Part III

DYNAMICS OF THE MID-CONTINENT POPULATION OF LESSER SNOW GEESE - PROJECTED IMPACTS OF REDUCTIONS IN SURVIVAL AND FERTILITY ON POPULATION GROWTH RATES

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INTRODUCTION

Our primary task was to generate a set of scenarios involving decreases in survival and reproductive success that reduce the annual growth rate of the mid-continent population of lesser snow geese. By implementing management actions corresponding to those scenarios, the numbers of lesser snow geese in the mid-continent population should decline. Once the population reaches a size that prevents further damage and allows recovery of damaged areas, management actions can be changed to use scenarios that hold the population size near that new level.

One of the problems modeling or monitoring the system is knowing how many geese there really are. Our best current estimates are from the mid-winter surveys. These serve as indices since the sample counts may miss some individuals (and groups) and may include some more than once. If we assume that the surveys are performed consistently (even if biased) and assume that annual changes in the indices are representative of changes in the entire mid-continent population, then annual growth rates based on the indices (indexed growth rates) can be taken as an unbiased estimate of the annual growth rate ($\lambda = N_{t+1} / N_t$) of the mid-continent population. The current indexed growth rate is $\lambda = 1.049$ (Figure 1) and is used both as an initial point of reference for our modeling and for monitoring purposes.

In this report, we develop scenarios that lead to growth rates over the range $\lambda = 1.05, ..., 0.5$. To provide some feel for the impact of instituting management plans corresponding to those growth rates, we modeled the dynamics of hypothetical populations of lesser snow geese that began at either 3,000,000 or 5,000,000 individuals (Figure 2a,b). The underlying model ($N_t = N_0 \times \lambda^t$) assumes no density dependence. This assumption is legitimate in the case of a population that has increased its numbers due to an increase in carrying capacity of the environment. We have indicated the Central and Mississippi Flyway Councils Regulatory Threshold value of 1,500,000 as a point of reference. Please note that there is no *a priori* reason to suppose that this is the population size that prevents further damage and allows recovery of damaged areas of the arctic ecosystem.

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Obviously, the lower the growth rate is below 1.0, the faster the population declines. It must be kept in mind, however, that habitat monitoring is a key component to this program and implementation may take 3 to 5 years. As such, it might be judicious to avoid extremely quick reductions (such as those achieved with values as low as $\lambda = 0.5$ or 0.6) since we might not have monitoring in place before the population was reduced substantially. Growth rates within the range of $\lambda = 0.7$ to 0.9 would seem more appropriate, at least for a population of 3,000,000.

In a more general fashion, it is possible to calculate the time it would take to reduce a population of unknown size by a specified proportion. We generated a set of such times for a range of reductions over a series of different growth rates (λ <1) and summarized them in Table 1. Again, allowing for time to get habitat monitoring in place, growth rates in the range of λ =0.7 to 0.9 may be the most reasonable.

MODEL

The annual cycle of lesser snow geese is illustrated in Figure 3. We evaluated annual population growth dynamics and developed our scenarios with a birth-pulse matrix projection model that coincides with the synchronous breeding pattern of the birds. Given what we know about age-specific differences in reproductive success, we used a 5 stage model of age classes i = 1, 2, 3, 4, 5+ that correspond to ages 0-1, 1-2, 2-3, 3-4, >4. We assumed a post-breeding census that begins accruing annual mortality immediately after each individual advances 1 age class and reproduces. We equated fledging with "birth" and used it as a point of reference for reproductive output. Finally, we collapsed seasonal mortalities into a single annual product.

The annual cycle can be reduced to the simple life cycle graph depicted in Figure 4. The 9 transition paths are estimated as:

$$F_i = BP_i \times (TCL_i / 2) \times (1 - TNF_i) \times P1_i \times P2_i \times (1 - TBF_i) \times P3_i \times s_a \quad \text{for } i = 1, 2, ..., 5$$

$$(1)$$

$$\mathbf{P}_1 = \mathbf{s}_0 \tag{2}$$

$$P_i = s_a \quad \text{for } i > 1 \tag{3}$$

where for age class i: BP is breeding propensity, TCL is clutch size, TNF is total nest failure, P1 is egg survival, P2 is hatching success, TBF is total brood failure, P3 is gosling survival and s_0 and s_a are the annual survival probabilities for juveniles (age = 0-1) and adults (age > 1) respectively. Additional technical details regarding these variables are found in Table 2. We reduced clutch size by $\frac{1}{2}$ to focus on females only.

The life cycle graph was cast as the Leslie style matrix \mathbf{A} for evaluation of annual growth rate of the population. The population was represented as the vector \mathbf{n} where the elements correspond to the number of individuals in each age class. The form of \mathbf{A} and \mathbf{n} are:

		0	F_{2}	F_3	F_4	F_5			n_1
		P_1	0	0	0	0			n_2
A	=	0	P_2	0	0	0	n	=	n_3
		0	0	P_3	0	0			n_4
		0	0	0	P_4	P_5			n_5

The population was modeled or "projected" through time as: $\mathbf{n}_t = \mathbf{A} \times \mathbf{n}_{t-1}$. The growth rate λ was estimated from \mathbf{A} using standard techniques of linear algebra.

CHOICE OF MODEL PARAMETERS

In selecting estimates for each of the parameters, we are limited by the fact that our best estimates come from the long-term study at La Pérouse Bay and may not be applicable to the entire mid-continent population. Adult survival for La Pérouse Bay birds has increased over the past 25 years but the pattern and extent do not appear to differ from less precise estimates for adults from either the Cape Henrietta Maria or West Hudson Bay colonies. Indeed, the increased survival of adults has likely been a major cause of the mid-continent population growth. The La Pérouse Bay estimate for this parameter seems generally applicable.

Reproductive success and first-year survival are more difficult issues. Reproductive success has declined substantially for those birds that continue to nest and rear their broods within the historical confines of the La Pérouse Bay colony. This reduction is no doubt related to habitat degradation in that region and the current estimates of reproductive success from La Pérouse Bay seem somewhat inappropriate for modeling the entire mid-continent population. For that reason, we have used estimates taken from the 1973 to 1984 period when the vegetation at La Pérouse Bay was above the threshold for adequate foraging and gosling growth.

A second problem using reproductive success estimates from La Pérouse Bay for modeling the midcontinent population is that La Pérouse Bay is one of the more southern colonies. As such, females may arrive with proportionately more food reserves and may be subject to fewer weather-related delays that could result in clutch size reduction through follicular resorption. The La Pérouse Bay females are also less prone to the irregular total failures associated with exceptionally late melt in the higher arctic. All else being equal, then, overall reproductive success at La Pérouse Bay might be higher than at more northern colonies.

Mortality during the first year $(1-s_0)$ reflects both hunting and non-hunting losses. Although non-hunting mortality accrues over the entire year, it is thought to be especially high during the immediate post-fledging period and during the early, staging portion of fall migration. Mortality related both to hunting and to the condition of

staging habitat, where birds from several colonies mix, should have the same impact on most juveniles, regardless of their colony of origin. In contrast, local habitat conditions may have a major impact on immediate post-fledging losses and this component of first-year mortality may be colony specific. Recent estimates of first year survival from La Pérouse Bay may be too low for modeling the mid-continent population since local habitat is severely degraded. However, values from the mid to late 1980's may provide a reasonable estimate since they predate severe degradation at La Pérouse Bay but include the more global impacts of hunting and the general 1 to 2 decade decline in the condition of common staging habitat in lower Hudson and James Bays.

The reproductive and survival parameter estimates from La Pérouse Bay for the period before habitat degradation began severely impacting local success are summarized in Table 2. The values of the associated Leslie matrix are illustrated in the life cycle graph given in Figure 5. The population growth rate based on these estimates is $\lambda = 1.107$ which is higher than the indexed estimate of $\lambda = 1.049$ (with 1.037-1.061 as the 95% confidence interval).

As explained above, it is possible that components of reproductive success estimated before severe habitat degradation at La Pérouse Bay could be higher than those for more northern colonies (which make up most of the mid-continent population). If that is the case and if we assume the indexed rate is correct, it seems reasonable to modify the estimates in Table 1 to generate a set of data more appropriate to modeling the entire mid-continent population. We changed adult survival to 0.88, the most recent (1987) value available from the analyses of the La Pérouse Bay band recovery data. We changed juvenile survival to 0.30, the corresponding value for that same year. The population growth rate incorporating only those two changes is $\lambda = 1.081$ which is still above the indexed estimate.

If we retain those more recent survival estimates and reduce our estimate of overall reproductive success by 18.6% - a value consistent with 1 complete failure every 9 years or a reduction in each reproductive component of 3%, we arrive at values for the Leslie matrix illustrated in the life cycle graph given in Figure 6. The growth rate for this set of estimates is $\lambda = 1.052$.

Since the true values for the fecundity components of the entire mid-continent population are not known, we proceeded using the two sets of estimates illustrated in Figures 5 and 6. We will refer to them as the **La Pérouse Bay** and **mid-continent** data sets, respectively. As will become clear in the following section on elasticity analyses, conclusions regarding management options and scenarios for reducing growth rate of the mid-continent population are largely independent of which of these sets is finally chosen.

ELASTICITY ANALYSES

The elasticity of any element in a Leslie matrix is its proportionate contribution to the growth rate of the population (they sum to 1). Each elasticity can also be viewed as the proportional change one would expect in the growth rate given a proportionate change in that element. Changing those elements with higher elasticity will alter the growth rate more than changing those with lower elasticities.

The elasticities of the 9 elements are depicted in Figure 7a along with the parameter estimates of those elements. Not surprisingly, the composite age elements (P_5 ; F_5) each have higher elasticities than their single age element counterparts ($P_1 P_2 P_3 P_4$; $F_2 F_3 F_4$). The elements P_2 , P_3 , P_4 and P_5 depend exclusively on the same demographic variable s_a (equation (3). The sum of their elasticities are 0.747 and 0.679 for the mid-continent and La Pérouse Bay data sets, respectively, indicating that these 4 elements account for 74.7% and 67.9% of the projected growth of the population.

To examine the generality of the latter result, we estimated elasticities for three example sets of estimates that cover a range of survivals, fertilities and growth rates (Figure 7a). In all cases, these 4 adult survival components account for more than 65% of the elasticity and are thus the primary determinant of population growth. As such, it is apparent that minor adjustments to the estimates of reproductive success, such as those to account for inter-colony differences, will have little impact on the overall dynamics or growth rate of the mid-continent population.

Adult survival (s_a) actually contributes more to the control of λ than pooling the elasticities of the elements P_2 , P_3 , P_4 and P_5 indicates. Since we used a post-breeding census model, as also contributes to the elements F_2 , F_3 , F_4 and F_5 (equation 1) and a portion of the elasticities of those matrix elements "belongs" to s_a . Similarly, life cycle parameters such as clutch size, nesting success, etc. contribute to more than one element in the matrix (i.e., F_2 , F_3 , F_4 and F_5 - equation 1). We estimated the contributions of each of the life cycle parameters (Table 2) to the elasticity of λ by partial differentiation. Those contributions, depicted in Figure 7b for the mid-continent and La Pérouse Bay data sets, are termed "lower level elasticities". While they do not sum to 1 (as do the higher level elasticities), they do provide a relative measure of the impact of a proportionate change in each parameter on λ .

Adult survival clearly makes the highest relative contribution to the growth rate of the mid-continent population. It is also the variable that offers the greatest numerical potential for altering that growth rate. For example, a 10% reduction in adult survival would result in more than a 5-fold greater reduction in λ than would a 10% reduction in any contributor to reproductive success. It must be kept in mind, however, that the management utility of such high elasticity variables also depends on whether they can be altered to the levels required to effect desired changes in growth rate. In some cases, it may be politically or economically more feasible to institute management actions that combine changes in both high and low elasticity variables.

SCENARIOS

Increasing Adult Mortality

We examined the effect of increasing adult mortality on population growth rate by decreasing adult survival from its initial estimate $s_a = 0.88$ (mid-continent) and $s_a = 0.86$ (La Pérouse Bay) to 50% of that initial estimate in 5% increments. (The series was s_a , .95× s_a , .90× s_a ,..., .50× s_a .) This resulted in reducing λ from 1.052 to 0.583 for the mid-continent data set (Figure 8a - adults only) and from $\lambda = 1.107$ to 0.629 for the La Pérouse Bay data set (Figure 8b - adults only).

Joint Harvest of Adults and Juveniles

Although one might attempt to selectively increase only adult mortality through harvest, it is likely that hunters would increase their direct harvest of juveniles at the same time. We investigated this for both data sets by decreasing both adult and juvenile survival at the same time. It is widely believed that part of the difference in adult and juvenile survival reflects an increased relative vulnerability of juveniles to hunting mortality. Unfortunately, it is not known whether that increased relative vulnerability itself depends on the level of adult mortality or harvest pressure.

To gain some insight into both effects, we performed two sets of simulations. In the first, we assumed that increased juvenile relative vulnerability was independent of the level of adult mortality. That is, we assumed the ratio of juvenile survival to adult survival (s_0 / s_a) did not change as adult mortality increased (Figure 9 - constant vulnerability). The decreasing survival series used in the simulations was: s_a , .95× s_a , .90× s_a , ..., .50× s_a

for adults and s_0 , $.95 \times s_0$, $..90 \times s_0$, ..., $.50 \times s_0$ for juveniles. The joint effects of these reductions are indicated by the "adult and juvenile - increased juvenile mortality constant vulnerability" plots on Figures 8a and b. The impact of increasing the mortality of both adults and juveniles (through harvest) is to lower λ at a faster rate.

In the second simulation, we increased the relative vulnerability of juveniles as adult mortality increased such that the ratio of juvenile survival to adult survival (s_0 / s_a) declined to 0 over the range of increased adult mortalities examined (Figure 9 - increasing vulnerability). We used this extreme rate of increase in vulnerability (juvenile survival reaches 0% of its initial value when adult survival reaches 50% of its initial value) in hopes of defining the extreme limit of such an effect. The decreasing series used was: s_a , $.95 \times s_a$, $.90 \times s_a$,..., $.50 \times s_a$ for adults and s_0 , $.90 \times s_0$, $..., .00 \times s_0$ for juveniles. The joint effects are indicated by the "adult and juvenile - increased juvenile mortality increased vulnerability" plots on Figures 8a and b. The impact of increasing adult mortality and both the mortality and relative vulnerability of juveniles at the same time is higher than the other scenarios. Since we used an extreme pattern of relative vulnerability, it is likely that reality lies between the two "adults and juveniles" curves on Figures 8a and b.

It is possible that increases in adult harvest could reduce juvenile survival independently of increases in juvenile harvest. If one or both parents are required to successfully shepard their young through their first migration south, their first winter and/or their return north the following spring, then increased adult harvest could increase non-hunting mortality of juveniles. If this were the only source of increased juvenile survival, then the relation of λ to increased adult mortality would be identical to the joint harvest situation with constant vulnerability in Figures 8a and b. If the increase in adult harvest results in this "parental care" effect as well as an increase in juvenile harvest, then again, reality likely lies between the two "adults and juveniles" curves on Figures 8a and b.

Egg Harvest

Harvesting eggs from the nests of laying and incubating females reduces the reproductive success of those individuals. From the perspective of our model, such egging can be viewed as a reduction in clutch size (TCL), an increase in nest failure (TNF) or a reduction in egg survival (P1). Since our projections of population growth rate use the product of these (and other) variables as a composite fertility (F_i in Figure 4 and equation (1)), we examined the potential impact of egging on population growth rate simply by decrementing overall fertility. The decreasing fertility series used was: F_i , $.95 \times F_i$, $.90 \times F_i$, ..., $.50 \times F_i$ with the reductions applied equally over the age classes. The effects of decreasing fertility on the population growth rate λ is depicted in Figures 10a and 10b for the mid-continent and La Pérouse Bay data sets, respectively. For reference, we included the effect on λ of reducing adult survival by the same proportionate amounts (s_a , $.95 \times s_a$, $.90 \times s_a$, ..., $.50 \times s_a$).

Consistent with the elasticity analyses, reductions in fertility do not have nearly as great an impact on λ as do equally proportionate reductions in adult survival. For the mid-continent data set, for example, it takes a 5.7% reduction in current adult survival (to .943×s_a) to make the population decline ($\lambda = 0.9999$). By contrast, it requires a 35.8% reduction in fertility (to .642×F_i) to achieve the same thing. To appreciate the magnitude of the latter action, assume that there are 2,500,000 nesting females in the mid-continent population and that the entire fertility reduction is to be accomplished by egging which we will view as a decrease in nesting success. Our current estimate for nesting success in the mid-continent data set is (1-TNF) = 0.7448, obtained by applying the entire 18.6% reduction in the La Pérouse Bay data set to nesting success (see above.) Reducing the current level of nesting success by 35.8% to 0.4782 (.642×.7448), we find that 1,304,500 (=2,500,000 × (1 - 0.4782)) nests would have to fail totally to force λ just below 1.0. This is an increase of 666,500 nests over the 638,000 nests currently expected to fail totally (=2,500,000 × (1 - 0.7448)). Assuming a modal clutch size of 4 eggs (averaged over the age classes), it would require the collection of 2,666,000 eggs from the additionally harvested nests to force the mid-continent population's growth to a level just below $\lambda < 1.0$.

As a last bench mark, reducing fertility by 5.7% (to $.943 \times F_i$) reduces λ from 1.052 to 1.044 rather than to $\lambda < 1$ as was the case when adult survival was reduced by this proportion (above). If that fertility reduction were again achieved solely through egging, it would require the collection of 142,000 eggs.

APPLICATIONS

The overall strategy of the Habitat Working Group is to: 1) **decrease** the growth rate of the midcontinent population to some $\lambda < 1$ using a management program of reduced survival and reproductive success and monitor the population to see that the appropriate decrease and reductions are achieved; 2) monitor the arctic coastal ecosystem and when the population size is at a level that is causing no further damage, **change** the management program to one that allows the population to stabilize with a growth rate of λ **1.0**. The size of that stabilized population should become the new Regulatory Threshold.

We presented a set of scenarios that relate λ to decreasing adult mortality, decreasing adult and juvenile mortality and decreasing fertility. Before choosing one or more of them, an appropriate initial value for the reduced λ must be selected after several factors are considered. These include both the size of the current mid-continent population and the time frame over which it should be reduced. The latter, of course, depends on the new regulatory threshold size - a value we can not really know in advance.

The simulations depicted in Figures 2a and 2b and the values in Table 1 provide some guidance. If we accept that it will take 3 to 5 years to get an ecosystem and goose monitoring program in place and begin collecting relevant data and if we use the current regulatory threshold of 1,500,000 as a first approximation of a new stabilized target, then $\lambda < 0.8$ seems too severe, even for a current population of 5,000,000. If the current population is closer to 3,000,000, then a growth rate closer to $\lambda=0.9$ would seem more appropriate. In the following example, we assume the current population is between these estimates and we set the initial reduced growth rate at $\lambda=0.85$.

Given the elasticities of the parameters, it is tempting next to appeal solely to adult survival and make it the focus of our management efforts. As mentioned above, this is not always best and our view is that an approach combining reductions in survival with reductions in fertility through increased harvest of eggs is a reasonable overall course of action to lower λ . It is also our view, however, that the elasticity of fertility is such that even a substantial increase in egg harvest will be insufficient to appreciably alter reduction scenarios based on adult mortality. As such, we will focus the rest of this section on increasing adult and juvenile mortality and calculating associated harvest estimates.

We center on the 3 models that consider joint harvest of adults and juveniles and only on the midcontinent data set. To that end, we have recast Figure 8a as Figure 11, adding a horizontal that corresponds to λ =0.85 and dropping perpendiculars from the intersections of the horizontal with the 3 models. Those perpendiculars intersect the x-axis at points that give the adult mortality needed to achieve λ =0.85 under each of the models. For the "adult only" model, an annual adult mortality of 0.312 is required to achieve λ =0.85. This model assumes that there is no increase in the harvest of juveniles in the face of increased adult harvest and does not seem too realistic. It was included primarily as a point of reference.

It is more reasonable to assume that there will be an increase in the harvest (or at least mortality) of juveniles associated with any increase in adult harvest. What is not clear is whether that increase will be proportional to the increased harvest of adults (Figure 8 - constant vulnerability) or whether juvenile mortality will increase disproportionately with increased adult harvest. The latter could result from increased vulnerability

(Figure 8a) and/or decreased parental care. Reality likely lies between these two models, indicated on Figure 11 by the 2 adults and juveniles lines. This gives us a range of adult mortalities from 0.27 to 0.29 that would lead to λ =0.85. It should be recalled that associated increases in juvenile mortality are built into the models and do not need to be expressly calculated.

We assume that increasing adult mortality from its current level of $0.12 (1-s_a)$ to a new level between 0.27 and 0.29 will be achieved with hunting mortality. As such, the final translation of increased adult mortalities into a management plan must consider the relative contributions of hunting and non-hunting sources to adult mortality. The approach we have taken is based on recoveries of banded individuals and the data we have used comes from the banding program at La Pérouse Bay.

By way of review, let:

- f = recovery rate (probability that a banded bird is shot, retrieved, and has the band reported)
- H = harvest rate (probability that a bird is shot and retrieved)
 - = reporting rate (probability that the band is reported from a banded, harvested bird)

K = hunting mortality rate (probability that a bird is lethally shot)

c = retrieval rate (probability that a lethally shot bird is retrieved)

K is the value we seek and it can be found from the relationships: H = f / and K = H / c so that K = f / / c.

Although recoveries of birds banded at La Pérouse Bay declined over the 20 year period from 1968 to 1988, there was little decline after 1980. We used the unweighted mean of the 1980-1988 estimates as an estimate of direct recovery rate f = 0.0254. Using traditional estimates from mallard duck banding studies of = 0.38 and a retrieval rate of c = 0.80, we find that K = 0.0836. If we define E as non-hunting mortality rate and assume additive mortality of the instantaneous rates, we find that annual adult survival rate $s_a = (1-K) \times (1-E)$. Given our estimates of $s_a = 0.88$ and K = 0.0836, we find E = 0.0398.

We then find the K's associated with our new mortality rates of $m_{low} = 0.27$ and $m_{high} = 0.29$ as:

$$K_{low} = 1 - (.73/.9602) = 0.2397$$

$$K_{high} = 1 - (.71/.9602) = 0.2605$$

To achieve $\lambda = 0.85$, then, we will have to increase the current hunting mortality rate K=0.0836 by a factor between 2.87 and 3.11.

The most recent average estimate of actual harvest, based on hunter surveys and the parts inventory, is approximately 305,000. If we assume that this estimate, like the mid-winter inventory, is a representative index of true harvest rather than the actual total harvest and if we assume that the retrieval rate remains the same, then to achieve a reduction in growth rate to λ =0.85, this harvest index will have to increase approximately 3-fold to 915,000 birds.

Once the population size begins going down, the actual total harvest required to sustain an adult mortality

between 0.27 and 0.29 will necessarily decrease. The latter stems from the relationship of hunting mortality rate to total harvest number and population size. If we let G be the total number of geese harvested and G/.8 be the total number killed by hunters, then the hunting mortality rate at time t can be estimated as $K_t = (G/.8) / N_t$ where N_t is the population size at time t. If G/.8 remains the same each year and N_t declines, then K_t must increase and so must the adult mortality rate. As the adult mortality rate increases, the population growth rate declines below λ =0.85 and the population will decline at an ever-increasing rate. While overshooting the annual mortality rate for a few years may not stress this population, the practice should not be continued indefinitely.

To avoid the situation, total number of geese harvested should be reduced as the population declines to hold adult mortality constant. If we view the actual harvest estimate as an index, then regulations must be adjusted annually so that it remains at approximately 3 times the current estimate. If we view it as the actual total harvest, then regulations must be adjusted annually so that it decreases at a rate that maintains adult mortality between .27 and .29.

As an alternative, comparative example, assume that we seek an initial reduction in the population growth rate that is less severe so that our initial $\lambda = 0.95$. From Figure 11, we can find $m_{low} = 0.20$ and $m_{high} = 0.21$. Following procedures outlined above, we then calculate $K_{low} = .1668$ and $K_{high} = 0.1773$. Referring to the current hunting mortality rate K = 0.0836, we find that to attain $\lambda = 0.95$ we will have to increase current hunting mortality rate by a factor of 1.99 to 2.12.

CONCLUSIONS

Our modeling is based on a strategy that seeks to reduce population growth rate to some sustained level with $\lambda < 1.0$ until a target population size can be achieved and stabilized by altering that strategy so that $\lambda = 1.0$. The estimates for mortality and harvest reached in the above examples are based on our assumptions regarding current population size, time span for reduction and a rough, first approximation of the stabilized target population that is approximately 50% of the current population size. Different assumptions will lead to somewhat different values under this type of strategy but will likely require that a harvest index be increased to a level 2 to 3 times the current values for several years. Such an increase in harvest will lead to a growth rate of between $\lambda = 0.85$ and $\lambda = 0.95$ and require 3 to 7 years to reduce the mid-continent population to 50% of its current level (Table 1). It is not known whether the coastal tundra can support a population of that reduced size without suffering further damage.

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