

RETROSPECTIVE ANALYSIS OF DEMOGRAPHIC RESPONSES TO ENVIRONMENTAL CHANGE: A LESSER SNOW GOOSE EXAMPLE

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Abstract. In general, analysis of population dynamics can proceed either prospectively or retrospectively. In the case of the former, asymptotic expectations are generally derived (analytically or numerically) from analysis of the potential effects of perturbation of the elements of the life table. However, the vital rates that are indicated by prospective analysis to contribute the most to projected growth rate are not necessarily those that have contributed to observed variation in growth rate over time. We used a retrospective analysis to analyze the life table responses of a population of long-lived herbivorous geese to a systematic reduction in food abundance within the traditional breeding colony. Typical of long-lived species, adult survival rate has been shown previously in a prospective perturbation analysis to have the largest potential impact on projected growth of the population. However, despite a significant long-term increase in adult survival over the course of the study, there has been a long-term decline in growth rates of the population inhabiting the traditional sampling areas, although absolute numbers of individuals in both populations increased over time. Retrospective assessment of the relative contributions of variation in underlying vital rates (adult and juvenile survival, in situ recruitment, emigration and immigration rates into the population) to projected growth showed that the long-term dynamics of the nesting population primarily reflected the combined effects of changes in postfledging juvenile survival, while changes in the postnesting population were most influenced by variation in juvenile survival and adult fidelity rate to the traditional brood-rearing areas. Decreases in both juvenile survival and fidelity reflect systematic reductions in food abundance over the course of the study. Our results confirm previous suggestions that philopatry to the brood-rearing areas may be a significantly more plastic trait than fidelity to nesting areas.

Key words: dispersal; eigenvalues; elasticity; environmental change; life table response experiment (LTRE); matrix population models; philopatry; sensitivity; Snow Geese; trophic cascade.

INTRODUCTION

The response of populations to environmental change is of fundamental theoretical, and practical, interest to ecologists. Life history variation is arguably an adaptation to particular patterns and forms of environmental heterogeneity, and analysis of variation in life histories necessarily focuses on the manner in which these responses, or adaptations, occur.

In the study of wild populations, analysis of demographic response(s) to variable environments can be broadly categorized as either prospective or retrospective. In the former case, the analysis considers the relative magnitude (and significance) of *potential* changes in the demography of the population that might occur given a change in one or more aspects of the life table. For example, sensitivity or elasticity analyses of stage or age-based projection matrices are prospective analyses, since they quantify the *expected* degree of perturbation to population growth given a

specified change in one (or more) element(s) of the matrix.

However, prospective analytical methods differ significantly from retrospective analyses, since the vital rate which contributes most to the observed variability in life histories is not necessarily the one to which life histories are the most sensitive (which is revealed by the prospective analysis), nor the one that will necessarily make the biggest contribution to variability in another environment (Horvitz et al. 1996, Caswell 2000). This is especially true in wild populations, where natural selection is likely to minimize variation in those parameters to which population growth (i.e., fitness; Caswell 1989) is potentially the most sensitive, such that observed variation in growth over time might reasonably be expected to reflect changes in one or more of the parameters to which growth is less sensitive (Caswell 1989, Pfister 1998).

We examined the response to environmental change of an obligate avian herbivore, the Lesser Snow Goose (*Anser c. caerulescens*; hereafter, Snow Goose), using data from a long-term study of a population breeding at La Pérouse Bay in sub-arctic Canada. In general, female Snow Geese exhibit strong philopatry to their

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natal colony and are traditional in their use of the same feeding and nesting areas where they were reared as goslings (Cooke and Abraham 1980). The colonial breeding, and foraging, and philopatry to specific feeding areas generally exhibited by Snow Geese reflect both a strategy to minimize mortality risk due to predation by predator saturation (Findlay and Cooke 1982), and a strongly synergistic relationship between the geese and their principal saltmarsh forage plants. Under moderate grazing conditions, there is a positive feedback between grazing intensity and fecal nitrogen deposition, and both net aboveground primary production and nitrogen content of food plants increase (Cargill and Jefferies 1984, Jefferies 1988a, b, Hik and Jefferies 1990). Under these conditions, Snow Geese at La Pérouse Bay feed largely on local saltmarsh vegetation, suggesting strong selection favoring use of traditional foraging sites. Lieff (1973) and Harwood (1974) have both demonstrated preferences for fertilized vegetation by grazing Snow Geese. In addition, there is evidence that these saltmarsh plants are required for optimal gosling growth during the first few weeks following hatching (Gadallah and Jefferies 1995).

The size of the La Pérouse Bay nesting population, however, has increased dramatically over the course of the study, from ~2000 nesting pairs in the early years to present estimates of 25 000–35 000 nesting pairs (Cooch et al. 1989, Cooke et al. 1995; R. F. Rockwell, *personal observation*). High intensity grazing and particularly early season grubbing by increased numbers of geese have reduced the standing crop of food available at La Pérouse Bay (Hik and Jefferies 1990, Hik et al. 1991, Williams et al. 1993), and precipitated a trophic cascade that has significantly reduced both the capacity of the forage plants to recover from grazing, and the standing crop of available forage (Bazely and Jefferies 1996, Abraham and Jefferies 1997, Jefferies 1997, 1999). Over the course of the study, ~70% of the saltmarsh graminoid swards have been severely damaged or destroyed, ~100% in some of the most heavily used traditional nesting and foraging areas at La Pérouse Bay.

This reduction in available food has had a number of long-term impacts on the demography of the birds remaining in this sample area. Although Snow Geese in general are classic “capital breeders” (bringing most of the nutrients they use for egg production with them to the breeding grounds during spring migration; sensu Ankney and MacInnes 1978), adults at La Pérouse Bay forage extensively during the pre-laying period (Ganter and Cooke 1996), and reduction in available biomass during this period is generally believed to have resulted in a significant long-term decline in the average number of eggs produced by each female (Cooch et al. 1989, Cooch and Cooke 1991, Ganter and Cooke 1996). In addition, growth and development of geese have been shown to be highly sensitive to variation in the quality

and quantity of food (Cooch et al. 1991a, b, Sedinger and Flint 1991, Larsson and Forslund 1992), and the decline in food availability has led to a significant long-term decline in growth and survival of goslings (Cooch et al. 1991a, Francis et al. 1992a, Williams et al. 1993), and a decline in size among those birds surviving to adulthood (Cooch et al. 1991b). However, despite the progressively smaller size of surviving adults, adult survival has in fact increased over time (Francis et al. 1992a), although there is some evidence that smaller adult size may have negative impacts on other life history traits (Sedinger et al. 1995; but see Cooch et al. 1992 and Cooke et al. 1995).

One response by the geese to these changes has been increased local dispersal during the posthatching brood-rearing period, away from the traditional feeding areas at La Pérouse Bay (see *Methods: Sampling regions*). Cooch et al. (1993) demonstrated that such dispersal can have significant fitness benefits (see also Lindberg and Sedinger 1998). It also has implications for analysis of variation in population growth rate, since abundance within the sampling region will clearly be affected by the rate of dispersal to other areas.

Thus over the course of the study at La Pérouse Bay, we have observed a long-term systematic reduction in food abundance, which has had significant collateral impacts on several demographic parameters of the geese; there have been significant long-term declines in measures of reproductive success (clutch size and gosling growth and survival), and significant increases in local dispersal following hatch. In contrast, there has been a significant increase in adult survival.

In this study, we used a retrospective analysis of variation in projected population growth rate to assess the relative impacts of variation in life history parameters on fitness (using projected growth rate as a measure of fitness).

METHODS

Demographic data were collected annually from 1969 to 1990 as part of a larger investigation of the breeding biology of Lesser Snow Geese at La Pérouse Bay, Manitoba, Canada (58°44' N, 94°28' W). The colony is in the southern portion of the species' breeding range, and is used periodically in spring as a temporary staging area for birds migrating to more northerly colonies (Fig. 1).

Each year, ~2000 nests were monitored at various stages from egg laying to hatching, and measures of reproductive success were recorded (see *Estimation of model parameters: Breeding ground recruitment*). Approximately five weeks after hatching, before the goslings were fully fledged, the adults molted their primary flight feathers and were temporarily flightless. By this time, nonbreeders have left the colony to distant molting sites. When the adults were flightless, ~1500 families (4000–5500 adults and goslings in most years) were rounded up, aged, sexed, and banded. A detailed

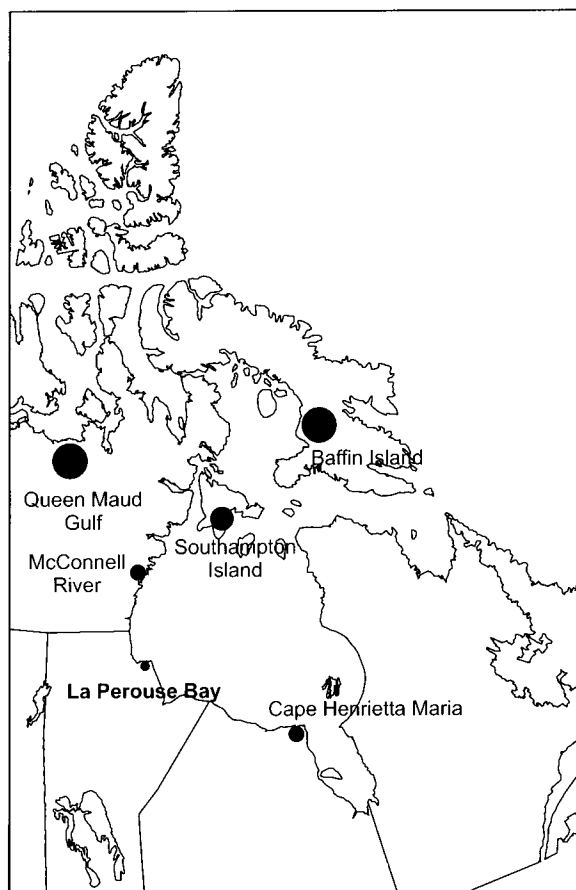


FIG. 1. Major nesting areas of mid-continent Lesser Snow Geese in northeastern Canada. Sizes of circles are proportional to estimated numbers of geese breeding at each colony in 1997 or 1998: Queen Maud Gulf, 1.4×10^6 ; Baffin Island, 1.8×10^6 ; Southampton Island, 0.7×10^6 ; Cape Henrietta Maria, 0.2×10^6 ; McConnell River, 0.15×10^6 ; La Pérouse Bay, $16\text{--}22 \times 10^3$.

description of the study site, and field methods, and data collection protocols are described in Cooke et al. (1995) and references therein. We briefly describe those particular methods relevant to this study.

Sampling regions

At La Pérouse Bay, the breeding habitat consists of several vegetational assemblages. Along the shoreline the geese traditionally feed, but do not nest on large areas of coastal salt marsh (now heavily degraded). These salt marshes are dominated by a stoloniferous grass, *Puccinellia phryganeodes*, and a rhizomatous sedge, *Carex subspathacea*, (Jefferies 1988a, b). We refer to these salt marshes as the “traditional brood-rearing areas” (Fig. 2). Prior to 1990, virtually all of our annual banding drives took place in these traditional brood-rearing areas. Inland from the coastal marshes is an area dominated by the willow *Salix brachycarpa* and dune lyme grass, *Elymus arenarius*. Most of the geese nested in this habitat, since (1) it is in

relatively close proximity to the preferred brood-rearing habitat on the coastal salt marshes and (2) it is typically the first area of the colony to become snow free in spring. We refer to these areas as “traditional nesting habitat” (Fig. 2). Further inland from the traditional nesting areas are denser stands of willow, interspersed with large areas of fresh water marsh.

In the early years of the study, ~2000–2500 pairs of geese nested primarily along the west coast of La Pérouse Bay. During the following 10–15 yr, the population grew at ~8–12% per year, and the nesting area progressively expanded north along the eastern coast of La Pérouse Bay and 3–5 km inland towards the southeast, progressively away from the traditional nesting regions (Fig. 2; Cooke et al. 1995, Ganter and Cooke 1998). Estimates of the size of the nesting population were 14 200 and 22 500 nesting pairs in 1985 and 1990, respectively (R. Kerbes, *personal communication*).

These long-term changes in the spatial extent of the colony make defining the “population” more difficult. For this study, we restricted our analysis to data from

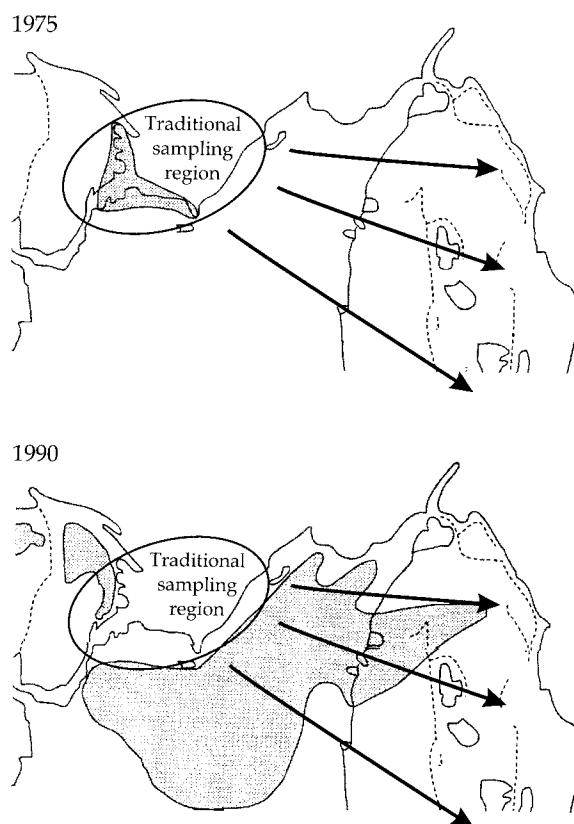


FIG. 2. Temporal and spatial variation in Snow Goose nesting (shaded regions) at La Pérouse Bay, 1975 and 1990 (adapted from Ganter and Cooke 1998). Ellipses indicate approximate spatial extent of “traditional sampling regions.” Arrows indicate the general direction of local dispersal of family groups with increasing habitat degradation (sensu Cooch et al. 1993).

the traditional sampling regions only (both during nesting, and during annual banding drives; Fig. 2). In the early years of our study, virtually all of the geese nesting at La Pérouse Bay were found in these traditional areas. However, with the increasing size of the colony, and the concurrent spatial expansion of habitat used by the geese (Cooch et al. 1993, Cooke et al. 1995, Ganter and Cooke 1998), this is no longer the case. However, the dynamics of the geese in the traditional sampling areas will influence the dynamics of the larger macro-population of birds nesting at La Pérouse Bay, and understanding those factors contributing significantly to the dynamics of the traditional colony will also influence (and, in turn, be influenced by) population processes at a larger scale.

Retrospective analysis of population dynamics

Our main interest is in exploring the relationship between changes in one or more vital rates and the population dynamics of the Snow Geese nesting at La Pérouse Bay. In the presence of (1) relatively high true adult survival (0.8–0.94; Francis et al. 1992a, Cooke et al. 2000) and (2) no detectable senescent decline in survival with age (Francis et al. 1992b), changes in adult survival will have a significantly greater impact on projected growth than would changes in any other parameter (Caswell 1989). An earlier prospective sensitivity analysis confirmed this prediction (Rockwell et al. 1997).

However, as noted earlier, the vital rate to which life histories are the most sensitive (as indicated by a prospective analysis) is not necessarily the one that has contributed most to the observed variability in the dynamics of the population, nor is it the one that will necessarily make the biggest contribution to variability in another environment (Horvitz et al. 1996, Caswell 2000). Identification of those factors that have contributed most to variation in the dynamics of the population requires a retrospective approach.

Traditional retrospective analytical methods have generally involved relating the pattern of changes in abundance with the pattern of variation in the underlying vital rates. In essence, this is the basis for key factor analysis and related techniques (*sensu* Varley and Gradwell 1960). However, such approaches make a number of limiting assumptions, and are known to have significant statistical problems (Vickery 1991 and references therein). Unfortunately, these problems have not precluded their continued use (e.g., Newton 1988, Møller 1989). Although various improvements to classical key factor analysis have been proposed (e.g., Podoler and Rogers 1975, Brown et al. 1993), most of these methods are still potentially flawed, since they rely on estimates of population abundance at each stage of the life cycle, yet do not properly account for sampling variances and covariances.

Recently, however, there has been a recognition that identifying contributions to population change may be

more usefully assessed in terms of contribution of the vital rates to variation in *projected* growth rate, rather than abundance (Caswell 1989, 1996a, 2000, Sibly and Smith 1998). In particular, projected growth rate is an omnibus *index* of the cumulative contributions of the underlying birth and death processes. Moreover, methods relying on analysis of projected growth rate are not affected by difficulties due to issues of age structure and postreproductive animals (Sibly and Smith 1998).

One approach for partitioning variation in growth rates is the life table response experiment (LTRE; Caswell 1989, 1996a, Horvitz et al. 1996). The LTRE relies on the fact that if projected population growth rate is measured as a deviation from a reference value, then “treatment” effects (i.e., variation in projected growth rate) can be decomposed into contributions from each of the vital rates, in a manner structurally (but not formally) analogous to analysis of variance. We used a LTRE analysis to retrospectively assess the response of the Snow Geese at La Pérouse Bay to long-term changes in the foraging environment.

Population models

We modeled the projected dynamics of Snow Geese at La Pérouse Bay using a linear time-invariant female-based matrix model:

$$\mathbf{n}(t + 1) = \mathbf{A}\mathbf{n}(t) \quad (1)$$

where $\mathbf{n}(t)$ is a vector giving the abundances of the stages in the population at time t , and \mathbf{A} is the population projection matrix, whose ij th entry a_{ij} gives the contribution of an individual in stage j to stage i over one time step. The projection interval (from t to $t + 1$) is one year. The matrix \mathbf{A} and the corresponding life cycle graph are shown in Fig. 3.

The dominant eigenvalue λ of the matrix gives the *projected* population growth rate. We differentiate between *projected* and *realized* growth rate (the ratio of successive population abundance values) elsewhere. The right and left eigenvectors \mathbf{w} and \mathbf{v} give the projected stable stage distribution and the stage-specific reproductive values, respectively.

The sensitivity s_{ij} of *projected* λ to a change in the matrix entry a_{ij} is given by

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle} \quad (2)$$

The elasticity e_{ij} of *projected* λ to a change in the matrix entry a_{ij} (i.e., the proportional effect of a change in a_{ij} on change in λ) is simply the sensitivity calculated on a log scale, and is given by

$$e_{ij} = \frac{\partial \log \lambda}{\partial \log a_{ij}} = \frac{a_{ij}}{\lambda} \cdot \frac{\partial \lambda}{\partial a_{ij}} \quad (3)$$

(Caswell 1989). Sensitivity and elasticity analyses are referred to collectively as perturbation analyses, since they reflect the *expected* change in growth rate follow-

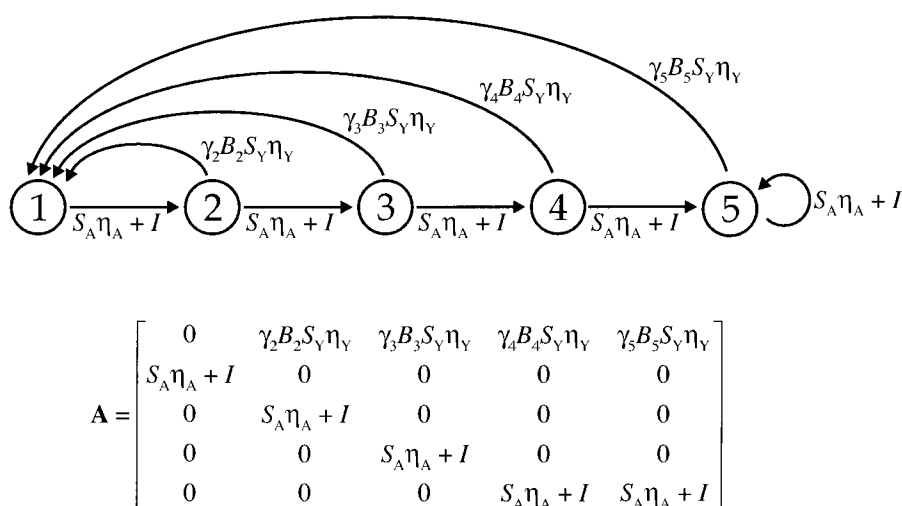


FIG. 3. Life cycle diagram and matrix model corresponding to a prebreeding census for Snow Geese. Node 1 represents yearlings. Transitions among nodes are determined by age-specific survival rates (S_x), fidelity rates (η_x) and breeding propensities (γ_x), and the immigration rate (I). Fertility contributions are products of survival and breeding success (B_i ; see Fig. 5).

ing a given perturbation (change) in one of the matrix elements.

Parameterization of the LTRE

In a single classification LTRE, a baseline or reference treatment is defined, to which other treatments may be compared. Following Caswell (1989), this can be written using the *analogy* of a linear model as

$$\lambda^{(m)} = \lambda^{(\cdot)} + \alpha^{(m)} \quad (4)$$

where $\alpha^{(m)}$ is the effect of the m th level of the treatment, measured as a deviation from the growth rate of the reference matrix ($\lambda^{(\cdot)}$). The effect $\alpha^{(m)}$ measures the effect of treatment m on λ , and incorporates all the differences in survival and fertility between the treatment matrix and the reference matrix. To decompose $\alpha^{(m)}$ into the contributions due to the differences in each matrix element, Caswell (1989) showed that to first-order

$$\begin{aligned} \hat{\alpha}^{(m)} &= \lambda^{(m)} - \lambda^{(\cdot)} \\ &= \sum_{i,j} (a_{ij}^{(m)} - a_{ij}^{(\cdot)}) \frac{\partial \lambda}{\partial a_{ij}} \bigg|_{(1/2)(A^{(m)} + A^{(\cdot)})} \end{aligned} \quad (5)$$

where the sensitivities ($\partial \lambda / \partial a_{ij}$) are evaluated halfway between the treatment matrix $A^{(m)}$ and reference matrix $A^{(\cdot)}$. If the reference matrix $A^{(\cdot)}$ represents the mean matrix, then $\sum \hat{\alpha}^{(m)} \approx 0$. This summation will differ from zero to the extent that λ is a nonlinear function of the a_{ij} . In situations where the first-order approximation may fail (implying that the second and higher order terms are sufficiently large that they cannot be neglected), Caswell (1996b) has shown that second-order terms can be accommodated by using the second derivative of λ with respect to the a_{ij} .

However, in general, there is no reason to expect the individual values of λ corresponding to each treatment

to be symmetrically distributed about the mean, and the more important criterion is whether or not the predicted value of $\tilde{\lambda}^{(m)}$,

$$\tilde{\lambda}^{(m)} = \lambda^{(\cdot)} + \tilde{\alpha}^{(m)} \quad (6)$$

is close to the actual value of $\lambda^{(m)}$ (H. Caswell, *personal communication*). Thus when the mean matrix was used as the reference, we used the first-order approximation, after first confirming a good fit of the predicted value of $\tilde{\lambda}^{(m)}$ with the observed value.

For our study, we partitioned the annual data into six contiguous 3-yr blocks of time (1973–1975, 1976–1978, 1979–1981, 1982–1984, 1985–1987, and 1988–1990). Each 3-yr block was regarded as one level (m) of a “systematic food reduction treatment” in a single-classification planned experiment, with the earliest 3-yr block (1973–1975) having the highest food abundance, and the latest period (1988–1990) having the lowest. A separate projection matrix $A^{(m)}$ was derived for each block.

This approach is *analogous* (at least heuristically) to fixed-effects ANOVA, and differs from a random effects model in that it examines the effects of some treatment on λ , relative to some predetermined baseline. In a random effects model, the goal is to partition the variance in λ into contributions from the variances and covariances in the individual matrix elements a_{ij} (Brault and Caswell 1993, Horvitz et al. 1996, Caswell 2000). We chose to adopt the “fixed-effects” formulation for two reasons. First, since the time axis also constituted the only level of replication in our study, variances and covariances among the individual matrix elements could only be estimated over time. Thus our “replicate” and “treatment” axes were co-linear, and estimates of variance

and covariance among the matrix elements would only be possible within treatment blocks, which were limited to 3-yr intervals. Second, comparative analysis of other goose populations suggests that, at least in broad terms, the food restrictions that occurred through time at La Pérouse Bay do reasonably constitute a fixed set of treatments, which can be replicated in other studies of this or related species, at other colonies.

While it is possible to apply the LTRE approach in a regression context (Caswell 1996c), we applied a single classification fixed design (Eq. 4). A regression approach is generally most appropriate when there are specific quantitative treatment levels. While we have strongly suggested that the long-term deterioration of the foraging conditions at La Pérouse Bay constitute changes in an underlying treatment variable that has significantly influenced the dynamics of the geese, deriving meaningful functions relating the set of vital rates a_{ij} to the changes in the plants (the critical step in applying a regression approach to a LTRE) would be extremely difficult. The changes in the plants are characterized by significant spatial and temporal heterogeneity, and the most appropriate metric (total plant abundance, relative biodiversity of the plant communities, plant chemical composition, etc.) is unknown. Instead, we adopted the single classification "fixed effects" LTRE, since we believed it was better suited to exploration of variation in response of the geese to systematic, yet qualitative, changes in the plants.

It should also be noted that the LTRE does not constitute a formal statistical analysis of variation (despite structural analogy with analysis of variance and other approaches based on linear models). There is no underlying null hypothesis being tested, and the only assumptions are fully specified in the first-order approximation (Eq. 5). Issues of independence of samples and non-additivity do not require the same consideration in terms of their impact on the validity of the LTRE approach (H. Caswell, *personal communication*). However, they may influence interpretation to some degree.

Partitioning $\alpha^{(m)}$.—The matrix entries a_{ij} for a matrix (particularly stage-based matrices) can often be expressed as combinations of two or more underlying vital rates. Because the contribution of a_{ij} to a treatment effect $\alpha^{(m)}$ on λ could reflect effects of the subcomponents of a_{ij} , we further partitioned the contributions of a_{ij} by rewriting the effects in terms of the subcomponents rather than the matrix entries themselves (Caswell 1996b). This is accomplished by recognizing that the matrix is fully defined by the subcomponents. If a given projection matrix is defined by the contribution of subcomponents $\theta_1, \theta_2, \dots, \theta_n$ (i.e., $a_{ij} = f\{\theta_1, \theta_2, \dots, \theta_n\}$) then to first-order we can rewrite Eq. 5 in terms of the contributions of the subcomponents as follows:

$$\hat{\alpha}^{(m)} = \lambda^{(m)} - \lambda^{(c)} \\ \equiv \begin{pmatrix} \sum_{ij} (\theta_{1ij}^{(m)} - \theta_{1ij}^{(c)}) \frac{\partial \lambda}{\partial \theta_{1ij}} \\ + \sum_{ij} (\theta_{2ij}^{(m)} - \theta_{2ij}^{(c)}) \frac{\partial \lambda}{\partial \theta_{2ij}} \\ \vdots \\ + \sum_{ij} (\theta_{nij}^{(m)} - \theta_{nij}^{(c)}) \frac{\partial \lambda}{\partial \theta_{nij}} \end{pmatrix}^{(1/2)(A^{(m)} + A^{(c)})} \quad (7)$$

where, in general,

$$\frac{\partial \lambda}{\partial x} = \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \cdot \frac{\partial a_{ij}}{\partial x}. \quad (8)$$

(Caswell 1989).

Written this way, each summation term is the contribution of a treatment effect to the overall effect on λ , expressed in terms of the underlying vital rates, rather than the matrix entries themselves (Caswell 1996b). However, the overall summation tends in general to differ from $\alpha^{(m)}$; this non-additivity seems to reflect the fact that the means of the individual parameters are not the same as the means of the a_{ij} themselves, rather than non-linearity between population growth and the individual a_{ij} (Appendix A). However, since we found no systematic bias in the *relative* contribution of the lower level vital rates, we discuss changes in relative contributions of each term to $\alpha^{(m)}$ over time.

Parameterizing the model

The elements (a_{ij}) of the matrix model used in our study were completely specified by seven primary parameters, which governed the rate of entry and departure of individuals into and from the population: *juvenile survival* (S_V ; survival over the first year of life), *adult survival* (S_A ; annual survival of a bird 1+ years old), *juvenile fidelity* (η_V ; the probability of returning to the population, conditional on surviving the first year of life), *adult fidelity* (η_A ; annual probability of a bird 1+ years old returning to the sampled population, conditional on being alive), *adult immigration rate* (I ; the probability that a bird present in the population at time i entered between time $i - 1$ and i), *breeding propensity* (α_x ; probability that an individual of age x years will breed in a given year, conditional on being alive), and *breeding ground reproductive success* (B_x ; the average number of female goslings reared to fledging per breeding female of age x). In our model (based on a pre-breeding census), immigration rate for adult females, I , would enter into the projection model in the diagonal and self loop a_{ij} elements (Fig. 3), such that for every one adult female at age x , we expect ($S_A \eta_A + I$) individuals at age $x + 1$. The sum ($S_A \eta_A + I$) can potentially be > 1 , indicating a net surplus of individuals in each age class due to immigration.

We truncated the life cycle at five years of age (such that the 5+ age class represented a terminal stage);

Snow Geese are reproductively mature at five years of age, with no evidence of significant senescent decline in any of our parameters (Francis et al. 1992b, Rockwell et al. 1993, Cooke et al. 1995). Previous analysis of data from La Pérouse Bay demonstrated that realized fertility (offspring production during the breeding period, and subsequent juvenile survival over the first year of life) has declined over the course of the study (Cooch et al. 1989, Francis et al. 1992a, Williams et al. 1993), while annual adult survival has increased significantly (Francis et al. 1992a). Thus to simplify some of our analyses, we structured our model assuming a prebreeding census, which structurally separates fertility from adult survival and immigration (Fig. 3; Caswell 1989).

It is important to note that the LTRE approach can be applied to any structurally consistent set of matrix models, regardless of whether or not they incorporate parameters that completely specify the dynamics of the population. The LTRE analyzes variation in projected growth rate, not realized growth rate. Projected growth rate, λ , is a mathematical property (dominant eigenvalue) of the underlying projection matrix, and gives the projected growth of the population under the assumption of time invariance, given the parameterization of the matrix. Projected λ is also an omnibus index of the cumulative contributions of all of the vital rates included in the matrix to the projected growth of the population under these same assumptions. Thus LTRE can be used to assess the relative contributions of any arbitrary set of parameters, a_{ij} , to projected growth. In our study, our intent was to examine the responses of the geese nesting at La Pérouse Bay to environmental change, regardless of their origin (i.e., local recruits or immigrants). Potentially, we could have done so using the LTRE approach without explicitly including estimates for immigration rate, since it is unlikely that variation in immigration rate reflects changes in the local environment. However, since immigration might actually influence both the rate of change in the environment at La Pérouse Bay and the pattern and rate of response of the geese currently nesting there, we included immigration rate explicitly in our model.

Estimation of model parameters

Some of the parameters used in our models were estimated using methods previously described for this study. Specific details are provided in Cooke et al. (1995), and references therein. Here we discuss elaborations of those methods relevant to this study.

Survival.—Survival rates for populations where some fraction of the population is individually marked are commonly estimated using either one of two approaches. Survival can be estimated using data from live encounters (recaptures or resightings). Estimates of survival derived from recapture (or resighting) data ("apparent" survival; ϕ) reflect the probability that the individual is alive (S) and in the sampling area (η ;

fidelity), and thus confound true mortality with permanent emigration. Thus whenever the fidelity rate η is <1.0 , apparent survival rate (ϕ) will always underestimate true survival rate (S) (since $\phi = S \times \eta$). Alternatively, survival rates can be estimated using data from recoveries of dead individuals. Since recoveries can occur anywhere within the migration and wintering range, survival estimated from dead recoveries represents estimates of true survival rate (S), and are not confounded by differences in site fidelity.

Comparison of estimates of survival derived from dead recovery and live encounter data provide ad hoc estimates of the rate of permanent emigration ($1 - \eta$) from the sampling area (since $\eta = \phi/S$; Hepp et al. 1987, Francis and Cooke 1993). Burnham (1993) has derived a formal method for direct estimation of true survival and *permanent* emigration rates (where permanent emigration refers to an individual leaving the sampling region permanently in the sense of never again being in the sample area at the time of sampling) using combined dead recovery and live encounter data. We used the approach described by Burnham to derive estimates of both adult and juvenile survival and fidelity rates (i.e., $1 - \text{emigration rate}$) for each 3-yr treatment block, using combined live recapture and dead recovery data for 22 556 females banded as goslings during postnesting banding drives at La Pérouse Bay from 1972 to 1990. We used only data from birds banded as goslings for two reasons. First, previous analysis indicated significant heterogeneity in fidelity rate between birds banded as goslings and birds banded as adults (Pradel et al. 1995). While it is possible to simultaneously estimate fidelity rate conditional on the age at which a bird was marked, we were particularly interested in the pattern of possible change in fidelity rate with increasing age and experience. This is generally difficult with birds banded as adults since they are generally of unknown age, and their natal brood-rearing area is unknown. This has implications for interpretation of estimated immigration rates. Encounter data consisted of (1) recoveries of dead individuals made between September and March (i.e., during the nonbreeding season), and (2) live recaptures made during annual banding drives made just prior to fledging of the goslings. Further details concerning survival estimation are given in Appendix B.

Emigration or mortality?—Mortality represents a permanent state transition; an individual who dies clearly cannot contribute to abundance at the next or any future census. Thus if annual survival is constant over years, then it is (by definition) invariant to when in the annual cycle it is estimated (i.e., winter to winter annual survival must be the same as summer to summer annual survival), conditional on no annual variation in survival.

The same is not necessarily true for emigration; an individual may be consistently absent from the sample area during a particular part of the year, yet return to

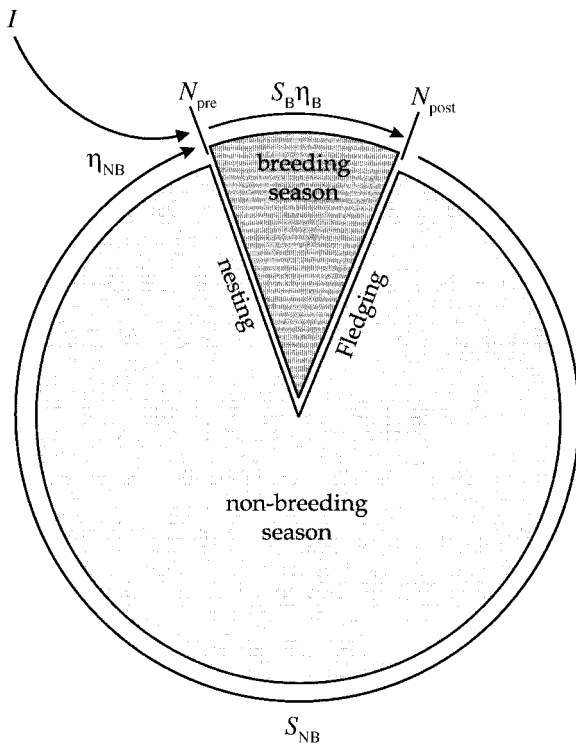


FIG. 4. Schematic representation of the annual cycle of Snow Geese, partitioned into a breeding and nonbreeding season (size of the respective sections is drawn proportionately to the portion of the year comprised by each period). Populations can be censused either prior to breeding (N_{pre}) or after breeding (N_{post}). Presence of natal recruits in the sample is conditional on surviving (S) and remaining in the sample (η).

the sample area in a subsequent part of the year. For example, consider the situation where the annual cycle is divided into a breeding and nonbreeding period (Fig. 4). Individuals can be censused either at the beginning or at the end of the breeding period. An individual may be in the sampled area at the start of breeding with probability η_{NB} , permanently emigrate during the breeding season with probability $(1 - \eta_B)$, such that it is never available to be enumerated during a postbreeding census (although for some species, the offspring of the individual may remain in the census area and contribute to abundance during the postbreeding census, even if the individual itself does not), and return to the sample at the start of breeding the following year with probability η_{NB} . In our study, permanent emigration could have the following forms: permanent emigration from the nesting sample ($1 - \eta_B$; Fig. 4), permanent emigration from the brood-rearing sample ($1 - \eta_{NB}$), or permanent emigration from both ($1 - \eta_B \times 1 - \eta_{NB}$). In the latter case, emigration has the same demographic consequences as does mortality.

With only a single annual census, it is not currently possible to assess the relative proportions of individuals that permanently depart the sample over the entire

annual cycle, and those which are present for some parts of the year and not others. If the proportion of those individuals that permanently emigrate over the entire life cycle is low (i.e., if $1 - \eta_B \times 1 - \eta_{NB} \approx 0$), then interpreting growth rate estimates will depend on when during the annual cycle emigration is believed to occur. Previous analysis of Snow Geese at La Pérouse Bay has suggested a marked dichotomy in the pattern of fidelity to the natal colony; although the probability of females returning to their natal colony, conditional on being alive, is very high ($>95\%$; Cooke et al. 1995), philopatry of adults and their offspring to brood-rearing areas (where the postnesting census occurs), although significant in the early years of the study (Cooke and Abraham 1980), was significantly lower than overall natal philopatry (Pradel et al. 1995). Further, the systematic changes in food abundance at La Pérouse Bay have strongly suggested, based on indirect measures, that the pattern of brood-rearing philopatry may have changed (decreased) significantly (Cooch et al. 1993), and in an age-specific way (Rockwell et al. 1993).

Thus we believe that the majority of the estimated permanent emigration from the traditional La Pérouse Bay sample occurs during the breeding season, primarily during brood rearing, with essentially no permanent emigration during the nonbreeding season. Under this assumption, the growth rate from models based on apparent survival rate (i.e., where η is assumed to be <1 ; Fig. 4) reflects projected growth of the population at the end of breeding. Conversely, under the same assumptions, projected growth rate from models based on true survival rate (assuming $\eta = 1$; Fig. 4) reflects projected growth of the population at the beginning of the breeding season. The opposite would be true if, in fact, most of the emigration occurred during the nonbreeding season.

Breeding ground recruitment: reproduction and immigration.—Recruitment into a population consists of the combined contributions of in situ reproduction and immigration, each of which may be affected by various ecological and demographic factors in different ways. Commonly, the fertility contributions in matrix models reflect in situ recruitment only, and do not accommodate additions to the sampled population through immigration. It is straightforward to parameterize a matrix model to include immigration rate if estimates are available (e.g., Hitchcock and Gratto-Trevor 1997). Hence projected growth rates will often be negatively biased if permanent recruitment of immigrants into the population occurs. Such permanent immigration has been previously documented at La Pérouse Bay (Geramita and Cooke 1982, Pradel et al. 1995). Thus, in our models, we incorporated estimates of both in situ fertility and immigration.

In situ fertility (B') for a given age class (x) is the product of age-specific prefledging reproductive success (B_x) and first year (juvenile) survival (P_y ; Fig. 3).

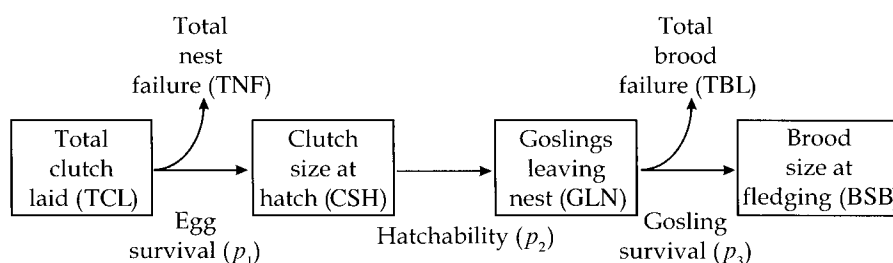


FIG. 5. Components of breeding ground reproductive success (B_i). TCL = total clutch laid; CSH = clutch size at hatch (when at least one egg in the clutch begins to hatch); GLN = goslings leaving nest (number of goslings that successfully hatch and leave the nest); BSB = brood size at fledging (number of goslings from a brood that successfully survive to fledging); TNF = total nest failure (probability of all eggs in a nest being depredated prior to hatching); TBL = total brood loss (loss of all goslings in a brood between hatch and fledging); p_1 = egg survival (CSH/TCL); p_2 = hatching success (GLN/CSH); p_3 = brood survival (BSB/GLN).

Procedures for survival estimation were discussed previously (see also Appendix B); here we describe estimation of the components of pre fledging reproductive success (B_x).

We used a compartment model to estimate the pre fledging reproductive success of individual adult females of different ages. Details are given in Rockwell et al. (1993) and Cooke et al. (1995). Data were derived from observation of ~35 000 individual nests over the course of the study.

The components of the model span the period from egg laying through fledging of the goslings (Fig. 5). The state variables correspond to sequential stages of the life cycle and each imposes a logical upper limit on the succeeding one. Succeeding pairs of state variables are used to estimate the transition probabilities (i.e., proportional survival between stages). Values less than one for the partial success transition indicate a decrement in fitness between stages of the reproductive cycle.

We defined two additional transition probabilities to account for total failure during incubation and brood rearing (Fig. 5). The absolute frequency of total brood loss cannot be estimated because the failure of a brood to appear in the sample did not imply that the entire brood died, only that it was not recaptured (Cooke and Rockwell 1988). A minimum estimate can be obtained from the proportion of nests for which both of the marked parents, but none of the goslings, were recaptured. Cumulative reproductive success was estimated for each age class as $B_i = TCL p_1(1 - TNF)p_2 p_3(1 - TBL)$. For some analyses, we partitioned B_i into a pre-hatching ($B_L = TCL p_1[1 - TNF]p_2$) and posthatching ($B_H = p_3[1 - TBL]$) component, since analysis of variation of the individual parameters indicated a strong difference in the magnitude in variation among years in pre- and posthatch fertility (Williams et al. 1993, Cooke et al. 1995).

Intuitively, mark-recapture data form the basis for estimation of immigration of adults into the breeding population, since adult immigrants will be unbanded at the time of entry into the population. We wish to

estimate the number of new adult recruits to the La Pérouse Bay population that are due to immigration. Following Pollock et al. (1990) and Nichols and Pollock (1990), consider a single, open (to emigration and immigration) animal population with two age classes. Total adult recruitment B_i between time i and $i + 1$ is estimated as the sum of recruitment due to in situ reproduction (i.e., natal recruitment), $B_i^{(A)}$ and immigration, $B_i^{(I)}$:

$$\hat{B}_i = \hat{B}_i^{(A)} + \hat{B}_i^{(I)}. \quad (9)$$

Expected in situ recruitment of adults $B_i^{(A)}$ is clearly a function of the number of individual offspring produced in previous years and the survival rate of the offspring to the age of recruitment. In the simplest case, with only two age classes (adult, A, and juvenile, J) and a 1-yr transition between juvenile and adult, $B_i^{(A)}$ is estimated as

$$\hat{B}_i^{(A)} = [\hat{N}_i^{(J)} - n_i^{(J)} + R_i^{(J)}]\hat{\phi}_i^{(J)} \quad (10)$$

where $n_i^{(J)}$ is the number of juveniles (offspring) captured at sampling occasion i , $R_{i-1}^{(J)}$ is the number of juveniles released at sampling occasion i , and $\phi_{i-1}^{(J)}$ is the probability that a juvenile encountered at sampling period $i - 1$ survives and is still in the sampled population at time i .

Similarly, the total number of immigrants entering the population between year i and $i + 1$, $B_i^{(I)}$, is estimated as the difference between the current size of the adult population next year (i.e., at time $i + 1$), $N_{i+1}^{(A)}$, and the sum of (1) the number of adults in the population in the current year, $N_i^{(A)}$, expected to survive from year i to $i + 1$, and (2) the expected number of in situ adult recruits:

$$\begin{aligned} \hat{B}_i^{(I)} = & \hat{N}_{i+1}^{(A)} - [\hat{N}_i^{(A)} - n_i^{(A)} + R_i^{(A)}]\hat{\phi}_i^{(A)} \\ & - [\hat{N}_i^{(J)} - n_i^{(J)} + R_i^{(J)}]\hat{\phi}_i^{(J)}. \end{aligned} \quad (11)$$

Thus for the simple case of two age classes, we calculate a net immigration rate, I_p , between time i and $i + 1$ as

$$\hat{I}_i = \left(\frac{\hat{B}_i - \hat{B}'_i(A)}{\hat{N}_i(A)} \right) = \left(\frac{B''_i(A)}{\hat{N}_i(A)} \right). \quad (12)$$

While the basic approach outlined by Pollock et al. (1990) is straightforward, the estimation and subsequent interpretation of immigration rate, I , at La Pérouse Bay is complicated by several factors. First, there are more than two age classes. Second, breeding does not begin until two years of age, and not all individuals recruit to the breeding population at the same age. Third, our sampling methods were not entirely appropriate for estimation of recruitment using standard approaches. We describe our approach to estimating immigration rate given these complications in Appendix C. Finally, our estimates of recruitment rate refer to the population sampled during our annual banding drives. Since birds encountered during banding were known to have bred during that year (i.e., only breeding birds are available for recapture), then immigration to the population censused after breeding (i.e., during banding) is equivalent to immigration into the nesting sample.

Breeding propensity.—Estimation of breeding propensity (α_x ; defined as the age-specific probability of breeding at age x conditional on being alive) in wild populations is complex. In principle, the proportion of females that begin breeding at each age can be determined by comparing the numbers of a given cohort that could (potentially) be breeding (i.e., the number remaining alive) with the numbers that actually are breeding. However, in many studies only breeding individuals are observed, and thus breeding propensity and recapture rate are confounded. Relative estimates of breeding propensity can be derived by using analysis of variation of recapture rates over time, since recapture rates estimate the probability that an individual will be encountered, which in our study is conditional on breeding.

While there has been significant annual variation in age-specific recapture rates among years (and hence, among blocks), recapture rate increased with age in all years; if the true probability of detecting an individual given that it remains in the sampled population is independent of age, then age-specific increases in recapture rate reflect increases in breeding propensity. In addition, there was no indication of significant trend in breeding propensity over time (Cooke et al. 1995, Cooch et al. 1999). This result is in contrast to recent analysis of Pacific Black Brant (Lindberg et al. 1998), where strong year-specific trends in breeding propensity within age class were found. Thus to improve the precision of our estimates, we derived age-specific recapture rates over all years combined. Breeding propensities were estimated from these values by scaling them relative to the recapture rate of the oldest age class, which was assumed to have the maximal breeding propensity.

However, we note that this approach somewhat con-

finds two separate and potentially important processes: *breeding propensity* and *age of maturity* (or age of first reproduction). Previous analysis of breeding data from La Pérouse Bay has clearly indicated that age-specific breeding propensity (the probability of breeding in a given year) is to some degree conditional on the age at which an individual first recruits to the breeding population (i.e., the age at which it first breeds; Viallefont et al. 1995a, b). This is consistent with life history theory suggesting a trade-off between age of first breeding and reproductive performance. Clearly, the probability of breeding (propensity) and the probability of breeding for the first time (recruitment) are logically equivalent only for the earliest age class at which breeding can occur (in Snow Geese, two years of age); for older age classes, the probability of breeding at four years of age in year i may be conditional on whether the individual bred for the first time (recruited) as a 2-yr-old, a 3-yr-old, or as a 4-yr-old bird. Ideally, estimated recapture rates should be conditioned on the age of first breeding. This is also true using more direct estimates of age of first breeding (sensu Cooch et al. 1995). In our present analysis using recapture rates as an index of breeding propensity, we were unable to do this, and thus the estimated recapture rates (and derived breeding propensities) confound birds that recruited at different ages. While it may be possible to separately estimate both parameters in some cases (Kendall and Nichols 1995), data from La Pérouse Bay were not collected appropriately for rigorous application of these methods.

While use of recapture rates to derive a scaled index to breeding propensity is clearly an ad hoc approach, the lack of significant trend suggests that the imprecision in estimates of breeding propensity will not affect the inter-block comparisons, since the proportional impact on projected growth will be the same among all treatment blocks.

RESULTS

Estimated parameter values for each treatment block are presented in Table 1. Details concerning the estimation of the survival, recapture, and fidelity rates are presented in Appendix B, while those for estimation of immigration rate are presented in Appendix C.

Consistent with the results of previous studies of this population (Cooch et al. 1989, Cooch and Cooke 1991, Francis et al. 1992a, Williams et al. 1993, Cooke et al. 1995), fertility, juvenile, and adult true survival (S) showed significant trends; fertility declined over time (i.e., among increasing 3-yr "treatment" blocks; 1973–1975 to 1988–1990) within each age class (Table 1), while juvenile survival decreased and adult survival increased significantly (Appendix B, Table B1).

Fidelity rate (η) varied among treatment blocks and between juvenile and adult birds. The most parsimonious model was a model with two age classes (juvenile

TABLE 1. Parameter estimates used in analysis of the population dynamics of Lesser Snow Geese at La Pérouse Bay, 1973–1990.

A) Breeding ground reproductive success								
Block	Pre-hatch (B_L) [†]				Post-hatch (B_H) [‡]			
	2	3	4	5+	2	3	4	5+
1973–1975	1.481	1.708	1.968	2.052	0.629	0.629	0.677	0.519
1976–1978	1.433	1.643	1.851	1.880	0.619	0.619	0.687	0.636
1979–1981	1.256	1.479	1.701	1.780	0.684	0.684	0.654	0.646
1982–1984	1.183	1.339	1.514	1.618	0.529	0.529	0.522	0.551
1985–1987	1.239	1.383	1.704	1.708	0.444	0.444	0.562	0.499
1988–1990	1.212	1.267	1.480	1.534	0.255	0.255	0.389	0.354
B) Survival and fidelity (see Appendix B)								
Block	Juvenile			Adult				
	S_Y [§]	η_Y	ϕ_Y [¶]	S_A	η_A	ϕ_A		
1973–1975	0.733	0.763	0.559	0.803	0.933	0.749		
1976–1978	0.646	0.727	0.470	0.815	0.918	0.748		
1979–1981	0.536	0.688	0.369	0.827	0.899	0.743		
1982–1984	0.418	0.644	0.264	0.837	0.877	0.734		
1985–1987	0.309	0.596	0.184	0.847	0.849	0.719		
1988–1990	0.219	0.545	0.119	0.856	0.817	0.699		
C) Immigration rate (see Appendix C, Fig. C2)								
Measure#	Overall mean			Maximum		Minimum		
\bar{I}_{block}	0.09			0.61		−0.23		
D) Breeding propensity								
Age class (x)	p_x			α_x ^{††}				
2	0.091			0.314				
3	0.177			0.612				
4	0.212			0.734				
5+	0.246			0.850				

[†] $B_L = \text{TCL}(1 - \text{TNF})p_1p_2$ (see *Methods: Estimation of model parameters: Breeding ground recruitment*; also see Fig. 5).

[‡] $B_H = (1 - \text{TBL})p_3$ (see *Methods: Estimation of model parameters: Breeding ground recruitment*; also see Fig. 5).

[§] S = “True” survival (based on analysis of dead recoveries; see *Methods: Estimation of model parameters: Survival*). True survival is the probability that a given individual will survive over a specified interval (see Appendix B).

^{||} η = Fidelity (based on joint analysis of dead recovery and live encounter data; see *Methods: Estimation of model parameters: Survival*). Fidelity is the probability that a given individual will return to the sampling region, conditional on being alive; emigration ($1 - \eta$) is assumed to be a permanent departure from the sample (see Appendix B).

[¶] “Apparent” survival (ϕ) is estimated as the product of true survival and the fidelity rate ($\phi = S \cdot \eta$; see *Methods: Estimation of model parameters: Survival*). Apparent survival is equivalent to survival estimated from live encounters alone.

[#] I = Immigration rate, estimated as the total number of new individuals in the population at occasion $i + 1$ which entered the population between i and $i + 1$, and which were not in the population at i . Thus, for every single adult female at age x , we expect ($S_A \eta_A + I$) individuals at age $x + 1$ (see Appendix C).

^{††} Breeding propensity (α) is the age-specific probability that a given individual will attempt to breed, conditional on being alive and in the sample. Breeding propensity is estimated by scaling recapture rates relative to 5+-yr-old age class and setting $\alpha_{5+} = 0.85$ (see *Methods: Estimation of model parameters: Breeding propensity*).

and adult), where fidelity for both age classes varied as a linear function of time, with a block \times age interaction (Appendix B, Table B1). For a given treatment, juveniles were $\sim 20\%$ less likely to show fidelity to the traditional brood-rearing areas than were older birds (Table 1). This model was ~ 2.9 times better supported by the data than was the next best model in the candidate model set (Appendix B, Table B1). There was also no strong support of models containing a threshold change in fidelity rate between the 1982–1984 and 1985–1987 treatment blocks. It should be noted that given the significant dependencies in our data (evidenced by lack of fit to the most general model, necessitating use of a quasi-likelihood adjustment to model AIC values; Appendix B, Table B1), differences in

relative support of this magnitude are unlikely to constitute a large degree of support for the superiority of one model over the other (Royall 1997). However, our primary purpose was not to compare the relative fit of various models to our data, but rather to derive the most parsimonious parameter estimates for our projection model(s). Model weights are still robust for use in deriving parsimonious parameter estimates by averaging parameter values among models in the models sets, weighted by individual model weights (sensu Buckland et al. 1997; also see Appendix B). Parameter estimates for each block, averaged over all models, showed a general monotonic decline in fidelity over time (Table 1).

For recapture rate (used to derive estimates of breed-

ing propensity), the most parsimonious model was one where recapture rate was held constant among blocks, but varied among age classes (Appendix B, Table B1); thus derived values for breeding propensity increased with age from 2 to 5+ yr (Table 1).

Immigration into the breeding population at La Pérouse Bay was markedly episodic (Appendix C, Fig. C2), with large numbers of immigrant birds entering the population in some years. For example, between 1977 and 1978, the immigration rate was estimated to be ~34%, such that for each adult in the population in 1978 that was also in the population in 1977, 0.34 immigrant adults had entered the population between 1977 and 1978.

Periodically high immigration into the La Pérouse Bay is seemingly at odds with the expectation of strong natal philopatry (i.e., no net immigration of adult females) in this species (Cooke et al. 1995, and references therein). However, natal philopatry is probably a conditional trait; the probability of adult females returning to the natal colony is very high in this species, provided they are not constrained from doing so. We believe that the years with marked immigration can be related to specific climatic events that inhibited departure of birds that normally use La Pérouse Bay as a temporary staging area prior to continuing migration to other, more northerly colonies (Fig. 1). Notably, we have shown previously that such "stopovers" result in permanent immigration into the breeding population (Pradel et al. 1995). For example, 1977 and 1980 were both significant drought years in the midwestern agricultural regions of North America. In those years, Snow Goose productivity was significantly lower than in other years, presumably because the birds arrived on the breeding grounds in poorer physiological condition than in other years (Davies and Cooke 1983). Snowmelt at La Pérouse Bay was also extremely early in both years. If Snow Geese in general were in poorer condition, then it is conceivable that some of the geese temporarily staging at La Pérouse Bay were unable to continue migration north, and taking advantage of the abnormally early season availability of nesting in both years, recruited to the La Pérouse Bay population. More typically, Snow Goose migration is periodically halted by extremely poor weather. For example, in 1983, breeding at La Pérouse Bay was the latest on record, with generally cold and snowy conditions throughout the regions of the eastern arctic with significant Snow Goose breeding colonies (Fig. 1). A large number of migrating geese were undoubtedly prevented from further northward migration by the very late snowmelt, which might explain the high immigration rate between 1983 and 1984.

Since there was no detectable trend in the occurrence of years with either positive or negative values for I , we used the mean value averaged over all years ($\bar{I} = 0.09$; Table 1) as our estimate of the net impact of immigration on recruitment to the adult population.

Variation in projected growth

Projected population growth rate λ for each 3-yr treatment block declined monotonically over time, for models both with and without accounting for differences in fidelity rate, η . However, the rate of the decline in projected growth was significantly greater when derived from the models that included variation in fidelity rate than from the models where fidelity was assumed to be absolute (Fig. 6), reflecting the significant long-term declines in both adult and juvenile fidelity rates (Table 1). Under the assumption that any permanent emigration from the traditional La Pérouse Bay sample occurs only during the breeding season, this corresponds to a significantly greater decline in growth of the postnesting population, relative to the nesting population. Projections based on block-specific growth rates from these two models predict that the nesting population size (i.e., the number of birds in the traditional nesting sample) would be expected to have increased significantly over time (Fig. 6). In contrast, the size of the postnesting population (i.e., the sample using the traditional brood-rearing areas at La Pérouse Bay) is expected to have shown a marginal increase over the first five treatment blocks (i.e., from 1973 to 1988), followed by an actual decline in numbers in the last few years (1988–1990; Fig. 6).

While estimating the actual size of both the nesting and postnesting populations is difficult (for both technical and logistical reasons), there is good agreement among various measures of abundance and the prediction of our projection models. Annual survey estimates of the size of the nesting population indicated that the population has increased ~11-fold, from ~2000 pairs in 1973 to ~22 500 pairs in 1990. This relative increase is very close to the projected increase of the nesting sample (12.6-fold increase; Fig. 6). The nesting sample underestimates the size of the total prebreeding population (since it only reflects breeding birds, and does not count nonbreeding individuals). Provided there is no systematic variation in the proportion of nonbreeding birds (Appendix B; see also Cooch et al. 1999), then the nesting sample is a robust index of the increase in the prebreeding population.

In contrast, annual mean visual counts of Snow Geese in the vicinity of fixed observation towers on the brood-rearing areas at La Pérouse Bay declined at a fairly gradual rate from 1979 (when the surveys were initiated) to 1987, at ~4–5% per annum. This value is also very close to the projected rates of change, which averaged –5.4%/yr. Jolly-Seber (J-S) estimates of the size of the adult population at banding (i.e., the size of the population in the traditional banding area sampled) were also generally consistent with the expectation based on our model projections (although there was considerable annual variation in our estimates reflecting the episodic pattern of immigration into the colony; Appendix C). A 3-yr moving average of these

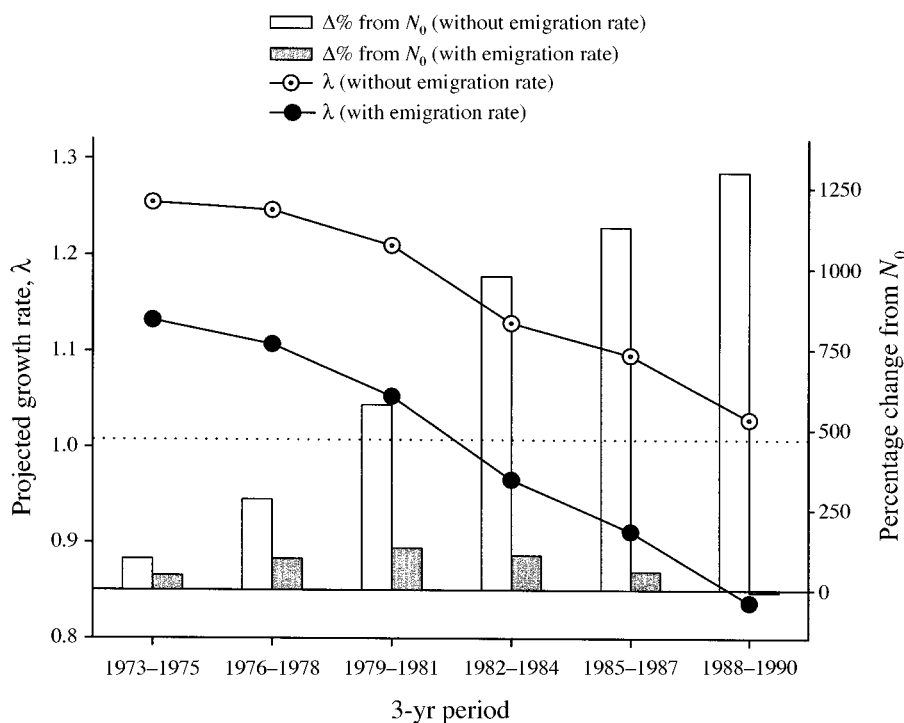


FIG. 6. Variation in projected population growth rate (lines) and percentage change in population abundance (bars) as a function of treatment block (1973–1975 to 1988–1990); and the presence or absence of emigration rate in the model, which corresponds functionally to prebreeding census (without emigration) or postbreeding census (with emigration). Projected abundance change is based on multiplication of initial starting vector (based on stable-stage vector for the first treatment block) by block-specific growth rates.

estimates increased from 1500 to 2000 in the early years of the study, peaking in about 1986 (slightly later than predictions based on the population projections; Fig. 6), with a slight decline in recent years.

Based on the good qualitative fit of our models to observed changes in prebreeding and postnesting abundance at La Pérouse Bay, we proceeded to partition the sources of the variation in projected growth using retrospective LTRE analysis.

Retrospective analyses: LTRE

We decomposed $\alpha^{(m)}$ (the difference in λ between the treatment and reference matrices; Eq. 4) into the contributions due to the differences in each matrix element (Eq. 5), for both models parameterized both with and without variation in fidelity rate. In each case, the mean matrix of the set of matrices for a given model type was used as the reference matrix. The accuracy of the first-order approximation was assessed by testing for concordance of observed and expected values of λ for a given treatment block (Eq. 6). In all cases, observed and predicted values of λ differed by $\ll 1\%$, suggesting the first-order approximation was satisfactory for this analysis.

Block-specific $\alpha^{(m)}$ declined over time, regardless of whether or not variation in fidelity rate was included in the model (Fig. 7). In both cases, fertility (the prod-

uct of breeding propensity, reproductive success during breeding, and juvenile survival: $\gamma_i B_i S_Y \eta_Y$; Fig. 3) contributed a significantly greater proportion of the variation in $\alpha^{(m)}$ than did the combined contributions of adult survival and immigration rate (Fig. 7). Thus although true adult survival (which has the greatest *potential* proportional contribution to growth based on a *prospective* perturbation analysis; Rockwell et al. 1997) increased significantly over the course of the study (Francis et al. 1992a; Table 1), the long-term declines in both breeding success and juvenile survival (B_i and S_Y) had a significantly greater impact, based on a retrospective analysis.

However, although the relative magnitude and sign of the *fertility* contributions to $\alpha^{(m)}$ are similar between the two models (increasingly negative with decreasing α), the contributions of *adult survival* to variation in α were (1) increasingly positive with decreasing α for the model based on “true” survival only ($\eta = 1$) and (2) a near constant positive contribution until the 1982–1984 block, after which the contribution was increasingly negative over time for the model based on “apparent” survival (i.e., when variation in fidelity rate was included in the model; $\eta < 1$). This difference reflects the interaction of changes in true survival and fidelity rate. For the model based on true survival only (i.e., assuming $\eta = 1$), the positive increasing contri-

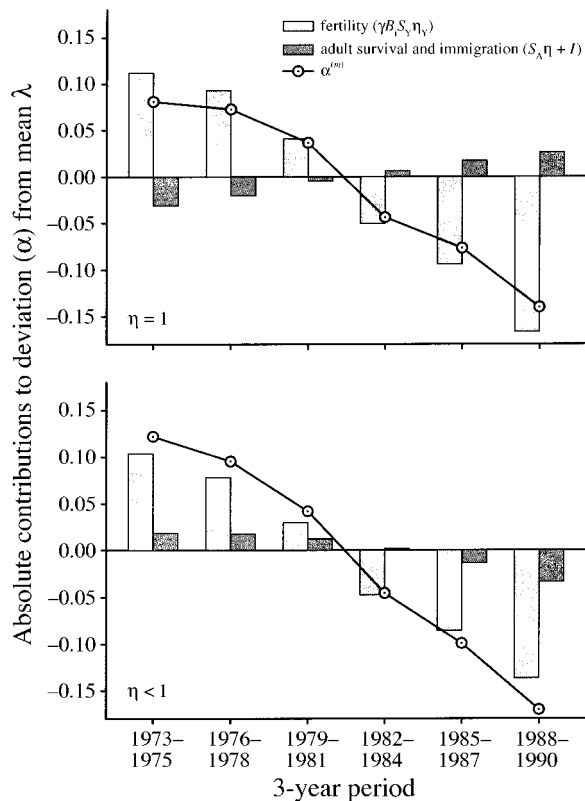


FIG. 7. Results of LTRE analysis of variation in growth rate among treatment blocks, using fixed-effects single-classification model. Lines connect estimates of block-specific overall $\alpha^{(m)}$ (deviation of block-specific λ from reference value based on mean matrix; Eqs. 4 and 5). Bars represent proportional contribution of principal underlying vital rates (fertility and adult survival; Fig. 1) to $\alpha^{(m)}$.

bution of the net adult survival reflects entirely the long-term increase in adult survival over the course of the study. All other things being equal, increasing adult survival would increase the growth rate of the population (and thus contribute positively to α). In contrast, apparent adult survival has not increased over the study, but has in fact declined over time in a nonlinear manner; while true survival (S_i) has increased, fidelity rate (η_i) has declined (Table 1). This is characterized by a slow increase in "apparent" survival over the first few time blocks, and a more rapid decline in recent years (Table 1). Thus the decrease in $\alpha^{(m)}$ after the 1982–1984 block (Fig. 7) suggests that the decreasing fidelity rate is contributing significantly more than true adult survival rate.

We further tested this hypothesis by assessing the relative contribution of each lower-level vital rate to variation in fidelity rate ($\eta = 1$), by far the greatest proportion of the relative variation in $\alpha^{(m)}$ is contributed by changes in first year postfledging survival (S_Y), with a slightly increasing contribution to $\alpha^{(m)}$ over time (Fig. 8). Of the remaining component vital rates, adult sur-

vival (S_A) and posthatch fertility (B_H) contribute approximately equally over time, while the contribution of changes in pre-hatch fertility (B_L) was generally inconsequential. Thus most of the variation in the growth of the nesting population at La Pérouse Bay (contingent on the assumption that a bird will return to the colony to attempt to breed, given that it is alive) reflects changes in postfledging juvenile survival. Although there has been a systematic decline in breeding ground reproductive success (Cooch et al. 1989, Williams et al. 1993; Table 1), these changes have contributed relatively little to long-term changes in growth potential of the nesting population; most of the variation in recruitment rate reflects changes in postfledging gosling mortality.

However, while the long-term decline in first year survival would seem to predict an eventual decline in the size of the nesting population at La Pérouse Bay (i.e., fewer goslings surviving their first year to be recruited into the breeding population), this is more than offset by both the high adult survival, and the significant numbers of adults immigrating into the nesting population on average each year over the period of the

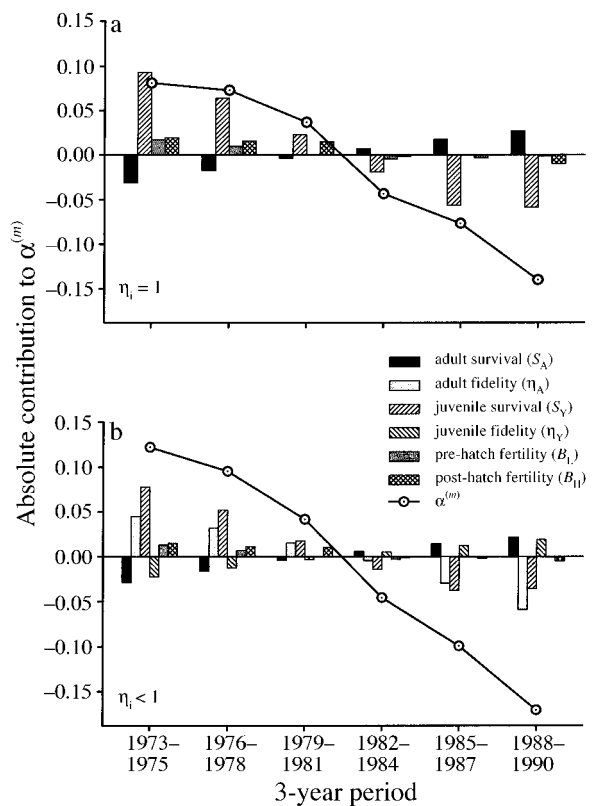


FIG. 8. Lower-level contributions of individual vital rates to variation in $\alpha^{(m)}$ for each treatment block, for models (a) without fidelity rate (i.e., $\eta = 1$) and (b) with emigration (fidelity) rate (i.e., $\eta < 1$). Bars represent the proportion of the contribution of each rate to $\alpha^{(m)}$. Since neither breeding propensity (γ_L) nor immigration rate (I) varies over time (Table 1), neither contributes to variation in I .

study. Thus while the projected rate of growth of the nesting population has declined over time (Fig. 6), the significant immigration into the breeding population has kept the population in a positive growth trajectory, albeit at a decreasing rate.

In contrast, when variation in fidelity rate was included in the model, the summed value of adult fidelity rate (η_A) and juvenile survival (S_Y) contributed >55% of the variation in α over all blocks (Fig. 8). Both factors have declined significantly over the course of the study (Table 1). As in the previous case, however, there was heterogeneity in the relative contribution of both factors to variation in α . In the early years of the study (blocks 1973–1975 and 1976–1978), juvenile survival contributed significantly more to variation in α than did the sum of adult fidelity and immigration rates. Since the 1976–1978 period, the apparent difference in relative contributions has decreased, and was reversed in the 1988–1990 block (adult fidelity contributing proportionately more to $\alpha^{(m)}$ than the contributions from juvenile postfledging survival). Since immigration rate, I , was held constant in our analyses, the progressive decline over time in postnesting abundance in the traditional sampling areas at La Pérouse Bay reflects decreasing first year survival, and to an increasing degree, a significant decline in adult fidelity, η , to the traditional brood-rearing areas.

DISCUSSION

We used retrospective analysis to explore the underlying factors contributing to variation in the dynamics of the Snow Geese breeding at La Pérouse Bay. There has been a long-term decline in the abundance and quality of food plants available to the birds at La Pérouse Bay (Williams et al. 1993, Abraham and Jefferies 1997, Jefferies 1997), which has led to systematic changes in various measures of Snow Goose fertility and survival. By treating the systematic changes in food abundance as “treatment levels” in a “natural experiment,” we examined the relative contributions of the changes in each of the vital rates to changes in projected growth rate over time.

Previous prospective perturbation analysis indicated that adult survival had the greatest potential impact on projected growth of the Snow Geese at La Pérouse Bay (Rockwell et al. 1997). However, growth rates of both the nesting and postnesting population (using both projected and realized measures of growth) declined significantly over time despite a significant long-term increase in adult survival. This clearly implied that changes in other factors must have been relatively more important. Retrospective analysis using the life table response experiment (LTRE) approach indicated that most of the variation in recruitment to the nesting population reflected a decline in postfledging survival of juveniles (S_Y ; Fig. 8). Posthatch fertility was the next most important factor. These observations are consistent with results from an earlier analysis (Cooke and

Francis 1993) and from Williams et al. (1993). Notably, although Snow Geese are a hunted species, the majority of postfledging mortality occurs before the geese reach the areas where hunting occurs in the fall (Francis et al. 1992a, Cooke and Francis 1993), reflecting increased mortality on the breeding grounds due to decreased growth of goslings. Thus most of the variation in recruitment to the nesting population reflects the impacts of progressively degraded foraging habitats on gosling growth and survival.

Our analyses indicated that juvenile survival was also important to variation in the projected growth of the postnesting population, but in addition, emigration of adults from the postnesting population had an increasingly large impact over time (Fig. 8). As foraging conditions at La Pérouse Bay have steadily declined, increasing numbers of family groups are locally emigrating from the traditional colony during brood rearing (Table 1). This result is consistent with a recent analysis of fidelity in Black Brant (Lindberg et al. 1998), which strongly implicated reduced fidelity with increasing population density. In contrast to the brant study, however, we found no evidence of significant age specificity in emigration rate beyond the second age class (Appendix B, Table B1). Juveniles were generally less likely to show fidelity to the traditional brood-rearing areas than were older birds; however, fidelity rate among adults also declined significantly. Since our analysis was based on data from birds marked as goslings, this result implies an age-specific plasticity in fidelity rate in this population; for a given treatment block, younger birds are less likely to return to the traditional brood-rearing areas. Among those birds that did exhibit fidelity during the first year, subsequent fidelity as an adult was significantly higher (Table 1; sensu Lindberg et al. 1998), which may be consistent with effects of age and experience on selection of brood-rearing location (Rockwell et al. 1993). Our analyses failed to support a significant threshold change in the fidelity rate (Appendix B), despite possible changes in the stability of the grazing ecosystem since 1982–1984 (R. L. Jefferies, *personal communication*). In addition, our estimate of the net emigration from the population is likely conservative, since it does not reflect heterogeneity of response of adult birds to being handled during banding. Our joint analysis of live recapture and dead recovery data was restricted to birds banded as goslings, whereas estimates of immigration rate, I , were based on the sample of individuals first banded as adults. Pradel et al. (1995) showed that for birds banded as adults (which will include some in situ adult recruits, and some immigrants), a significant proportion (~25%) permanently emigrate from the sampling area the year following marking. However, Pradel et al. (1995) did not detect a significant difference in the probability of emigrating from the traditional banding sample following marking as an adult between adults known to have been hatched at La Pérouse Bay (web-tagged adults),

and adults of unknown origin. The effect of handling on newly banded adults did not seem to be specific to birds likely to consist of some unknown number of immigrants. Thus we believe that the effect of handling on net emigration of adult birds from La Pérouse Bay is a latent process occurring in all years of our study, notably offset in some years by significant immigration of birds into the population.

In our analyses, we assumed that any permanent emigration occurred after nesting (i.e., during the interval between nesting and the postbreeding census; Fig. 4). Given this assumption, the consequences of emigration do not affect the growth of the nesting population directly. However, these consequences might do so through differential reproductive success between birds that remain at La Pérouse Bay and those that emigrate (*sensu* Cooch et al. 1993) if offspring from dispersed families are recruited into the La Pérouse Bay nesting sample. Departure of adults during brood rearing has direct impact on the postnesting population. Permanent emigration during brood rearing is demographically equivalent to mortality prior (and relative) to the postnesting census, and increasing emigration is equivalent to decreasing apparent survival (Table 1). In contrast to the nesting sample, where true survival has increased, the postnesting sample decline reflects a significant decrease in apparent survival.

This heterogeneity has several consequences for drawing general conclusions about the dynamics of the La Pérouse Bay population. Decreasing first year survival suggests that there will be an eventual decline in the number of birds nesting in the sampled area, if the assumption of a constant net immigration rate is met. Projecting the pattern of such changes is likely to be complicated by increasing numbers of birds nesting outside of the traditional La Pérouse Bay nesting area, and closer to the brood-rearing areas that are currently used (Fig. 2). In our present analysis, we implicitly assumed that the frequency of this event is low (such that the estimated emigration rate for birds banded as goslings reflects emigration during the breeding season). However, philopatry to the La Pérouse Bay nesting colony will likely become maladaptive eventually, and there is good reason to believe that emigration during the nonbreeding season will increase (*sensu* Lindberg et al. 1998). Testing this hypothesis will require sampling at least twice during the season (e.g., at the beginning and end of the nesting season), which is logistically difficult at La Pérouse Bay.

The changes in abundance of birds using the brood-rearing areas at La Pérouse Bay has been much more rapid, and dramatic; in recent years there are very few Snow Geese from the traditional La Pérouse Bay nesting population that continue to use the traditional brood-rearing areas. Since the mid 1980s, there has been an increasing rate of emigration from La Pérouse Bay during brood rearing (Table 1; see also Cooch et al. 1993), with significantly higher reproductive suc-

cess among dispersing individuals. This observation characterizes one of the difficulties in assessing the causes and consequences of variation in population dynamics in wild populations. Many times, assessments are restricted to localized sampling areas, and projecting the consequences over a larger scale is potentially difficult. At La Pérouse Bay, the postnesting population within the traditional sampling areas has been in serious decline for some time, and there are recent indications that recruitment to the prebreeding nesting colony, at least in the traditional nesting areas, is also experiencing a decline, albeit more slowly than the postnesting population (Fig. 2). And yet the larger "super population" of Snow Geese in the La Pérouse Bay and Cape Churchill area has been steadily increasing, reflecting both the higher reproductive success among dispersing individuals (Cooch et al. 1993), and significant permanent immigration into the population in some years (Appendix C; Pradel et al. 1995).

It is intriguing to consider the larger role such immigration may play in the dynamics of the La Pérouse Bay ecosystem. Migratory geese generally arrive in large numbers early in the season, when little (if any) aboveground biomass is available. Early in the season, geese engage in "grubbing" of roots and other forms of belowground biomass, which significantly damages immediate survival and long-term viability of their preferred forage plants. It has been suggested that it is principally this early season grubbing, particularly by large numbers of "nonresident" birds, which has precipitated the trophic cascade at La Pérouse Bay (Bazely and Jefferies 1996, Abraham and Jefferies 1997, Jefferies 1999). However, while growing numbers of geese at La Pérouse Bay (including both in situ recruits and immigrants) have undoubtedly increased the extent of destructive grubbing, they will also contribute to increased grazing pressure on emergent aboveground biomass during nesting, and later during brood rearing following hatch. While the primary saltmarsh food plants have been shown to respond positively to moderate levels of grazing pressure (e.g., Cargill and Jefferies 1984, Hik and Jefferies 1990), it is possible that grazing pressure has significantly exceeded this capacity, and that grazing itself may be a more significant factor in the progressive degradation of the La Pérouse Bay colony than previously thought. This is currently under investigation.

Management and conservation efforts clearly benefit from analysis of the pattern of demographic variation in the species in question, but as our study demonstrates, partitioning the effects of this variation on the status of the population needs to be considered carefully in the context of the timing and spatial scope of the analysis. Our results indicate philopatry to the brood-rearing areas may be a significantly more plastic trait than fidelity to nesting areas, supporting the original suggestions made by Abraham (1980) and Cooke and Abraham (1980), and that the rates of change in

the size of the population censused at the start and end of the breeding season may differ significantly. We concur with Lindberg et al. (1998) that more careful study of the role of immigration and emigration (and movement in general) in population dynamics, using robust estimates of emigration and survival rates, are needed.

*Retrospective analysis—asymptotic,
or direct analysis?*

The LTRE has been proposed as a robust method for retrospective analysis of the effect of variation in vital rates on population dynamics (Caswell 2000). However, it should be noted that the LTRE approach is based on prospective perturbation (sensitivity) analysis (Eq. 5), and assesses the influence of the underlying vital rates on *projected* asymptotic growth (although it may be possible to consider retrospective analysis based on transient rather than asymptotic dynamics; see Fox and Gurevitch 2000), relative to a reference value, rather than assessing *realized* (i.e., observed) changes in growth rate directly. Recently, Nichols et al. (2000) have described an approach for direct analysis of a time series of realized growth rates, based on analysis of mark-recapture data. Their approach rests on the duality that mark-recapture methods for estimation of the probability of departure from the population (emigration, mortality) can be used equivalently to estimate the probability of entry into the population (in situ recruitment, immigration). Estimates of the realized rates of departure and entry fully specify the actual growth of the population. Nichols et al. (2000) have shown that it is possible to directly estimate the realized contribution of one or more vital rates to observed differences in growth.

Clearly, both approaches rely on the same underlying vital rates, and both methods consider the effect of differences in one or more vital rates on some measure of the cumulative effect of all of the vital rates considered simultaneously; that effect being the growth of the population (either realized, or projected). The relationship between projected growth (deterministic or stochastic), the variance and covariance of the vital rates, and the observed (retrospective) variation in realized growth rate, is clearly in need of more study.

However, regardless of which measure of population growth is used in a retrospective analysis, it is important to remember that such studies generally rely on analysis of a single realization of a complex set of underlying stochastic processes, which may limit the degree to which retrospective analysis may (or may not) inform prospective applications. As Caswell (1989:20) notes, "Interpreted as projections, the results of demographic analyses reveal something about *present* conditions, not about the *future* behavior of the population." Renshaw (1991) has also strongly cautioned against making prospective inferences from single realizations of the dynamics of a population (see

also Caswell 2000). This issue warrants consideration in any retrospective analysis, regardless of whether variation in growth of the population is analyzed directly (sensu Nichols et al. 2000) or not (e.g., LTRE analysis; Caswell 1989, 2000).

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APPENDIX A

NON-ADDITIVITY IN ANALYSIS OF LOWER-LEVEL CONTRIBUTIONS IN LIFE TABLE RESPONSE EXPERIMENTS: THE PROBLEM OF SUMS AND PRODUCTS

Consider a set of Leslie projection matrices with the structure

$$\begin{bmatrix} 0 & F_2 & F_3 \\ S_1 & 0 & 0 \\ 0 & S_2 & 0 \end{bmatrix} = \begin{bmatrix} 0 & C_2 S_1 & C_3 S_1 \\ S_A & 0 & 0 \\ 0 & S_A & 0 \end{bmatrix}.$$

The fertility elements are products of C_i (age-specific clutch size, say), and S_j (first-year survival rate), while the survival elements along the diagonal represent adult survival, S_A . From Eq. 7 (following Caswell 1996b), the overall deviation ($\alpha^{(m)}$) from the reference matrix (m) can be written in terms of the underlying component vital rates (C_i , S_j and S_A):

$$\hat{\alpha}^{(m)} = \lambda^{(m)} - \lambda^{(\cdot)}$$

$$\equiv \left(\sum_i (C_i^{(m)} - C_i^{(\cdot)}) \frac{\partial \lambda}{\partial C_i} + \sum_j (S_j^{(m)} - S_j^{(\cdot)}) \frac{\partial \lambda}{\partial S_j} + \sum_i (S_A^{(m)} - S_A^{(\cdot)}) \frac{\partial \lambda}{\partial S_{A_i}} \right) \frac{1}{(1/2)(A^{(m)} + A^{(\cdot)})} \quad (\text{A.1})$$

where in general,

$$\frac{\partial \lambda}{\partial x} = \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \cdot \frac{\partial a_{ij}}{\partial x}.$$

Assume that the mean matrix is used as the reference matrix. We note that each term in Eq. A.1 consists of two parts: the first is the difference between the value of a given lower-

level parameter given matrix (m), and the mean of that parameter average over all matrices (\cdot). The second part is the partial derivative of λ with respect to the same parameter (i.e., the sensitivity). In the former case, when using the mean matrix as the reference, the difference is calculated with respect to the mean of that individual parameter over all matrices in the analysis. However, the partial derivative is calculated using a sensitivity matrix derived relative to the mean matrix, calculated using the mean of the a_{ij} values over all matrices. In other words, the first term is a function of the mean of the individual parameters, whereas the second term is a function of the mean of a_{ij} values, which may represent single parameters, or (commonly) products of lower-level parameters. However, the means of the individual parameters are not the same as the means of the a_{ij} themselves, since

$$\frac{(a \cdot b) + (c \cdot d)}{2} \neq \frac{(a + c)}{2} \cdot \frac{(b + d)}{2}.$$

In the present example,

$$\frac{(C_1^A \cdot S_1^A) + (C_1^B \cdot S_1^B)}{2} \neq \frac{(C_1^A + C_1^B)}{2} \cdot \frac{(S_1^A + S_1^B)}{2}.$$

This inequality (essentially Jensen's inequality) may create a systematic bias in the estimation of the contribution of the lower-level elements. Further, this bias does not seem to be corrected by adding second-order terms (Caswell 1996b) to the linear approximation.

For example, consider the situation with two levels of a particular treatment, yielding matrices **A** and **B**, respectively, each having the form

$$\begin{bmatrix} 0 & F_2 & F_3 \\ S_1 & 0 & 0 \\ 0 & S_2 & 0 \end{bmatrix} = \begin{bmatrix} 0 & C_2 S_1 & C_3 S_1 \\ S_A & 0 & 0 \\ 0 & S_A & 0 \end{bmatrix}$$

where the parameters are as previously defined. The parameter values for the two matrices are:

A	B
$C_2 = 1.5$	$C_2 = 1.7$
$C_3 = 1.7$	$C_3 = 2.0$
$S_1 = 0.4$	$S_1 = 0.45$
$S_A = 0.85$	$S_A = 0.75$

Thus,

$$\mathbf{A} = \begin{bmatrix} 0 & 0.60 & 0.68 \\ 0.85 & 0 & 0 \\ 0 & 0.85 & 0 \end{bmatrix} \quad \mathbf{B} = \begin{bmatrix} 0 & 0.765 & 0.90 \\ 0.75 & 0 & 0 \\ 0 & 0.75 & 0 \end{bmatrix}$$

where the mean matrix is $(\mathbf{A} + \mathbf{B})/2$:

$$\begin{bmatrix} 0 & 0.6825 & 0.7900 \\ 0.8000 & 0 & 0 \\ 0 & 0.8000 & 0.8000 \end{bmatrix}.$$

The projected growth rates for the matrices **A** and **B**, and mean matrix, are 1.001, 1.032, and 1.021, respectively. If the mean matrix represents the reference matrix against which the other two are compared, then clearly, the overall contribution of matrix **A** will be negative, while that for matrix **B** will be positive. A single-classification LTRE (using the first-order approximation) yields estimates of α_i consistent with this expectation: $\alpha_A = -0.0199$ and $\alpha_B = 0.0112$.

The α_i values represent the sum of the contributions of the individual a_{ij} values. The corresponding contribution matrices (\mathbf{C}_i) are as follows:

$$\mathbf{C}_A = \begin{bmatrix} 0 & -0.0271 & -0.0295 \\ 0.0247 & 0 & 0 \\ 0 & 0.0119 & 0 \end{bmatrix}$$

$$\mathbf{C}_B = \begin{bmatrix} 0 & 0.0252 & 0.0254 \\ -0.0268 & 0 & 0 \\ 0 & -0.0126 & 0 \end{bmatrix}.$$

The contribution matrices provide the expectations for the sum of the contributions of the lower-level elements to α_i . For example, considering "treatment A," and using the mean matrix as the reference, the mean adult survival S_A (averaged over matrix **A** and **B**) is 0.8. The sensitivity matrix evaluated halfway between matrix **A** and the mean matrix is

$$S_A = \begin{bmatrix} 0 & 0.3284 & 0.2678 \\ 0.4938 & 0 & 0 \\ 0 & 0.2386 & 0 \end{bmatrix}.$$

Thus,

$$\begin{aligned} \sum_i (S_{Ai}^A - S_{Ai}^C) \frac{\partial \lambda}{\partial S_{Ai}} \\ = [(0.85 - 0.8)(0.4938)] + [(0.85 - 0.8)(0.2386)] \\ = 0.0247 + 0.0119 = 0.0366. \end{aligned}$$

We note that 0.0247 and 0.0119 match precisely the corresponding elements of the \mathbf{C}_A matrix ($a_{2,1}$ and $a_{3,2}$, respectively).

However, these two elements are a function of S_A only. What about the fertility elements, F_i , which are functions of two lower-level parameters ($F_i = C_i S_i$)? We start with C_i . The first step involves deciding what mean C value to use in the calculations in Eq. A.1. The most obvious choice is to simply sum the respective C_i values and divide by two. Doing this yields 1.6 and 1.85 as the mean C_2 and C_3 values, respectively. Using these mean values, the contribution of C_i to the overall α_i for matrix **A** is calculated as

$$\begin{aligned} \sum_i (C_i^A - C_i^C) \frac{\partial \lambda}{\partial C_i} \\ = [(1.5 - 1.6)(0.3284)(0.4)] + [(1.7 - 1.85)(0.2678)(0.4)] \\ = -0.01314 - 0.01607 = -0.02921. \end{aligned}$$

For the parameter, S_j and using the appropriate mean value (0.425), the contribution of S_j to the α_i value for matrix **A** is calculated as

$$\begin{aligned} \sum_i (S_{ji}^A - S_{ji}^C) \frac{\partial \lambda}{\partial S_{ji}} \\ = [(0.4 - 0.425)(0.3284)(1.5)] \\ + [(0.4 - 0.425)(0.2678)(1.7)] = -0.01232 - 0.01138 \\ = -0.02370. \end{aligned}$$

In both cases, where lower-level parameters are analyzed, there is a discrepancy between the sum of the lower-level contributions and the observed value(s) for α_i . For example, for the parameter F_2 , the overall contribution (matrix \mathbf{C}_A) was calculated in the LTRE as -0.0271 . However, summing the lower-level contributions yields $(-0.01314 + -0.01232) = -0.02546$. The same situation exists for parameter F_3 ; the overall contribution was calculated as -0.0295 , but the sum of the lower-level contributions is again higher $(-0.01607 + -0.01138 = -0.02745)$. When considering the overall α_A value (calculated to be -0.0199 in the LTRE), the total of the calculated lower-level contributions is $(0.0366 + -0.0292 + -0.0237) = -0.0163$. The same thing is true (in reverse) for the other matrix (**B**).

While the differences in this example are arguably small, they can become large, especially for stage-based matrices where many of the individual a_{ij} elements are product terms. And, in each case, the discrepancy appears when

partitioning a_{ij} contributions that are products when using the mean matrix as a reference matrix, since the means of the individual parameters are not the same as the means of the a_{ij} .

APPENDIX B

COMBINED ANALYSIS OF RECOVERY AND RECAPTURE DATA FROM GOSLINGS BANDED AT LA PÉROUSE BAY, 1973–1990

We used the approach described by Burnham (1993) to derive estimates of both adult and juvenile survival and fidelity rates (i.e., 1–emigration rate) for each 3-yr treatment block, using combined live recapture and dead recovery data for 22 556 females banded as goslings at La Pérouse Bay from 1972–1990. Program MARK (White and Burnham 1999) was used for all estimations. We used only data from female geese banded as goslings since previous analysis indicated significant heterogeneity in emigration rate between birds banded as goslings and birds banded as adults (Pradel et al. 1995).

Following Burnham and Anderson (1998), we first defined a candidate model set, which included a general global model which (1) was sufficiently parameterized to include all of the effects believed relevant to the analysis (variation among treatment block, and among age classes within treatment blocks), and (2) reflected results from previous analysis of one or more of the individual parameters. The global model was parameterized to allow full (block \times age) interaction. For survival, and recovery rates we used a two-age-class model, with the first age class spanning one year; previous analyses indicated significant differences between first-year and subsequent survival, but no differences among older age classes (Francis et al. 1992a). For estimation of emigration rate, we used a five-age-class model. A recent analysis of Pacific Black Brant (*Branta bernicla nigricans*) indicated strong age specificity in several components of fidelity (Lindberg et al. 1998). We restricted our general model to five age classes since that was the maximum age class in our matrix projection models. We also used a five-age-class model for estimation of the recapture rate. The age specificity in recapture rate was incorporated to accommodate differences in breeding propensity among age classes; in Snow Geese, the probability of being recaptured is conditional on being alive and in breeding state, since only breeding birds remain in the sample area to be recaptured (Cooke et al. 1995). Five age classes were used since reproductive maturity in Snow Geese is reached at five years of age, with the recapture rate for the first age class fixed to zero (yearling Snow Geese do not breed).

Our candidate model set consisted of the global model, plus a series of 24 reduced parameter models, which were broadly divided into two structural types. Since previous analysis (Francis et al. 1992a, Cooch et al. 1993, Cooke et al. 1995) indicated significant long-term trends in all four parameters, in some of the models estimates were constrained to be linear functions of 3-yr treatment blocks (the blocks

are ordinal, and the rank ordering of blocks is a natural linear covariate), with sequentially reduced interaction structure between age and the linear time covariate for each parameter.

In addition, we also included a series of models where the parameter changed as a step function between a specific pair of treatment blocks, to accommodate the possibility of a threshold (rather than linear) change in estimates. Previous analysis indicated that components of the fertility parameters of our model, particularly those occurring between hatching and fledging (Cooch et al. 1993, Rockwell et al. 1993, Williams et al. 1993, Cooke et al. 1995), had changed in a threshold fashion, approximately between the 1982–1984 and 1985–1987 treatment blocks. Model notation followed Lebreton et al. (1992). The factorial structure of the model is represented by subscripting the primary parameters using “a” for putative age effects, “b” for block differences, “c” for pre/post-threshold differences, “lin” for linear time effects, and “.” for constant effects. Relationships among factors were indicated using standard linear models notation.

Selection among models in the candidate model set was based on comparison of the QAIC_c (Lebreton et al. 1992, Burnham and Anderson 1998):

$$\text{QAIC}_c = \frac{-2 \ln(L)}{\hat{c}} + 2np + \frac{2np(np + 1)}{n_{\text{ess}} - np - 1}$$

where L is the model likelihood, np is the number of estimable parameters, n_{ess} is the effective sample size, \hat{c} and is the quasi-likelihood adjustment for over dispersion in the data. The model likelihoods, number of estimable parameters, and the effective population size are estimated directly by program MARK (White and Burnham 1999). The quasi-likelihood parameter was estimated using a parametric bootstrap approach. The estimate of \hat{c} was derived by dividing the observed deviance for the general model by the mean deviance for the bootstrapped models. This approach assumes that the mean of the simulated deviances represents the expected value of the deviance under the null model of perfect fit of the model to the data. If the model fits the data well, \hat{c} is asymptotically 1.0. The model with the lowest QAIC_c is accepted as the most parsimonious model for the data.

Comparisons among models in the candidate set were accomplished by deriving an index of relative plausibility, using normalized Akaike weights (Burnham and Anderson 1998). Individual model Akaike weights, w_i were calculated as

$$w_i = \frac{e^{(-\Delta\text{QAIC}_c/2)}}{\sum \{e^{(-\Delta\text{QAIC}_c/2)}\}}$$

TABLE B1. Summary of model testing for female Snow Geese goslings banded at La Pérouse Bay, Manitoba, Canada.

Model	QAIC _c	ΔQAIC_c	QAIC _c weight	np^\dagger	Deviance
$S_{a2-\text{lin-lin}}P_{a5-././././}r_{a2-\text{lin-lin}}\eta_{a2-\text{lin+lin}}$	15272.35	0.00	0.655	15	3330.97
$S_{a2-\text{lin-lin}}P_{a5-././././}r_{a2-\text{lin-lin}}\eta_{a2-\text{lin}}$	15274.47	2.12	0.227	14	3344.77
$S_{a2-\text{lin-lin}}P_{a5-././././}r_{a2-\text{lin+lin}}\eta_{a2-\text{lin+lin}}$	15275.80	3.45	0.117	14	3349.24
General model	15292.58	20.23	0.000	40	3230.87

Notes: Models were sorted by increasing QAIC_c value. Models with QAIC_c weights >0.005 are listed, with the most parsimonious model at the top. The factorial structure of the model is represented by subscripting the primary parameters. Relationships among factors were indicated using standard linear models notation.

† Number of estimated parameters (which is less than or equal to the number of parameters that are potentially estimable given the structure of the model).

where ΔQAIC_c is the absolute numerical difference in QAIC_c between a given model and the model in the candidate model set with the lowest QAIC_c . The ratio of w_i between any two models indicates the relative degree to which the model with the greater Akaike weight is better supported by the data than the other model. To account for uncertainty in model selection (Burnham and Anderson 1998), we report parameter estimates $\hat{\theta}$ and associated standard errors derived by averaging over all models in the candidate model set, weighted by Akaike model weights (sensu Buckland et al. 1997):

$$\text{avg}(\hat{\theta}) = \sum_{i=1}^R w_i \hat{\theta}_i$$

where w_i reflects the Akaike weight for model i .

Goodness of fit (GOF) of the general model $\{S_{a2-b^*b}P_{a5-b/b}b/bb^*r_{a2-b^*b}^*r_{a2-b^*b}\}$ to the data was assessed by comparing the observed deviance of the general model against the distribution of deviances from 100 bootstrapped data sets. Fit of the general model to the data was poor ($P \ll 0.001$); the mean value of quasi-likelihood parameter \hat{c} calculated from the bootstrapped samples was 1.85. As noted in the text, \hat{c} is asymptotically 1.0 if the model fits the data perfectly.

Although there is clear lack of fit between our general model and the data, we chose to proceed with the analyses, applying the quasi-likelihood correction to the model fits. We did so for several reasons. First, the conceptual basis of all models is "data = structure + residual variation." In general, the structure of the residual variation is unknown, but for multinomial distributions, it is known. If the model structure is "correct," then the then the variance of the residual "noise" is 1.0 (where variance is defined as the expected value of the GOF χ^2 divided by its degrees of freedom). Adjustment of the model fit using values of $\hat{c} \leq 3$ is generally robust (Lebreton et al. 1992; D. Anderson *personal communication*). Second, our model imposed a significant structure to the data. The use of contiguous 3-yr treatment blocks is clearly artificial, and much of the lack of fit to the data undoubtedly reflects this structuring.

We applied the quassi-likelihood adjustment to the results from our candidate model set (Table B1). Only models where the QAIC_c weight is >0.005 are shown (the influence of models with weights <0.005 on model averaged parameter estimates is extremely small).

APPENDIX C

PARTITIONING RECRUITMENT INTO COMPONENTS REFLECTING IN SITU PRODUCTION AND IMMIGRATION IN AN OPEN POPULATION

Following Pollock et al. (1990) and Nichols and Pollock (1990), the rate of immigration into an open population can be estimated as

$$\hat{I}_i = \left(\frac{\hat{B}_i - \hat{B}'_i^{(A)}}{\hat{N}_i^{(A)}} \right) = \left(\frac{B_i^{(A)}}{\hat{N}_i^{(A)}} \right)$$

where \hat{B}_i (the expected total number of recruits into the population between time i and $i + 1$) is the sum of the expected number of in situ recruits, $B'_i^{(A)}$ (from Eq. 10), and the number of adult immigrants, $B''_i^{(A)}$ (from Eq. 11).

However, both Eqs. 10 and 11 as written assume that the interval between birth and recruitment is only one year (i.e., that there are only two age classes, juvenile and adult, with a 1-yr transition between the juvenile and adult age classes). However, yearling Snow Geese do not breed. Therefore, the interval between natal year and age of first breeding is at least two, and not one year (Cooke et al. 1995). Hence, the number of in situ recruits between year i and $i + 1$ must be conditioned on the number of goslings produced in year $i - 1$, times the product of juvenile and adult survival over the next two years:

$$\hat{B}_i^{(2)} = \hat{N}_i^{(J)} \hat{\phi}_{i-1}^{(J)} \hat{\phi}_i^{(A)}.$$

We use the superscript (2) in $B_i^{(2)}$ in this case to indicate in situ recruitment to the 2-yr-old age class in year $i + 1$. We use the superscripts J and A to indicate juvenile and adult survival, respectively; survival varies as a function of these two age groupings only.

However, we also note that the preceding expressions specify the expected number of *potential* recruits. In many populations, only a proportion of those individuals surviving to be recruited (i.e., the pool of *potential* recruits) actually recruit to the breeding population (*realized* recruit) at a given age. In general, the probability of a potential recruit becoming a breeding individual is different from what we referred to previously as breeding propensity, α_x . Breeding propensity (as we have defined it) is the probability of breeding at a given age; the breeding event may be the first breeding attempt for this individual (in which case breeding propensity and the probability of recruitment are the same), or it may be the result of a underlying stochastic process conditioned on having recruited (bred) at an earlier age. For example, the

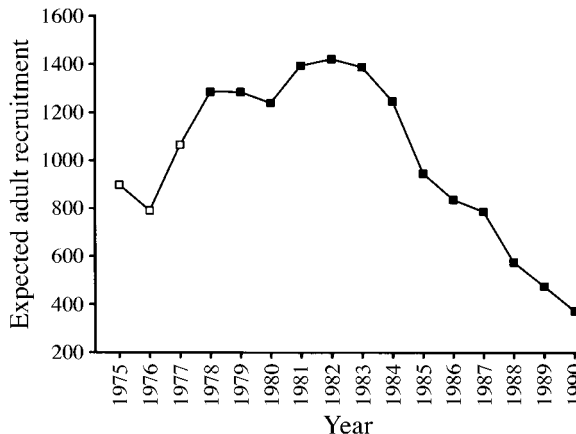
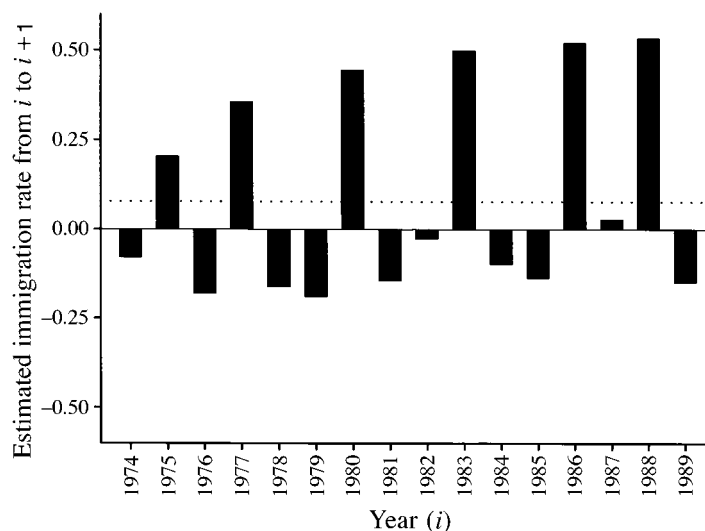


FIG. C1. Annual variation in expected number of in situ adult recruits ($B'_{i,n}^{(A)}$) into La Pérouse Bay population. Empty symbols (□) indicate values estimated using summation over <4 age classes.

probability of breeding at (say) four years of age in year i may be conditional on whether the individual bred for the first time (recruited) as a 2-yr-old, a 3-yr-old, or as a 4-yr-old bird (sensu Viallefont et al. 1995a, b). Individuals which do not recruit at age x may subsequently recruit at later ages, conditional on being alive and in the sample, and a recruit in year i at age x may or not breed in a subsequent year.

Thus, a precise derivation of the expected number of in situ recruits would require estimates of both age of recruitment and subsequent breeding propensity. Unfortunately, our data do not permit separate estimation of both parameters (such that age-specific breeding probabilities α_x were estimates as ratios of recapture rates p_x), and thus we chose to derive estimates of the expected number of in situ recruits using our age-specific estimates of breeding propensity, α_x (Table 1). For the purposes of estimating the number of in situ recruits, we assume that the breeding propensities are probabilities of independent events; an individual which does

FIG. C2. Annual variation in estimated immigration rate I_i (estimated as B'_i/\hat{N}_i) at La Pérouse Bay. Immigration rate I_i is the probability of an individual entering the population between $i - 1$ and i . Mean immigration rate (\bar{I}) is indicated by dashed line.



not breed at two years of age (with probability $1 - \alpha_2$) becomes a potential recruit at three years of age, conditional on surviving. Thus, for example, *the expected number of realized recruits as 2-yr-old birds over the interval from i to $i + 1$ in year due to in situ reproduction is*

$$\hat{B}_{i,r}^{(2)} = \hat{N}_{i-1}^{(j)} \hat{\phi}_{i-1}^{(j)} \hat{\phi}_i^{(A)} \alpha_2.$$

We add the subscript r to indicate “realized” recruits. There is no time specificity in the breeding propensity term α_2 , since our analyses did not indicate significant annual variation in the probability of a 2-yr-old adult female recruiting to the breeding population (see Table 1). The expected number of potential 2-yr-old recruits which do not recruit at two years is

$$\hat{B}_{i,p}^{(2)} = \hat{N}_{i-1}^{(j)} \hat{\phi}_{i-1}^{(j)} \hat{\phi}_i^{(A)} (1 - \alpha_2).$$

We use the subscript p to indicate potential recruits. Of these $B_{i,p}^{(2)}$ individuals, some proportion will survive to become potential recruits as 3-yr-old birds the following year:

$$\hat{B}_{i+1,p}^{(3)} = \hat{N}_{i-1}^{(j)} \hat{\phi}_{i-1}^{(j)} \hat{\phi}_i^{(A)} (1 - \alpha_2) \hat{\phi}_{i+1}^{(A)} \alpha_3$$

and so on. In general, the total expected adult recruitment due to in situ reproduction in year i (i.e., summing total number of expected recruits over all contributing age classes x) is given as

$$B_{i,r}^{(A)} = \sum_{x=2}^5 N_{i-x}^{(j)} \phi_{i-x}^{(j)} \alpha_x \left(\prod_{y=1}^{x-1} \phi_{i-x+y}^{(A)} (1 - \alpha_y) \right) \quad (C.1)$$

where $\alpha_1 = 0$.

We use the superscript A in the B' term to indicate total adult recruitment (over all age classes). Since only breeding Snow Geese (which are, by definition, recruits) are observable at La Pérouse Bay, we only need to account for realized recruits in a given year (i.e., recruitment rate is conditioned on the size of the breeding population, not the total population, which would consist of both realized and potential recruits). Since the number of expected recruits in older (>5 yr) age classes is very small ($<4\%$ of the total number of in situ recruits in most years), we arbitrarily constrained the limit on the summation to five years.

While α_x , $\hat{\phi}_i^{(j)}$ and $\hat{\phi}_i^{(A)}$ can all be estimated directly from the data, there are several difficulties in estimating the $N^{(v)}$ terms in the preceding expressions. First, it is generally not possible to derive an estimate of $N_i^{(j)}$ (where $\hat{N}_i^{(j)} = n_i/\hat{p}_i^{(j)}$), since the capture probability for goslings, $\hat{p}_i^{(j)}$, cannot be estimated from standard age-specific capture–recapture models

for open populations. Pollock et al. (1990) note that for some populations (or in this case, age classes) where births and immigration are known to be negligible, it is possible to estimate $\hat{N}_i^{(v)}$ using a special case of the standard capture–recapture models for open populations which allows for losses (deaths and emigration) (Jolly 1965, Seber 1982). At La Pérouse Bay, it is reasonable to assume that during the brood-rearing period when we conducted our annual banding drives, there were no additional “births” into the gosling (and adult) population, and only “deaths” occurred. Unfortunately, the deaths only model requires knowing (1) the number of individuals that are released during banding sample i (within a year) and that are recaptured at a later banding occasion in the same year, and (2) the number of individuals captured before banding sample i (within a year), not captured in banding sample i , and captured again later. These data were not collected for either goslings or adults at La Pérouse Bay.

However, if we assume that recapture rate for goslings is the same as the recapture rate for adults (i.e., $p_i^{(j)} = p_i^{(A)}$), then given $n_i^{(j)}$ (the total number of goslings captured in the i th sample, which is known), $N_i^{(j)}$ can be estimated as $\hat{N}_i^{(j)} = n_i^{(j)}/\hat{p}_i^{(A)}$. Recapture rates for adults are estimable from standard capture–recapture models for open populations (Pollock et al. 1990, Lebreton et al. 1992). The assumption of equal capture probabilities for both goslings and adults in the sampled area is probably reasonable for snow geese, since the family bonds during brood rearing for this nidifugous species are sufficiently strong that the probability of capturing an adult is strongly correlated with the probability of capturing her young. At La Pérouse Bay, $>80\%$ of web-tagged goslings are captured in the same banding drives as their parents. To derive an estimate of the size of the gosling population using this approach (hereafter referred to as the Jolly-Seber (J-S) estimate of $N_i^{(j)}$), we used $\hat{p}_{s+} = 0.246$ (see Table 1) as the capture probability for goslings. This value represents our best estimate of the true capture rate of breeding adults. While it is likely that this estimate is biased, this bias is unlikely to be systematic; we did not detect a significant interaction of recapture rate with age over time in our data.

Using this approach, we derived estimates for $N_i^{(j)}$, using the ratio of the total number of goslings captured in a given year to the assumed recapture rate for goslings. As a check, we also derived an estimate of the size of the gosling population in year i by multiplying the estimated size of the adult female population $\hat{N}_i^{(A)}$ in year i (using Jolly-Seber estimates based on the sample of individuals banded as adults; Seber

1982, Pollock et al. 1990) times the gosling:adult ratio observed during annual banding drives in year i . (The J-S estimates of $N_i^{(A)}$ are known to be biased with respect to the entire La Pérouse Bay population [Cooke et al. 1995], but are probably robust with respect to the size of the population using the brood-rearing areas, which represents some proportion of the nesting population). There was a significant positive correlation between these two different estimates of $\hat{N}_i^{(J)}$ ($r_s = 0.68$, $P < 0.01$), with most of the differences occurring in the early years of the study; in the early years of our study (1973–1975), the size of the gosling population estimated using the gosling:adult ratios was significantly lower than the J-S estimates. This difference was probably due to a higher recapture rate for all birds in the early years of the study (when the population was smaller, and a given capture effort probably resulted in a higher sampling fraction than in later years); a higher capture rate would lower the J-S estimate for gosling population size. To minimize bias as much as possible, we used the mean of the two different estimates of $\hat{N}_i^{(J)}$ to derive annual estimates for $B_i'^{(A)}$ (using Eq. C.1). However, our method for estimating $\hat{N}_i^{(J)}$ did not allow us to estimate the precision of the estimate, which prevented us from deriving estimates of the precision of $B_i'^{(A)}$. In addition, because the expression for expected $B_i'^{(A)}$ (Eq. C.1) uses summation and products of parameters up to and including year $i - 4$, and since our data set begins in 1973, the earliest year for which we could derive the expected number of in situ adult recruits using summation over ages 2–5+ yr is 1978. However, because the contributions from 2- and 3-yr olds to the expected recruitment constituted ~80% of

the expected recruitment in most years, there was a very high correlation ($r > 0.95$) between expected recruitment using all available age classes, and the total expected number of 2- and 3-yr-old recruits. Thus, we were able to derive estimates of the number of recruits for years 1975–1977, using a linear model based on a regression of the total number of expected recruits against the total number of expected 2- and 3-yr-old recruits.

Consistent with expectations from our other analyses (Table 1), expected in situ recruitment at La Pérouse Bay first increases as the total size of the colony grows, then declines significantly over time as fertility and first year survival decline (Fig. C1). Thus, any differences between changes in the size of the population over time and changes expected if only in situ recruitment (and survival of recruited adults) are operating must reflect immigration.

For estimation of $N_i^{(A)}$, we used J-S estimates based on analysis of mark-recapture data from all females banded as adults (Seber 1982, Pollock et al. 1990). We estimated $B_i''^{(A)}$ (Eq. 3) using (1) the J-S estimates of $N_i^{(A)}$, (2) estimates of $\hat{\phi}_i^{(A)}$ from our analysis of combined recapture and recovery data (Appendix B; Table 1), and (3) estimates of $B_i'^{(A)}$ (Eq. C.1). Immigration rate, I_i , was estimated as the ratio ($B_i'' : \hat{N}_i$ (Eq. 14), for 1975–1990 (Fig. C2). Positive values indicate a net immigration into the population. However, negative values do not necessarily indicate a net emigration from the population; this would only be true if we had used \hat{S} rather than $\hat{\phi}$ in estimating B_i . In using $\hat{\phi}$, emigration is already accounted for. Thus negative values probably reflect sampling variation.