

THE RELATIVE IMPACT OF A SPRING HUNT ON SNOW GOOSE POPULATION DYNAMICS

Charles M. Francis

Bird Studies Canada, P. O. Box 160, Port Rowan, Ontario, Canada N0E 1M0

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 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 directed at young geese. If it were necessary to set quotas for aboriginal hunters, these results could 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 non-aboriginal hunting season for waterfowl in North America is currently restricted to autumn and early winter by the Migratory Bird 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 non-hunting 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 several-fold 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. 1999). Because it is unlikely that such an increase could be achieved within current regulatory frameworks, a variety of measures has 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 non-aboriginal hunt in autumn and winter. Thus, one way to estimate the impact of a spring harvest is to compare its impact to 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 due to 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 1992a). Thus, in this paper, I shall assume strictly additive mortality.

A second factor that differs between spring and autumn is that the population size 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 non-native hunt, young geese are disproportionately killed. 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, that do not breed until their second or third year, 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 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 due to weather and other variables, so any experiment would need to 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) 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. 1991; Francis et al. 1992a, 1992b; Rockwell et al. 1993).

Before developing a model, it is important to consider the definitions of a spring 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/June. For the non-aboriginal hunt, the “autumn” season actual 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 non-aboriginal 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 which 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 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 due to rapid colony growth and consequent overgrazing (Rockwell et al. 1993). Because it may not be valid to generalise 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 either took place in early September or in early May. Hunting mortality appears to be largely additive to other forms of mortality in geese (Francis et al. 1992a, Rexstad 1992). On this assumption, I modelled annual survival (S) for age class i with the equation

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

for the autumn harvest, and

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

for the spring harvest, where M_{winter}^i represents natural mortality from 1 September to 30 April, M_{summer}^i represents natural mortality from 1 May through 31 August, H_{autumn}^i and H_{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 been reduced by over-winter mortality, hence the construction of the model.

The total harvest at each time of year was apportioned among age classes based on estimates of the relative vulnerability and abundance of that age class at the time of harvest. Band recovery data (mainly from non-aboriginal 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 ranging from 1-3 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 non-aboriginal hunt has not been allowed. Thus, it was necessary to simulate various possibilities. First-year birds are likely to have reduced vulnerability compared to 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, by late spring they may become more vulnerable. 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 also modelled vulnerability of young as ranging from 1-3 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 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, 1992b). Mean annual adult survival between 1970 and 1988 at La Pérouse Bay was about 0.83, but 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. 1999). Adult survival rates in the absence of non-aboriginal 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 La Pérouse Bay banded in late July, shortly before fledging, was about 0.42, 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 post-fledging ranging from 0.07 to 0.70 (Francis et al. 1992b). The proportion of mortality due to non-aboriginal 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. 1999).

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 due to disease (e.g., cholera), and starvation on the breeding grounds or elsewhere (Ankney 1975). For young, mortality was greatest in years when nesting was late and growth rates were slow, and was inversely related to hunting kill (Francis et al. 1992a, 1992b). 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 this pre-season mortality was 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 young after August, was assumed to be uniformly distributed through 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 La Pérouse Bay. 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 2-year old, 3-year old, and older females at 0.13, 0.26, and 0.30 respectively (unpublished analyses).

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 2-year old geese, relative to adults, is $0.13/0.30 = 0.44$, and for 3-year old geese $0.26/0.30 = 0.86$. To determine the absolute proportion of breeders requires an estimate of the proportion of older birds that breed. I assumed this to be about 0.90, though 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 post-fledging (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_{fail} represents the proportion of birds that fail to breed due to mate loss. I varied P_{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 (λ) 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 non-linear (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. 1991, Francis et al. 1992) prevent 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 first to estimate the effect of the autumn harvest, then 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 harvest.

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 La Pérouse Bay was about 7.4% per year ($\lambda = 1.074$). This represents a 4.5 times increase in population size over 20 years, which is consistent with the observed increase in the colony at La Pérouse Bay from about 2,000 to 8-9,000 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 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 λ of 1.11. There were several differences in the parameter estimates they used, of which the most important 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-continental population of Snow Geese which suggest a λ of 1.05-1.06 (Cooke et al. 1999). Differences among colonies are expected due to differences in productivity (for example northern colonies have more variable productivity (Francis et al. 1992b) and likely have lower mean values), as well as different hunting mortality due 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 harvest. 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 harvest 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 are either 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 non-aboriginal 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, if all harvest occurred in early autumn 6.7% more geese could be shot 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 post-fledging 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 for 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 (Figure 1). At one extreme, if the spring harvest is entirely of young (Figure 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 (Figure 1, top line), the spring harvest will always have a greater impact. The impact of shooting a spring adult 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, the autumn harvest 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 non-aboriginal hunt) but young are equally vulnerable to adults in spring, the relative impact would be between 1.22 to 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 (Figure 2). If young and adults were 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 (Figure 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 early in 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. comm.). 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 impact of a spring hunt, assuming young are 2-3 times more vulnerable than adults in autumn, but not in spring, becomes 1.32 to 1.42 that of an autumn hunt.

3.5 *Effect of annual variation in productivity*

The preceding estimates were based upon deterministic models, that assumed 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 season.

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 most birds shot in either season are adults. Similarly, the difference between a spring and 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 (May 1) versus early autumn (September 1). For adults, assuming 8% annual mortality from natural causes, the difference was 7%, indicating that 7% more adults can be harvested in autumn for the same impact on population growth. For young, the difference was larger, because of higher natural mortality after September 1, at 20%.

Furthermore, these differences represent extremes, because they assume an 8-month interval between the autumn and spring harvest. In fact, the current non-aboriginal 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 or a hunt in April, due to natural mortality alone, would be almost negligible.

Of much greater importance was 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 only be 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 to adults in spring, the impact of a spring harvest would be 20-30% greater than the

autumn harvest.

From the perspective of the non-aboriginal 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 under-estimate 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 the age classes. The Louisiana sample was generally banded slightly later in winter, though 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 this survey, hunters are asked to submit tails for geese 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 or Mississippi flyways ($n = 67,000$). The 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. This decline is substantially greater than expected based on reductions in the proportion of young available to be harvested (due to both hunting and natural mortality). The proportion in the harvest in February approaches that which is expected in the population at that time, though a more complex analysis, considering variation in productivity among colonies and among years, is needed to confirm this. If this were the case, this would suggest that the relative vulnerability of young and adults was similar in spring.

A confounding factor in the analysis could be changes in 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 non-breeding adults than breeding adults and suggested this could be due to differential migration (i.e., being harvested in different areas), or to 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 (in litt.) 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. Chris Davies, pers. comm.), 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 non-aboriginal hunters (Ken Abraham, pers. comm.). 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 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 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 number of hunters, their behaviour, number of locations where geese encounter hunters, and number and distribution of refuges where geese can feed undisturbed. These factors are not necessarily correlated with 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 only be relevant 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 for the people, 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 an autumn harvest.

Some goose populations harvested by aboriginal peoples are declining or at relatively low population 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 relative impact of a spring harvest was 25% higher than 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 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 Lesser 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 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 took place in spring (Prevett et al. 1983), and 13% of the Quebec harvest (Reed 1991). A more recent survey in 1991 (Berkes et al. 1992) suggested 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. 1999). 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 non-aboriginal 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 for birds losing mates to 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 than 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 young average about twice as vulnerable as adults over the regular season, but are similar in vulnerability to adults in spring, and allowing for the fact that the mean harvest date in the regular season is about 2 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 U.S., on average during the hunting seasons from 1990-1997, 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 (for example, 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. (1999) predicted that a further increase of 2.1-4.7 fold in the harvest, relative to the harvest estimate for 1997, would be required to start reductions of the Snow Goose population in 1999. 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 whether they are likely to be sufficient to control the population.

6. Research Needs

These models highlighted 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 non-aboriginal 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 non-aboriginal hunt is already available, at least through February, based on tail fan surveys. Additional surveys involving inspection of whole birds would be desirable, because ageing birds based solely on tail fans may become less reliable later in the season due to 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 through the season.

The second factor is the breeding success of females widowed at different times through 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 measure accurately the effects of spring harvest on goose population dynamics.

Acknowledgements

An earlier draft of this paper was written in 1994 on contract for the Canadian Wildlife Service, to consider the effect of spring hunting by aboriginal peoples around Hudson Bay. Revision of the paper to consider the additional context of controlling population growth, was supported, in part, by Bird Studies Canada. I especially thank Hugh Boyd for encouraging me to revise and update the paper. P. Dwyer, H. Boyd, S. Wendt, K. Dickson, K. Abraham, J. D. Nichols, A. W. Diamond, J. C. Davies, R. G. Bromley, B. Trost, and M. Bausfield provided data on aboriginal harvests and/or helpful suggestions for the modelling and writing of this paper. P. Padding and S. Williams provided U.S. harvest data, while H  l  ne L  vesque provided Canadian harvest data. C. D. Ankney provided a critical review of the paper.

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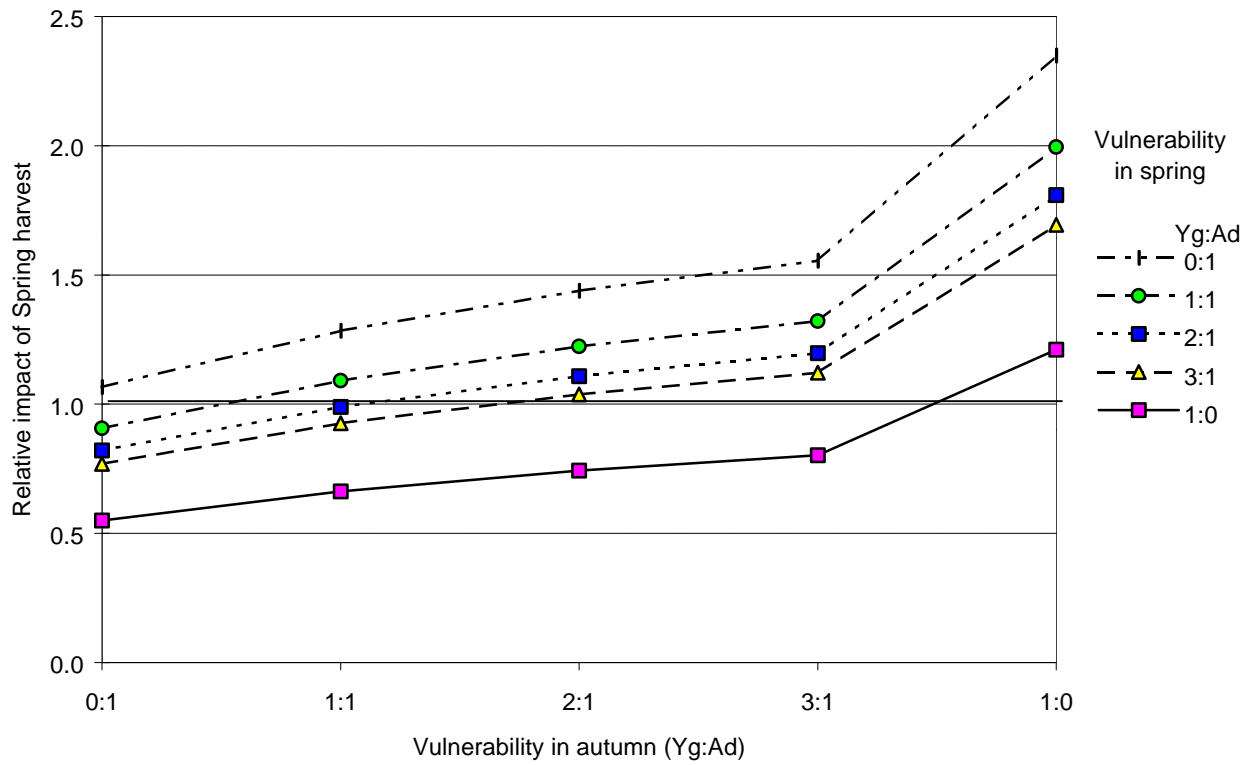


Figure 1. Impact of harvesting Snow Geese in spring relative to harvesting an equivalent number of birds in autumn in relation to the relative vulnerability of young and adults in each season. The ratio of 0:1 represents harvesting only adults in spring (top line) or autumn (left edge). The ratio of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

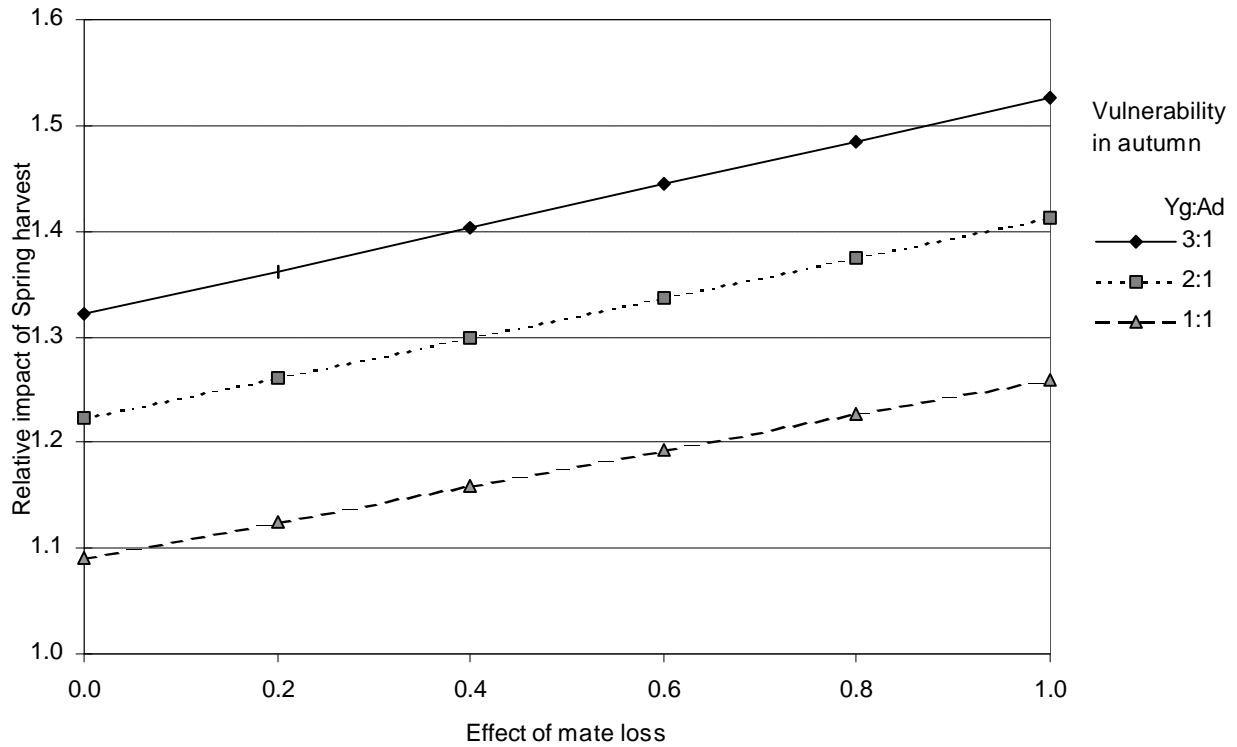


Figure 2. Impact of harvesting Snow Geese in spring relative to harvesting an equivalent number of birds in autumn in relation to the effect of mate loss on subsequent breeding success, where an effect of 0.0 indicates no effect (i.e. all females that lose mates, pair again, with no loss of breeding success), while 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 three times as vulnerable as adults in autumn. All lines assume that young and adults are equally vulnerable in spring.