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

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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**

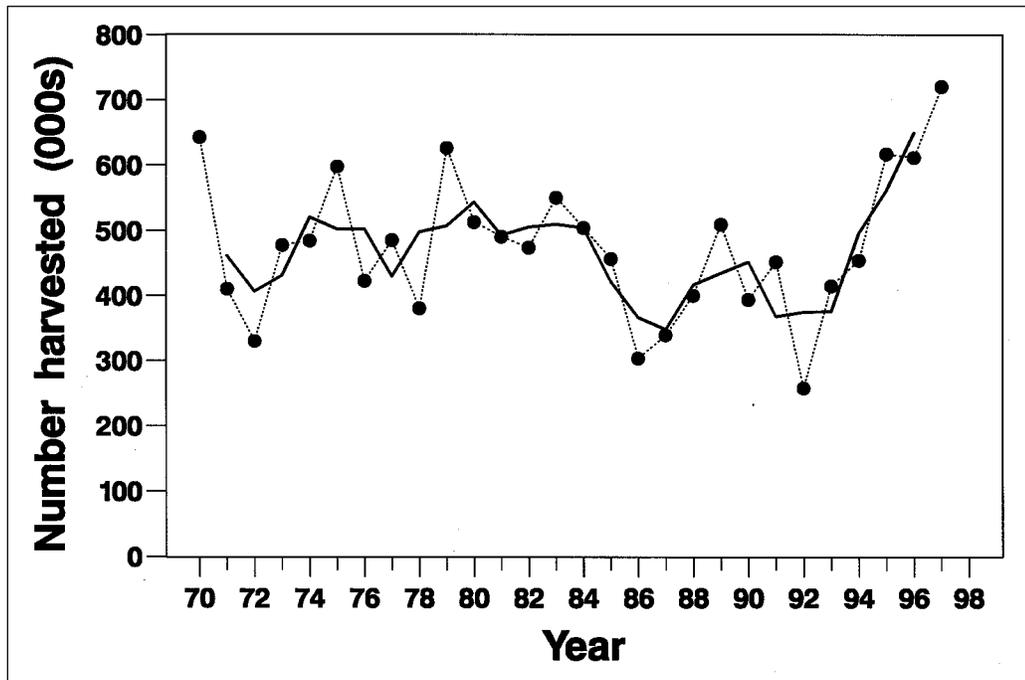
Estimated mean annual harvest for Lesser Snow Geese in mid-continental North America by five-year periods as estimated from harvest surveys in the United States (Mississippi and Central flyways) and Canada (Saskatchewan, Manitoba, and Ontario)

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 ( $K$ )

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

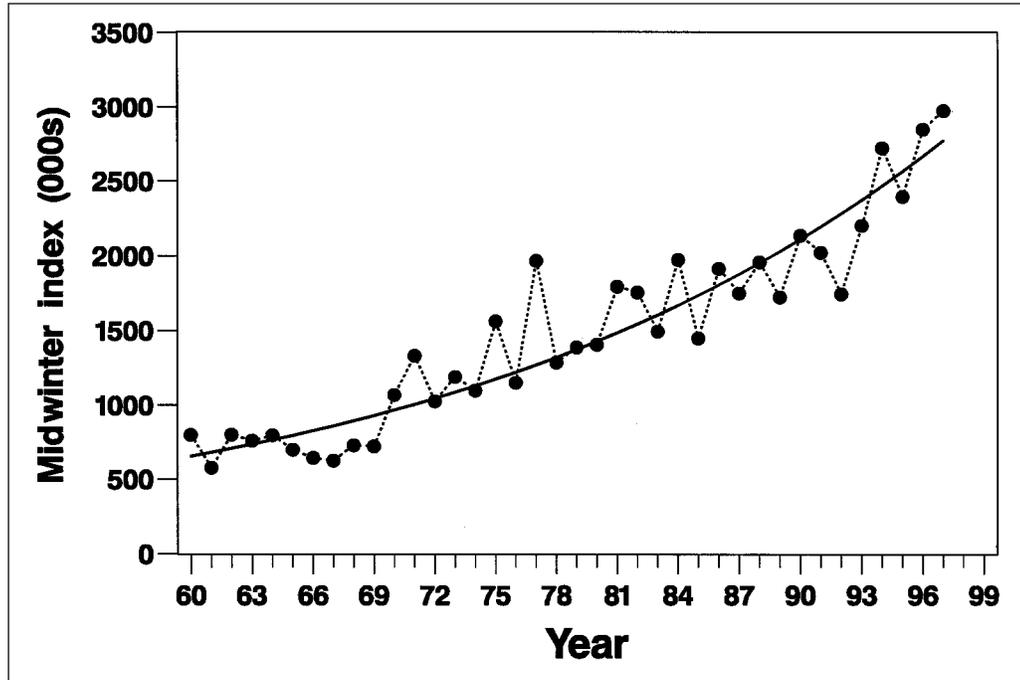
then the kill rate ( $K$ ) corresponding to a given adult survival rate ( $s_a$ ) and natural mortality rate ( $E$ ) is given as

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

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.

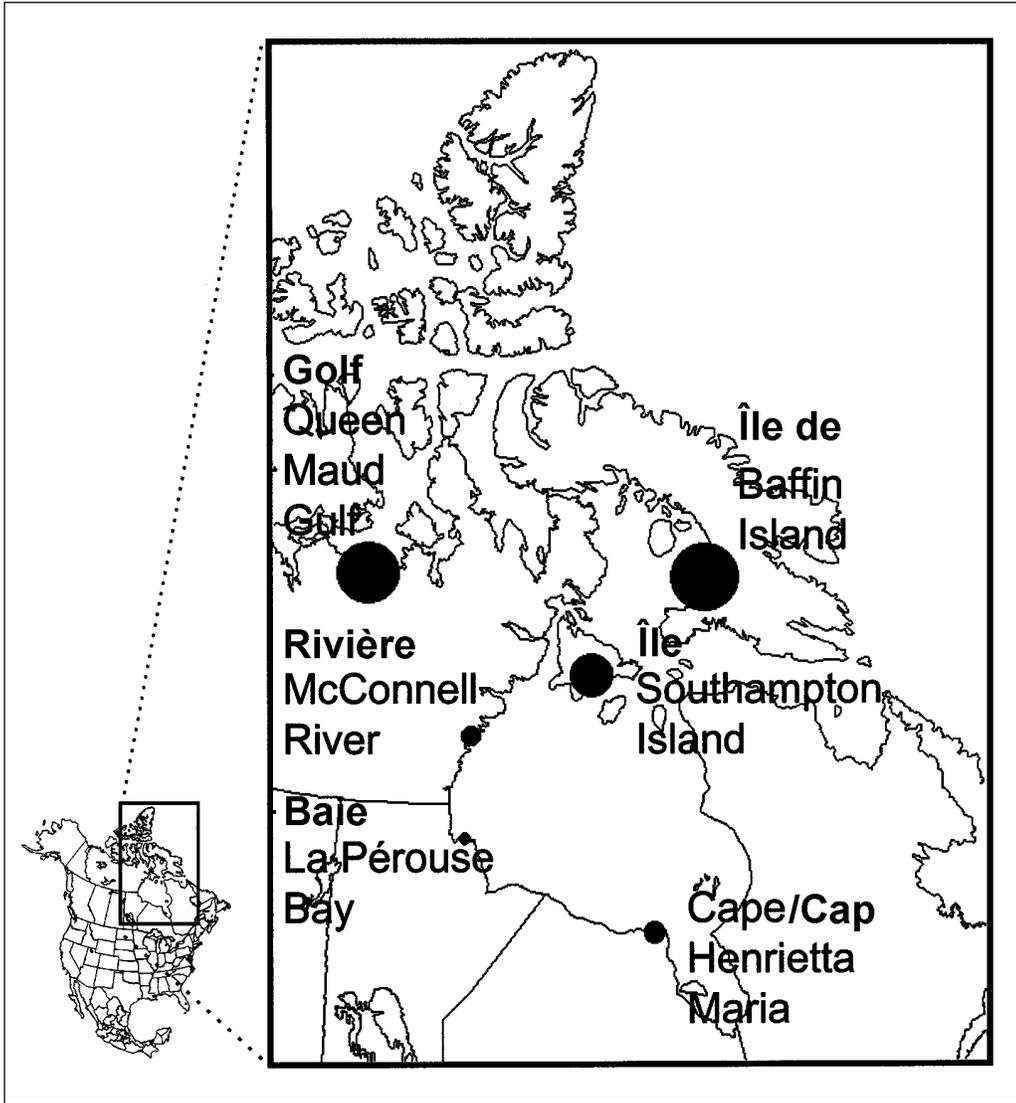
### 3.2.3 Survival rate required to reduce $\lambda$ to 0.95

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.

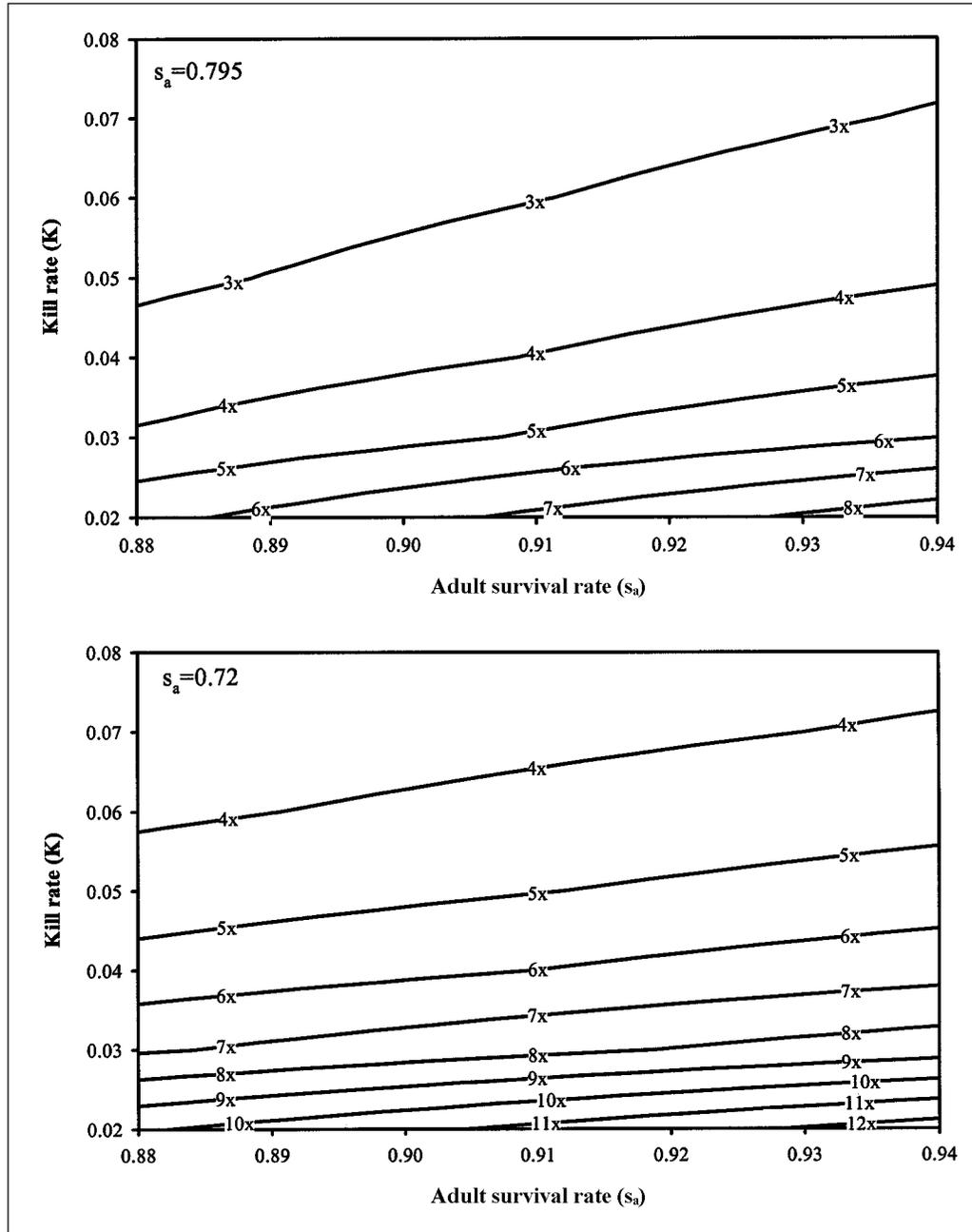
If we consider the total estimated harvest during 1994 of 230 000 adults (see above), a three- to fivefold increase (as required to reduce  $s_a$  to 0.795) implies a harvest between 0.7 and 1.1 million adult geese, whereas a 4.5- to 7.3-fold increase (to reduce  $s_a$  to 0.72) implies a harvest between 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.