or both. Rockwell et al. (1997) carried out a sensitivity analysis of their model for population dynamics of Snow Geese and showed that population growth rate is most sensitive to changes in adult survival rates. This conclusion is consistent with expectations for any population with relatively high adult survival and little or no evidence of senescent decline in reproductive value (Caswell 1989; Francis et al. 1992b; Rockwell et al. 1993). Based on this analysis, Rockwell et al. (1997) concluded that the most efficient way to control Snow Goose populations would be through increasing adult

**Table 1**

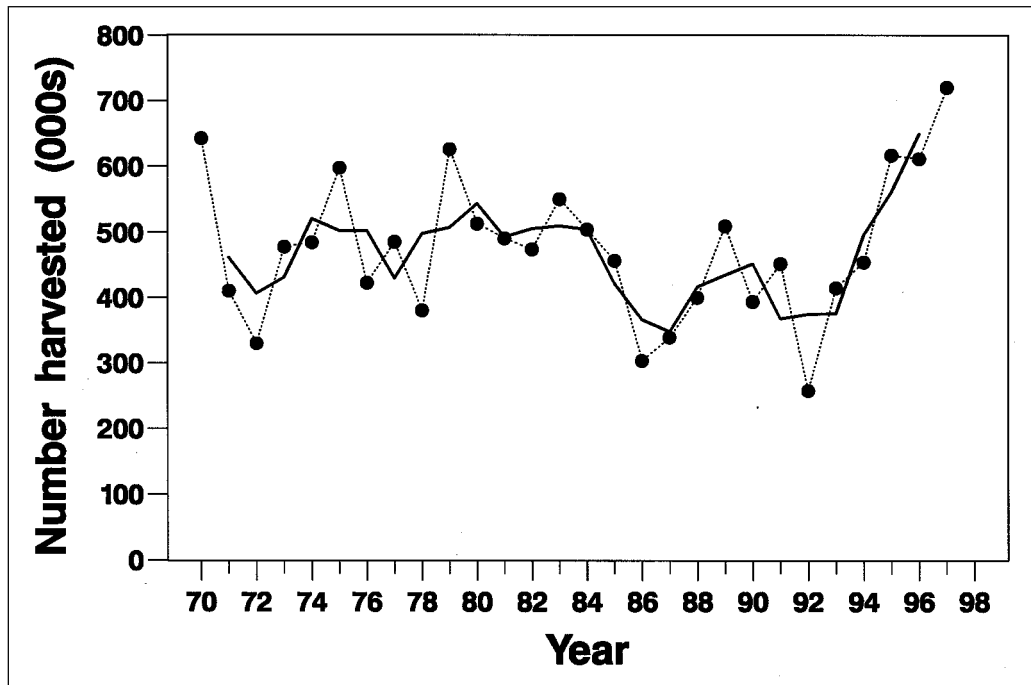
Estimated mean annual harvest for Lesser Snow Geese in mid-continental North America by five-year periods as estimated from harvest surveys in the United States (Mississippi and Central flyways) and Canada (Saskatchewan, Manitoba, and Ontario)

Time period	Mean annual harvest (000s)		
	U.S.A.	Canada	Total
1970–1974	399	— <sup>a</sup>	— <sup>a</sup>
1975–1979	427	75	503
1980–1984	394	112	506
1985–1989	292	110	402
1990–1994	317	77	395
1995–1997	540	103	643

<sup>a</sup> Comparable harvest estimates are not available for the Canadian prairies during this period.

**Figure 1**

Estimated total numbers of Lesser Snow Geese harvested in the Mississippi and Central flyways of the U.S.A. and central Canada (Ontario, Manitoba, Saskatchewan) from 1970 to 1997. Reliable data for Canada were not available for 1970–1974, so they were estimated from the mean for 1975–1979. Solid line represents a running three-year mean. Years with unusually low harvest (e.g., 1992) were associated with low proportions of young in the harvest and were probably due to poor breeding success rather than reduced hunting effort.



mortality. In most goose populations that have been studied, natural and hunting mortality appear to be additive (Francis et al. 1992a). This implies that the mortality rate due to natural causes ( $E$ ) is not affected by hunting mortality, at least within observed limits. If we assume the natural mortality rate is not otherwise changing over time (as was done by Rockwell et al. 1997), it follows that the overall mortality rate will increase if hunting kill ( $K$ ) is increased. Rockwell et al. (1997) estimated the degree to which hunting kill would need to be increased to reduce growth in the following way. Using their model, they first determined the degree to which adult survival ( $s_a$ ) would need to be reduced to achieve the desired population growth rate (values of  $\lambda = 0.95$  and  $\lambda = 0.85$  were both used). Let this desired lower adult survival rate be  $s'_a$ . Since adult survival is a function of both natural ( $E$ ) and hunting mortality ( $K$ )

$$s_a = (1-K)(1-E) \quad (1)$$

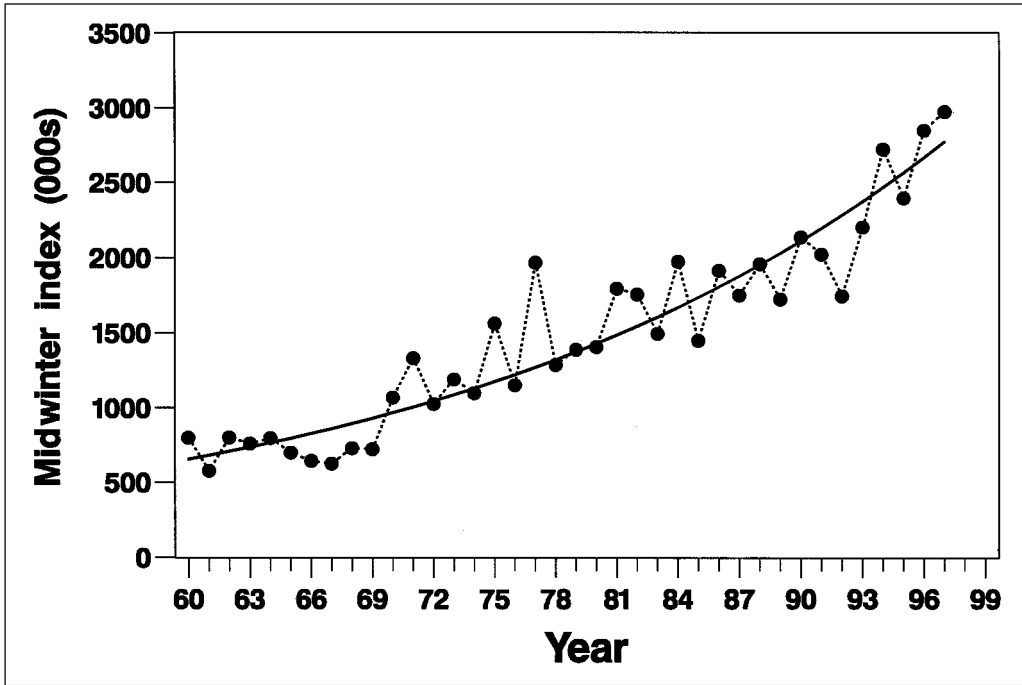
then the kill rate ( $K$ ) corresponding to a given adult survival rate ( $s_a$ ) and natural mortality rate ( $E$ ) is given as

$$K = 1 - \frac{s_a}{(1-E)} \quad (2)$$

Thus, the relative degree to which kill rate  $K$  would need to be increased from present levels to reduce population growth to a specified value is

**Figure 2**

Midwinter counts of Lesser Snow Geese in the Mississippi and Central flyways from 1960 to 1997. The curve was fitted by log-linear regression and suggests a growth rate of 4% per year. A regression from 1970 onwards suggests a growth rate of only 3% per year, but data from breeding ground counts suggest that the true population growth rate was 5% per year or higher (see text).



$$\frac{K_{\text{needed}}}{K_{\text{present}}} = \frac{1 - \frac{s'_a}{(1-E)}}{1 - \frac{s_a}{(1-E)}} = \frac{s'_a + E - 1}{s_a + E - 1} \quad (3)$$

where  $s'_a$  is the desired survival rate and  $s_a$  is the present survival rate. To solve this expression, only estimates of  $s_a$  and  $E$  are required. Alternatively, this can be rewritten in terms of  $s_a$  and  $K$  only:

$$\frac{K_{\text{needed}}}{K_{\text{present}}} = \frac{s'_a (K_{\text{present}} - 1) + s_a}{s_a K_{\text{present}}} \quad (4)$$

In the Original Model, Rockwell et al. (1997) used the former approach (in principle) and estimated  $E$  by first estimating the kill rate  $K$  corresponding to what they assumed to be current estimates of adult survival ( $s_a$ ). Kill rate  $K$  can be estimated from analysis of recovery data as

$$K = f / \phi / c \quad (5)$$

where  $f$  (recovery rate) is the probability that (a) a banded bird is shot (killed), (b) the shot bird is retrieved, and (c) its band is reported;  $\phi$  (reporting rate) is the probability that a banded bird will have its band reported, given that it was shot and retrieved; and  $c$  (retrieval rate) is the probability that a lethally shot banded bird is retrieved. Generally, only the recovery rate  $f$  can be estimated directly from recovery data, and kill rate  $K$  must be derived using known or assumed values for reporting and retrieval rates. Given an estimate for kill rate and adult survival rate, natural mortality rate is derived by rearranging equation 1 as

$$E = 1 - \frac{s_a}{(1-K)} \quad (6)$$

Making specific assumptions about recovery, reporting and retrieval rates, and current survival rate, Rockwell et al. (1997) derived an estimate for  $K$  and (using the preceding expression) for natural mortality rate  $E$ . They determined that hunting kill rate (and thus the total number of birds harvested at a given population size) would need to be approximately doubled relative to current values to reduce growth to  $\lambda = 0.95$  and approximately tripled to reduce growth even further, to  $\lambda = 0.85$ .

### 3.2 Evaluation of key assumptions in the Original Model

From equation 4, it is clear that estimates of three parameters are needed to determine the change in harvest required to control the population: current survival rate  $s_a$ , current kill rate  $K_{\text{present}}$ , and survival rate  $s'_a$  required to achieve a particular  $\lambda$ . In this section, we consider three potential problems with the estimates for these parameters used in the Original Model: temporal variation in survival and harvest rates; geographic variation in these rates; and uncertainty in the estimate of  $s'_a$ .

#### 3.2.1 Temporal changes in recovery and survival rates

The Original Model of Rockwell et al. (1997: 98–99) used a recovery rate ( $f$ ) corresponding to the mean value obtained by Francis et al. (1992a) for the colony at La Pérouse Bay (LPB) from 1980 to 1988 ( $f = 0.0254$ , which was close to the estimated value for 1983). Similarly, the Original Model assumed an adult survival rate  $s_a = 0.88$ ,

corresponding to the value estimated by Francis et al. (1992a) for 1987. These rates would be appropriate only if recovery and harvest rates had not changed since those times. In fact, the population nearly doubled between 1983 and 1997, when their report was written (assuming  $\lambda = 1.05$ ), while harvest remained at or below the 1983 levels, at least through 1994 (Fig. 1, Table 1). Since harvest rate is simply the ratio of the total number of birds harvested to the total number of birds in the population at the start of the hunting season, then, assuming constant natural mortality, we expect a doubling of population size to *reduce* recovery rate to approximately half. Under assumptions of additivity, this will *increase* adult survival rate. Francis et al. (1992a) demonstrated that both rates changed significantly in the predicted directions between 1970 and 1988 and argued that the changes were largely a consequence of increases in population size without concomitant increases in harvest. Given that the population continued to grow after 1988, without further increases in harvest, at least until 1995, it seems likely that these rates have continued to change.

Thus, values used in the Original Model to calculate how much harvest needs to be increased to reduce  $\lambda$  were based on an assumed recovery rate  $f$  that was higher, and an assumed adult survival rate  $s_a$  that was lower, than was likely to have applied during the range of years used in the original analysis.

### 3.2.2 Geographic variation in survival and recovery rates

A second challenge to the Original Model is that values for  $f$  and  $s_a$  were based upon data from LPB, which is one of the smaller colonies of Snow Geese (Fig. 3) and may not be typical of the rest of the mid-continent population. Recovery rates of Snow Geese banded at LPB were higher than those of Snow Geese banded at either Cape Henrietta Maria (CHM) or McConnell River (McC) during the same years (Francis and Cooke 1992a). Reporting rates for Snow Geese at LPB appear to be comparable to those of other species of waterfowl and were not affected by colour bands (Appendix 2), suggesting that these differences in recovery rates were due to intercolony variation in either harvest or survival rate.

Geese from different colonies around Hudson Bay follow different migration routes and hence are subject to different harvest pressures (Francis and Cooke 1992a). In the case of geese from CHM, recovery rates were lower than those of geese from LPB, but survival rates were similar. Francis and Cooke (1992a) suggested that this was due to harvest of CHM geese by aboriginal hunters around James Bay, who rarely reported bands. During the 1970s, the annual harvest by Cree around James Bay and Hudson Bay was estimated at about 31 000 birds in Quebec (Boyd 1977) and about 45 000 in Ontario (Prevett et al. 1983). The total is comparable to the total reported harvest of mid-continent Snow Geese elsewhere in Canada during this period (Table 1). The proportion of birds harvested in James Bay that originate from CHM, as opposed to Baffin Island, is unknown, but it is plausible that the aboriginal harvest was large enough to reduce survival rates of birds from CHM to a level comparable to that of birds from LPB, despite lower harvest (as indexed by recovery rates) in other areas of North America.

In contrast, most geese from McC migrate farther west, where many fewer are harvested by aboriginal hunters.

In this case, the lower recovery rate at McC may indicate a lower harvest rate than at LPB. Assuming no additional sources of natural mortality, this would imply that survival rates were higher at McC than at LPB. The point estimates of adult survival rates from McC were higher than those from LPB (Francis and Cooke 1992a); however, because banding at McC continued for only two years, despite very large sample sizes, the precision was not adequate to confirm this.

If harvest rates differ among colonies, as suggested by these analyses, then values from LPB are not necessarily appropriate for estimating demographic parameters of the entire mid-continent population.

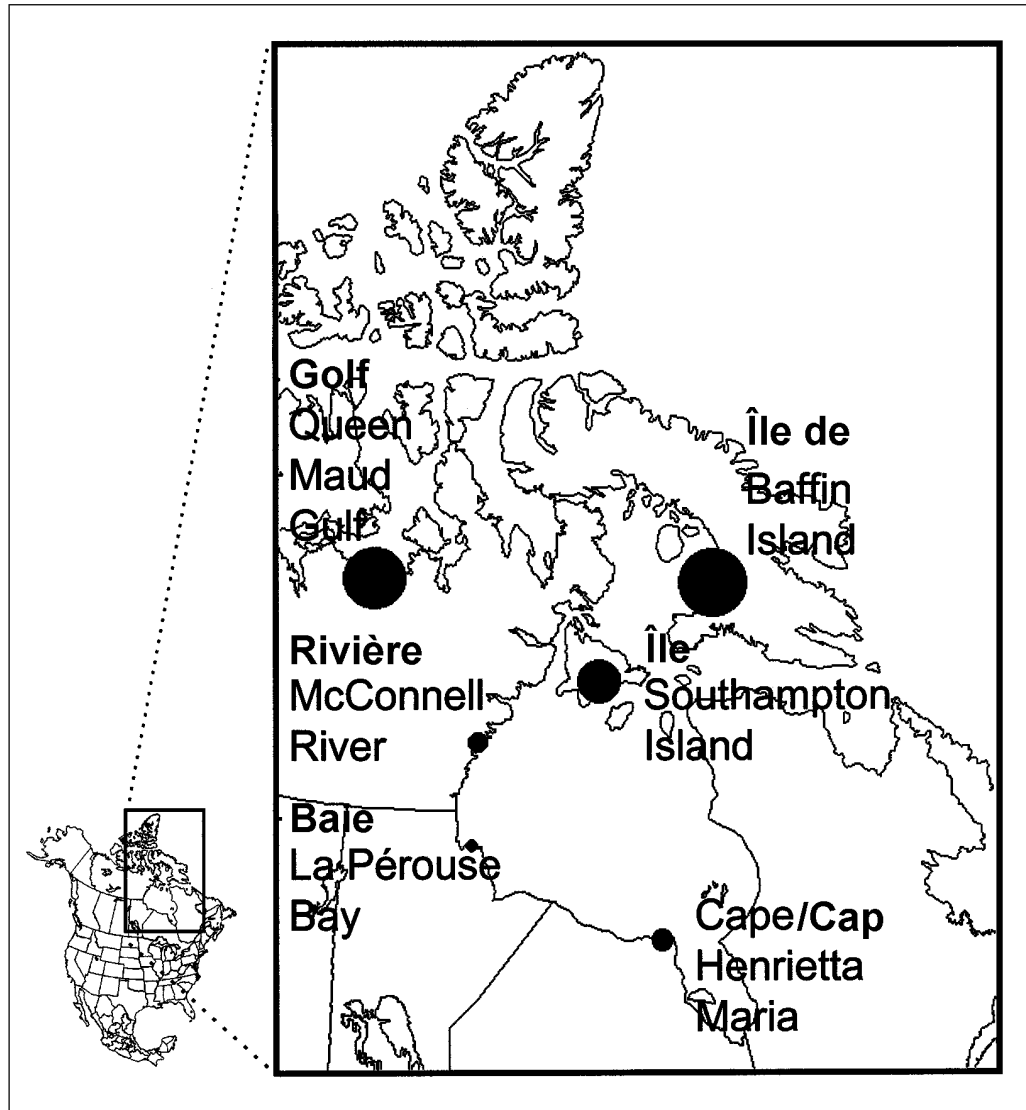
### 3.2.3 Survival rate required to reduce $\lambda$ to 0.95

Using the Original Model, Rockwell et al. (1997) concluded that a survival rate of  $s_a = 0.795$  would be sufficient to reduce  $\lambda$  to 0.95, corresponding to a 5% per year reduction in the population. This value was derived from the projection matrix used to model the mid-continent population and is analytically correct, given that matrix. However, there are several reasons to question the validity of projections from that matrix. In the Original Model, the matrix elements were modified *a posteriori* to derive a matrix yielding an expected value for  $\lambda$  that matched the observed growth rate of the mid-continent population (assumed to be 5% per year). This was done using logical expectations based largely on data from LPB.

The problem with using growth rate  $\lambda$  as a criterion for model selection is that there is an infinite set of combinations of survival and fertility values that will yield the same growth rate (Caswell 1989). Thus, it is not possible to verify the validity of any particular matrix without additional data. Such data were not available from other colonies for the same period, but there is retrospective evidence that suggests that the matrix used in the Original Model was not appropriate. Specifically, the value of adult survival of 0.795 required to reduce growth to 0.95 was nearly the same as the estimate for average adult survival rate at LPB from 1970 to 1978 ( $s_a = 0.80$ ), a period when both the LPB population (Cooch and Cooke 1991; Francis et al. 1992a) and the mid-continent population in general were growing rapidly (Reed et al. 1987; Kerbes 1994). If  $s_a = 0.795$  were actually sufficient to reduce population size now, this implies that either (1) average productivity of young throughout the mid-continent population is now much lower than it was at LPB during the 1970s or (2) adult survival rates were higher at colonies other than LPB, or both. We think that both explanations are insufficient. First, although there are clear differences in expected productivity among colonies (fecundity, especially nesting success and immature survival, is likely to be lower at the larger, more northern colonies than at LPB, because of the shorter nesting season and more frequent total breeding failure), age ratios in the harvest show no long-term changes in the proportion of immature geese in the mid-continent population (C.M. Francis, unpubl. data). This suggests that average fecundity of the mid-continent population was not significantly higher during the 1970s than at present. Second, assuming that natural mortality was at least as great for geese nesting in northern areas with a longer migration and harsher breeding conditions as for geese at LPB, higher adult survival rates at northern colonies would have to be due to lower hunting

**Figure 3**

Major nesting areas of mid-continent Lesser Snow Geese in northeastern Canada. Sizes of circles are proportional to estimated numbers of geese breeding at each colony in 1997 or 1998: Queen Maud Gulf, 1 384 000 (Alisauskas et al. 1998); Baffin Island, 1 767 000; Southampton Island, 708 000; Cape Henrietta Maria, 200 000; La Pérouse Bay, 66 000; McConnell River, 154 000 (R.H. Kerbes, pers. commun.).



mortality. While this appeared to be the case in the comparison of McC and LPB data, estimates of kill rates from harvest surveys and breeding ground counts suggest that the average mid-continent harvest rate may actually be higher than that for LPB (see Section 4.1, below). Thus, there is little compelling evidence to suggest that survival rates averaged higher at northern colonies than at LPB.

Estimating the adult survival value  $s'_a$  needed to reduce growth rate based on a single projection matrix (which necessarily makes simplifying assumptions about homogeneity among colonies and no changes over time) is potentially prone to significant bias. A more robust approach would require developing a spatially and temporally structured metapopulation model, which is beyond the scope of the current paper. Nevertheless, we note that, given the uncertainty surrounding the validity of the projection matrix, it may be prudent to use a lower target survival rate to increase the likelihood of satisfactorily reducing the population. A value of  $s'_a = 0.795$  may not be sufficient to stop

population growth, and a target of  $s'_a = 0.72$ , as recommended in the Original Model to reduce  $\lambda$  to 0.85, may be more appropriate to ensure that the realized  $\lambda$  is actually  $<1.0$ .

#### 4. Consequences of revised assumptions

In the preceding section, we showed that estimates of two of the key parameters, kill rates and survival rates, in the Original Model may have been inappropriate. In this section, we use available data to obtain better estimates of these parameters and then recalculate the changes in harvest that would be required to reduce the population at an adequate rate. Apart from revising these estimates, we have retained, as much as possible, the assumptions and design of the Original Model.

We carried out this analysis in two stages. We first calculated the increase in harvest that would have been required in the 1994 hunting season to control the



population. That year was chosen for two reasons. First, it was the most recent year of harvest data used in the development of the Original Model. As a consequence, our results can be compared directly with those of Rockwell et al. (1997). Second, most of the available data on recovery and survival rates of Snow Geese, on which we base our calculations, are available only up until that date. The 1994 harvest was similar to the mean over the previous decade.

As a second step, we then predicted the changes in harvest that would be required in 1999, relative to the most recent harvest estimate available (1997–1998 season). Because we do not have adequate data to measure directly the consequences of increases in harvest from 1995 onwards (Table 1, Fig. 1), we base this prediction on observed relationships between harvest and survival rates in earlier years.

From equation 4, we see that the magnitude of the increase in kill needed to achieve the desired reduction in population growth (under the assumptions of the model used by Rockwell et al. 1997) is dependent only on the kill rate and the adult survival rate, so we proceed to estimate those.

#### 4.1 Estimated kill rate in 1994

As pointed out by Rusch and Caswell (1997), there are two ways in which harvest rate (which is proportional to kill rate) could be estimated. The first is from band recoveries, following equation 5. The second requires estimates of the total population before the hunting season, as well as the total harvest. We shall consider both of these approaches in turn.

We estimated the recovery rate for 1994 based on a modelled relationship between recovery rate and time, rather than using the point estimate of recovery rate for 1994, to improve the precision of the estimate and to obtain an estimate that may better predict changes in the future. We based our initial analyses on data from LPB, which was the only breeding colony of Snow Geese with extensive banding from the 1970s to the 1990s and hence with sufficient data to estimate the relationship between recovery and survival rates. Starting in 1988, many birds did not receive colour bands, but, as shown in Appendix 2, this did not affect recovery rates, so we pooled data from birds with and without coloured legbands. We based our estimates of recovery rates only on direct recoveries (those in the season immediately following banding), for two reasons. First, we could pool data from the sexes, thus increasing the precision of estimates. Second, recovery rates of previously banded birds tend to be lower than those of newly banded birds, possibly because of changes in breeding status (Francis et al. 1992b).

The results indicate that recovery rates declined, at least through 1994 ( $P < 0.001$ ; Table 2), as we had predicted from a constant or declining harvest and growing population. Mean recovery rates in the 1990s were about one-quarter of what they were in the early 1970s, as predicted by the arguments in Section 2 of this paper. The estimated value for 1994 was 0.011 (95% confidence limits 0.009–0.013). Assuming a reporting rate of 0.38 and a retrieval rate of 0.8, this corresponds to a kill rate of 0.036 (range 0.029–0.044 based on the 95% confidence limits of the recovery rate estimate).

We also estimated recovery rates for Snow Geese banded from 1990 to 1997 at QMG, the only other breeding

**Table 2**

Mean direct recovery rates of Lesser Snow Geese banded at La Pérouse Bay, Manitoba, and Queen Maud Gulf, Nunavut, from 1970 to 1995 by five-year periods<sup>a</sup>

Location/time period	Adult recovery rate		Immature recovery rate	
	Mean	SE	Mean	SE
<b>La Pérouse Bay</b>				
1970–1974	5.19	0.49	9.44	0.46
1975–1979	4.42	0.44	8.49	0.37
1980–1984	3.06	0.15	5.52	0.54
1985–1989	1.87	0.24	2.53	0.53
1990–1994	1.28	0.22	2.22	0.52
1995 <sup>b</sup>	1.38	0.40	1.46	0.40
<b>Queen Maud Gulf</b>				
1990–1994	1.00	0.24	1.95	0.76
1995–1997 <sup>b</sup>	1.67	0.16	2.89	0.65

<sup>a</sup> For this analysis, sexes were pooled, as were birds with and without colour legbands, because neither of these factors influences direct recovery rates.

<sup>b</sup> Note that reporting rates may have increased during this period because of the use of a toll-free telephone number starting in 1995 to report bands.

colony where large numbers of birds have been banded every year recently. We included only birds that had received either a single metal legband or a metal band on one leg and a coloured band on the other leg. The latter were applied to most of the immature females but none of the adults. We excluded birds with neck collars, because their recovery rates were about twice those of birds marked concurrently with only legbands (C.M. Francis, unpubl. data). During 1990–1994, mean recovery rates of both adults and young were similar to, but slightly lower than, those estimated for LPB during the same period (Table 2). The estimated adult recovery rate for 1994, based on linear regression over time, was 0.0078 (95% confidence limits 0.002–0.014). These data are consistent with the earlier McC data suggesting that recovery rates may be lower for some of the more western colonies than for LPB, as discussed above (Section 3.2.2). Assuming similar reporting rates at these colonies, as at LPB, these correspond to a kill rate of 0.026 (range 0.007–0.047).

An alternative approach for estimating harvest and kill rates is based on estimates of the total population at the start of the hunting season and the total harvest. Current estimates of the total legal harvest (g) by licensed hunters of Snow Geese in Canada and the United States, based on the harvest survey data, are believed to be reasonably unbiased (Cooch et al. 1978; Geissler 1990), although this must be taken partly on faith, as there are many uncertainties related to questionnaires that are not returned, as well as to the kill by unlicensed hunters. On the other hand, estimates of the population at the start of the hunting season are not available directly. Francis et al. (1992a) used midwinter inventory data (N) to derive a crude estimate of directions of change in harvest rate with the formula  $g/(g + N)$ . However, that approach is not suitable for quantitative measures of harvest rates, for several reasons. First, the midwinter inventory is, at best, only an index of the total population, which may represent less than 50% of the true winter population (e.g., Kerbes 1975). Without an estimate of the correction factor required to convert midwinter counts to total population size, g and N cannot meaningfully be added together. Second, the proportion of the population counted on the midwinter survey has likely been changing over time, as increasing proportions of Snow Geese winter in agricultural fields away

from the coast. Third, the midwinter survey takes place before the end of the hunting season, so that part of the harvest ( $g$ ) represents birds counted in the midwinter survey. Fourth, the preceding equation does not consider crippling loss and natural mortality between the start of the hunting season and the time of the midwinter survey. Fifth, the midwinter survey does not differentiate between Ross' Geese *Anser rossii* and white-phase Snow Geese, which have potentially been increasing at different rates. Finally, harvest rates differ by age class, but the midwinter survey provides no information on the age composition of the population (although age composition has been estimated for flocks in some areas since the 1950s; U.S. Fish and Wildlife Service 1997).

An alternative source of information on population size is from counts of breeding colonies (Fig. 3). These counts, based mostly on aerial photography, are believed to provide reasonable estimates of the number of breeding individuals on each colony surveyed (Kerbes 1975, 1994; Alisauskas et al. 1998). These surveys have not been carried out every year, but, during 1997 and 1998, all known moderate to large breeding colonies in the Arctic were surveyed (Fig. 3). The total estimated breeding population in those colonies at that time was 4.38 million adults. This underestimates the total population to the extent that geese are nesting in colonies that were not surveyed or were outside the boundaries that were surveyed. The extent of the underestimate is thought to be small (R.H. Kerbes, pers. commun.), but it is obviously unknown. In contrast, this could overestimate the 1994 population to the extent that the population continued to grow through 1997–1998. To estimate the number of adults in the fall flight in 1994, we assume that those two factors cancelled each other out. We also assumed that the numbers of these geese that were harvested in other flyways (e.g., the Pacific Flyway) were comparable to the numbers of geese from more western colonies (e.g., Banks Island) that were included in the Central Flyway harvest. To estimate the adult harvest rate in 1994, we also need to estimate the number of nonbreeding adult geese present during the fall flight. We used matrix models, with the same parameters as the models of Rockwell et al. (1997), to estimate the nonbreeders at 28% of the number of breeding geese (E.G. Cooch, unpubl. data). This is similar to the proportion of nonbreeders estimated by Alisauskas et al. (1998) to be present on the colony at QMG (32% of the number of breeders). Using the mean of these two estimates (30%), we estimated the fall flight in 1994 at approximately 5.6 million adults. The mean total harvest during 1985–1994, which was similar to the estimated harvest in 1994, was 400 000. The estimated average age ratio in the harvest during this period, based on parts surveys by the U.S. Fish and Wildlife Service and the Canadian Wildlife Service, was 0.575. Thus, the estimated adult harvest was 230 000, and the estimated harvest rate was  $230\,000/5\,600\,000 = 0.04$ . Allowing for a retrieval rate of 0.80, as we did in the recovery rate analysis, this represents a kill rate of 0.05. This is close to the estimated kill rates obtained from recovery rate analyses, especially considering the unknown precision and accuracy of most of the parameters used in obtaining the estimates.

## 4.2 Estimated survival in 1994

If mortality associated with hunting is additive to other sources of mortality, and if nonhunting mortality has not changed over time (as was assumed in the Original Model), then it follows that a decrease in harvest rates, as indicated by the decline in recovery rates, should be associated with an increase in survival rates. To test this, again using banding data from LPB, we used SURVIV (White 1983) to estimate adult survival rates using models derived from those in Brownie et al. (1985). We used data from birds banded as both adults and immatures. The most general model we fitted allowed all survival and recovery rates to vary among years (model H1). However, adult survival rates were estimated with very poor precision from that model, especially in recent years, owing to declining sample sizes banded as well as declining numbers recovered. To increase sensitivity for detecting changes in survival rates, we then fitted a model in which survival rates were constrained to be constant over each five-year period from 1970 to 1994 (the final year for which survival rates could be estimated, because banding stopped in 1995). We compared this with models in which survival was constrained to be constant for the final 15 or final 10 years of the period, corresponding with the assumptions of the models of Rockwell et al. (1997).

For data from both male and female Snow Geese, the most parsimonious model, as determined by the Akaike Information Criterion, allowed adult survival to differ among five-year periods, with the final five-year period different from earlier five-year periods (Table 3). In a one-tailed test of the hypothesis that mean adult survival rates increased in the final period (as predicted by the change in harvest rates), versus the hypothesis that they had not increased, the hypothesis of no change was rejected for males and females ( $P < 0.05$  in both cases).

We also estimated survival rates based upon adult banding data from 1989 to 1995 at QMG. We used the same criteria as in the recovery rate analysis, except that we also included 1989 data (the start of banding at that site) to increase the sample. Although precision was poor, the mean estimates for both sexes were remarkably close to the most recent estimates for LPB (Table 3), reaffirming the suggestion that adult survival rates are currently higher than postulated by Rockwell et al. (1997).

Although it seems likely that survival continued to increase from 1990 to 1994, our best estimates of survival rates for 1994 from these models are the estimates of mean survival during the final period, of approximately  $s_a = 0.94$ . Unfortunately, even if we pool data from males and females, the standard error (SE) of this estimate from LPB is relatively high at  $\pm 0.029$ . This corresponds to 95% confidence limits for survival between 0.88 and 1.0, representing mortality rates between 0.12 and 0.0.

An alternative approach to estimating survival rates for 1994 is to model survival as a linear function of recovery rates (Francis et al. 1992a). Following Francis et al. (1992a), we fitted this model using data from birds banded only as adults, with males and females pooled. The resultant model, including data from 1970 to 1995, was nearly identical to that derived by Francis et al. (1992a) using only data through 1988:  $s_i = 0.92 - 2.9f_i$ , where  $s_i$  is adult survival rate in year  $i$  and  $f_i$  is the adult recovery rate in year  $i$ . Based on our earlier

**Table 3**

Adult survival rates of Lesser Snow Geese banded at La Pérouse Bay, Manitoba, and Queen Maud Gulf, Nunavut, from 1970 to 1995 by five-year periods<sup>a</sup>

Location/time period	Male survival rate		Female survival rate	
	Mean	SE	Mean	SE
<b>La Pérouse Bay</b>				
1970–1974	0.80	0.019	0.80	0.020
1975–1979	0.82	0.015	0.81	0.017
1980–1984	0.86	0.014	0.84	0.017
1985–1989	0.86	0.018	0.83	0.020
1990–1994	0.94	0.039	0.94	0.042
<b>Queen Maud Gulf</b>				
1989–1995	0.94	0.063	0.92	0.064

<sup>a</sup> Parameters were estimated with SURVIV, independently for each sex, using a model that assumed that adult survival remained constant within each five-year period, but immature survival rates and all recovery rates varied among years (birds banded as immatures were included in the analyses for La Pérouse Bay only).

estimate of 0.011 for the recovery rate in 1994, this suggests a survival rate that year of 0.89, near the lower confidence limit of the direct estimate. A third approach is to model survival as a linear function of time. Although survival obviously cannot increase indefinitely in a linear fashion, this model was an equally good fit to the regression in relation to recovery rates within the range of years analyzed (1970–1994). The estimated survival rate for 1994 from this model was 0.91.

#### 4.3 Impact of revised parameters on required harvest estimates in 1994

In the preceding sections, we estimate adult kill rates for 1994 at 0.026 and 0.036 based on recovery data from QMG and LPB, respectively, or at 0.05 based on estimates of total harvest and total fall adult population. The differences between QMG and LPB were similar to the differences between McC and LPB in the late 1970s. The lower values based on banding data could be due to any of several factors: (1) reporting rates of banded birds were lower than we assumed (despite two independent derivations of a similar value); (2) harvest rates from at least one of these colonies were lower than the mean for the population; (3) the harvest surveys are biased high, perhaps because of nonresponses; or (4) the fall flight of adults was underestimated, perhaps as a result of overlooked colonies, inaccurate counts, or a proportion of nonbreeders that was higher than estimated. There are insufficient data to determine which of these may be most important; in any case, standard errors are not available for several of the components of both estimates. We suspect that the estimate of 0.026, although potentially appropriate for some colonies, is too low for the mid-continent population as a whole, because this implies that either fall flight of adults was twice as high as we estimated or that actual harvests average only half as large as estimated by harvest surveys. Although errors of this magnitude are possible, they seem unlikely, so we will restrict our analyses to the range from 0.036 to 0.05 (if 0.026 was correct, the required increase in harvest would be even greater than we estimate).

Direct modelling of survival suggests a value of 0.94 for both LPB and QMG, but, as noted above, the confidence limits are fairly wide. Comparison with the preceding

estimates of kill rate suggests that these estimates are probably too high, as they imply a natural mortality rate ( $E$ ), based on equation 1, between 0.01 and 0.03. These are considerably lower than the estimate of  $E = 0.08$  derived from the long-term relationship between recovery and survival rates at LPB (Francis et al. 1992a). They are also much lower than mortality estimates from a nonhunted population of Barnacle Geese *Branta leucopsis* (Owen 1984), although the latter may be expected to be greater than for Snow Geese because of a longer, more arduous migration flight over the ocean. Although ready availability of food on staging and wintering areas may have led to low natural mortality of adult Snow Geese, it seems unlikely to be less than 0.03, and it could well be higher. Estimated survival from long-term models was between 0.89 and 0.91, implying natural mortality rates between 0.04 and 0.08. The true average value for the population in 1994 was likely between these limits of 0.89 and 0.94, so we base our analyses on these limits.

Based on the models of Rockwell et al. (1997),  $s_a$  must be reduced to 0.795 to reduce  $\lambda$  to 0.95 and to 0.72 to reduce  $\lambda$  to 0.85. From equation 4, for the ranges of parameters just mentioned, we estimate that an increase in kill rate between three- and fivefold would have been required to reduce  $s_a$  to 0.795 in 1994, and between 4.5- and 7.3-fold to reduce  $s_a$  to 0.72 (Fig. 4). These results contrast with the conclusions of Rockwell et al. (1997) that doubling the kill rate for the first rate and tripling it for the latter rate would have been sufficient. Furthermore, as we noted in Section 3.2.3, reducing survival to 0.80 may not be sufficient to reduce  $\lambda$  below 1.0, so the estimates for  $s_a = 0.72$  may be more appropriate.

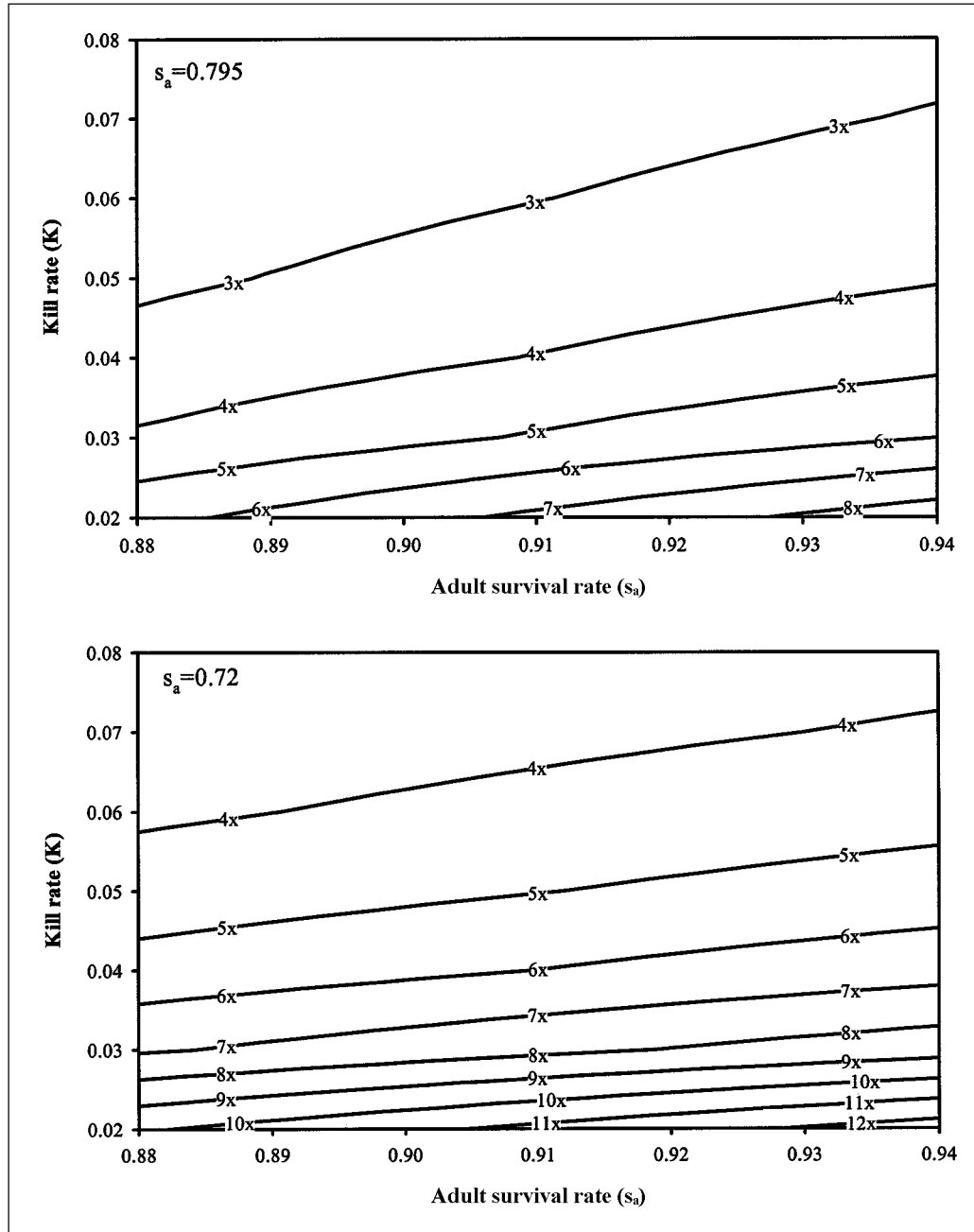
If we consider the total estimated harvest during 1994 of 230 000 adults (see above), a three- to fivefold increase (as required to reduce  $s_a$  to 0.795) implies a harvest between 0.7 and 1.1 million adult geese, whereas a 4.5- to 7.3-fold increase (to reduce  $s_a$  to 0.72) implies a harvest between 1.0 and 1.6 million adults. Assuming an age ratio of 57% adults in the harvest, these ranges correspond to a total harvest (including young birds) somewhere between 1.2 and 2.8 million geese.

#### 4.4 Predicted increase required for 1999

Survey data indicate that the Snow Goose harvest has increased since 1994, with the total estimated harvest for 1997 about 80% higher than the 1985–1994 mean (Table 1). Mean recovery rates of geese marked at QMG were about 60% higher in 1995–1997 relative to 1990–1994 (Table 2), suggesting that this increased harvest led to increased harvest rates. However, the increased recovery rates could also be due to the introduction of a toll-free telephone number to report goose bands in 1995, as well as increased efforts to promote band reporting. Thus, we cannot use these recovery rates to estimate harvest and kill rates directly. Instead, we predict the required harvest for 1999 based on estimated changes in population size. We note that even an 80% increase in harvest was far less than our minimum estimate of a threefold increase required to stop population growth. If the population continued to grow at 5% per year ( $\lambda = 1.05$ ), it would be about 27% larger in 1999 than it was in 1994. Even allowing for some reduction in the growth rate due to increased harvest, it seems likely that the population will be

**Figure 4**

Effect of different values of current adult survival and kill rate on estimated increase in kill rate needed to reduce adult survival to 0.795 or 0.72, the values required to achieve growth rates of  $\lambda = 0.95$  and  $0.85$ , respectively, based on the assumed matrix in the Original Model of Rockwell et al. (1997). Lines represent pairs of survival and kill rate values corresponding to a specified number of times increase in kill rate. For example, if current adult survival rate is 0.91 and current kill rate is 0.04, then reducing  $s_a$  to 0.795 will require an approximately 3.8- to 4.0-fold increase in kill.



at least 20% larger in 1999 than it was in 1994. Under this assumption, the total harvest required to control the population in 1999 would be about 20% higher than was estimated in the previous section. Thus, the total required harvest would be between 0.85 and 1.9 million adults, which, assuming no changes in age ratios (the estimated age ratio in the 1997 harvest was again 57%), represents between 1.5 and 3.4 million geese. Relative to the most recent harvest estimate available, of 720 000 birds for 1997, this corresponds to a further 2.1- to 4.7-fold increase.

If we assume that the harvest and fall flight estimates we used for 1994 were reasonably accurate and that  $s_a$  must

be reduced from 0.89 to 0.72 to ensure adequate reduction in the population, then our best estimate of the required harvest in 1999 would correspond to about 2.1 million geese out of a predicted fall flight of 9.2 million geese (assuming 20% growth from 1994 to 1999 and 27% immatures in the flight). However, we caution that we cannot be sure that harvest or breeding population estimates are more accurate than estimates from recovery rates, and the required harvest could be anywhere between 1.5 and 3.4 million, based on our current knowledge.

## 5. Discussion

We agree with Rockwell et al. (1997) that a deterministic stage-based matrix model can be a valuable tool for modelling demography of animal populations, including Snow Geese. However, as was shown by Francis et al. (1992a), there have been long-term changes in survival rates of both adult and immature geese, as well as large annual fluctuations in productivity and postfledging survival. Under these circumstances, the stable age distribution assumed in the standard analyses of matrix models will not be reached (Caswell 1989), and use of mean values of demographic parameters, especially survival rates, may be of limited utility for population modelling. Although it is still possible to use matrix population models, their predictions will be accurate only if the model parameters include the current age distribution of the population and current values of demographic parameters. Furthermore, the ability of the model to predict beyond the immediate future will depend upon the extent to which it models changes in these demographic parameters and the precision to which they can be estimated. As Figure 4 clearly shows, the relative increase in kill needed to achieve management objectives is very sensitive to estimates of adult survival and kill rates.

In this paper, we have concentrated on estimating these two demographic parameters. We have accepted, for the moment, the assumptions in the Original Model regarding most parameters, such as mean age-specific reproductive output, but we have shown that the values used by Rockwell et al. (1997) for survival and kill rates were not appropriate for the mid- to late 1990s. We predict that the harvest must be increased 1.5- to 3.0-fold more than was estimated in the Original Model to achieve the required reductions in adult survival rates.

The preceding estimates (like those presented in the Original Model) were calculated in terms of increasing adult harvest but are expressed in terms of increases in the total harvest, assuming no long-term change in age ratios in the harvest. Because the reproductive value of young birds is substantially less than that of adults, the increased harvest of young birds will have a proportionately much smaller effect on population growth (E.G. Cooch, J.D. Lebreton, and F. Cooke, unpubl. data), but it will still have an effect. Using a model developed by Francis (this volume), we estimated that a threefold increase in the total harvest would be roughly equivalent to a fourfold increase in the adult harvest with no change in the immature harvest (C.M. Francis, unpubl. data). Considering that harvest rates of immature geese have also been decreasing over time (as indexed by recovery rates; Table 2), an increase in their harvest is probably required to meet the assumptions of the Original Model. Whether this should be increased by more or less than the adult harvest could be determined only by revisiting all of the assumptions of the Original Model, which is beyond the scope of the current paper.

It is worth noting that if it were possible to increase the proportion of adults in the harvest by selectively shooting adults or by hunting in areas or at times when adults are more vulnerable, this would reduce the amount of increase required in the total harvest. On the other hand, if an increase in the overall harvest resulted in a higher proportion of immature birds being taken, then an even greater increase in the total harvest would be required to achieve the desired growth rate targets.

Although we have concentrated on the consequences of using inappropriate values of survival and recovery rate estimates, there is a need to reconsider other assumptions in the Original Model. Here, we restrict ourselves to outlining some of the possible variations to the assumptions that need to be considered. If management actions are to be taken based upon these models, we feel that it should be a very high priority to develop new models to test the effects of varying these assumptions.

One of the more critical assumptions was that  $\lambda$  was stable over time and that 1.05 was an accurate estimate of  $\lambda$ . Rockwell et al. (1997) constructed a matrix based upon the best available estimates of individual parameters and found that the estimated growth rate was higher than suggested by measures of change in overall population size. They then argued that, because some of the input parameters of the model were not well measured (e.g., the proportion of adult females that breed each year), it was appropriate to adjust some of the other parameters to match the observed  $\lambda$ . We agree that poorly measured parameters should be adjusted to match those that are measured more precisely.

Unfortunately, there is some uncertainty about the population growth rate over the period in question. The estimate of 1.05 reported by Rockwell et al. (1997) was derived incorrectly from the midwinter surveys by a simple linear regression of abundance against year for the period 1970–1994. A more appropriate analysis of the midwinter surveys, using the logarithm of abundance against year, gives  $\lambda = 1.03$  for the period 1970–1997 or  $\lambda = 1.04$  for the period 1961–1997 (Fig. 2). Assuming a constant growth rate, constant harvest, and asymptotic age distributions,  $\lambda$  can also be estimated from changes in recovery rate. Under these assumptions, population size at any time  $t$  is given by:

$$N_t = N_0 \lambda^t$$

and recovery rate at time  $t$  is:

$$f_t = f_0 \lambda^{-t}$$

Based on recovery rate estimates from either LPB or CHM (Francis et al. 1992a),  $\lambda$  was 1.06, which is higher than estimates from winter counts. Allowing for the slight decrease in harvest between 1970 and 1995 (Table 1), 1.05 may be consistent with these estimates.

The parameter  $\lambda$  can also be estimated from breeding ground counts. Most of the colonies in the central and eastern Canadian Arctic were surveyed using aerial photography, combined with some ground counts, in 1973 (Kerbes 1975) and again in 1997–1998 (Alisauskas et al. 1998; R.H. Kerbes, pers. commun.; Fig. 3). Interpolating estimates for colonies that were surveyed in other years, the total mid-continent population increased from about 1.1 to 4.19 million breeding adults, which corresponds to  $\lambda = 1.057$ . Some colonies, such as those around QMG, have been growing much more quickly (Alisauskas et al. 1998), but this may be due partly to immigration from other colonies that have been declining. This  $\lambda$  is similar to the estimate derived from the recovery rate analysis and substantially higher than the estimate from winter counts: over a 25-year period, a growth rate of 1.057 corresponds to a fourfold increase, while a growth rate of 1.031 represents only a 2.1-fold increase.

Even if the mean value of  $\lambda$  has been close to 1.05 over the study period, there is reason to believe that  $\lambda$  may have changed over time, because survival rate has been increasing. If this has not been compensated by reductions in other demographic parameters, then  $\lambda$  must have been increasing as well. If  $\lambda$  was actually higher than 1.05 in 1994, then the Original Model may have underestimated the extent to which survival rates need to be reduced to cause the population to decline. As noted above (Section 4.3), the Original Model suggested that  $s_a = 0.795$  would be sufficient to reduce  $\lambda$  to 0.95, whereas empirical data from LPB indicate that adult survival was approximately equal to that value from 1970 to 1978 (Francis et al. 1992a), a period when the population was increasing rapidly. This discrepancy could be due to use of inappropriate fecundity parameters owing to incorrect assumptions about  $\lambda$  and whether it was changing over time.

The issue of possible density-dependent processes should also be considered. The parameters used in the Original Model were derived from a colony that had large reductions in reproductive output and immature survival rates between the early 1970s and the late 1980s. The Original Model assumed that reproductive output was constant over time and that Snow Geese, considering the mid-continent population as a whole, avoided density-dependent reductions in reproductive output by moving to new breeding sites when conditions deteriorated at any given locality. Indeed, analyses of age ratios in the long-term harvest data provide no evidence for long-term reductions in productivity (C.M. Francis, unpubl. data). However, some of the values used in the Original Model were based upon mean values from 1973 to 1984. Rockwell et al. (1997: 83) assert that, during this period, "the vegetation at La Pérouse Bay was above the threshold for adequate foraging and gosling growth," but this is not consistent with the observations that growth (Cooch et al. 1991) and survival rates (Francis et al. 1992a) of immature geese had already declined dramatically by 1978. Without revisiting all of the assumptions of the Original Model, it is unclear how this may affect the conclusions.

If density-dependent effects were causing changes in the nonhunting mortality rate  $E$ , this would also affect the conclusion. Increased nonhunting mortality of immature Snow Geese was demonstrated at LPB, apparently as a result of deterioration of feeding conditions on their breeding colony (Francis et al. 1992a). Although some geese, especially young ones, may be able to avoid this effect by moving to new breeding areas, many mature adults continue to return to the same breeding areas despite deterioration of the breeding environment (Cooch et al. 1993; Ganter and Cooke 1998). As a result, increasing deterioration of habitat on breeding colonies is likely to have at least some negative effects on population growth. It is conceivable that this could also increase nonhunting mortality of adults, although no data are available to test this. If so, a smaller increase in harvest may be sufficient to reduce survival rates to values necessary to control the population. On the other hand, if  $E$  were increasing as a result of any sort of compensatory effects, then larger increases in harvest might be required, because at least some of the increased harvest might be compensated by reductions in other forms of mortality. Unfortunately, our estimates of  $E$  depend upon the assumption that mortality has been additive, so we cannot test this directly.

The ultimate test of any model will be through measuring changes in growth rate of the population if the harvest is increased. Obviously, close monitoring will be required to measure any such changes in demographic parameters, including population size, growth rate, survival rate, and harvest rate. Such monitoring will not be without considerable financial cost and logistic difficulties. Monitoring survival rates requires continued banding of large numbers of birds at the same site for many years, preferably sites that have been used extensively in the past. Unfortunately, with the current very low recovery rates, even banding several thousand birds per year may provide survival estimates with insufficient precision to measure the expected changes in survival rates. For example, after banding about 5000 geese at QMG between 1989 and 1996 (excluding neck-collared birds, which differ in recovery and probably survival rates), the 95% confidence limits of mean adult survival for sexes combined ranged from 0.84 to 1.0 (Table 3). These cover a very wide range of population growth rates. Increased recovery rates owing to greater harvest, the recent introduction of toll-free numbers for reporting bands, and efforts to promote band reporting should improve precision. At the same time, some of those measures mean that recovery rates can no longer be interpreted as indices of harvest rates, at least until new estimates of reporting rates are available. Thus, it will also be critical to develop a reward band study for mid-continent Snow Geese to measure the new reporting rates, once the effects of efforts to increase reporting rates have stabilized.

## 6. Management implications

Any mathematical model of population growth in a population of wild animals necessarily involves a simplification of reality, with a variety of assumptions. If the assumptions are appropriately chosen and the critical components of the system are adequately represented, then the model may provide useful predictions of the consequences of various management options. Although the differences between our assumptions and those of the Original Model appear to be quite small, the change in the predictions is very large.

A major recommendation of the Arctic Goose Habitat Working Group of the Arctic Goose Joint Venture was to reduce the population growth rate to an annual level between 0.85 and 0.95 by increasing the harvest to between *two and three times* the mean harvest levels at the time (Batt 1997: 118–119). However, with revised assumptions, which are supported by analyses of recent data, we estimate that a *3.0- to 7.3-fold increase* relative to the harvest at that time would have been required in 1994. Despite a nearly 1.8-fold increase in the estimated harvest by 1997 relative to the earlier mean values, we estimate that a further *2.1- to 4.7-fold increase* would still be required in 1999 to reduce the population adequately. For the mid-continent population, this corresponds to a total harvest, as measured by the harvest surveys, of between 1.5 and 3.4 million geese.

We emphasize the uncertainty in these estimates. If the true value required is close to the higher of these estimates, then achieving the lower value would likely be insufficient to stop population growth. Conversely, if the true value is at the lower limit, then harvest at the upper limit would lead to a much faster decline in the population than intended. We also caution that there is likely to be variation

among colonies in current harvest and growth rates. For example, estimated recovery rates from QMG were lower than those from LPB, suggesting that the QMG geese may be subject to lower than average harvest rates. Other colonies may be subject to higher harvest rates. Depending upon the distribution of increased harvest, some colonies could be disproportionately affected by changes in harvest and could decline much more rapidly than others. Finally, we note that we have considered uncertainty in only some model parameters. There is an urgent need to revisit all of the assumptions of the Original Model and carry out a new modelling exercise, using stochastic rather than deterministic models (Nations and Boyce 1996), to obtain the best possible estimates of the effects of various management actions on the colonies.

Even considering the lower limit of our estimates, managers need to determine whether planned measures will be sufficient to achieve the required changes in harvest. If not, successfully reducing the population could require additional control measures. Efforts to reduce productivity have been suggested, although Rockwell et al. (1997) showed that proportionately much larger changes are required in productivity than in survival parameters. Any alternative options should again be modelled prior to implementation. If management actions are not able to reduce the population growth rate  $\lambda$  to less than 1.0, the population will continue to grow until it is limited by external factors, such as reduced availability of food on wintering or staging areas, loss of habitat on the breeding areas, or large-scale disease outbreaks.

Whatever measures are adopted, continued monitoring of total population size and demographic parameters is essential to determine the effectiveness of those measures. Monitoring should include detailed studies at multiple nesting colonies, to determine whether any colonies are disproportionately affected. Any such monitoring should be preceded by appropriate modelling and power analyses to determine the level of precision with which various parameters can be measured, to ensure optimal allocation of resources among monitoring programs.

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## Appendix 1

Annual estimated midwinter survey counts and harvest totals for Lesser Snow Geese in the Mississippi and Central flyways and the Canadian provinces of Ontario, Manitoba, and Saskatchewan from 1970 onwards<sup>a</sup>

Year	No. of Snow Geese (000s)				
	Midwinter survey		Harvest estimates		
	Central	Mississippi	Central	Mississippi	Canada
1970–1971	412.4	654.9	314.3	258.4	–
1971–1972	394.5	937.3	180.7	159.7	–
1972–1973	493.0	532.3	151.1	109.2	–
1973–1974	657.4	532.3	254.8	153.0	–
1974–1975	655.4	441.5	241.3	173.2	–
1975–1976	870.8	691.6	350.1	167.6	80.1
1976–1977	579.0	571.3	256.5	102.3	63.7
1977–1978	1172.9	794.1	306.3	126.8	52.0
1978–1979	772.5	513.0	189.0	133.9	57.6
1979–1980	793.5	594.2	338.4	165.6	122.7
1980–1981	901.7	504.6	251.8	144.4	116.9
1981–1982	925.7	868.3	269.9	110.8	110.0
1982–1983	923.4	832.1	241.7	124.4	107.6
1983–1984	905.5	588.9	245.7	187.2	117.8
1984–1985	980.4	992.7	292.8	101.5	109.6
1985–1986	837.6	611.7	216.9	99.0	140.9
1986–1987	900.5	1013.3	149.9	69.7	84.1
1987–1988	735.9	1014.6	182.6	56.5	100.0
1988–1989	598.1	1358.0	250.8	51.4	98.3
1989–1990	661.3	1063.0	286.3	97.3	125.7
1990–1991	799.9	1335.9	211.8	92.8	89.3
1991–1992	908.4	1113.5	250.0	110.7	91.2
1992–1993	896.0	848.2	149.5	60.2	48.1
1993–1994	1015.2	1185.6	270.2	71.7	73.2
1994–1995	1203.4	1521.7	270.5	99.0	85.1
1995–1996	835.6	1562.6	332.0	191.3	94.2
1996–1997	1208.6	1642.3	299.2	231.1	81.7
1997–1998	1058.7	1918.5	349.0	239.0	132.8

<sup>a</sup> Midwinter survey and U.S. harvest data from Sharp and Moser (1998); Canadian harvest data from computer files provided by H el ene L evesque of the Canadian Wildlife Service.

## Appendix 2

Effects of colour bands on band reporting and recovery rates

Most geese at LPB were banded with supplementary alpha-numeric coloured legbands. These are often assumed to increase reporting rates, but here we use an indirect approach to show that average reporting rates of these geese are comparable to those of other species of waterfowl, and we also show that reporting rates of geese banded at LPB with and without colour bands were similar.

The reporting rate assumed in the Original Model was 0.38, as taken from studies of Mallard *Anas platyrhynchos* reporting rates (Nichols et al. 1991). This value is similar to that reported by Martinson and McCann (1966) for Canada Geese *Branta canadensis*. Although no direct measures of reporting rates are available for Snow Geese, analyses of the relationship between recovery and survival rates provide independent evidence that this value was reasonable for geese banded at LPB. Francis et al. (1992a) used an ultra-structural model to estimate the relationship between survival rate in year *i* (*s<sub>i</sub>*) and recovery rate in the same year (*f<sub>i</sub>*) as *s<sub>i</sub>* = 0.92 - 2.9*f<sub>i</sub>*. If we assume that the nonhunting mortality rate is unaffected by hunting mortality (complete additivity), then this equation can be rewritten as *s<sub>i</sub>* = *s<sub>0</sub>* (1 - *b f<sub>i</sub>*), where *s<sub>0</sub>* = 0.92 represents the survival rate in the absence of hunting, and *b* = 2.9/0.92 = 3.1. This implies that every bird reported represents 3.1 birds killed, so the correction from kill rate to recovery rate is (3.1)<sup>11</sup> = 0.32. This correction incorporates both the retrieval rate (the proportion of birds killed that are retrieved) and the reporting rate. If we return to the Original Model assumption of a reporting rate of 0.38 and a retrieval rate of 0.8, then the corresponding conversion from kill rate to recovery rate is 0.8 × 0.38 = 0.30. The similarity of these two values, despite their derivation from independent sources, suggests that they may be close to the true average value for LPB.

To test whether colour bands affected recovery rates directly, we analyzed data for LPB from 1988 to 1993, when some geese received colour bands and standard legbands, while others received only standard legbands. These were not randomly assigned by sex (females were much more likely to receive colour bands than males); however, Francis and Cooke (1992b) showed that, although recovery rates in years after banding differed by sex, owing to emigration of males, there were no differences between the sexes in direct recovery rates. Thus, we could pool across sexes for analysis of direct recovery rates. We compared direct recovery rates relative to presence or absence of colour bands on a year-by-year basis, using composite Z-test analyses (described in Brownie et al. 1985). Separate analyses by year were necessary because recovery rates varied among years, as did the numbers of birds with and without colour bands. There was no evidence that colour bands affected reporting rates (Table A-1). Thus, we conclude that, at least for data from LPB during this time period, colour bands did not lead to any increase in reporting rates.

**Table A-1**

Comparison of direct recovery rates between Lesser Snow Geese banded with supplementary colour bands and without colour bands, La P erouse Bay, Manitoba<sup>a</sup>

Age	Year	No colour bands			Colour bands			Z <sup>b</sup>
		No. banded	No. recovered	Rate (%)	No. banded	No. recovered	Rate (%)	
Adult	1988	606	13	2.15	1551	23	1.48	1.08
	1992	913	7	0.77	2377	33	1.39	-1.46
	1993	1199	16	1.33	1198	13	1.09	0.56
	Mean			1.42			1.32	0.10
Young	1988	1292	27	2.09	1383	28	2.02	0.12
	1989	386	4	1.04	462	2	0.43	1.04
	1990	431	10	2.32	417	6	1.44	0.94
	1991	1190	33	2.77	1191	41	3.44	-0.94
	1992	368	8	2.17	406	13	3.20	-0.88
	1993	2189	76	3.47	1213	29	2.39	1.75
Mean			2.31			2.16	0.82	

<sup>a</sup> Includes only years with >100 of an age class in each category.

<sup>b</sup> Positive values indicate recovery rates are higher for birds without colour bands, negative values the reverse. None of the differences is significant.

# Snow Geese: Can we pay down the mortgage?

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We are pleased that Professor Cooke and coauthors (Cooke et al., this volume) have focused on increased harvest of adults as the most efficient way to reduce numbers of Lesser Snow Geese *Anser caerulescens caerulescens* (hereafter referred to as Snow Geese), as was proposed by Rockwell et al. (1997). What remains to be determined is how many adult Snow Geese need to be harvested per year to accomplish the goal of preventing further destruction of Arctic ecosystems. Herein, we will show that despite Cooke et al.'s (this volume) commendable use of current data, some of which were unavailable to Rockwell et al. (1997), they have produced estimates of required harvest that, in absolute terms, are more erroneous (too high) than were those of Rockwell et al. (1997) (too low). First, we will note how several of their assumptions have affected the accuracy and validity of their estimates. Because our goal is to aid in the solution of a current problem, we will limit our commentary to their present-day rather than their historic estimates. Second, we will show that a simpler approach to meeting the goal of reducing the mid-continent Snow Goose population to its target level by the year 2005 is via a constant annual harvest. Finally, we will give our best "guesstimate" of that harvest.

Rockwell et al. (1997) showed that adult survival ( $s_a$ ) has the greatest impact on Snow Goose population growth rate. Subsequent elasticity analyses (R.F. Rockwell, unpubl. data) show that this is true even when the original model is modified to incorporate density dependence, environmental stochasticity, and metapopulation structure. Thus, it is not surprising that  $s_a$  remains a key variable in Cooke et al.'s (this volume) analyses. They estimate that this variable currently ranges from 0.89 to 0.94 and base their harvest projections on this range. Although we can accept the lower estimate, the upper one is far too high. One of the best estimates of the growth rate of the mid-continent population of Snow Geese is based on Kerbes' breeding colony surveys done in the early 1970s and late 1990s (R.H. Kerbes, pers. commun.) and assumes no systematic change in breeding propensity or nesting success. Although we agree with Cooke et al. (this volume) that there is some variation among the growth rates of specific colonies and some variance associated with an overall estimate, the current point estimate for the overall mid-continent population is between 1.053 and 1.057 (R.F. Rockwell, unpubl. data, and Cooke et al., this volume, respectively; both based on R.H. Kerbes, pers. commun.). Substituting  $s_a = 0.94$  into Rockwell et al.'s

(1997) projection matrix for the mid-continent population (rather than the original  $s_a = 0.88$ ) leads to an estimated growth rate of  $\lambda = 1.11$ , which far exceeds the current estimate of  $\lambda \approx 1.05$ . Of course, it is possible that estimates of reproductive success and/or juvenile survival in that original matrix were too high for the present; perhaps they declined during the period when adult survival purportedly increased to 0.94, thereby reducing population growth rate in a compensatory fashion. However, given the low elasticity of those variables, such a decline would have had to have been large. We examined this further and found that a 42% reduction in either variable (to 58% of its original value) or a 24% reduction in both would be required to compensate for the 7% increase in adult survival from 0.88 to 0.94. We feel that such an increase is unrealistic, especially in the face of unpublished analyses (cited in Cooke et al., this volume, Section 3.2.3) that age ratios and fecundity of the mid-continent population have not changed over time. We feel that their estimate of 0.94 for adult survival is biologically unrealistic and that harvest projections from it are not meaningful. (No doubt about it, Snow Geese are survivors, but parrots and albatrosses they ain't.)

A stated goal of the Arctic Goose Habitat Working Group was "to reduce the population growth rate to some sustained level with  $\lambda < 1.0$ " (Rockwell et al. 1997: 99) and monitor the resulting population size and its continuing impact on the Arctic ecosystem. To provide managers with some flexibility, scenarios were developed for reductions in adult survival that led to population growth rates of  $\lambda = 0.85$  and  $\lambda = 0.95$ . Cooke et al. (this volume) assert that it may be prudent to use the estimated adult survival associated with  $\lambda = 0.85$  "to ensure that realized growth rate is actually  $\lambda < 1.0$ ." This appears to stem, in part, from their uncertainty as to whether the original projection matrix, based primarily on data from La Pérouse Bay, is accurate for the entire mid-continent population, owing to potential heterogeneity among nesting colonies in reproductive success or survival or to changes in these variables over time. However, as indicated above, their analyses found no change in age ratio (or fecundity) over time. Moreover, their most reasonable estimate of current adult survival of 0.89 (the one they use for their "best" projection — Section 4.4) is not that much higher than the original value of 0.88 and, if substituted, would lead to the mid-continent population growing at  $\lambda = 1.06$ . However, given that such a matrix differs from the

original only by adult survival, the estimate of adult survival required to achieve  $\lambda = 0.95$  remains the same at  $s_a = 0.795$ . As such, harvest projections based on this reduced value for adult survival should lead to a declining mid-continent population.

In fact, if we view the matrix as a mean with elements that vary stochastically over time and incorporate the reduced adult survival of  $s_a = 0.795$ , then the average growth rate of the stochastically growing population will actually be less than  $\lambda = 0.95$ , and the population will decline faster than 5% annually (average growth rate *sensu*  $\ln(\lambda)$  of Caswell [1989], and Tuljapurkar [1990]). Although we agree that using adult survival associated with a deterministic growth rate of  $\lambda = 0.85$  will reduce the population faster, it is not clear to us why such an approach is more prudent given that the goal is to reduce the population size with  $\lambda < 1.0$ . Clearly, use of the  $\lambda = 0.85$  adult survival target will require a higher annual harvest.

Cooke et al. (this volume, Section 4.4) provide a “best estimate” of 2.1 million geese as the 1999 harvest required to adequately reduce the population, assuming a current value for adult survival of 0.89 and a target survival value of 0.72, corresponding to  $\lambda = 0.85$ . They note that there is uncertainty associated with this and suggest that the real estimate could be between 1.5 and 3.4 million birds. While we generally applaud the presentation of ranges, in this case it is misleading. The upper estimate assumes that current adult survival is 0.94 and uses the target survival value associated with  $\lambda = 0.85$ . As noted above, the former is biologically unrealistic and the latter is more extreme than needed to begin reducing the population. Using their method but restricting it to the more reasonable adult survival estimate of 0.89 and an average of their two estimates of recovery rate, we find the limits of 1.6 and 2.5 million geese, corresponding to reduction rates of 5% and 15%, respectively, in the first year. We think this is a biologically more meaningful range of estimated harvest given a goal of reducing the mid-continent population by a fixed annual rate.

To avoid its misuse, it is important to stress that Cooke et al.’s (this volume) estimate of 2.1 million geese is the total harvest for the *first year only* of a fixed annual rate reduction program. As is thoroughly explained in Rockwell et al. (1997), because such programs assume that the hunter harvest rate is a constant over the management period, the number of geese in the total harvest will necessarily decrease each year as the population declines. Representatives of at least one group that is critical of Snow Goose management plans have (inadvertently?) multiplied such first-year estimates by the projected management period to obtain absurdly high values for total harvest and then used them in arguments against the management program.

Although the foregoing method will lead to a decline in Snow Goose numbers, we feel that a more realistic alternative is to reduce the population by a fixed *number* rather than by a fixed *rate* each year. This is analogous to paying down a mortgage whereby a fixed amount is paid each month (or year) so as to pay off the principal in a fixed time given a fixed interest rate. Notably, in the first year of the mortgage, most payment goes to interest costs and little to reducing the principal. In subsequent years, increasing amounts go towards the principal.

**Table 1**

Projections of mid-continent Lesser Snow Geese from 1998 through 2006 using a fixed annual total harvest number and estimates in Cooke et al. (this volume)

Year	Total fall flight population (millions)	Total harvest <sup>a</sup> (millions)	Annual growth rate
1998	8.87	1.41	
1999	8.33	1.41	0.94
2000	7.72	1.41	0.93
2001	7.01	1.41	0.91
2002	6.20	1.41	0.88
2003	5.28	1.41	0.85
2004	4.21	1.41	0.80
2005	3.00		0.71
<b>1997 harvest rate<sup>b</sup></b>			
2005	3.00	0.25	
2006	3.11		1.037
<b>Readjusted harvest<sup>c</sup></b>			
2005	3.00	0.34	
2006	3.00		1.00

<sup>a</sup> The estimate of 1.41 million is from  $0.8 \times C$ , where 0.8 is the retrieval rate and C is:

$$C = \frac{N_t \phi^i \lambda^i - N_{t+i}}{\sum_{j=1}^i \phi^{j-1} \lambda^j}$$

where:

$N_t = 8.87$  million

$N_{t+i} = 3.00$  million

$i = 7$

$\lambda = 1.037$

$\phi = 1 + [(0.73 \times 0.0915) / 0.635]$

where:

0.73 is the proportion of adults in fall flight

0.0915 is hunter kill rate estimated from 1997 harvest and fall flight

0.635 is the proportion of adults in the harvest (correct correspondent to

Cooke et al.’s [this volume] harvest age ratio of 0.575)

<sup>b</sup> If harvest in 2005 is reduced to the rate associated with the 1997 harvest, the population will grow.

<sup>c</sup> If harvest is readjusted using the fixed-number approach, the population does not grow.

For mid-continent Snow Geese, if we use Cooke et al.’s (this volume) adult fall flight estimate for 1994 of 5.6 million, their 20% growth rate for 1994–1999 (i.e., an annual interest rate of 3.7% [ $\lambda = 1.037$ ]), and their estimate of 27% juveniles in the fall flight, then the projected total fall flight in 1998 was 8.87 million. This is the principal, and the question becomes: “How large is the annual payment (harvest) required to reduce a mortgage of 8.87 million Snow Geese to a specified target in a fixed time period given a 3.7% interest rate?” Unlike most mortgages where the target is zero, the goal of the Arctic Goose Habitat Working Group (Batt 1997: 118) was to reduce the mid-continent population to 50% of its current numbers by 2005. Using Abraham and Jefferies’ (1997) upper estimate for 1994 of 6 million (which was then “current”), the target is 3 million, which is about one-third of the now-current number. Given these estimates and the most recent (1997) harvest statistics (required since the population growth rate reflects reproductive success and mortality, some of which stems from harvest), simple calculations show that the required annual harvest (payment) is 1.41 million.

We summarize an example projection using the fixed-number method in Table 1. The declining annual population growth rate through 2005 reflects the shift, noted above, from “more interest” in the payment to “more principal” as the mortgage period proceeds. To compare projections from this method to one based on a fixed rate of reduction, we note that our example corresponds to an overall fixed annual reduction rate of 14.5% ( $\lambda = 0.857$ ). Using the corresponding target annual adult survival rate of 0.725 from Rockwell et al. (1997) and the same example estimates from Cooke et al. (this volume), the first-year total harvest required under a fixed-rate program is 2.12 million — a value 50% higher than that required under the fixed-number method.

It is important to stress that our method achieves the target population size of 3 million in 2005 using a fixed total number of geese in the annual harvest. If that fixed harvest is removed after the target date and harvest returns, for example, to a total based on the harvest rate that existed before the reduction program, then the population will begin growing at the original rate (Table 1). Again using the 1997 harvest rate estimates as a basis, if we readjust harvest from 0.25 million to a fixed total of 0.34 million, the population does not grow ( $\lambda = 1.0$ ). The small size of this adjustment (0.09 million) shows how reasonably the mid-continent population can be managed at a level more in tune with its Arctic ecosystem *once its numbers are reduced*. This small number also provides some insight as to how the population might have gotten out of hand. Small payment shortfalls will be quickly translated into increased principal and rapidly accruing compound interest. Such extreme sensitivity is an inherent property of fixed-number harvests and is the reason management plans using such strategies must be closely monitored (e.g., Cooch et al., in review). We note that close monitoring is also required for fixed-rate strategies, as explained in Rockwell et al. (1997).

We think that reducing the Snow Goose population by a fixed number per year is a sensible approach given that there is a relatively fixed number of Snow Goose hunters who will hunt a relatively fixed number of days per year. Further, we think that an annual harvest of 1.41 million Snow Geese is easily attainable by these hunters and, perhaps, more easily monitored than recovery and harvest rates associated with fixed-rate strategies. In the 1997–1998 season, before any special seasons or regulations were in place, hunters harvested 720 000 mid-continent Snow Geese, more than 50% of the target number. Information provided by representatives from the Central and Mississippi flyways indicates that more than 1 million Snow Geese were harvested during the 1998–1999 season. This is a remarkable accomplishment, given that only 14 of 24 states and one Canadian province used at least some of the special options that became available for only the latter part of the 1998–1999 season.

We are confident that, given the opportunity, hunters can easily exceed the target harvest of 1.41 million Snow Geese, especially in the first several years of this endeavour. Note that any excess harvest in the first years reduces the need to harvest as much in later years (analogous to making “extra” payments on a mortgage). Such savings will also accrue from the adult bias in harvest that appears to occur, at least initially, using electronic callers (A.D. Afton, pers. commun.) or that which should occur in low-productivity

years. The increased harvest not only will begin solving the problem but also will provide part of the data critical for monitoring the mid-continent population. We must now focus on the various analyses and research projects that are needed to evaluate our first attempts to manage an overabundant waterfowl population and to improve our estimates of its demographic variables. There is much that can be learned about Arctic ecosystems, Snow Goose dynamics, Snow Goose behaviour, and hunting. So, let’s just keep paying down the mortgage.

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