Metapopulation dynamics of mid-continent lesser snow geese: implications for management

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Abstract: The rapid increase in abundance of lesser snow goose (LSG; *Chen caerulescens caerulescens*) numbers and their devastating effects on arctic and subarctic habitats has inspired much research on the use of population models for defining appropriate management policies. We use the not-yet considered metapopulation approach to examine the elasticity of mid-continent LSG population dynamics to changes in underlying vital rates to determine whether management efforts aimed at decreasing burgeoning numbers should be reevaluated. After considering a variety of geographic scenarios in the metapopulation model, we found that changes in survival would still have a larger impact on population dynamics relative to equal proportionate changes in other vital rates, but where these changes geographically occur could be of critical importance. In some instances, changes in reproductive output could have notable effects on eventual abundance. These new findings suggest that spatial structure in demographic vital rates that underlie abundance distributions across locations and dispersal among colonies require additional research to help guide the management of lesser snow goose numbers.

Key words: human–wildlife conflicts, lesser snow geese, management, matrix model, metapopulation dynamics, population momentum, transient dynamics

Human–wildlife conflicts complicate conservation and management efforts worldwide, especially since human populations are increasing and inhabiting ever-greater geographic areas (Conover 2002). Anthropogenic developments often have deleterious effects on the environment (McKinney 2002, Forester and Machlis 1996). However, agricultural practices can have beneficial impacts on wildlife populations. North American goose populations, for example, were declining in the early 1900s, but rebounded and expanded as the efficiency of grain agriculture increased throughout their migration and wintering areas (Ankney 1996, Abraham et al. 2005). The mid-continent population of lesser snow geese (LSG; *Chen caerulescens caerulescens*) increased quickly at a rate of 5 to 7% per year due to increased waste grain and expansion of rice agriculture in the Gulf Coast states (Robertson and Slack 1995, Jefferies et al. 2003, Abraham et al. 2005). This has become a great concern, as growing snow goose-colonies have (1) led to increased damage of standing and fall-seeded cereal crops; (2) provided a reservoir for the bacterium that causes avian cholera, which can easily be transmitted to other bird species; and (3) caused ecosystem-level changes to their arctic breeding grounds (Johnson 1997, Abraham et al. 2005, Jefferies et al. 2006).

In addition, long-term data indicate that the harvest rate has generally declined in Canada and the United States as LSG numbers increased (Cooke et al. 2000). There are many possible reasons for declines in harvest rates, such as flocks becoming larger, making them more difficult to decoy, and a larger proportion of experienced adults in the population (Rockwell et al. 1997). Further, LSG populations have grown so quickly that they now swamp out their main predator (Holling 1959), North American waterfowl hunters, whose numbers have been declining for the last 2 decades (Pergams and Zaradic 2008).

To alleviate the many deleterious impacts of increasing LSG abundance, the Arctic Goose Working Group suggested that the continental LSG population be reduced by 50% below

numbers in the late 1990s. The modeling portion of *Arctic Ecosystems in Peril* (Rockwell et al. 1997) depicted how a reduction in the size of the mid-continent population of LSG requires a long-term reduction of the population growth rate to $\lambda < 1.0$. They also used the model to explore how various combinations of reductions in reproductive success and survival might achieve this goal. Using an elasticity analysis, Mills and Lindberg (2002) argued that reductions in adult survival would reduce the growth rate more rapidly than equivalent proportional reductions in reproductive output. This was particularly appealing because reductions in adult survival potentially could be achieved by increasing LSG mortality through changes in hunting regulations. 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 whether an increase in harvest could begin shifting the population's dynamics in the right direction and would be the most humane method for accomplishing this task. As a result, a 1998 Conservation Order amendment to U.S. migratory bird law was implemented to liberalize harvest regulations (e.g., initiation of a spring hunt, allowing use of unplugged shotgun magazines and electronic calls, and allowing large bag limits), were later made in Canada. This landmark change in harvest policy seems to have increased harvest rates since 1998 and reduced adult LSG survival in some areas but not in others (Alisauskas et al. in press).

It thus appears that different segments of the mid-continent population of LSG may be subject to different levels of adult mortality. If so, a metapopulation model may be a closer approximation to reality. Mills and Lindberg (2002) suggested that failure to include spatial structure in the LSG model used by Rockwell et al. (1997) could change the conclusion that adult survival has the largest functional effect on λ, and that in the presence of dispersal, other vital rates could be more important. Their point raises an interesting issue, especially in light of current survival data that indicate the mid-continent population may actually be a metapopulation where the subpopulations experience different survival (Alisauskas et al. in press).

We explored the ramifications of a metapopulation model on both regional and global dynamics. We used population modeling tools to examine: (1) the metapopulation's current projected growth in light of the best estimates of survival and reproductive output available (Cooch et al. 2001, Alisauskas et al. in press); (2) the elasticity of the metapopulation dynamics to changes in the underlying vital rates against a backdrop of possible dispersal and spatial-structure scenarios; and (3) transient dynamics and momentum when conducting elasticity analyses of the metapopulation dynamics. Recent research has shown that rapid shifts in demographic variables, such as that anticipated when management action is taken, can lead to unanticipated changes in short-term transient growth that have long-term influences on population abundance (i.e., population momentum; Koons et al. 2005, 2006).

Materials and Methods

We examined the 3 objectives listed above within a deterministic framework that mid-continent LSG dynamics behave similarly under both deterministic and stochastic frameworks (Rockwell et al. in press).

Building on a single population projection model

Rockwell et al. (1997) developed a 5 age-class, birth-pulse, Lefkovitch model to project the mid-continent population of LSG using the following life cycle:
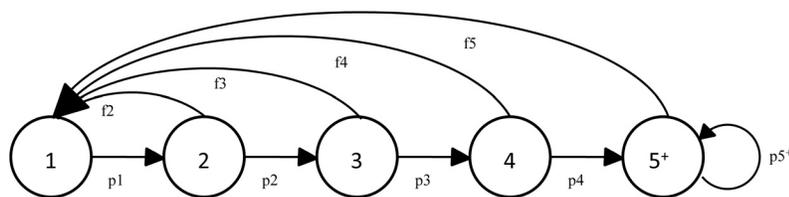
where 1,2,…5+ represent individuals with ages of ≤1 year, almost 2 years, and ≥5 years of age,

respectively. Thus, the population projection matrix model (A) pertaining to this life-cycle diagram is:

$$\mathbf{A} = \begin{bmatrix} 0 & f_2 & f_3 & f_4 & f_{5+} \\ p_1 & 0 & 0 & 0 & 0 \\ 0 & p_2 & 0 & 0 & 0 \\ 0 & 0 & p_3 & 0 & 0 \\ 0 & 0 & 0 & p_4 & p_{5+} \end{bmatrix} \quad (1)$$

Here, we used a pre-breeding census projection because it better corresponds to the timing of breeding-ground surveys, and allows for simpler interpretation of elasticity analyses (Caswell 2001, Cooch et al. 2003). The latter can be seen from the matrix fertility parameterizations that quantify recruitment to 1 year of age:

$$f_i = 0.5 \times BP_i \times TCL_i \times TNS_i \times P1_i \times P2_i \times TBS_i \times P3_i \times s_0 \quad (2)$$

where for age class i, BP is breeding propensity, TCL is the size of the total clutch laid, NS is the probability of nest success, $P1$ is the probability of egg survival in nests that did not totally fail, $P2$ is the probability that an egg hatches (hatchability), BS is the probability of brood success, $P3$ is the probability that a gosling from a brood that did not totally fail fledges, s_0 is the survival probability from fledging to just before the next breeding season, and p_i is the annual survival probability from age class i to $i + 1$ of fully grown individuals. All of the demographic variables contributing to recruitment are found only in the first row, and only survival of fully grown individuals is found in the non-zero entries in the rest of the matrix. We used nesting and brood success (i.e., survival; NS, BS) rather than failure rates (e.g., nest mortality) to facilitate elasticity comparisons and to be consistent with using survival rather than mortality throughout the model (Link and Doherty 2002; Tables 1a, b).

Precise and accurate estimates of these fertility components are available only for the La Pérouse Bay colony (58º44′ N, 94º28′ W) where reproductive success has declined substantially in parallel with severe habitat degradation (Cooch et al. 2001). The most recent estimates of reproductive success from La Pérouse Bay may be inappropriate for modeling the entire mid-continent population where habitat degradation has not yet reached the severe levels at La Pérouse Bay. For that reason, we use estimates taken from a time period when the vegetation at La Pérouse Bay was above the threshold for adequate foraging and gosling growth (Rockwell et al. 1997; Rockwell et al., in press). Future studies should nevertheless examine this limiting assumption.

Metapopulation model

We built on the single-population model described above to develop a metapopulation model based primarily on 2 intensively studied colonies within the mid-continent population of LSG; one is located at Queen Maud Gulf (~ 68° N, 103° W) and the other at La Pérouse Bay (~ 58° N, 94° W; Cooch et al. 2001, Alisauskas et al. in press). Breeding colonies within the Mid-continent population might be subjected to different levels of mortality (Alisauskas et al. in press), and connected via immigration and emigration (henceforth dispersal). Thus, we suspect that a metapopulation model might be more realistic than modeling each population separately. Although a number of other nesting colonies exists (Kerbes et al. 2006), the lack of long-term banding and reproductive studies at these locations makes it difficult to ascertain where important geographic differences in demography truly exist. We considered 2 contrasting geographic scenarios in our metapopulation analyses.

Geographic scenarios. In one set of scenarios, we considered a North versus South separation in survival, based on R. T. Alisauskas et al. (in press) who indicated that, since 1998, LSG colonies north of 60° N experienced higher survival rates than those colonies south of 60° N. These differences could occur because of differences in habitat quality on the breeding grounds, differential harvest rates related to differences in the timing of migration, or both (Alisauskas et al. 2009; R. T. Alisauskas, unpublished data). Accordingly, we parameterized adult survival in the North and South segments of our metapopulation model (see below) using the temporal average of Alisauskas' estimates of adult survival between 1998 and 2005 for northern and southern colonies, respectively.

Most banding has occurred in the central Canadian Arctic (at and near Queen Maud Gulf; 26% of banded mid-continent LSG during 1989

to 1997 and 25% during 1998 to 2006) and at southern colonies in the eastern Canadian Arctic (at and near La Pérouse Bay, Cape Henrietta Maria, Akimski Island; 72 and 59% of total bands released during respective time periods). Much less funding and effort have been devoted to banding at northern colonies in the eastern Canadian Arctic (i.e., Baffin Island, Southampton Island, and western Hudson Bay, 1% and 16%, respectively; Alisauskas et al. in press) where the majority of mid-continent LSG breed (Kerbes et al. 2006; Kerbes et al. unpublished report). Given the historically unbalanced sampling effort, future banding across a wider geographic region may be needed to identify true underlying geographic differences in survival over time. Inconsistent with a North–South difference in survival (as discussed above), northern colonies in the eastern Canadian Arctic recently have declined like their southern counterparts, whereas colonies in the central Arctic have continued to increase rapidly (Kerbes et al., unpublished report). Although not explicitly considered in recent survival analyses (Alisauskas et al. in press; Dufour et al. in press), an East versus West (i.e., colonies east of 95° W; colonies west of 95° W, respectively) split in demography and geographic structure is another possibility that deserves attention. We designed such scenarios and parameterized adult survival in the East and West segments of this version of the metapopulation model (Figure 1) using Alisauskas' results for the north (dominated by samples from Queen Maud Gulf west of 95° W) in the West segment, and results for the south, dominated by samples from southern colonies east of 95° W, in the East segment. This modeling assumption considers the possibility of an East-West separation in survival driven by differences in Mississippi and Central Flyway harvest or by habitat differences along spring migration corridors, but should be tested when more banding data becomes available.

Based on aerial surveys of nesting colonies,

Table 1a. Age-specific demographic variables contributing to recruitment of the mid-continent population ofl snow geese.

Age classes	1	2	3	4	5+
	Fertility components (lower-level estimates)[a]				
BP	0	0.3500	0.7700	0.8300	0.8500
TCL	0	3.3995	3.9500	4.2545	4.4179
NS	0	0.7450	0.7450	0.7450	0.7450
$P1$	0	0.9719	0.9677	0.9787	0.9840
$P2$	0	0.9340	0.9340	0.9340	0.9340
BS	0	0.9265	0.9265	0.9265	0.9265
$P3$	0	0.7053	0.7053	0.6659	0.6659
s_0	0	0.3000	0.3000	0.3000	0.3000
	Overall fertility				
f	0	0.079	0.201	0.222	0.238

[a] Fertility components: BP = breeding propensity; TCL = total clutch laid; NS = nesting success; $P1$ = egg survival; $P2$ = hatchability; BS = brood success; $P3$ = fledging probability; s_0 = survival from fledging to the next reproductive event (Rockwell et al. 1997). We denoted f as the overall fertility, which varied across age classes (i.e., 2, 3, 4, and 5), but remains the same across all locations (i.e., North, South, East, and West). For model clarity, we named these estimates as follows: $fes2$, $fes3$, $fes4$, $fes5$, for the East or South colonies, and $fwn2$, $fwn3$, $fwn4$, $fwn5$ for the West or North colonies (See Figure 1).

Table 1b. Age-specific demographic variables contributing to survival of fully grown individuals in the mid-continent population of lesser snow geese; p corresponds to annual survival of adults (i.e., 2, 3, 4, and 5+) and age-class 1 individuals, and varied across locations (West or North relative to East or South). We named these estimates as follows: $pes2$, $pes3$, $pes4$, $pes5$, and $pes5+$ for the East and South colonies, and $pwn2$, $pwn3$, $pwn4$, $pwn5$, $pwn5+$ for the West and North colonies (see Figure 1).

	Age classes				
	1	2	3	4	5+
p_{wn}	0.871	0.871	0.871	0.871	0.871
p_{es}	0.831	0.831	0.831	0.831	0.831

the most plausible split in the distribution of mid-continent LSG abundance under a North-South (i.e., *N-S*) scenario would be that approximately 90% currently breed in the North, and 10% breed in the South. Under an East-West (i.e., *E-W*) scenario the most plausible split would be that approximately 70% breed in the East and 30% in the West (Kerbes et al. 2006;
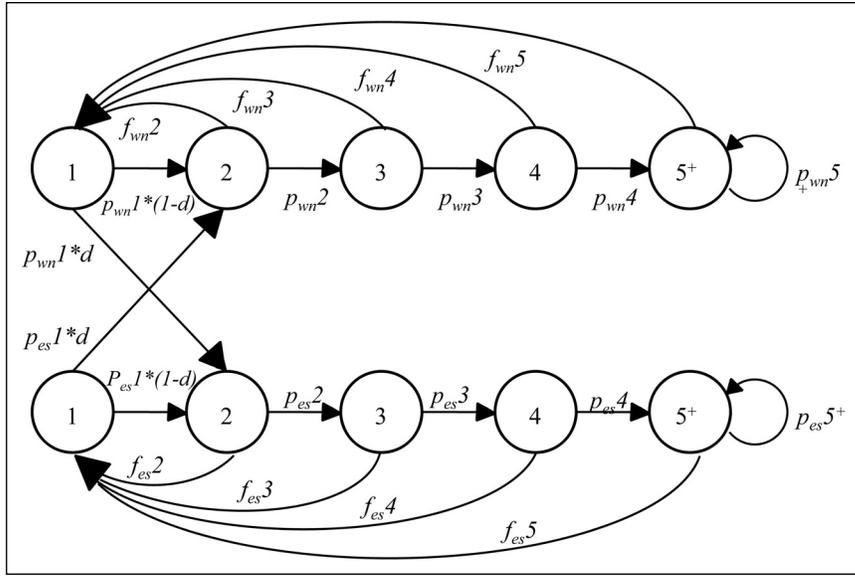
Figure 1. Metapopulation life cycle representation: *es* and *wn* = the different geographic segments; *f, p,* and *d* = fertility, survival, and dispersal respectively.

Kerbes unpublished report). We considered a range of percentage splits for both geographic scenarios to address uncertainty in the spatial structure of mid-continent LSG abundance associated with aerial surveys (Alisauskas et al. 2009). Of key importance, the majority of the metapopulation (residing in the north) experiences high survival in the *N-S* scenarios, whereas the majority of the metapopulation (residing in the east) experiences low survival in the *E-W* scenarios.

Dispersal. There is limited information on dispersal probabilities among nesting colonies in the mid-continent population of LSG. However, dispersal is likely low given the high fidelity LSG have to their breeding grounds (Cooch et al. 2001). We ,therefore, assessed the impact of various low to moderate dispersal scenarios on metapopulation dynamics (i.e., dispersal probabilities *d* of 0.05, 0.1, 0.2, and 0.3) and allowed only age-class 1 birds, which are the most likely to disperse (Cooch et al. 2001), to move between the geographic segments. Specifically, we assumed that most individuals disperse

between ages 1 and 2 years, whereby they experience the survival of their natal geographic location and disperse immediately before their second year of life, during the spring migration to the breeding grounds. Thereafter, dispersing individuals assume the demography of their new geographic location. For simplicity, we assumed the same probability of dispersal in either direction (i.e., North to South and South to North, or East to West and West to East, depending on the scenario of geographic splits).

Metapopulation projection model. We used a 10-stage, pre-breeding census matrix to model geographic structure as well as age-specificity in demographic vital rates and abundance (see Figure 1):

$$\mathbf{B} = \begin{bmatrix} 0 & f_{wn2} & f_{wn3} & f_{wn4} & f_{wn5} & 0 & 0 & 0 & 0 & 0 \\ p_{wn1}\times(1-d) & 0 & 0 & 0 & 0 & p_{es1}\times d & 0 & 0 & 0 & 0 \\ 0 & p_{wn2} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & p_{wn3} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & p_{wn4} & p_{wn5+} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & f_{es2} & f_{es3} & f_{es4} & f_{es5} \\ p_{wn1}\times d & 0 & 0 & 0 & 0 & p_{es1}\times(1-d) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & p_{es2} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & p_{es3} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p_{es4} & p_{es5+} \end{bmatrix} \quad (3)$$

The upper-left portion of the matrix represents the North or West location and the

lower right the South or East location; *d*, *f*, and *p* denote dispersal, fertility, and survival, respectively; *wn* denotes a parameter specific to either the West or North locations; and *es* is specific to East or South locations, depending on the scenario considered.

Long-term dynamics: symptotic analysis

Asymptotic analysis of matrix population models provides valuable information, the most informative quantity being λ, which represents the long-term geometric rate at which a population will grow or shrink once its stage distribution has reached stability (i.e., the Stable Stage Distribution [SSD], which, in our study, is defined by geographic locations and age classes; Caswell 2001).

We calculated elasticities for lower-level parameters (θ_v), such as dispersal, age-specific clutch size, etc., that affect matrix entries (a_{ij}) according to the following:

$$e_v = \frac{\theta_v}{\lambda} \frac{\partial \lambda}{\partial \theta_v} = \frac{\theta_v}{\lambda} \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial \theta_v} \qquad (4)$$

A complete elasticity analysis can help identify the demographic parameter(s) that has (have) the potential to affect the growth rate the most, if changed. Elasticity analysis often is used to inform conservation and management decisions (Doak et al. 1994, Rockwell et al. 1997). We provide the classically used asymptotic elasticities as a point of comparison to elasticities that may be more relevant to management in the near future (see short-term dynamics section, below). Elasticities do not, however, indicate how easily a vital rate can be changed or how costly it is to change 1 vital rate relative to another. Exploratory computations of the costs and applicability of alternative ways to control LSG numbers exist (Johnson and Ankney 2003), and when empirical data becomes available, it should be incorporated into a perturbation analysis used to guide management (see Nichols and Hines 2002, Baxter et al. 2006).

Short-term dynamics: transient dynamics and population momentum

A major limiting assumption of asymptotic perturbation analysis is that of an SSD. In reality, catastrophes, natural disturbances, selective harvest regimes, and animal release and relocation programs significantly alter a population's structure, causing it to be unstable much of the time. For example, given that juveniles are more vulnerable to harvest than are adults (Francis et al. 1992), the introduction of spring hunts and increased bag limits may have perturbed the age structure of mid-continent LSG in certain locales. Following any perturbation to population structure, the relative abundance in each stage will approach stability in a damped cyclic fashion; this causes the population growth rate also to change in a transient fashion (see Caswell 2001, Koons et al. 2005). Because management objectives are often focused on the near future, the short-term transient dynamics following perturbations to population structure may be more relevant than long-term asymptotic dynamics (Koons et al. 2006, Caswell 2007). We focus on transient population growth rates 5 years ($\lambda_{t5} = (N_5 / N_0)^{1/5}$) following an initially unstable population structure (i.e., $\mathbf{n}_0$ denotes the initial total population abundance).

Short-term transient dynamics can have long-term inertial effects on population abundance, a process also known as population momentum. Koons et al. (2006) explain the relevance of momentum in a management setting. We calculated momentum as:

$$M = \frac{N_{a,\mathbf{n}_0}}{N_{a,\text{SSD}}} \qquad (5)$$

where N_a denotes the asymptotic total abundance for a population with an initially unstable stage distribution ($\mathbf{n}_0$) relative to one with an initially SSD. It is important to note that large magnitudes of population momentum (i.e., values differing greatly from 1) signify populations whose long-term abundance is greatly affected by historically unstable stage distributions, not ones that are resistant to such effects.

To examine how transient growth rates and population momentum respond to changes in underlying vital rates, we measured their elasticities to changes in the lower-level vital rates (θ_v ; Tables 1a, b.). For the sake of

conciseness, we refer the reader to Caswell (2007) and Koons et al. (2007) for details on the calculation of transient growth rate and momentum elasticities, respectively. To simplify elasticity results for making inference, we summed up elasticities corresponding to important components of reproductive output across age classes, such as the e_{f1} egg laying (i.e., *BP+TCL*), e_{f2} egg hatching (i.e., *NS+P1+P2*), and e_{f3} gosling fledging (i.e., *BS+P3*) components. We also presented an elasticity for total reproductive output "e_f" (i.e., $e_f = e_{f1} + e_{f2} + e_{f3}$), and total survival elasticity "e_p" (i.e., $e_{s0} + e_{p1} + e_{p2-5+}$).

We used the following equation to provide managers with information of how much a vital rate would need to be changed in order to achieve a metapopulation growth rate of 0.95 over the next 5 years:

$$\Delta vital\ rate \approx \frac{\Delta growth\ rate}{elasticity} \qquad (6)$$

where Δ represents proportional change (Heppell 1998).

Results

We focus on results for scenarios with a 90:10% abundance split between North and South regions as well as 70:30% split between East and West regions. Results pertaining to other scenarios can be found in Appendices A, B, and C. We present asymptotic and short-term metapopulation growth rates under various location-specific, abundance splits, and dispersal levels in Appendix A. Although we focus on transient results over 5 years, results for the similar 10-year transient dynamics can be found in Appendix B. In Appendix C, we present long-term and short-term elasticities of population growth rate to changes in overall survival and total reproductive output across abundance and geographic split scenarios that were not presented in the manuscript.

Long-term dynamics

Because of higher adult survival, the North and West segments had higher local asymptotic population growth rates (i. e., 1.0423) than the South and East segments (i.e., 1.0004) in the absence of dispersal. When combined in a metapopulation context, the North and West segments thus serve as 'strong source populations' whereas the South and East segments serve as 'weak sources' (in the respective *N-S* and *E-W* metapopulation scenarios).

Increasing probabilities of dispersal gradually brought asymptotic metapopulation growth rate away from that of the strong source and toward that of the weak source (Table 2a.) because of more individuals being moved toward locations with lower survival rates (i.e., net larger movement toward either South or East segments, depending on the geographic scenario considered). The different splits of abundance across geographic locations had no impact on the metapopulation's long-term dynamics because of the ergodic properties of λ (i.e., independence of initial conditions; Caswell 2001).

When dispersal was low (d = 0.05), the majority of individuals in the SSD belonged to the North or West segments in age class 5+ (42.74%), and the remaining population was divided among the younger age classes. The proportionate abundance in the South or East segments was much smaller (<6%; Table 3). This was an expected pattern because survival was much lower (i.e., 0.831) in the South and East segments (Table 1b), and, thus, received a greater net number of dispersants relative to the North and West segments, where P = 0.871. Although the SSD remained concentrated in the oldest age class in the North or West segments as we increased dispersal, the proportion of the population residing in the South or East segments steadily increased (Table 3).

Elasticities of λ to changes in dispersal e_d were small relative to those for other vital rates (Figure B1, Appendix B). Nevertheless, the relationship between the elasticity of λ to infinitesimal changes in dispersal relative to the dispersal scenarios was not always monotonic, as elasticities peaked at d = 0.1 under the *E-W* scenario with a 70:30% abundance split (Figure B1, Appendix B), but monotonically decreased under the *N-S* scenario with a 90:10% abundance split (Appendix A).

Elasticities of λ to changes in total reproductive output (i.e., e_f) and survival (i.e., e_p) for the North and South segments were qualitatively similar to those of West and East segments, respectively (asymptotic elasticities presented in Figure 2a).

Table 2a. Asymptotic and short-term measures of metapopulation growth under various geographic splits *N-S* or *E-W*, location-specific abundance splits (i.e., 70:30% for the *E-W* split and 90:10% for the *N-S* split*)*, and dispersal levels (i.e., *d* = 0.05, 0.1, 0.2, or 0.3*)*.

	$\lambda_{asymptotic}$	λ_{t_5}		M	
		N-S (90:10)	E-W (70:30)	N-S (90:10)	E-W (70:30)
d = 0.05	1.0366	1.0303	1.0107	1.0349	0.4614
d = 0.1	1.0326	1.0301	1.0108	1.1111	0.6054
d = 0.2	1.0281	1.0296	1.0111	1.1433	0.7842

Table 2b. Proportional change in vital rates (i.e., total reproductive output or survival) needed to achieve a metapopulation growth rate of 0.95 over the next 5 years for various location-specific (i.e., North–South and East–West), abundance-specific (i.e., 90:10% and 70:30% respectively) and dispersal scenarios (*d* = 0.05 or 0.3).

Location and abundance splits	Dispersal scenarios	Proportional change in λ_{t_5}	Proportional change in reproductive output	Proportional change in survival
North 90:10 split	*d* = 0.05	0.0779	0.0901	0.0461
	d = 0.3	0.0769	0.0937	0.0480
South 90:10 split	*d* = 0.05	0.0779	0.8744	0.4531
	d = 0.3	0.0769	0.5850	0.2941
East 70:30 split	*d* = 0.05	0.0601	0.1808	0.0922
	d = 0.3	0.0607	0.1745	0.0878
West 70:30 split	*d* = 0.05	0.0601	0.0945	0.0496
	d = 0.3	0.0607	0.0977	0.0519

Table 3. Stable Stage Distributions (SSD) for various geographic locations, which happen to be equivalent between *N-S* (90:10% location-specific abundance split) and *E-W* split scenarios (70:30% abundance split) because of the independence of SSD on initial conditions. Thus, SSDs in the North and West (*N-W*) locations are equivalent, as are the SSDs in the South and East (*S-E*) locations. SSDs do, however, change with dispersal levels (*d* = 0.05, 0.1, 0.2, or 0.3). The distributions are presented in percentages (%).

	Age 1		Age 2		Age 3		Age 4		(St)age 5+		Sum	
	N-W	S-E	N-W	S-E	N-W	*S-E*	*N-W*	*S-E*	N-W	S-E	N-W	*S-E*
d = 0.05	14.3	2.19	11.51	2.27	9.67	1.82	8.12	1.46	42.74	5.9	86.34	13.64
d = 0.1	12.8	3.75	10.02	3.79	8.45	3.05	7.13	2.46	38.42	10.13	76.82	23.18
d = 0.2	11.08	5.52	8.4	5.45	7.12	4.4	6.03	3.56	33.44	15.01	66.07	33.94
d = 0.3	10.23	6.4	7.63	6.23	6.48	5.05	5.5	4.09	30.94	17.44	60.78	39.21

As expected, e_p and e_f were always far superior in the strong-source geographic locations (North or West), relative to the weak-source locations (South or East; Figure 2a.). Under the *N-S* split scenarios, the largest elasticity corresponded to the elasticity of λ to changes in adult survival in the northern colonies (Figure 2a). The elasticity values for northern vital rates decreased slightly as dispersal increased, but they increased for southern vital rates because of the net movement toward the south (given our assumption of equal probabilities of dispersal in both directions; Figure 2a.). We observed similar findings for the *E-W* split scenario, whereby the highest elasticity was again found to be adult survival in the West. But as dispersal
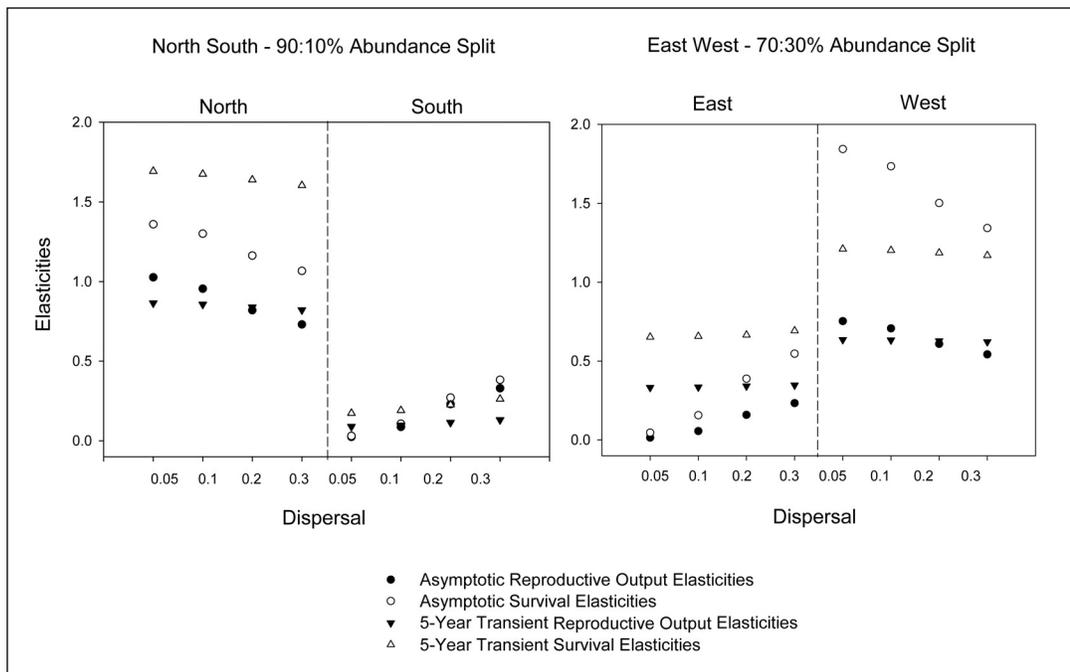
Figure 2a. Asymptotic and 5-year transient elasticities of λ to changes in total reproductive output (e_f) and survival (e_p) across dispersal regimes (i.e., 0.05, 0.1, 0.2, and 0.3) for East–West (70:30% abundance split) and North–South (90:10% abundance split) geographic split scenarios.

Figure 2b. Elasticity of momentum to changes in total reproductive output and survival across dispersal regimes (i.e., 0.05, 0.1, 0.2, and 0.3) for East–West (70:30% abundance split) and North–South (90:10% abundance split) geographic split scenarios.
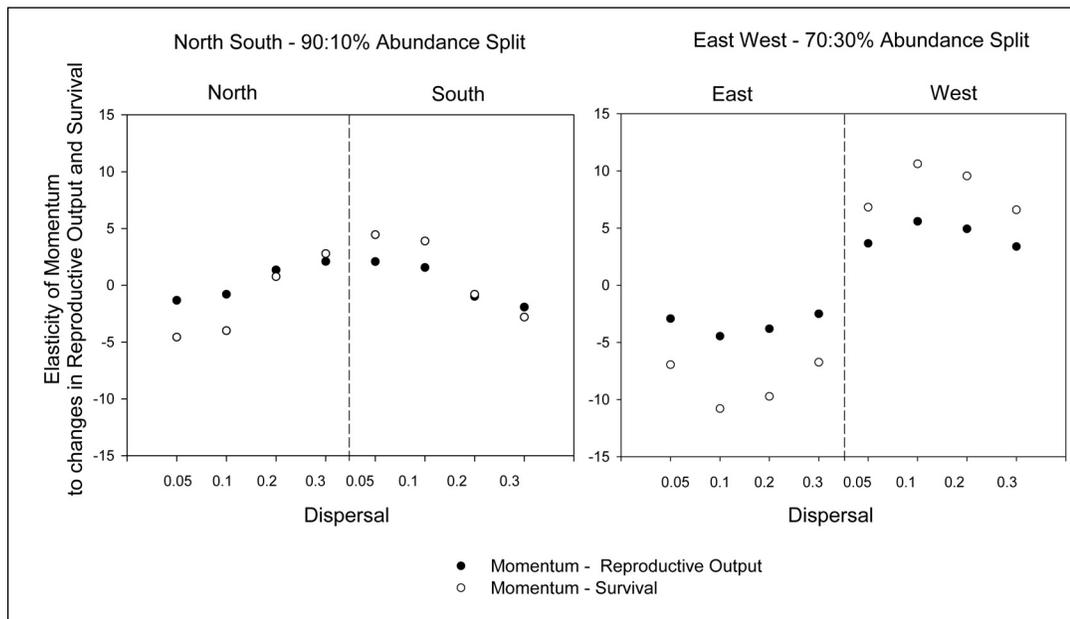
increased, survival and reproduction elasticity values decreased in the western colonies and increased slightly in the eastern colonies (Figure 2a).

Short-term dynamics

Consistent with the transient nature of population dynamics following an unstable
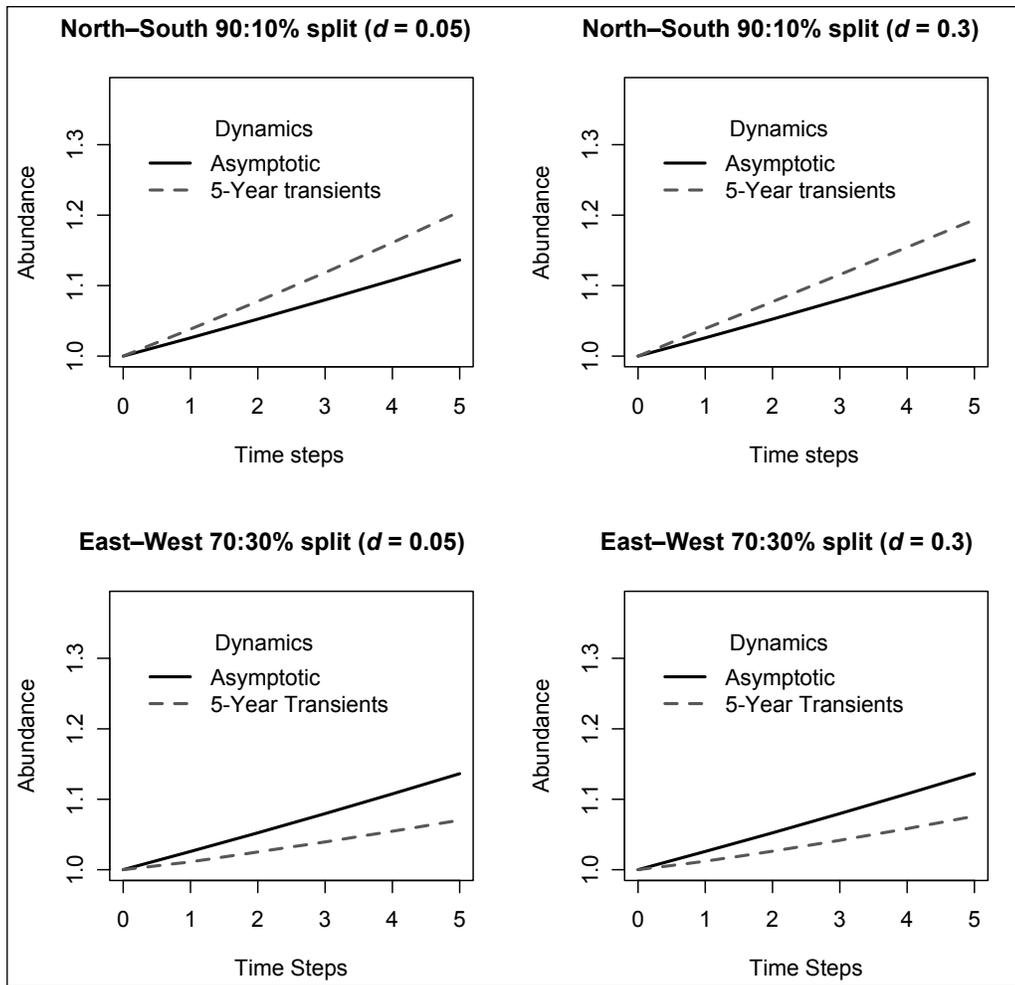
Figure 3. Illustration of differences in abundance between asymptotic and transient dynamics for North–South under a 90:10% population abundance split (top) and East–West locations under a 70:30% abundance split (bottom) locations, under either low (*d* = 0.05, left-hand side) or high dispersal regimes (*d* = 0.3, right-hand side) .

population structure, the pattern of transient growth rates (λ_{t_5}) and population momentum (*M*) across the geographic split scenarios and various dispersal levels was variable and often very different than projected asymptotic dynamics (Table 2a). This is perhaps because each population structure defined by unique geographic splits (90:10% split between *N-S* and 70:30% split between *E-W*) differs from the respective SSD for a given dispersal regime in unique ways (Table 3). This may cause transient trajectories of abundance to be higher or lower than the asymptotic trajectories (Figure 3), thus, causing unique differences in transient population growth rates and momentum.

Under the *N-S* scenario, elasticities of transient population growth rates to changes in viral rates were generally different than asymptotic elasticities across dispersal regimes. For example, transient reproductive output elasticities were inferior to asymptotic reproductive output elasticities in most cases (i.e., *d* < 0.3), but transient survival elasticities, on the other hand, were superior to asymptotic survival elasticities, thus, making the gap between survival and reproductive output elasticities even larger (Figure 2a). The results were similar for the 70:30% and the 80:20% abundance split scenarios (Figures B1 and B2, Appendix B).

Momentum elasticity patterns across dispersal levels in the North were almost a mirror image of those in the South. Elasticity values were negative at low levels of dispersal

for the North and at high levels of dispersal for the South, and vice versa (Figure 2b), whereby, a negative elasticity implies that an increase in the vital rate will decrease the numerical value of population momentum. Moreover, the directional pattern in the elasticity of momentum to changes in survival and reproductive output increased across dispersal levels for the North but decreased in the South (Figure 2b); the qualitative nature of this pattern did not change across other splits in abundance (i.e., 70:30% and 80:20%; Figures C1 and C2, Appendix C). At high-dispersal levels ($d > 0.1$), elasticities of population momentum to changes in reproductive output were sometimes similar and even superior to elasticities of population momentum to changes in survival (Figure 2b).

Under the *E-W* scenario, the qualitative patterns of transient elasticities were similar to results for the *N-S* split scenarios, whereby elasticity results for the West and East segments were roughly similar to those from the North and South segments, respectively. However, the numerical gap between transient survival and reproductive output elasticities in the West was smaller than the asymptotic difference (Figure 2a). Moreover, there were several differences in the population momentum elasticities between *N-S* and *E-W* scenarios. First, elasticities of momentum to changes in dispersal were always positive in the *E-W* scenarios (Figure B1), but were sometimes negative in the *N-S* scenarios at high levels of dispersal (i.e., $d = 0.3$; Table B1, Appendix B). Second, absolute values of momentum elasticities were larger under the *E-W* scenario compared to the *N-S* scenario. Third, elasticities of population momentum to changes in both reproductive output and survival exhibited opposite signs, depending on the location considered; elasticities were always negative across dispersal regimes in the East, but were always positive in the West (Figure 2b). Lastly, there was a nonmonotonic relationship between momentum elasticities and dispersal regimes under the *E-W* scenarios (maximum absolute values reached at $d = 0.1$), whereas the relationships were monotonic under the *N-S* scenarios.

Further, we calculated the proportional change in total reproductive output or survival that would be needed in order to achieve a metapopulation growth rate of 0.95 in the next

5 years (Table 2b). We found that independent of the location- and abundance-split scenarios, a lesser proportionate change in survival would be needed to reach this goal relative to changing overall reproductive output. The most demographically efficient strategies to achieve this goal would be to reduce survival in either the North or West locations (Table 2b). Demographically, attempts to reduce reproductive output in the South would by far be the least efficient approach (Table 2b).

Discussion

The rapid increase in abundance of LSG populations and their devastating effects on arctic and subarctic habitats have inspired seminal papers on the population dynamics of LSG and their use in defining appropriate management policies (Ankney 1996; Rockwell et al. 1997; Cooch et al. 2001; Alisauskas et al., in press). Ankney (1996) motivated managers to think about the potential consequences of short-term actions on long-term management. In this regard, short-term population dynamics and perturbation analyses are very useful tools for better understanding how management actions can affect short-term and long-term dynamics. It is thus crucial to make proper use of such tools to help management reach LSG population targets.

Given that geographic differences in LSG survival exist (Alisauskas et al., in press), our metapopulation model of mid-continental LSG provides a basis for gaining initial insight into the dependence of population dynamics on geographic structure and dispersal between geographic locations. The metapopulation approach provided results that were consistent with those attained from single LSG population analyses (Rockwell et al. 1997, Cooch et al. 2001, Koons et al. 2005, 2007). The metapopulation approach also provided novel insight into LSG dynamics that may be informative for management. For example, because LSG populations appear to be growing everywhere, asymptotic metapopulation growth rates were in between local growth rates of the strong-source and weak-source locations, but did not depend on the specific geographical splits in model structure (*N-S* versus *E-W*). Short-term growth rates, however, were sensitive to the structural split in abundance between

geographic locations and the degree of dispersal between locations (Table 2a). Thus, if managers would like to achieve a target growth rate (e.g., 0.95) for the overall mid-continent LSG population in the near future, determination of spatial structure in abundance, demographic vital rates, and dispersal among colonies may require more attention.

Mills and Lindberg (2002) suggested that use of a metapopulation model could change the conclusion that adult survival has the largest functional effect on population growth rate (Rockwell et al. 1997), but we did not find this to be true. In both the North-South and East-West split scenarios, the largest elasticity of λ corresponded to changes in survival at the strong-source locations (North or West). The elasticity of transient growth rates were always much larger to changes in survival, relative to changes in reproductive output or dispersal, as well. However, survival and reproductive output elasticity values were closer in the weak-source locations (Figure 2a). Following from these results, reproductive output would have to be changed (proportionately) by at least twice as much as survival in order to achieve the same target growth rate of 0.95 for the overall mid-continent LSG population in the next 5 years (Table 2b). This conclusion is conditional on our modeling assumptions.

Managers focused on reducing the growth rate of mid-continent LSG may, thus, want to continue focusing on reducing survival, but should try to determine where, geographically, such changes would have the largest overall impact. Given that liberalized harvest regulations have not yet had the desired impact on LSG survival, the social issues and monetary cost of alternative management actions directed at survival may need to be reconsidered (Johnson and Ankney 2003).

The geographic split in the structure and demography of mid-continent LSG could have massive effects on long-term abundance via population momentum (Table 2a, Figure 3), depending on the degree to which the structures differ from projected SSDs (Table 3). Management actions that cause change in vital rates could perturb population structure even further and alter the force of momentum on long-term abundance. Assessment of the elasticities of population momentum to changes

in vital rates may thus be just as important for guiding management as perturbation analyses of population growth rates (Koons et al. 2007).

We found that metapopulation momentum was always <1, thus, decreasing abundance relative to asymptotic projections when the proportionate abundance in the strong-source locations was less than that in the SSD for given geographic and dispersal scenarios (Tables 2a and 3). The contrary was true when the proportionate abundance in the strong-source locations was greater than that in the SSD (Figure 3).

Moreover, we found that location-specific elasticities of momentum to changes in survival often were larger relative to changes in reproduction or dispersal. Elasticities of momentum to changes in survival often were negative for the abundance-rich locations (North or East) and positive for the abundance-poor locations (South or West). There were, however, a few exceptions to this pattern. At high-dispersal levels ($d > 0.1$), momentum elasticities to changes in survival were positive in the North and negative in the South, whatever the proportionate abundance split scenario considered (Figures 3a, b, c). For those scenario-combinations, M was always >1, and SSDs were always below the proportionate abundances (i.e., 90%) in the North and above the proportionate abundances (i.e., 10%) in the South. Thus, at high-dispersal levels under a North–South split, momentum could generate increased abundance. Moreover, at high-dispersal levels ($d > 0.1$), elasticities of momentum to changes in reproductive output were as large as those to changes in survival. Hence, geographic variation could be very important, and depending on the scenario, managers should focus their efforts on changing both survival and reproduction in efforts to alter population momentum in ways that will reduce mid-continent LSG abundance (Koons et al. 2006).

Dispersal elasticities were small (Table B1, Appendix B), indicating that it makes a small direct functional contribution to asymptotic and transient dynamics and to population momentum. However, the level of dispersal had important indirect effects on the elasticity of population dynamics to changes in other vital rates (Figure 2a). The secondary effects of

dispersal illuminated through the functional contribution of survival to population dynamics may be quite strong, especially in eastern and western locations. Overall, our findings suggest that research on where the important differences in demographic performance and abundance actually occur in the real world (*N-S*, *E-W*, or perhaps more fine-scaled geographic structure) is direly needed for directing appropriate management actions.

Conclusions and perspectives

In general, management actions that can change adult LSG survival in the future will still have a larger impact on the mid-continent LSG population than equivalent actions targeted at egg laying, nesting, gosling life-cycle stages, or actions that attempt to simultaneously reduce all reproductive components. However, reproductive output could have the potential to significantly influence population momentum and abundance of mid-continent LSG, depending on how the metapopulation is structured.

Liberalization of harvest regulations has not affected survival probabilities at the north-central Queen Maud Gulf colonies, and reductions in survival at La Pérouse Bay seem to have reached a threshold (Alisauskas et al. in press). Diminishing numbers (Pergams and Zaradic 2008), and interest of waterfowl hunters may limit their ability to effectively control LSG survival and abundance. If so, the alternative methods for reducing survival laid out by Johnson and Ankney (2003) may now need to be reconsidered.

On the other hand, Canadian provinces have not liberalized their spring harvest regulations to the degree of that in some states. Many non-First Nation residents in northern communities depend on geese as a subsistence food resource, and season restrictions often curtail their potential harvest of LSG resources during their northward migration. Increased liberalization of spring season lengths in Canada, combined with social programs directed at bringing back subsistence cultures such as egging (particularly for LSG) among First Nation youths, could be a potent strategy for reducing mid-continent LSG numbers more effectively.

Strategically focusing on specific geographic segments of the mid-continent population could be more efficient than blanket application of management to the continental population as a whole. Where to focus management to achieve objectives in the most efficient manner will require more detailed research on the spatial structure (*N-S*, *E-W*, and on a smaller spatial scale, underlying key demographic vital rates (i.e., adult survival and dispersal), as well as empirical tests of the cost-effectiveness, logistical feasibility, and the social and legal acceptance of alternative management actions (Johnson and Ankney 2003).

Acknowledgments

Literature cited

Abraham, K. F., R.L. Jefferies, and R. T. Alisauskas. 2005. The dynamics of landscape change and snow geese in midcontinent North America. Global Change Biology 11:841–855.

Alisauskas, R. T, K. L. Drake, and J. D. Nichols. 2009. Filling a void: abundance estimation of North American populations of Arctic geese using hunter recoveries. Environmental and Ecological Statistics 3:463–489.

Ankney, C. D. 1996. An embarrassment of riches: too many geese. Journal of Wildlife Management 60:217–223.

Baxter, P. W. J., M. A. McCarthy, H. P. Possingham, P. W. Menkhorst, and N. McLean. 2006. Accounting for management costs in sensitivity analyses of matrix population models. *Conservation Biology* 20:893–905.

Caswell, H. 2001. Matrix population models. Second edition. Sinauer, Sunderland, United Kingdom.

Caswell, H. 2007. Sensitivity analysis of transient population dynamics. Ecology Letters 10:1–15.

Conover, M. R. 2002. Resolving human–wildlife conflicts: the science of wildlife damage management. CRC Press, Boca Raton, Florida, USA.

Cooke, F., C. M. Francis, E. G. Cooch, and R. T. Alisauskas. 2000. Impact of hunting on population growth of mid-continent lesser snow geese. Pages 17–31 *in* H. Boyd, editor. Population monitoring and management of snow geese. Canadian Wildlife Service, Occasional Paper 102. Ottawa, Ontario, Canada.

Cooch, E. G., R. F. Rockwell, and S. Brault. 2001. Retrospective analysis of demographic responses to environmental change: a lesser snow goose example. Ecological Monographs 71:377–400.

Cooch, E. G., G. Gauthier, and R. F. Rockwell. 2003. Apparent differences in stochastic growth rates based on timing of census: a cautionary note. Ecological Modeling 159:133–143.

Doak, D., P., Kareiva, and B. Klepetka. 1994. Modeling population viability for the desert tortoise in the Western Mojave Desert. Ecological applications 4:446–460.

Dufour, K., R. Alisauskas, R. Rockwell, and E. Reed. In press. Temporal variation in survival and productivity of mid-continent lesser snow geese and its relation to population reduction efforts. *In* B. Batt, editor. Arctic ecosystems in peril: report of the Arctic goose habitat working group. Arctic Goose Joint Venture, Canadian Wildlife Service, Ottawa, Ontario, Canada, and U.S. Fish and Wildlife Service, Washington, D.C., USA.

Forester, D. J., and J. E. Machlis. 1996. Modeling human factors that affect the loss of biodiversity. Conservation Biology 10:1253–1263.

Francis, C. M., M. H. Richards, F. Cooke, and R. F. Rockwell. 1992. Changes in survival rates of lesser snow geese with age and breeding status. Auk 109:731–747.

Heppell, S. S. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 1998:367–375.

Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Canadian Entomologist 91:293–320.

Jefferies, R. L., A. P. Jano, and K. F. Abraham. 2006. A biotic agent promotes large scale catastrophic change in the coastal marshes of Hudson Bay. Journal of Ecology 94:234–242.

Jefferies, R. L., R. F. Rockwell, and K. F. Abraham. 2003. The embarrassment of riches: agricultural food subsidies, high goose numbers, and loss of Arctic wetlands—a continuing saga. Environmental Reviews 11:193–232.

Johnson, M. A. 1997. Management strategies to address the mid-continent lesser snow goose overpopulation problem. Pages 101–111 *in* B. Batt, editor. Arctic ecosystems in peril: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture, Canadian Wildlife Service, Ottawa, Ontario, Canada, and U.S. Fish and Wildlife Service, Washington, D.C., USA.

Johnson, M. A., and C. D. Ankney, editors. 2003. Direct control and alternative harvest strategies for North American light geese, report of the Direct Control and Alternative Harvest Measures Working Group. Arctic Goose Joint Venture, Canadian Wildlife Service, Ottawa, Ontario, Canada, and U.S. Fish and Wildlife Service, Washington, D.C., USA.

Kerbes, R. H., K. M. Meeres, R. T. Alisauskas, F. D. Caswell, K. F. Abraham and R. K. Ross. 2006. Surveys of nesting mid-continent Lesser Snow Geese and Ross's Geese in eastern and central arctic Canada 1997-1998. Technical Report Series 447, Canadian Wildlife Service, Prairie and Northern Region, Saskatoon, Saskatchewan, Canada.

Koons, D. N., J. B. Grand, B. Zinner and R. F. Rockwell. 2005. Transient population dynamics: relations to life history and initial population state. Ecological Modeling 185:283–297.

Koons, D. N., R. R. Holmes, and J. B. Grand. 2007. Population inertia and its sensitivity to changes in vital rates and population structure. Ecology 88:2857–2867.

Koons, D. N., R. F. Rockwell, and J. B. Grand. 2006. Population momentum: implications for wildlife management. Journal of Wildlife Management 70:19–26.

Link, W. A., and P. F. Doherty. 2002. Scaling in sensitivity analysis. Ecology 83:3299–3305.

McKinney, M. L. 2002. Urbanization, biodiversity, and conservation. Bioscience 52:883–890.

Mills, L. S., and M. S. Lindberg. 2002. Sensitivity analysis to evaluate the consequences of conservation actions. Pages 338–366 *in* S. R. Beissinger and D. R. McCullough, editors. Population viability analysis. University of Chicago Press, Chicago, Illinois, USA.

Nichols, J. D, and J. E. Hines. 2002. Approaches

for the direct estimation of λ, and demographic contributions to λ, using capture-recapture data. Journal of Applied Statistics 29:539–568.

Pergams, O. R. W, and P. A. Zaradic. 2008. Evidence for a fundamental and pervasive shift away from nature-based recreation. Proceedings of the National Academy of Science USA 105:2295–2300.

Robertson, D. G., and R. D. Slack. 1995. Landscape change and its effects on the wintering range of a lesser snow goose (*Chen caerulescens caerulescens)* population: a review. Biological Conservation 71:179–185.

Rockwell, R. F., E. G. Cooch, and S. Brault. 1997. Dynamics of the mid-continent population of lesser snow geese: projected impacts of reductions in survival and fertility on population growth rates. Pages 73–100 *in* B. Batt, editor. Arctic ecosystems in peril: report of the Arctic

goose habitat working group. Arctic Goose Joint Venture, Canadian Wildlife Service, Ottawa, Ontario, Canada, and U.S. Fish and Wildlife Service, Washington, D.C, USA.

Rockwell, R. F., and C. D. Ankney. 2000. Snow geese: can we pay down the mortgage? Pages 32–34 *in* H. Boyd, editor. Population monitoring and management of snow geese. Canadian Wildlife Service Occasional Paper 102. Ottawa, Ontario, Canada.

Rockwell, R. F., K., Dufour, E. Reed, and D. Koons. In press. Modeling the mid-continent population of lesser snow geese. In B. Batt, editor. Arctic ecosystems in peril: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture, Canadian Wildlife Service, Ottawa, Ontario, Canada, and U.S. Fish and Wildlife Service, Washington, D.C, USA.

Appendix A

We considered scenarios where 90, 80, or 70% of the current mid-continent population bred in northern colonies with respective complements (10, 20, or 30 %) breeding in southern colonies (i.e., *N-S*). In addition, we considered scenarios where 90, 80, or 70% of the current mid-continent population bred in eastern colonies with respective complements breeding in western colonies (i.e., *E-W*). We examined the effects of various dispersal regimes on the long-term and short-term metapopulation dynamics of LSG (i.e., *d* = 0.05, 0.1, 0.2, or 0.3) as a function of these geographic splits. We present here the asymptotic and short-term measures of metapopulation growth under various location-specific abundance splits, geographic splits *N-S* or *E-W*, and dispersal levels.

Geographic splits in abundance (%)		λ	λ_{t_5}		$\lambda_{t_{10}}$		M	
			N-S	E-W	N-S	E-W	N-S	E-W
70:30	d = 0.05	1.0366	1.0239	1.0107	1.0307	1.0150	0.8438	0.4614
	d = 0.1	1.0326	1.0238	1.0108	1.0302	1.0154	0.9425	0.6054
	d = 0.2	1.0281	1.0236	1.0111	1.0293	1.0161	1.0236	0.7842
	d = 0.3	1.0259	1.0234	1.0114	1.0285	1.0168	1.0397	0.8673
80:20	d = 0.05		1.0271	1.0073	1.4014	1.0195	0.9393	0.3485
	d = 0.1		1.0269	1.0075	1.0343	1.0203	1.0268	0.5058
	d = 0.2		1.0266	1.0079	1.0337	1.0216	1.0834	0.7134
	d = 0.3		1.0263	1.0083	1.0324	1.0229	1.0828	0.8164
90:10	d = 0.05		1.0303	1.0038	1.0378	1.0062	1.0349	0.2703
	d = 0.1		1.0301	1.0041	1.0370	1.0072	1.1111	0.4369
	d = 0.2		1.0296	1.0046	1.0353	1.0089	1.1433	0.6645
	d = 0.3		1.0291	1.0052	1.0338	1.0105	1.1259	0.7811

Appendix B

Table B1. λ, λ_{t_5}, $\lambda_{t_{10}}$ and *M* elasticities to changes in dispersal for North-South and East-West geographic scenarios with 70:30%, 80:20%, and 90:10% abundance splits across various dispersal levels (*d* = 0.05, 0.1, 0.2, and 0.3).

Table B2a. λ, λ_{t_5}, $\lambda_{t_{10}}$ and *M* elasticities to changes in the F1, F2, and F3 reproductive components (as described in the Methods section of the text) and overall survival (P) for North-South locations across various dispersal levels for a 70:30% split in abundance between locations.

Table B2b. ____ for an 80:20% split in abundance between locations.

Table B2c. ____ for a 90:10% split in abundance between locations.

Table B3a. λ, λ_{t_5}, $\lambda_{t_{10}}$ and *M* elasticities to changes in the F1, F2, and F3 reproductive components (as described in the text) and overall survival (P) for East-West locations across various dispersal levels for a 70:30% split in abundance between locations.

Table B3b. ____ for an 80:20% split in abundance between locations.

Table B3c. ____ for a 90:10% split in abundance between locations.

Table B1.

			Dispersal		
		Asymptotics	5-year transients	10-year transients	Momentum
North-South	*d* = 0.05	-0.003	0.000	0.000	0.153
	d = 0.1	-0.003	0.000	0.000	0.244
	d = 0.2	-0.002	-0.001	-0.001	0.231
	d = 0.3	-0.001	-0.001	-0.001	0.168
East-West	*d* = 0.05	-0.003	0.000	0.000	0.119
	d = 0.1	-0.003	0.000	0.000	0.144
	d = 0.2	-0.002	0.001	0.001	0.068
	d = 0.3	-0.001	0.001	0.001	0.012
North-South	*d* = 0.05	-0.003	0.000	0.000	0.111
	d = 0.1	-0.003	-0.001	-0.001	0.119
	d = 0.2	-0.002	-0.001	-0.001	0.027
	d = 0.3	-0.001	-0.002	-0.002	-0.027
East-West	*d* = 0.05	-0.003	0.000	0.001	0.162
	d = 0.1	-0.003	0.001	0.001	0.269
	d = 0.2	-0.002	0.001	0.002	0.271
	d = 0.3	-0.001	0.002	0.003	0.207
North-South	*d* = 0.05	-0.003	0.000	0.000	0.102
	d = 0.1	-0.003	-0.001	-0.001	0.094
	d = 0.2	-0.002	-0.002	-0.002	-0.014
	d = 0.3	-0.001	-0.002	-0.002	-0.066
East-West	*d* = 0.05	-0.003	0.000	0.000	0.170
	d = 0.1	-0.003	0.001	0.001	0.294
	d = 0.2	-0.002	0.002	0.002	0.312
	d = 0.3	-0.001	0.002	0.002	0.246

Table B2a.

		Asymptotics					5-year transients					10-year transients					Momentum				
		F1	F2	F3	F4	P	F1	F2	F3	F4	P	F1	F2	F3	F4	P	F1	F2	F3	F4	P
North	$d = 0.05$	0.22	0.32	0.49	0.49	0.87	0.20	0.30	0.20	0.74	0.64	0.20	0.30	0.20	0.77	0.67	-0.53	-0.80	-0.53	-2.81	-2.55
	$d = 0.1$	0.20	0.30	0.45	0.48	0.82	0.20	0.30	0.20	0.73	0.63	0.20	0.30	0.20	0.75	0.65	-0.58	-0.87	-0.58	-3.28	-2.99
	$d = 0.2$	0.17	0.26	0.38	0.46	0.71	0.20	0.29	0.20	0.72	0.62	0.19	0.29	0.19	0.73	0.63	-0.11	-0.16	-0.11	-1.40	-1.34
	$d = 0.3$	0.15	0.23	0.34	0.43	0.63	0.19	0.29	0.19	0.71	0.61	0.18	0.27	0.18	0.71	0.61	0.16	0.24	0.16	-0.15	-0.23
South	$d = 0.05$	0.00	0.01	0.01	0.01	0.02	0.07	0.11	0.07	0.26	0.23	0.18	0.27	0.18	0.71	0.20	0.74	1.12	0.74	2.81	2.44
	$d = 0.1$	0.02	0.02	0.05	0.03	0.07	0.07	0.11	0.07	0.27	0.23	0.07	0.10	0.07	0.25	0.21	0.83	1.24	0.83	3.28	2.86
	$d = 0.2$	0.05	0.07	0.12	0.09	0.18	0.08	0.12	0.08	0.28	0.24	0.08	0.11	0.07	0.27	0.23	0.28	0.42	0.28	1.40	1.26
	$d = 0.3$	0.07	0.10	0.16	0.13	0.26	0.08	0.12	0.08	0.29	0.25	0.08	0.12	0.08	0.29	0.25	-0.04	-0.07	-0.04	0.15	0.18

Table B2b.

		Asymptotics					5-year transients					10-year transients					Momentum				
		F1	F2	F3	F4	P	F1	F2	F3	F4	P	F1	F2	F3	F4	P	F1	F2	F3	F4	P
North	$d = 0.05$	0.22	0.32	0.49	0.49	0.87	0.22	0.34	0.22	0.82	0.71	0.22	0.33	0.22	0.84	0.73	-0.46	-0.68	-0.46	-2.59	-2.37
	$d = 0.1$	0.20	0.30	0.45	0.48	0.82	0.22	0.33	0.22	0.82	0.70	0.22	0.32	0.22	0.83	0.72	-0.40	-0.60	-0.40	-2.67	-2.47
	$d = 0.2$	0.17	0.26	0.38	0.46	0.71	0.22	0.33	0.22	0.80	0.69	0.21	0.31	0.21	0.79	0.69	0.14	0.21	0.14	-0.46	-0.53
	$d = 0.3$	0.15	0.23	0.34	0.43	0.63	0.21	0.32	0.21	0.79	0.68	0.20	0.30	0.20	0.77	0.67	0.38	0.57	0.38	0.69	0.51
South	$d = 0.05$	0.00	0.01	0.01	0.01	0.02	0.05	0.06	0.05	0.18	0.15	0.04	0.05	0.04	0.16	0.14	0.67	0.79	0.67	2.59	2.26
	$d = 0.1$	0.02	0.02	0.05	0.03	0.07	0.05	0.06	0.05	0.18	0.16	0.05	0.06	0.05	0.17	0.15	0.64	0.76	0.64	2.67	2.35
	$d = 0.2$	0.05	0.07	0.12	0.09	0.18	0.05	0.07	0.05	0.20	0.17	0.06	0.07	0.06	0.21	0.18	0.00	0.02	0.00	0.46	0.46
	$d = 0.3$	0.07	0.10	0.16	0.13	0.26	0.06	0.07	0.06	0.21	0.19	0.06	0.08	0.06	0.23	0.20	-0.30	-0.31	-0.30	-0.69	-0.55

Table B2c.

		Asymptotics					5-year transients					10-year transients					Momentum				
		F1	F2	F3	F4	P	F1	F2	F3	F4	P	F1	F2	F3	F4	P	F1	F2	F3	F4	P
North	$d=0.05$	0.22	0.32	0.49	0.49	0.87	0.25	0.37	0.25	0.91	0.78	0.24	0.36	0.24	0.91	0.79	-0.38	-0.57	-0.38	-2.38	-2.19
	$d=0.1$	0.20	0.30	0.45	0.48	0.82	0.24	0.37	0.24	0.90	0.78	0.23	0.35	0.23	0.89	0.78	-0.23	-0.34	-0.23	-2.06	-1.94
	$d=0.2$	0.17	0.26	0.38	0.46	0.71	0.24	0.36	0.24	0.88	0.76	0.22	0.34	0.22	0.86	0.74	0.38	0.57	0.38	0.47	0.28
	$d=0.3$	0.15	0.23	0.34	0.43	0.63	0.23	0.35	0.23	0.86	0.74	0.21	0.32	0.21	0.82	0.71	0.60	0.89	0.60	1.54	1.24
South	$d=0.05$	0.00	0.01	0.01	0.01	0.02	0.03	0.04	0.03	0.09	0.08	0.02	0.04	0.02	0.09	0.08	0.59	0.89	0.59	2.38	2.08
	$d=0.1$	0.02	0.02	0.05	0.03	0.07	0.03	0.04	0.03	0.10	0.09	0.03	0.04	0.03	0.11	0.09	0.44	0.67	0.44	2.06	1.84
	$d=0.2$	0.05	0.07	0.12	0.09	0.18	0.03	0.05	0.03	0.12	0.10	0.04	0.06	0.04	0.14	0.12	-0.28	-0.42	-0.28	-0.47	-0.33
	$d=0.3$	0.07	0.10	0.16	0.13	0.26	0.04	0.06	0.04	0.14	0.12	0.05	0.07	0.05	0.18	0.15	-0.55	-0.83	-0.55	-1.54	-1.27

Table B3a.

		Asymptotics					5-year transients					10-year transients					Momentum				
		F1	F2	F3	F4	P	F1	F2	F3	F4	P	F1	F2	F3	F4	P	F1	F2	F3	F4	P
East	$d=0.05$	0.00	0.01	0.00	0.02	0.02	0.09	0.14	0.09	0.35	0.30	0.11	0.16	0.11	0.40	0.35	-0.83	-1.25	-0.83	-3.68	-3.26
	$d=0.1$	0.02	0.02	0.02	0.08	0.07	0.10	0.14	0.10	0.35	0.30	0.11	0.16	0.11	0.41	0.36	-1.27	-1.91	-1.27	-5.71	-5.08
	$d=0.2$	0.05	0.07	0.05	0.21	0.18	0.10	0.15	0.10	0.36	0.30	0.11	0.16	0.11	0.42	0.37	-1.09	-1.63	-1.09	-5.14	-4.59
	$d=0.3$	0.07	0.10	0.07	0.29	0.26	0.10	0.15	0.10	0.37	0.32	0.11	0.17	0.11	0.44	0.38	-0.71	-1.07	-0.71	-3.54	-3.19
West	$d=0.05$	0.22	0.32	0.22	0.98	0.87	0.18	0.27	0.18	0.65	0.56	0.16	0.24	0.16	0.60	0.52	1.05	1.57	1.05	3.68	3.16
	$d=0.1$	0.20	0.30	0.20	0.92	0.82	0.18	0.27	0.18	0.65	0.56	0.16	0.24	0.16	0.59	0.51	1.60	2.40	1.60	5.71	4.91
	$d=0.2$	0.17	0.26	0.17	0.79	0.71	0.18	0.27	0.18	0.64	0.55	0.16	0.24	0.16	0.58	0.50	1.41	2.12	1.41	5.14	4.43
	$d=0.3$	0.15	0.23	0.15	0.71	0.63	0.18	0.27	0.18	0.63	0.54	0.16	0.23	0.16	0.56	0.49	0.97	1.45	0.97	3.54	3.06

Table B3b.

		Asymptotics					5-year transients					10-year transients					Momentum				
		F1	F2	F3	F4	P	F1	F2	F3	F4	P	F1	F2	F3	F4	P	F1	F2	F3	F4	P
East	$d=0.05$	0.00	0.01	0.00	0.02	0.02	0.07	0.10	0.07	0.24	0.21	0.08	0.11	0.08	0.29	0.25	-0.91	-1.36	-0.91	-3.90	-3.44
	$d=0.1$	0.02	0.02	0.02	0.08	0.07	0.07	0.10	0.07	0.25	0.22	0.08	0.12	0.08	0.31	0.27	-1.45	-2.17	-1.45	-6.32	-5.60
	$d=0.2$	0.05	0.07	0.05	0.21	0.18	0.07	0.11	0.07	0.26	0.23	0.09	0.13	0.09	0.33	0.29	-1.33	-2.00	-1.33	-6.07	-5.41
	$d=0.3$	0.07	0.10	0.07	0.29	0.26	0.07	0.11	0.07	0.28	0.24	0.09	0.14	0.09	0.36	0.31	-0.93	-1.40	-0.93	-4.39	-3.93
West	$d=0.05$	0.22	0.32	0.22	0.98	0.87	0.21	0.25	0.21	0.76	0.65	0.19	0.22	0.19	0.71	0.61	1.12	1.31	1.12	3.90	3.34
	$d=0.1$	0.20	0.30	0.20	0.92	0.82	0.21	0.25	0.21	0.75	0.65	0.19	0.22	0.19	0.69	0.60	1.79	2.08	1.79	6.32	5.42
	$d=0.2$	0.17	0.26	0.17	0.79	0.71	0.21	0.24	0.21	0.74	0.63	0.18	0.21	0.18	0.67	0.58	1.69	1.93	1.69	6.07	5.23
	$d=0.3$	0.15	0.23	0.15	0.71	0.63	0.20	0.24	0.20	0.72	0.62	0.18	0.21	0.18	0.64	0.55	1.22	1.36	1.22	4.39	3.78

Table B3c.

		Asymptotics					5-year transients					10-year transients					Momentum				
		F1	F2	F3	F4	P	F1	F2	F3	F4	P	F1	F2	F3	F4	P	F1	F2	F3	F4	P
East	$d=0.05$	0.00	0.01	0.00	0.02	0.02	0.04	0.05	0.04	0.13	0.11	0.04	0.07	0.04	0.17	-2.19	-0.98	-1.48	-0.98	-4.12	-3.62
	$d=0.1$	0.02	0.02	0.02	0.08	0.07	0.04	0.06	0.04	0.14	0.12	0.05	0.07	0.05	0.19	-1.94	-1.62	-2.43	-1.62	-6.93	-6.12
	$d=0.2$	0.05	0.07	0.05	0.21	0.18	0.04	0.06	0.04	0.16	0.14	0.06	0.09	0.06	0.24	0.28	-1.58	-2.37	-1.58	-7.01	-6.22
	$d=0.3$	0.07	0.10	0.07	0.29	0.26	0.05	0.07	0.05	0.18	0.16	0.07	0.10	0.07	0.27	1.24	-1.15	-1.72	-1.15	-5.24	-4.66
West	$d=0.05$	0.22	0.32	0.22	0.98	0.87	0.24	0.36	0.24	0.87	0.75	0.23	0.34	0.23	0.83	2.08	1.20	1.80	1.20	4.12	3.52
	$d=0.1$	0.20	0.30	0.20	0.92	0.82	0.24	0.36	0.24	0.86	0.74	0.22	0.33	0.22	0.81	1.84	1.98	2.98	1.98	6.93	5.94
	$d=0.2$	0.17	0.26	0.17	0.79	0.71	0.24	0.35	0.24	0.84	0.72	0.21	0.32	0.21	0.76	-0.33	1.98	2.96	1.98	7.01	6.02
	$d=0.3$	0.15	0.23	0.15	0.71	0.63	0.23	0.35	0.23	0.82	0.70	0.20	0.30	0.20	0.73	-1.27	1.47	2.21	1.47	5.24	4.50

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Appendix C

The following 2 figures provide long-term and short-term elasticities of population growth rate to changes in overall survival and total reproductive output across abundance and geographic split scenarios that were not presented in the manuscript (for the sake of conciseness).
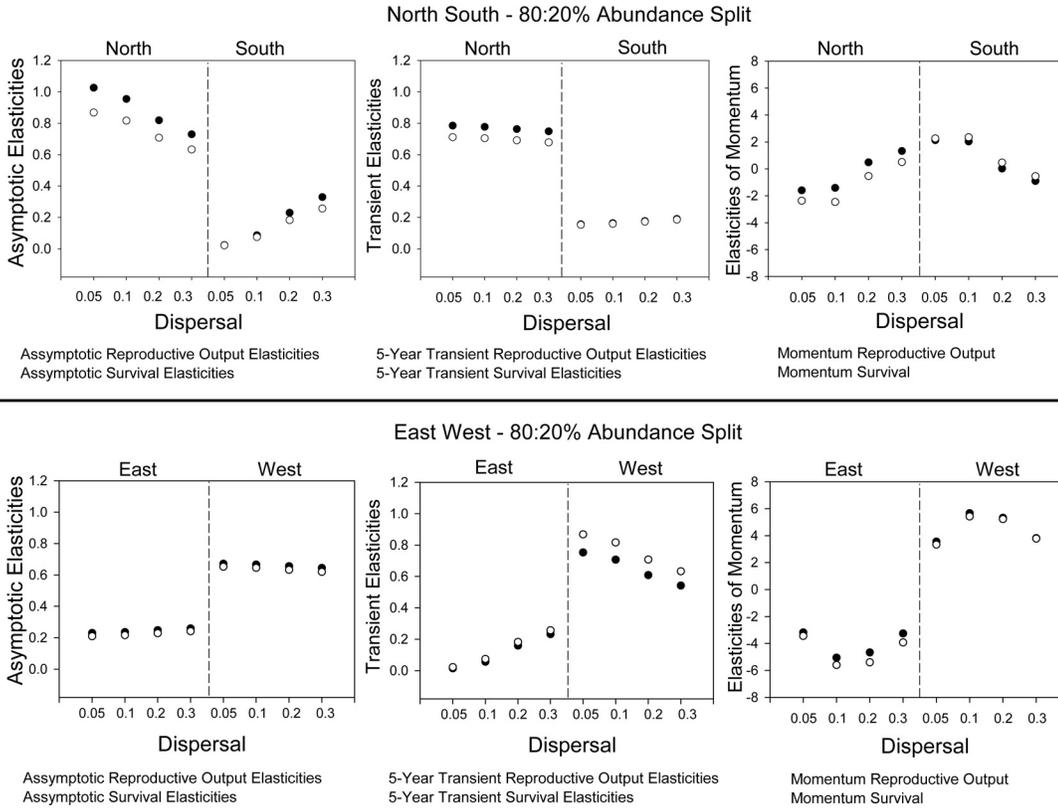

Figure C1. Asymptotic elasticities, 5-year transient elasticities, and elasticities of population momentum to changes in total reproductive output and survival across dispersal regimes (i.e., 0.05, 0.1, 0.2, and 0.3) for North-South and East-West geographic scenarios subjected to an 80:20% abundance split.
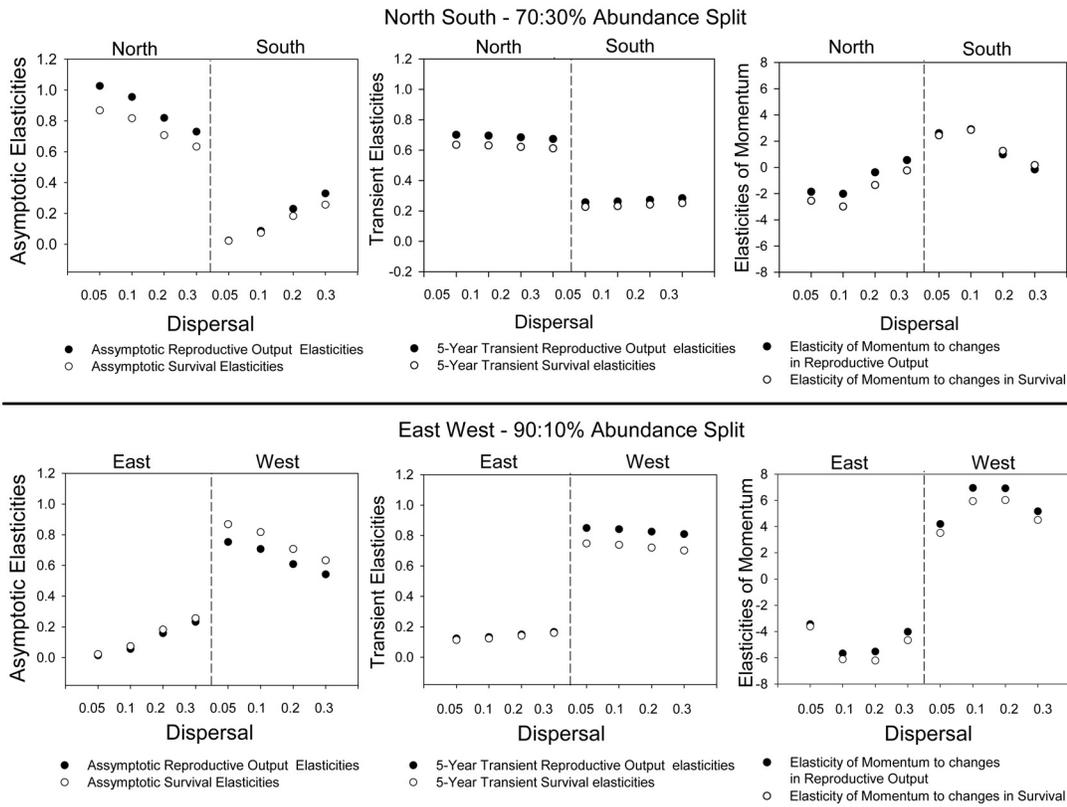
Figure C2. Asymptotic elasticities, 5-year transient elasticities, and elasticities of population momentum to changes in total reproductive output and survival across dispersal regimes (i.e., 0.05, 0.1, 0.2, and 0.3) for the North-South geographic scenario under a 70:30% abundance split, and for the East-West geographic scenario under a 90:10% abundance split.

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