Modeling the Midcontinent Population of Lesser Snow Geese

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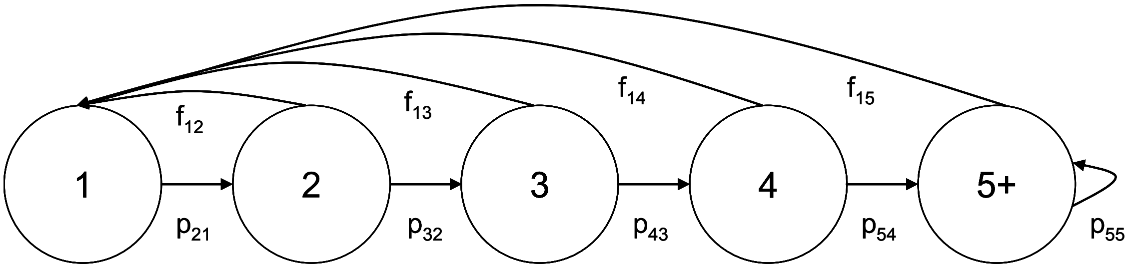
Introduction

The modeling portion of *Arctic Ecosystems in Peril* (Rockwell et al 1997) depicted how a reduction in the size of the Midcontinent Population of lesser snow geese requires that the population growth rate be reduced to $\lambda<1.0$ for some period of time. We also used the model to explore how various combinations of reductions in reproductive success and age-specific survival might achieve this goal. Consistent with the results of an elasticity analysis, it was argued that reductions in adult survival would be a more efficient means of reducing the growth rate to a point where the population should decline. This was particularly appealing since reductions in adult survival could be obtained by increasing hunting mortality through changes in harvest regulations, thus using North American hunters as the main management tool. Although there was subsequent debate over the level of harvest required to achieve management goals (Cooke et al 2000, Rockwell and Ankney 2000), there was no disagreement over the fact that an increase in harvest would begin shifting the population's dynamics in the right direction.

In this chapter, we use the same basic modeling approach to examine several issues that have emerged since the publication of *Arctic Ecosystems in Peril*. First, we examine the population's current projected growth in light of our best estimates of current adult survival. We present this against a backdrop of the possible combinations of survival and reproductive success that control the population's dynamics. We also examine the potential impact of stochastic variation on these projections. Recent research on transient dynamics has shown that rapid shifts in demographic variables, such as the anticipated shift in adult survival, can lead to unanticipated changes in population size related to transient dynamics and momentum (Koons et al 2005, 2006). We examine the potential impact of momentum on this system. Finally, it appears that different segments of the Midcontinent Population of lesser snow geese may be subject to different levels of adult mortality. If so, a metapopulation model may be a closer approximation to reality and we explore the ramifications of such a model on both regional and global dynamics as well as elasticity. Finally, we highlight data needs for continued monitoring of the Midcontinent Population of lesser snow geese.

Projection Model

We used a 5 age class, birth pulse, Lefkovitch model to project the Midcontinent Population of lesser snow geese that corresponds to the following life cycle diagram:



where 1,2,…5+ represent individuals that are produced but not yet 1-year-old, 1 but not yet 2-years-old, through individuals that are at least 5 years old, respectively. The transitions $f_{1,j}$ and $p_{i,j}$ correspond to reproductive input to age class 1 from classes j and the survival of individuals age j to age i over the interval t to t+1, respectively. The life cycle diagram is cast as a projection matrix A of the form:

$$A = \begin{matrix} 0 & f_{1,2} & f_{1,3} & f_{1,4} & f_{1,5+} \\ p_{2,1} & 0 & 0 & 0 & 0 \\ 0 & p_{3,2} & 0 & 0 & 0 \\ 0 & 0 & p_{4,3} & 0 & 0 \\ 0 & 0 & 0 & p_{5+,4} & p_{5+,5+} \end{matrix} \tag{1}$$

Rockwell et al (1997) used the same life cycle diagram and matrix but used a post-breeding census approach to parameterize the matrix. Here, we have switched to a pre-breeding census projection since it better corresponds to the timing of breeding ground censuses, avoids any potential confoundments of covariance in stochastic situations (Cooch et al 2003) and allows simpler interpretation of elasticity analyses (Caswell 2001, Cooch et al 2003). The last can be seen from the actual parameterization in which:

$$f_{1,j} = 0.5 \times BP_j \times TCL_j \times (1-TNF_j) \times P1_j \times P2_j \times (1-TBF_j) \times P3_j \times s_0 \tag{2}$$

$$p_{i,j} = s_a \tag{3}$$

where for age class j

BP is breeding propensity
TCL is the size of the total clutch laid
TNF is the probability of total nest failure
P1 is the probability of egg survival in nests that did not fail totally
P2 is the probability that an egg hatches
TBF is the probability of total brood failure
P3 is the probability that a gosling from a brood that did not totally fail fledges
and
s_0 is the survival probability from fledging to just before the next reproductive effort
s_a is the annual adult survival probability

All of the demographic variables contributing to recruitment are found only in the first row and only adult survival is found in the non-zero entries in the rest of the matrix. Since elasticity accrues for the matrix elements, the sum of the first row's elasticities will yield the overall elasticity for recruitment and the sum over the remaining elements yields the elasticity of adult survival. This contrasts with the situation for a post-breeding census where adult survival contributes to first row elasticities (Caswell 2001). Since the terms in the first-row elements are multiplied together, the lower level elasticity of each age-specific demographic variable is simply estimated as the elasticity of the appropriate matrix cell.

Basic Dynamics

Although substantial effort has gone into estimating the current level of adult survival and whether it has changed in response to the management actions initiated after the publication of *Arctic Ecosystems in Peril*, little effort (or funding) has been centered on monitoring or improving estimates of the demographic variables leading to recruitment. Because they have substantially lower elasticity values (and therefore less potential to change population growth rate), this is not necessarily an unwise decision given limited resources (Caswell 2001). Because of this, we are forced to use the recruitment estimates from the original report as our best baseline estimates for the purposes of this chapter. It is worth noting, however, that preliminary analyses of juvenile to adult ratios in the Canadian fall flight have not substantially changed over a period that begins before the onset of the harvest management actions and continues to the present (Dufour et al This Document).

The underlying demographic variables vary with age (e.g. Rockwell et al 1993, Cooch et al 2001) and are summarized in Table 1. The recruitment estimates across the 5 age classes of our pre-breeding census projection matrix (the first row of A) are:

$$a_{1,j} = \begin{bmatrix} 0 & 0.08 & 0.20 & 0.22 & 0.24 \end{bmatrix} \tag{4}$$

To provide a better view of the population's potential growth rate should these estimates be high or low, and to examine the population's growth potential over a wide range of combinations of recruitment and adult survival, we estimated growth rate λ over a large portion of the potential parameter space. In doing this, we examined the range of adult survival rates reported in the literature for migratory geese (0.65 to 0.97) and combined those with a scalar change from 0.2 to 3.5 times the recruitment vector given in (4) to obtain representative growth rates. We have summarized these trials in Figure 1 by depicting isobars for all those combinations of recruitment and adult survival leading to population growth rates of $\lambda = 1$, $\lambda = 1.05$ and $\lambda = 0.95$. All combinations of recruitment and adult survival "northeast" of the $\lambda = 1.0$ isobar lead to population growth while all combinations to its "southwest" lead to declines. The large difference in scales of the X and Y axes highlights the fact that it takes greater changes in recruitment than adult survival to change the population's growth rate. This reflects the different elasticities of adult survival versus recruitment (0.87 versus 0.13).

As part of their evaluation of the potential impact of altered hunting regulations associated with management of the Midcontinent Population of lesser snow geese, Alisauskas et al (In Review) estimated the annual adult survival rates for birds tarsally banded at Queen Maude Gulf, La Pérouse Bay, and other colonies. Here, we computed means for the longest-studied colonies, Queen Maude Gulf and La Pérouse Bay, for the period 1998 to 2003 (beginning in the first year after the management program went into effect) by weighting their annual adult survival estimates by the inverses of their respective standard errors. The mean adult survival rates are 0.8536 for Queen Maude Gulf and 0.8227 for La Pérouse Bay and are indicated in Figure 1 (note that these estimates do not include birds banded at other colonies as in other chapters of this document). While the projected growth rate for populations with a La Pérouse Bay adult survival rate is slightly below λ=1.0, populations with an adult survival rate like that from Queen Maude Gulf are projected to continue growing. We reexamine this issue in the section titled Metapopulation Dynamics.

Stochastic Population Growth

The modeling presented in *Arctic Ecosystems in Peril* (Rockwell et al 1997) was based on deterministic projections in which the demographic variables did not change over the time intervals modeled. Although this approach simplified computations and allowed precise analytical estimates of elasticity and the like, it was chosen primarily because data were inadequate to provide robust estimates of overall variances for the variables, and were certainly not sufficient for isolating the process variance (that due exclusively to environmental fluctuations rather than sampling) that is truly meaningful in the real world. Although we still believe that models should be no more complex than available data (cf. Williams et al 2001), we also realize that there are differences between deterministic and stochastic growth that should at least be examined. For example, it is well established that the relationship between deterministic (λ_1) and stochastic (λ_s) growth rates is $\lambda_1 \geq \lambda_s$ and that the extent of the inequality increases with variance in the demographic variables (assuming no covariance, and no positive relationships between mean and variance) (Caswell 2001). As such, it seems reasonable to examine the potential extent of stochastic effects on the projected growth rate of the Midcontinent Population of lesser snow geese. Because there is substantially more evidence for variation in demographic variables contributing to reproductive output than to adult survival, we have concentrated our examination to the former (Cooke et al 1995; Cooch et al 2001).

To examine the potential difference between estimates of growth rate for deterministically and stochastically projected populations, we used a pre-breeding census version of the projection matrix employed by Rockwell et al (1997) that had an asymptotic deterministic growth rate of λ_1 = 1.0517. As explained earlier, the elements in the first row of the pre-breeding census matrix are the age-class-specific products of all contributors to the reproductive output of each age class, beginning with courtship at time = t (breeding propensity) through the production of a clutch, its survival, hatching of eggs, fledging and survival of the offspring to just before the next reproductive effort begins at time = t+1. As such, the first-row elements can be viewed as the annual recruitment rates for each age class. Although we do not have precise or robust estimates of variance for the components or their product, we can examine the potential impact of their variation on population growth by incorporating different levels of variance of recruitment rate into sets of model projections. We accomplished this by sampling independent year-specific values for each first-row element from beta distributions defined by our best mean estimates of age-class-specific recruitment and a range in coefficient of variation ($CV=\sigma/\overline{X}$) for that mean. An example of the sampling distribution for recruitment for age-class 4 adults with a 20% coefficient of variation is depicted in Figure 2.

Each model projection was initialized with the asymptotic stable age distribution and tracked for 100 years. The stochastic population growth rate (λ_s) was estimated using the Heyde-Cohen equation and verified for conformity with its expected asymptotic stability (Caswell 2001). The projection was repeated using the same parameterized beta distributions 1000 times and the mean and both upper and lower 2.5 percentiles of the λ_s values were recorded as the estimate and precision of stochastic population growth for a given coefficient of variation. We examined the effect of the extent of variation on stochastic growth rate for coefficients of variation ranging from 0.1 to 0.5. This spans ranges of total relative variance reported for many bird species (Johnson et al 1987, Clutton-Brock 1988; Newton 1989). It is worth noting that coefficients of process variation only would be lower (e.g. Hitchcock and Gratto-Trevor 1997).

The simulation results are depicted in Figure 3 where the deterministic expectation for the mean projection matrix is included for reference. While it is clear that the relation $\lambda_1 \geq \lambda_s$ holds and that the inequality increases with variation, the actual difference is vanishingly small, being only 0.1% for the projection set with the highest variance (CV=0.5). Further, the deterministic expectation is well within the 95% confidence limits of the stochastic growth rate estimates in all cases. Since the Heyde-Cohen estimator is asymptotically stable, the values of the confidence limits are specific to the 100 year projections, although they are indistinguishable from those based on projections as short as 10 years.

Although there is no information on the level of stochastic variation in adult survival, we can gain some insight on its potential impact using an approximation from Tuljapurkar recast in terms of elasticities (eqn. 14.77 in Caswell 2001). Focusing on a single demographic variable the relationship between the natural logs of stochastic and deterministic growth can be approximated as: $\ln(\lambda_s) \approx \ln(\lambda_1) - e_v \times V_v$ where e_v and V_v are the elasticity and variance of the variable of interest. If we assume, as a "worst case" scenario that the variance in adult survival is the same as that in recruitment and focus on the highest level we examined (CV=0.5), then we can simply rescale the difference in the natural logs of deterministic and stochastically projected growth rates by 0.87/0.13, the ratio of elasticities of adult survival and recruitment. Doing this we find a stochastic growth rate of $\lambda_s = 1.0445$ as opposed to $\lambda_s = 1.0506$ for stochastic variance in recruitment. This represents a reduction in the projected growth rate of 0.6% (as opposed to 0.1%) due to stochasticity. As indicated above, this would be a worst case approximation so the anticipated effect of stochastic variation in adult survival on population growth is less.

Given these minor effects of stochasticity in recruitment or adult survival on λ, we feel that the deterministic approximations of population growth and its response to various management options presented in Rockwell et al (1997) are more than adequate. Because the effects of stochastic variation in recruitment are so small and since real data on actual process variance are so scant, we will use deterministic projections throughout this chapter (cf. Williams et al 2001).

Transient Dynamics and Momentum

When an age-structured population is initialized with an arbitrary proportion of individuals in each age class, it will grow (or decline) at a variable rate until the proportion of individuals in each age class reaches its "stable age distribution". At that point, the population as a whole will grow (or decline) at a single rate (or remain stationary at $\lambda=1.0$). The stable age distribution (SAD) and the single, long-term growth rate (λ_1) are formally known as the dominant eigenvector and dominant eigenvalue. Both are properties of the matrix controlling the population's projection. Until a population reaches its SAD, it displays transient dynamics that are controlled by other properties of the matrix. Transient dynamics are also displayed when a population has reached its SAD but is suddenly subjected to an instantaneous change in one or more of its demographic variables. For example, if a population growing according to its SAD is suddenly subjected to a reduction in adult survival, such as that anticipated from substantial changes in hunting regulations, a period of transient dynamics will ensue.

Under such a pulse perturbation, the projection matrix is instantaneously altered and the corresponding SAD and long-term growth rate are also changed. Assuming no subsequent changes in underlying demographic variables, the new SAD and growth rate will be attained after the transient period. The situation is somewhat more complex, however, if one were to examine the actual population size rather than the age distribution or long term growth rate. In the case of a reduction in adult survival, the SAD anticipated after the perturbation will be shifted to a higher proportion of individuals in the younger age classes. However, the age distribution immediately after the perturbation will reflect the previous SAD and have disproportionately more individuals in older age classes. The mismatch, in this case a surplus of older, highly reproductive individuals (recall the recruitment rate vector) will continue producing during the transient period and the population size will be higher than expected had the population instantly shifted to its new (lower) growth rate. The surplus of individuals is referred to as population momentum (see Caswell 2001 for an overview). The analogy for this example would be a large ship that attempted to turn east at a fixed point from a northerly course. By the time the ship achieved a perfect easterly bearing, it would have drifted north of the point of the turn, a displacement resulting from the ship's momentum.

In demographic situations, momentum results from a mismatch between the age distribution at the point of the perturbation and the SAD corresponding to the new projection matrix. In the previous example, the shift was to a younger distribution and the temporary surplus of older, and in this case more productive, adults (Koons et al 2005). Until that mismatch is resolved by passage through the transient period, the population grows at a higher than anticipated rate. Negative momentum can be generated if the pulse perturbation reduces the reproductive output such that the post-perturbation matrix is older than that existing before the shift. Detailed explanations and examples of both situations are given in Koons et al (2006).

The shift in hunting regulations associated with attempts to control the Midcontinent Population of lesser snow geese represents a pulse perturbation and in light of the recent work on momentum, it is appropriate to examine the potential effects of the resulting transient dynamics and associated momentum on the population. To examine this, we used a pre-breeding census version of the projection matrix employed by Rockwell et al (1997) that resulted in growth of $\lambda = 1.0517$ and initialized a population with the SAD of that matrix. After 5 years of projection, we changed the adult survival elements of the matrix to $0.8897 \times s_a$ so that the resulting post-perturbation matrix had $\lambda_1 = 0.95$, one of the desired goals of the management program. We continued projecting the population for 5 years. As a point of reference, we also projected the population from year 5 to 10 by scalar $\lambda_1 = 0.95$, the rate anticipated were there an instant change and no period of transient dynamics. The results are depicted in Figure 4. As anticipated, the population projected with the post-perturbation matrix and experiencing transients is larger at year 10 although the magnitude of the effect is not terribly large: $N_{observed}=3{,}003{,}341$ while $N_{asymptotic}=2{,}986{,}141$ (a 0.58% surplus in the observed projection).

Under the new management regulations, however, hunters have not just increased the harvest of adults but have also increased the harvest of young of the year. As such, they have potentially reduced juvenile survival (s_0) as well as adult survival (s_a). Recall that in a pre-breeding census projection s_0 is included in the first-row matrix elements as part of fertility. We examined the potential effect of this complexity by again initializing a projection with the SAD from baseline matrix but at year 5 we changed adult survival to $0.90329 \times s_a$ and juvenile survival to $0.90329 \times s_0$, a combination resulting in a post-perturbation matrix with $\lambda_1 = 0.95$. (We assumed for simplicity that increased harvest affected adults and juveniles equally.) We again used a scalar projection with $\lambda_1 = 0.95$ as a point of reference. The results are depicted in Figure 5, where it appears that the “positive momentum” of the s_a shift is slightly outdone by a “negative momentum” expected from just an s_0 shift. The actual difference does not show in the graph. At $t = 10$, $N_{observed} = 2{,}985{,}364$ while $N_{asymptotic} = 2{,}986{,}141$ (a 0.026% deficit in the observed projection).

The negative momentum generated by reducing only s_0 (to $0.3395 \times s_0$) is depicted in Figure 6 for reference. The more extreme momentum response relates in part to the higher proportionate change required in s_0 (a lower elasticity variable) to reduce λ_1 to 0.95. At $t = 10$, $N_{observed} = 2{,}934{,}263$ while $N_{asymptotic} = 2{,}986{,}141$ (a 1.73% deficit in the observed projection).

While we can show that transient dynamics and momentum may operate as a result of the pulse perturbation nature of the management action, it is not likely to have much of an effect on the dynamics of a closed lesser snow goose population (i.e., with no dispersal). This is in great part the result of the increased harvest altering both adult and juvenile survival leading to positive and negative momentum mitigating each other.

Metapopulation Dynamics

A recent analysis of banding and recovery data (Alisauskas et al In Review) indicates that adult survival differs between the nesting colonies at Queen Maude Gulf and La Pérouse Bay, the only sites with large-scale, long-term banding data. In the absence of any compensation in recruitment rates, these findings imply that there are localized differences in population growth rates. If the adult survival estimates from these two colonies are representative at some more regional level, then modeling the Midcontinent lesser snow geese as a single population could lead to erroneous or at least imprecise estimates of projected population growth. It would be more appropriate to model the system as a metapopulation structure composed of several segments that may be connected through immigration and emigration (henceforth dispersal). It should be noted that we are using the term metapopulation in its broadest, perhaps population genetics, context (see Esler 2000) and not in the restrictive sense of Hanski and Gilpin (1991) that examines only the extirpation and colonization of satellite segments without regard to their population size. It is our intent in this section to examine potential dynamics of a metapopulation approach to modeling the Midcontinent Population of lesser snow geese and to see how important realistic estimates of key parameters might be. Although our assumptions are simple and in places arbitrary, we feel the results are general and may be quite useful for future management.

Consistent with admonitions that models should not be more complex than available data or biological knowledge will support (Williams et al 2001), we constructed a basic two segment metapopulation model for which the segments differ only in adult survival. Since our purpose is to examine the potential impact of a metapopulation structure on both local and global dynamics of the Midcontinent Population, we parameterized this model under two contrasting scenarios. In one, the more proximate basis for the difference in adult survival estimates is related to “East” versus “West” geography (perhaps related to Central versus Mississippi Flyway harvest differences or habitat differences along spring migration corridors) while the other assumes a “North” versus “South” bias possibly related to habitat quality at the nesting colonies or timing of migration. Under the North versus South scenario, much of the Midcontinent Population migrates through the range of southern nesting colonies and the habitat there appears more impacted which could contribute to an annual survival difference for residents. If geese from more southern colonies began fall migration earlier, they may be subjected to heavier harvest by simply being the first to arrive at hunting grounds (e.g. Alisauskas et al In Review).

We parameterized the two metapopulation structures using data from Kerbes et al.’s (2006) estimates of nesting colony sizes for the Midcontinent Population. Our **East West Structure** assigns all geese from the West Hudson Bay complex and colonies east of there to the East segment and all geese west of there to the West segment. This leads to an initial split of the Midcontinent Population of 0.81 in the Eastern segment and 0.19 in the Western. Our **North South Structure** assigns all the geese from the West Hudson Bay complex and colonies south of there to the South segment and all geese north of there to the North segment. This leads to an initial split of 0.84 to 0.16 (North to South). Although the relative splits for the two structures are about the same, they differ in whether the larger segment is projected to be growing or declining. The most recent evaluation of adult survival (Alisauskas et al In Review) is more consistent with the **North South Structure**, although some of the banding data samples are rather small. As will be seen, however, the projected dynamics under the two structures question the veracity of that consistency and the contrast in dynamic structures highlight the data needed to realistically model the Midcontinent Population in light of survival variation among colonies or broader regions.

A metapopulation model requires some level of dispersal among its segments. There is limited evidence on the mixing of geese from the nesting colonies across broad geographic ranges. We arbitrarily chose a dispersal probability of 0.20 per individual and allowed only age class 1 birds (the most likely dispersers) to move between the segments. Although the dispersal rate is symmetrical between the segments, the numbers of immigrants and emigrants are not since there are initial differences in the sizes of the segments. We assume that adult survival is segment-of-residence specific so that immigrants take on the adult survival value of their "new" segment.

We used a 5-stage, pre-breeding census matrix to project the segments and lacking adequate data on stochastic variation, we used deterministic projections. There is wide overlap in growth rates under deterministic and stochastic projections, as shown above. The matrices for the two segments (W and E or N and S) are:

$$\mathbf{W}=\mathbf{N}= \begin{array}{ccccc} 0 & 0.08 & 0.20 & 0.22 & 0.24 \\ 0.85 & 0 & 0 & 0 & 0 \\ 0 & 0.85 & 0 & 0 & 0 \\ 0 & 0 & 0.85 & 0 & 0 \\ 0 & 0 & 0 & 0.85 & 0.85 \end{array} \qquad \mathbf{E}=\mathbf{S}= \begin{array}{ccccc} 0 & 0.08 & 0.20 & 0.22 & 0.24 \\ 0.82 & 0 & 0 & 0 & 0 \\ 0 & 0.82 & 0 & 0 & 0 \\ 0 & 0 & 0.82 & 0 & 0 \\ 0 & 0 & 0 & 0.82 & 0.82 \end{array} \qquad (5)$$

with asymptotic growth rates of $\lambda_{W=N}$ = 1.0241 and $\lambda_{E=S}$ = 0.9917 respectively.

The two segments of a given structure were projected simultaneously and we assumed that dispersal between the segments was associated with spring migration such that immigration and emigration occurred immediately before reproduction. Immigration and emigration were implemented using an age-specific dispersal matrix (Gilliland et al 2009). We present the model projections for the first 10 years since such near-term dynamics are often more instructive and potentially more useful in management situations than are equilibrium or asymptotic solutions (Koons et al 2006). For completeness, however, we do discuss more long-term and equilibrium dynamics. In monitoring the dynamics of a metapopulation structure, it is necessary to examine growth of both segments as well as the overall metapopulation. Growth of a segment (local growth) in the presence of dispersal is a combination of "intrinsic growth" (that expected from fertilities and survival , e.g. $\lambda_{W,N}$ = 1.0241) and the difference between emigration and immigration. The latter are the product of the dispersal rate (0.2 in this exercise) and the size of the relevant segment. We use the term “population growth” in its population dynamics sense of lambda which indicates a population is increasing when λ>1, declining when λ<1 and stable when λ=1.

In the absence of dispersal (and as a point of reference), each segment of the **East West Structure** changes according to its intrinsic growth rate – the East segment declines (λ = 0.992) and the West segment increases (λ = 1.024) (Figure 7 solid lines). The dynamics of the metapopulation (Figure 7 solid line) are primarily controlled by the growth rate of the larger segment (East) in the beginning and the metapopulation declines until the two segments are of equal size (approximately 45 years). At that point, the growth rate of the metapopulation increases and is ultimately equal to the intrinsic rate of the West segment. At that point, the East segment would no longer exist.

Under 20% dispersal (Figure 7 dashed lines), the West segment initially grows faster (λ = 1.074) than expected from its intrinsic growth rate (λ = 1.024) since the number of immigrants from the substantially larger East segment is greater than the number of emigrants from the West. (Recall that the number of immigrants or emigrants is the dispersal rate times the abundance of the relevant segment.). Similarly, the East segment declines faster (λ = 0.975) than expected from its intrinsic rate (λ = 0.992). The dynamics of the metapopulation reflect the combined effects of segment-specific intrinsic rates and the dispersal between the different-sized segments and the metapopulation begins to grow slowly (λ = 1.001). As population sizes in the 2 segments equalize (about 23 years), the growth rate of the West segment begins to slow and that of the East segment begins to increase as immigration from the growing West segment overcompensates for losses from emigration and its intrinsic declining growth rate. Ultimately, the growth rates of both segments and the metapopulation approach an equilibrium that balances intrinsic rates with immigration and emigration gains and losses at λ = 1.012. Unlike the situation with no dispersal, both segments are maintained in standard source/sink fashion. The only odd twist is that initially, the East segment, which at λ = 0.992 would traditionally be called a “sink”, is behaving like a “source” owing to the high relative number of emigrants it provides.

In the absence of dispersal (again simply as a point of reference), each segment of the **North South Structure** changes according to its intrinsic growth rate – the South segment declines (λ =0.992) and the North segment increases (λ = 1.024) (Figure 8 solid lines). The dynamics of the metapopulation (Figure 8 solid line) are primarily controlled by the growth rate of the larger segment (North) and the metapopulation increases. As the South segment continues to decline (and ultimately disappear), the growth rate of the metapopulation approaches the intrinsic rate of the North segment.

Under 20% dispersal (Figure 8 dashed lines), the South segment increases (λ = 1.068) since immigration from the larger, growing North segment overcompensates for its intrinsic growth rate (λ = 0.992) and its emigration. Growth of the North segment is less than expected (λ = 1.004) from its intrinsic rate (λ = 1.024) since the number of emigrants is far greater than the number of immigrants. The initial growth of the metapopulation (λ = 1.017) reflects the combined effects of segment-specific intrinsic rates and the dispersal between the different-sized segments. Since growth of the South segment reflects overcompensation of its intrinsic decline overbalanced by immigration from the North segment, it remains smaller and the two segments eventually reach an equilibrium where intrinsic growth (and decline) are balanced by immigration and emigration from appropriately-sized segments. At that point, both segments and the metapopulation grow at the same rate of λ = 1.0121. Again, both segments are sustained in a source/sink fashion.

Although a complete analysis of the dependency of these dynamics on dispersal probability is beyond the scope of this chapter, we did examine the dynamics over a set of dispersal probabilities ranging from 0.1 to 0.4 to gain some insight of the robustness of the pattern and extent of shifts in local growth rates related to our arbitrary dispersal probability of 0.2. For the East West Structure, growth of the West segment increased over a range from λ = 1.05 to λ = 1.09 while that of the East Segment decreased over a range from λ = 0.98 to λ = 0.96 (for dispersal ranging from 0.1 to 0.4). For the North South Structure, growth of the South segment increased over a range from λ = 1.03 to λ = 1.10 while that of the North segment decreased over a range from λ = 1.01 to λ = 0.99. For both structures, the pattern of the shifts in local growth rate related to dispersal is the same over a four-fold range of dispersal values. While there are some differences in the extent of shifts as a function of the dispersal probability, it is clear that in both cases, the near-term growth rates of the initially smaller segment are substantially higher than their intrinsic potential. The source/sink dynamics of the metapopulation structures described above thus seem to be reasonably robust to differences in actual dispersal probability, at least over the range examined.

Although the two metapopulation structures we examined were somewhat hypothetical and the levels of dispersal were arbitrary, the dynamics of the systems are instructive and highlight the interplay between intrinsic growth rates, apportionment of the Midcontinent Population and dispersal. It is clear that local dynamics are not a simple function of local intrinsic growth characteristics nor are local dynamics necessarily predictive of more global metapopulation dynamics. Over the long-term (>50 years) and under a given level of dispersal, both structures ultimately reach the same asymptotic growth rate. Since that rate is a composite of intrinsic rates of the segments balanced by equilibrium levels of immigration and emigration between them, the overall asymptotic growth rate is lower than that projected for the more rapidly growing segment. This is typical of source/sink systems.

The near-term dynamics are more interesting and are more likely something managers can measure and respond to. For example, under the East West Structure, the West segment is projected to grow at a rate far in excess of its intrinsic expectation, owing to the disproportionate input of immigrants from the slowly declining East segment. This result is consistent with recent observations at the Queen Maude Gulf colony whose apparent growth rate has been λ = 1.08 (Alisauskas, personal communication), a value far greater than its projected intrinsic rate λ = 1.02 but similar to the projections here for the West segment under dispersal ranging from 10% to 40%. By contrast, under our North South Structure, the smaller (and intrinsically declining) South segment is projected to grow rapidly while the larger segment is projected to be nearly stable. This is inconsistent with estimates at both La Pérouse Bay and the southern Hudson and James Bay colonies which are stable or declining (Abraham, personal communication) and at Queen Maude Gulf. One could argue that from a metapopulation view, apportioning the Midcontinent Population into segments for which the larger one has an intrinsic growth rate less than 1 is more consistent with available data, at least for near-term dynamics over this range of dispersal values.

While such speculation is interesting and even testable, the real point of this section is to highlight that metapopulation dynamics are not necessarily indicative of local intrinsic growth rates nor local dynamics. Rather, they are a composite of local intrinsic growth rates and the relative impacts of immigration and emigration. The latter, in turn, are a function of individual dispersal probabilities and the relative sizes of donor and recipient segments. Given there are differences in adult survival among the northern breeding colonies of the Midcontinent Population of lesser snow geese, it is crucial that we obtain estimates of the relative size of each segment with a different survival rate and estimates of dispersal among them. It seems clear that any further attempt to model or project the Midcontinent Population of lesser snow geese must rely on a metapopulation approach with robust estimates of these parameters.

Elasticity Analyses

Elasticity analysis is a prospective tool that allows one to examine how equal proportionate changes in demographic characters alter a population's future growth rate. The technique is not intended to provide insights as to how the population came to possess a particular set of demographic character values nor their associated growth rates. Rather, elasticities of the demographic characters should be viewed as measures of the relative change in the population growth rate that can be achieved by manipulating those characters. As such, they offer managers a tool with which to weigh the outcomes of various possible actions and choose accordingly. The final choices, however, must be tempered by biological and social realities since some scenarios may be intractable while others are financially not feasible (cf. Rockwell et al. 1997; Schmutz et al. 1997).

Using the best available demographic data for the Midcontinent Population of lesser snow geese, Rockwell et al. (1997) showed that the elasticity of adult survival was substantially higher than that of any other demographic character. Because elasticity estimates can be sensitive to precise combinations of values of demographic variables and emergent growth rates, they showed further that the result was robust over a wide range of demographic characters that led to growth rates ranging from $\lambda=1.008$ to $\lambda=1.107$. Those evaluations used analytical solutions that relied on asymptotic (equilibrium) conditions. Subsequent perturbation analyses incorporating stochastic variation and near-term (5 to 10 year) simulations revealed the same pattern of relative effects for the demographic variables (Rockwell, unpublished). So too did models incorporating density-dependent effects, although in those scenarios one must examine the relative effects of equal proportionate changes of the demographic variables on the reactivity of growing or declining populations to the perturbation or the displacement of a perturbed equilibrium ($\lambda=1.0$) population and its return to equilibrium (Rockwell, unpublished).

Mills and Lindberg (2002) imply that failure to include immigration and emigration in the lesser snow goose model used by Rockwell et al (1997) calls into question the veracity of the analyses and conclusions reached. In their reevaluation, they used a more retrospective approach (Life-stage Simulation Analysis) and concluded that including immigration and emigration (set to be equal) can change the relative reactions of the La Pérouse Bay population to changes in other demographic variables. They argued: "…this example demonstrates that connectivity, or movement, is nontrivial in terms of its impact on λ for this population" (p. 354). While this could be true locally, it ignores the fact that the original analysis was for the entire Midcontinent Population. However, their point raises an interesting issue, especially in light of current survival data that indicate the Midcontinent Population may actually be a metapopulation structure whose segments are controlled by different levels of at least some of the demographic variables.

To examine this further, we used a perturbation approach to evaluate the relative effects on metapopulation growth of equal proportionate changes in demographic variables including recruitment and adult survival within segments as well as dispersal among segments. We used the two metapopulation structures described in the previous section that apportion the Midcontinent Population into an East West Structure and a North South Structure. Intrinsic projected growth rates of the segments within the two structures are based on the estimates of recruitment and survival described above, and are: $\lambda_{W,N} = 1.0241$ and $\lambda_{E,S} = 0.9917$. Recall from the previous section that for the East West Structure, the larger (East) segment (0.81 of the total initially) has the lower growth rate while for the North South Structure the larger (North) segment (0.84 of the total initially) has the higher growth rate. Consistent with Mills and Lindberg (2002), we assumed immigration and emigration for each segment (henceforth dispersal) involved a constant proportion of individuals and in the absence of real data allowed the proportion of individuals moving from one segment to the other to be one of several values (0.05, 0.10, 0.20, and 0.30).

As in the previous section, the model followed a time line that began with dispersal followed by birth-pulse reproduction and survival. The latter two were subsumed in a 5 stage class, Lefkovitch, pre-breeding census projection matrix. Each segment was initialized with its asymptotic stable age distribution and the metapopulation structure was projected for 10 years. The growth rates of both segments and the overall metapopulation were estimated using the Heyde-Cohen equation (Caswell 2001). We perturbed dispersal, adult survival of each segment and first-year (juvenile) survival (s_0) of each segment in turn by 1% from their baseline values (recall we used 4 "baseline" values of dispersal). We used juvenile survival as a way of perturbing recruitment in each segment since it is a multiplicative component of the pre-breeding census matrix's first row and is not itself dependent on stage class. The relative effects of each perturbation on the metapopulation growth rate were evaluated as:

$$\mathrm{re} = \left(\lambda_{\mathrm{baseline}} - \lambda_{\mathrm{perturbed}}\right) / \lambda_{\mathrm{baseline}} \; / 0.01$$

following Schmutz et al. 1997, who explained that these are equivalent to lower level elasticities of the demographic variables being perturbed. It is important to note that these are near-term relative effects (see Koons et al 2005) in that they are based on growth projected for just 10 years rather than at the systems equilibrium (asymptotic relative effects). We chose this time frame since it provides a better overview of the responsiveness of the system changes imposed by the management plan under review.

The results of the perturbation trials are summarized in Figure 9 where several trends are clear. First, the relative effect of dispersal is near 0 and lower than the relative effects of any other demographic variables. Second, the relative effect of adult survival of the "source" segment is highest for both the East West and North South Structures and is higher than the relative effect of the smaller segments' adult survival. Recall, that the source segment is the larger of the two in both structures and is thus initially providing the bulk of the dispersers. As such, its highest elasticity parameter tends to control overall dynamics at least in the near term. This difference in the relative effect of adult survival of the 2 segments declines as dispersal increases for both structures. This reflects the more rapid approach to equilibrium conditions of relative size, immigration, emigration and intrinsic growth expected with faster mixing of the two segments. Finally, the relative effects of recruitment are less than that of adult survival in all situations.

The conclusion that adult survival has the greatest proportionate effect on the growth of lesser snow geese (Rockwell et al 1997) is valid whether the Midcontinent Population is treated as a single population or a metapopulation structure. Dispersal within the metapopulation has no effect on this conclusion.

Conclusions and Data Needs

Although we agree with Williams et al (2001) that models should not be more complex than the available data, we are also believers in the famous admonition by Box (1979) that "all models are wrong, some models are useful". Thus, in a spirit of realistic pragmatism, we have endeavored to examine the dynamics of the Midcontinent Population of lesser snow geese with a series of models that are simplistically consistent with available data while being mindful of potentially more complex biological underpinnings and the overall concerns of managers. Where actual data were not available, we explored the effects of a realistic range of possibilities. Several generalities emerged from these explorations and a few key data needs became apparent.

Regardless of which demographic variables changed historically and led us to a population that is numerically outstripping its resources, adult survival emerges as the vital rate that holds the most potential for changing the growth rate of the Midcontinent Population of lesser snow geese. If it is reduced through increased hunter harvest, juvenile survival, a component of recruitment, will also be reduced since juveniles are a part of the overall hunter harvest. Given the current estimates of adult survival and recruitment, the projected growth rate of the Midcontinent Population of lesser snow geese is still positive with $\lambda > 1.0$. If a reduction in the Midcontinent Population is to be achieved using hunter harvest, that harvest will have to be increased. Since reduction of juvenile survival has a smaller effect on reducing the population growth rate, every attempt must be made to maintain a high proportionate harvest of adults. It is also important to stress that the observed **population growth rate** is a consequence of the current values of survival and recruitment. If the size of the Midcontinent Population is reduced through means other than a reduction in survival and/or recruitment (e.g. a one-time removal of a large portion of the population), the surviving population will still have the same positive growth rate ($\lambda > 1.0$) unless survival and/or recruitment are also reduced.

Although analysts and modelers prefer to have precise estimates of all variables that enter their projections, certain variables become the driving forces by their disproportionate effects on overall dynamics. Those are the variables for which robust estimates with high precision are necessary. From our current work, three variables emerge as critical for accurate monitoring and modeling of this system. The first is *adult survival* which, as shown, has a profound impact on dynamics of a single population or of a metapopulation structure and its segments. The second is the *relative proportion* of the Midcontinent Population belonging to metapopulation segments that have different adult survival rates. Without knowing these relative proportions, it is not possible to accurately project the overall growth rate of the entire metapopulation for even a single year. The third is the *dispersal rates* of individuals between the segments. These rates are required for multi-year projections and may also serve as a character that could be manipulated in aid of management. For example, in the absence of any dispersal, the fastest growing segment of a metapopulation structure becomes disproportionately larger. If dispersal from that segment to a slower growing segment could be achieved, the growth rate of the overall metapopulation would be lowered. If dispersal was to a declining segment, then the overall metapopulation could actually be reduced. In that vein it is also critical to see if dispersal is primarily limited to young birds, as assumed here, or if all age classes do or could be enticed to disperse.

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variable	**age class**				
	1	**2**	**3**	**4**	**5+**
BP	0	0.3500	0.7700	0.8300	0.8500
TCL	0	3.3995	3.9500	4.2545	4.4179
TNF	0	0.2550	0.2550	0.2550	0.2550
p1	0	0.9719	0.9677	0.9787	0.9840
p2	0	0.9340	0.9340	0.9340	0.9340
TBF	0	0.0735	0.0735	0.0735	0.0735
p3	0	0.7053	0.7053	0.6659	0.6659
s_0	0	0.3000	0.3000	0.3000	0.3000

Table 1. Age class specific demographic variables contributing to recruitment of the Midcontinent Population of lesser snow geese. BP=breeding propensity; TCL=total clutch laid; TNF=total nesting failure; p1=egg survival; p2=hatchability; TBF=total brood failure; p3=fledging probability; s_0=survival from fledging to the next reproductive event. See text for more details and Rockwell et al (1997) for citation information.

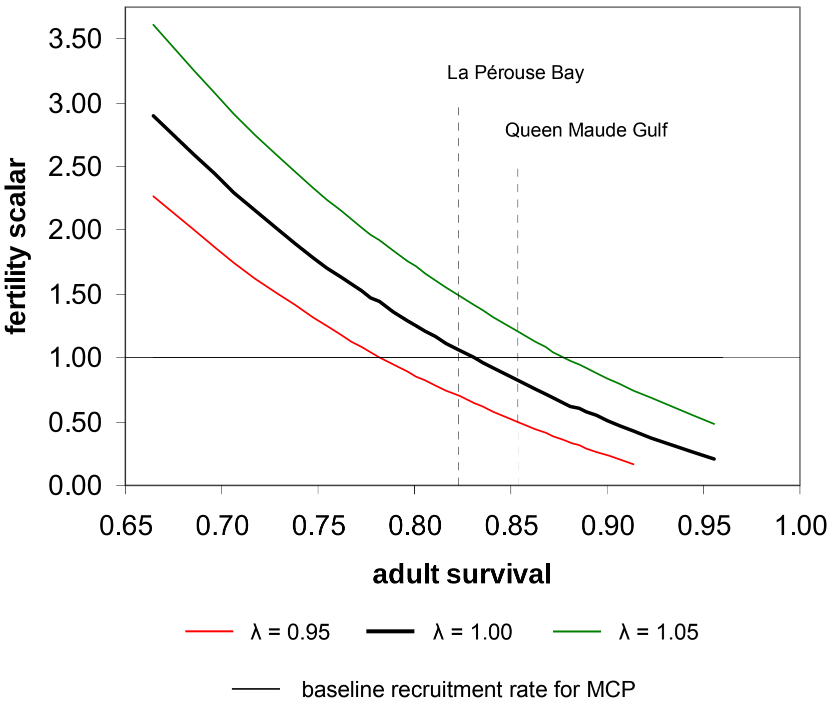


Figure 1. Growth rate potential of the Midcontinent Population of lesser snow geese. The baseline recruitment rate is the best estimate for the Midcontinent Population and is the age-specific vector [0, 0.08, 0.20, 0.22, 0.24] (see text). It corresponds to the fertility scalar value of 1 in the Figure. The corresponding values for fertility scalar 2 are [0, 0.16, 0.40, 0.44, 0.48], etc. The current mean estimates of adult survival for Queen Maude Gulf (0.8536) and La Pérouse Bay (0.8227) are indicated by verticals.

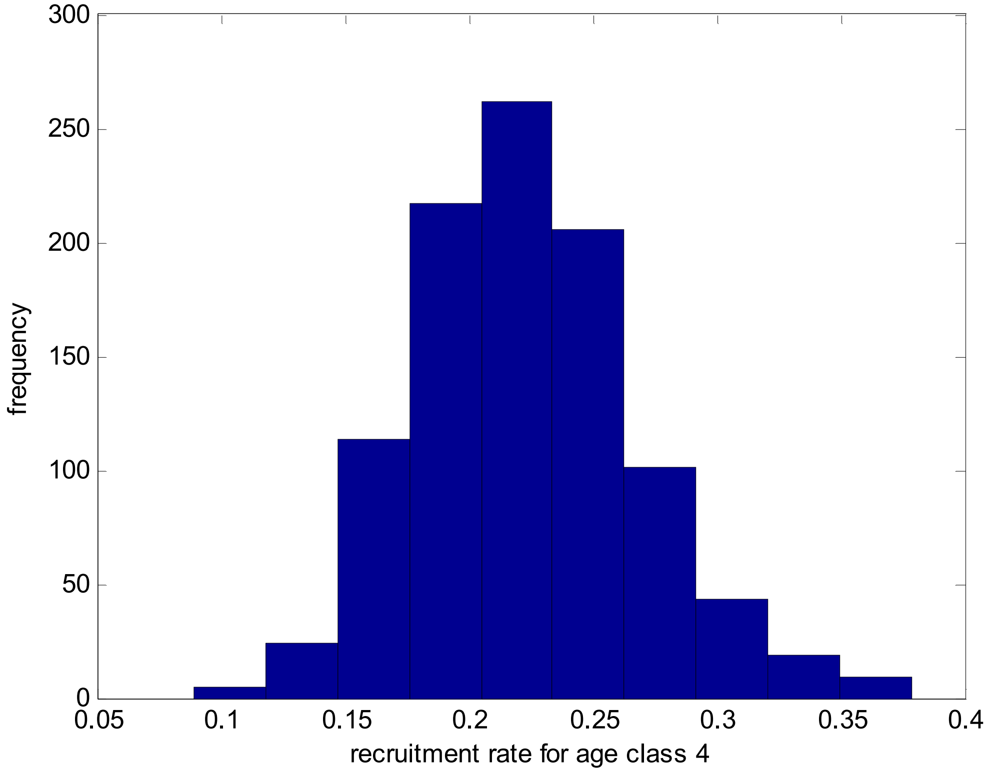


Figure 2. Frequencies of possible recruitment rates for 4-year-old lesser snow geese based on a mean of 0.2225 and a coefficient of variation of 0.2. The values are produced from a beta distribution with the shaping parameters a = 19.2150 and b = 67.1446 computed from the given mean and coefficient of variance.

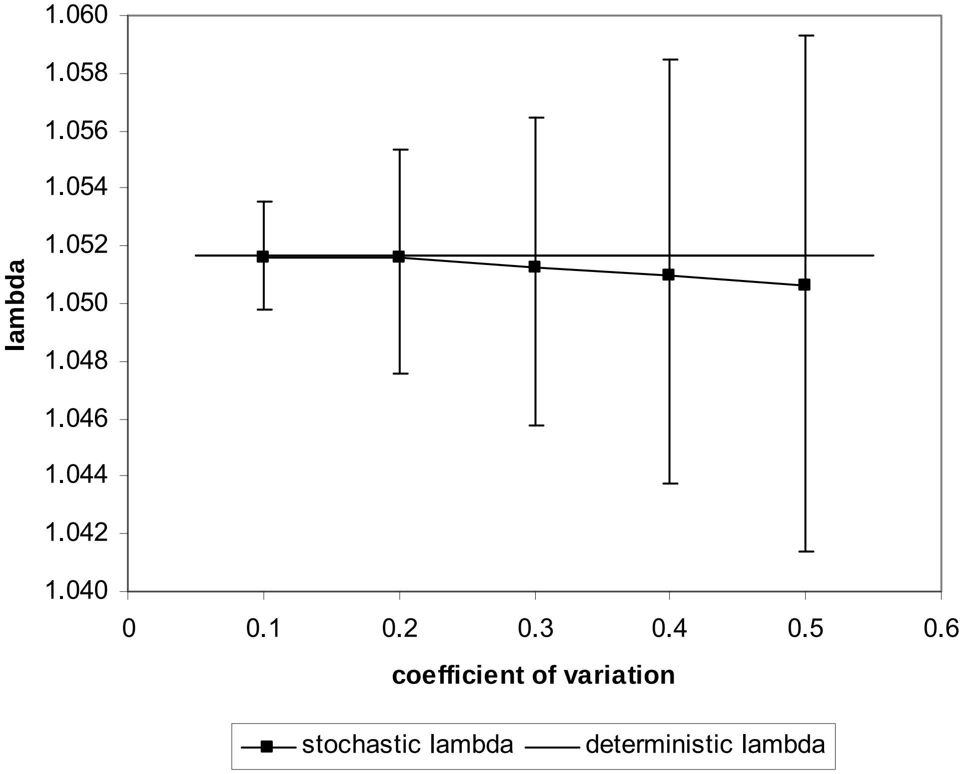


Figure 3. The effect of increasing variance on the stochastic growth rate of a population of lesser snow geese.

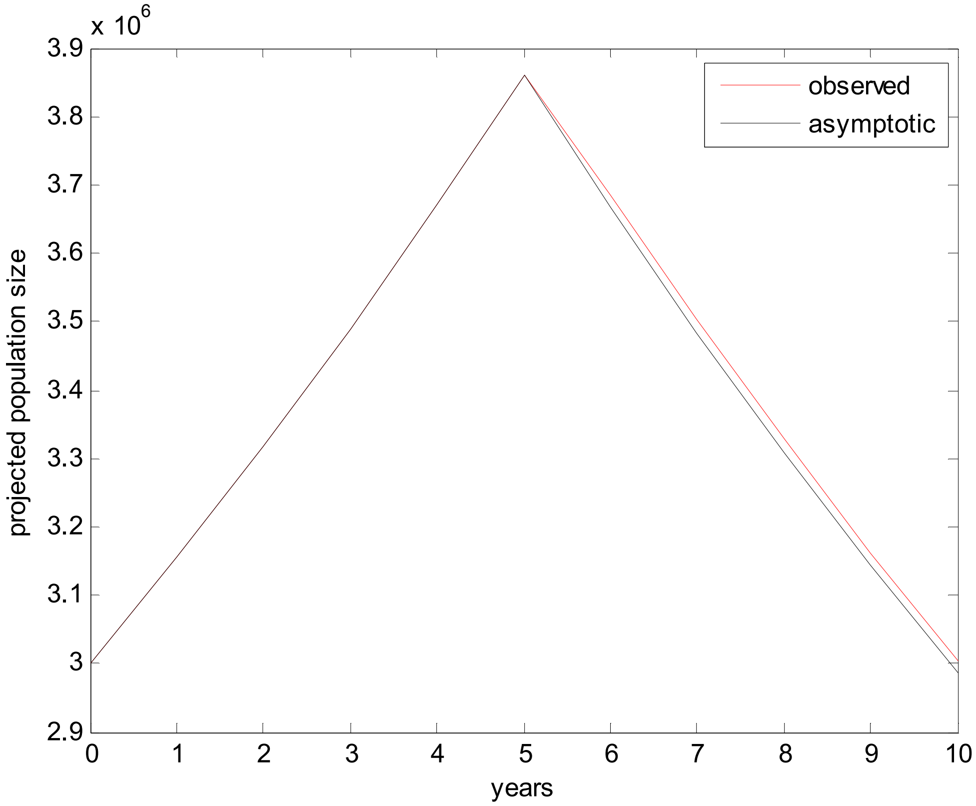


Figure 4. Effect of a shift from λ = 1.0517 to λ = 0.95 by reducing adult survival to 0.8897×s_a. The "observed" projection made use of the post-perturbation matrix ($\mathbf{n}_{t+1} = \mathbf{A} \times \mathbf{n}_t$) for $t \geq 5$ while the "asymptotic" projection was based on the asymptotic growth rate of the post-perturbation matrix ($\mathbf{n}_{t+1} = \lambda_1 \times \mathbf{n}_t$) for $t \geq 5$. See text for further details.

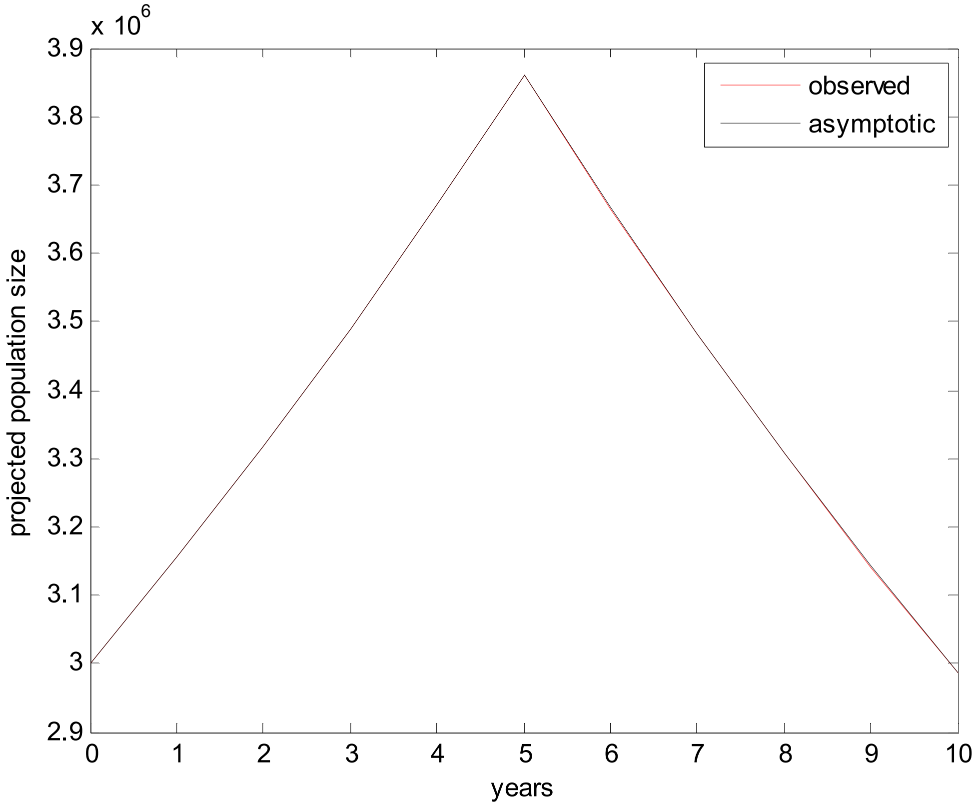


Figure 5. Effect of a shift from $\lambda = 1.0517$ to $\lambda = 0.95$ by reducing adult survival and juvenile survival to $0.90329 \times s_a$ and $0.90329 \times s_0$, respectively. The "observed" projection made use of the post-perturbation matrix ($\mathbf{n}_{t+1} = \mathbf{A} \times \mathbf{n}_t$) for $t \geq 5$ while the "asymptotic" projection was based on the asymptotic growth rate of the post-perturbation matrix ($\mathbf{n}_{t+1} = \lambda_1 \times \mathbf{n}_t$) for $t \geq 5$. See text for further details.

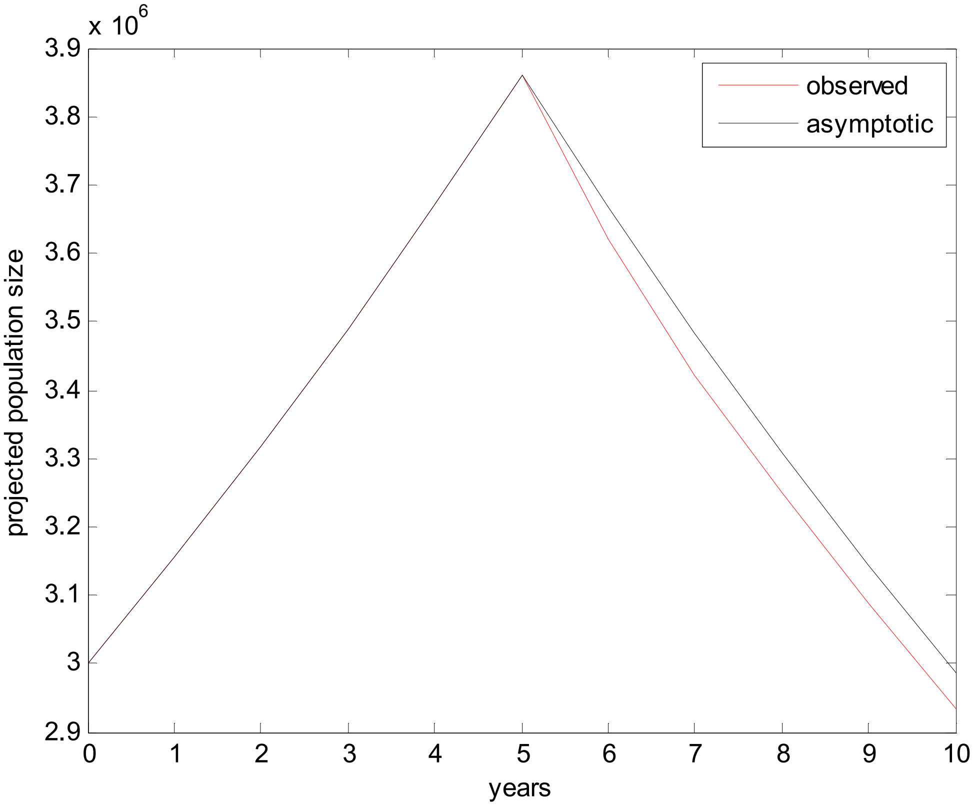


Figure 6. Effect of a shift from λ = 1.0517 to λ = 0.95 by reducing juvenile survival to 0.3395×s_0. The "observed" projection made use of the post-perturbation matrix ($\mathbf{n}_{t+1} = \mathbf{A} \times \mathbf{n}_t$) for $t \geq 5$ while the "asymptotic" projection was based on the asymptotic growth rate of the post-perturbation matrix ($\mathbf{n}_{t+1} = \lambda_1 \times \mathbf{n}_t$) for $t \geq 5$. See text for further details.

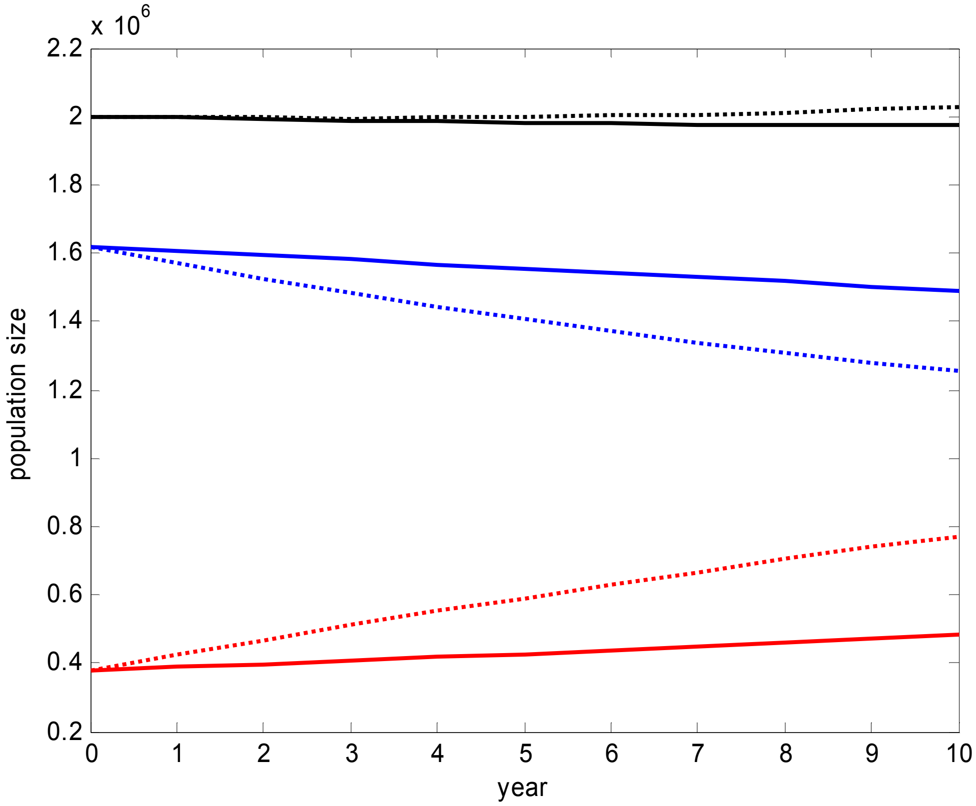


Figure 7. Projections of the Midcontinent Metapopulation and its East and West segments assuming an 0.81 (East) to 0.19 (West) initial split of the nesting geese both without (solid) and with (dashed) 20% dispersal of first-year birds. Midcontinent Population (MCP) ——; East Segment (East) ——; West Segment (West) ——. The 10-year realized growth rates based on the Heyde-Cohen equation (Caswell 2001) are: with no dispersal MCP $\lambda = 0.9986$; East $\lambda = 0.9917$; West $\lambda = 1.0241$; with dispersal MCP $\lambda = 1.0013$; East $\lambda = 0.9747$; West $\lambda = 1.0736$. (See text for more details.)

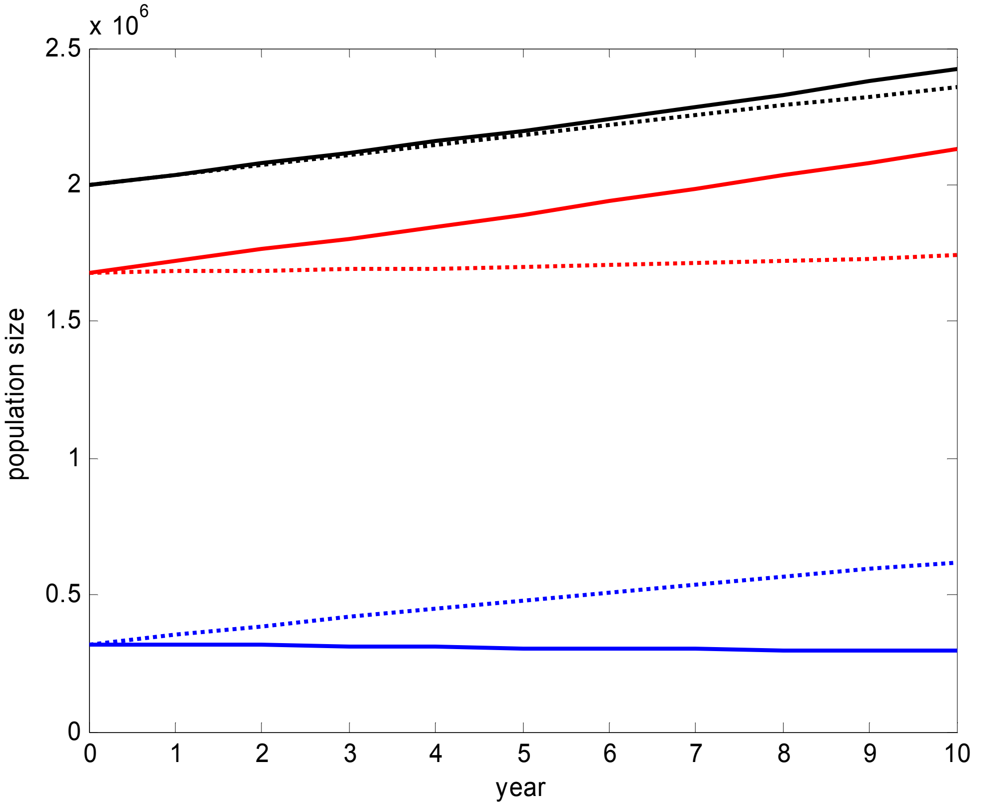
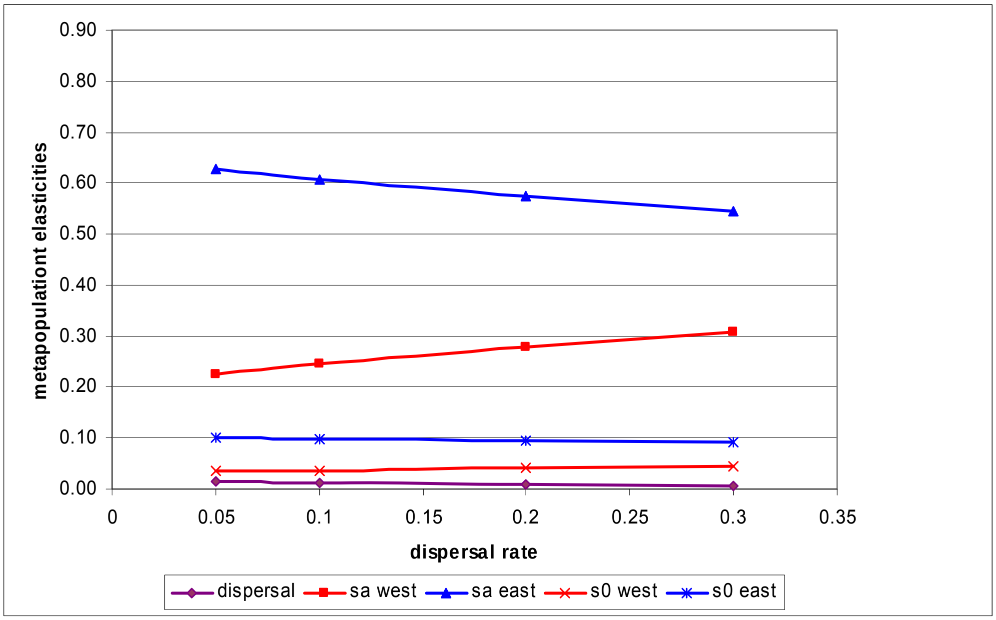


Figure 8. Projections of the Midcontinent Metapopulation and its South and North segments assuming a 0.84 (North) to 0.16 (South) initial split of the nesting geese both without (solid) and with (dashed) 20% dispersal of first-year birds. Midcontinent Population (MCP) ——; South Segment (South) ——; North Segment (North) ——. The 10-year realized growth rates based on Heyde-Cohen equation (Caswell 2001) are: with no dispersal MCP λ = 1.0195; South λ = 0.9917; North λ = 1.0241; with dispersal MCP λ = 1.0167; South λ = 1.0681; North λ = 1.0036. (See text for additional details.)


East West Metapopulation Structure

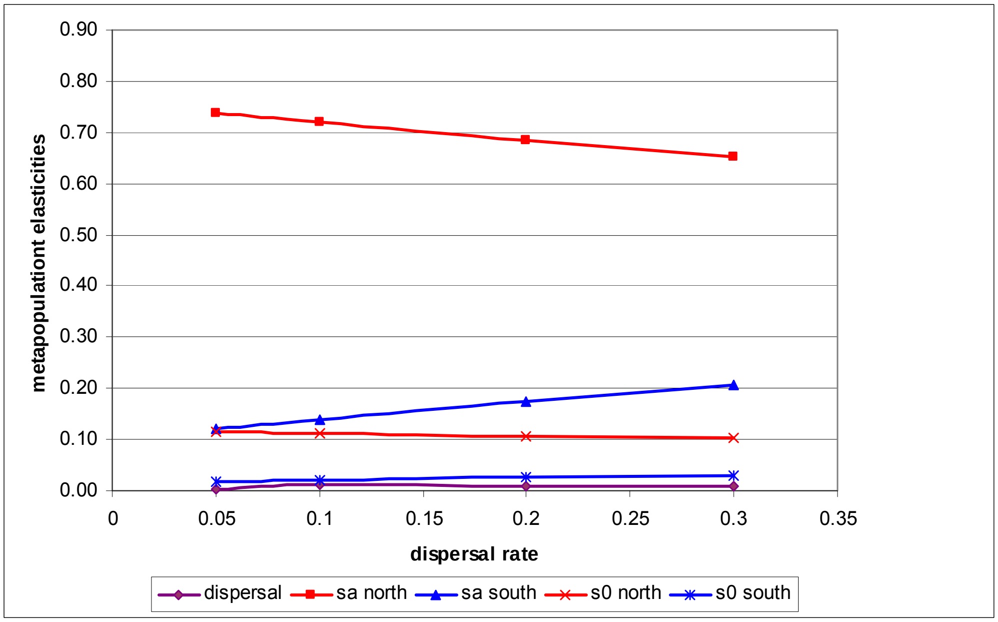

North South Metapopulation Structure

Figure 9. Relative effects of equal proportionate changes in the recruitment (s0) and adult survival (sa) of the segments of the metapopulation structures and dispersal between them for both the East West and North South metapopulation structures.