*Research Papers*

# Lesser Scaup Population Dynamics: What Can Be Learned from Available Data?

# Dynamique des populations de Petit Fuligule: que peut-on apprendre des données disponibles?

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ABSTRACT. Populations of Lesser Scaup (*Aythya affinis*) have declined markedly in North America since the early 1980s. When considering alternatives for achieving population recovery, it would be useful to understand how the rate of population growth is functionally related to the underlying vital rates and which vital rates affect population growth rate the most if changed (which need not be those that influenced historical population declines). To establish a more quantitative basis for learning about life history and population dynamics of Lesser Scaup, we summarized published and unpublished estimates of vital rates recorded between 1934 and 2005, and developed matrix life-cycle models with these data for females breeding in the boreal forest, prairie-parklands, and both regions combined. We then used perturbation analysis to evaluate the effect of changes in a variety of vital-rate statistics on finite population growth rate and abundance. Similar to Greater Scaup (*Aythya marila*), our modeled population growth rate for Lesser Scaup was most sensitive to unit and proportional change in adult female survival during the breeding and non-breeding seasons, but much less so to changes in fecundity parameters. Interestingly, population growth rate was also highly sensitive to unit and proportional changes in the mean of nesting success, duckling survival, and juvenile survival. Given the small samples of data for key aspects of the Lesser Scaup life cycle, we recommend additional research on vital rates that demonstrate a strong effect on population growth and size (e.g., adult survival probabilities). Our life-cycle models should be tested and regularly updated in the future to simultaneously guide science and management of Lesser Scaup populations in an adaptive context.

RÉSUMÉ. Les populations de Petit Fuligule (*Aythya affinis*) montrent un déclin marqué en Amérique du Nord depuis le début des années 1980. Lorsque l'on considère les options permettant de redresser la situation, il serait utile de comprendre la relation fonctionnelle entre le taux d'accroissement de la population et les taux vitaux, de même que les taux vitaux qui affectent le plus ce taux d'accroissement (qui sont présumément ceux qui ont entraîné le déclin historique des effectifs). Afin d'établir un fondement quantitatif pour comprendre l'histoire naturelle et la dynamique des populations de Petit Fuligule, nous avons compilé les estimés (publiés ou non) de taux vitaux mesurés entre 1934 et 2005 et développé à partir de ces données des modèles matriciels de cycle de vie pour les femelles nichant dans la forêt boréale, la forêt-parc des prairies et les deux régions combinées. Ensuite, nous avons utilisé l'analyse des perturbations afin d'évaluer les effets de changements dans divers taux vitaux sur le taux intrinsèque d'accroissement des populations et l'abondance. Comme chez le Fuligule milouinan (*Aythya marila*), le taux d'accroissement des populations obtenu pour le Petit Fuligule était particulièrement sensible aux variations unitaires ou proportionnelles du taux de survie des femelles adultes durant la saison de nidification ou le reste de l'année, mais beaucoup moins sensible aux variations des paramètres de fécondité. Curieusement, le taux d'accroissement des

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populations était aussi très sensible aux variations unitaires ou proportionnelles du succès d'éclosion moyen et des taux de survie des canetons ou des juvéniles. Étant donné les faibles effectifs d'échantillons disponibles pour certains aspects-clé du cycle de vie du Petit Fuligule, nous recommandons que des travaux additionnels soient effectués sur les taux vitaux qui ont une influence majeure sur l'accroissement des populations et leur effectif (ex. taux de survie des adultes). Nos modèles de cycle de vie devraient être testés et mis à jour régulièrement afin de guider l'étude et la gestion des populations de Petit Fuligule dans un contexte adaptatif.

## INTRODUCTION

Breeding numbers of Lesser and Greater Scaup (*Aythya affinis* and *A. marila*), which are surveyed collectively, have declined markedly since the early 1980s and, in 2006, the continental estimate was 48% below the North American Waterfowl Management Plan (NAWMP) goal of 6.3 million scaup (Wilkins et al. 2006). Greater Scaup primarily breed in Alaska and tundra regions of northern Canada (Kessel et al. 2002) where scaup numbers have remained stable or increased since the early 1980s (Afton and Anderson 2001). Scaup numbers have also remained stable on the prairies and most parts of the parkland region, which are breeding grounds for Lesser Scaup but not Greater Scaup (Afton and Anderson 2001). Much of the decline in scaup numbers has occurred in Canada's western boreal forest and isolated parts of the parkland region where primarily Lesser Scaup breed (Austin et al. 1998, 2000, Afton and Anderson 2001, Koons and Rotella 2003a).

Waterfowl biologists and managers strive to understand what can be done to reverse this trend and increase abundance of Lesser Scaup (Austin et al. 2006, Wilkins et al. 2006). Although general life-history information exists (e.g., Afton 1984, Austin et al. 1998), there is no published model of the Lesser Scaup life cycle. The potential uses of life-cycle models are many (see Caswell 2001). For example, parameterization of a life-cycle model forces an objective examination of the amount and quality of existing demographic data (e.g., sample size, spatial and temporal coverage, etc.), which helps identify information gaps. Life-cycle models also help managers and scientists understand how vital rates (e.g., clutch size, duckling survival, adult survival, etc.) and age structure affect population abundance and growth rate. Crude predictions about these

functional relationships can be derived from basic attributes of a species' life history (Sæther and Bakke 2000). Compared with rates for prairie dabbling ducks such as the Mallard (*Anas platyrhynchos*) (Hoekman et al. 2002), reproductive effort (e.g., renesting probability) and net fertility may be much lower for Lesser Scaup (Trauger 1971, Afton 1984). Thus, given avian life-history patterns (Sæther and Bakke 2000), we might predict that adult female survival should be an important determinant of population growth rate in Lesser Scaup, as was found for Greater Scaup breeding in Alaska (Flint et al. 2006). However, such a prediction could be tenuous for a declining population (Mertz 1971), variable environments (Tuljapurkar 1990), or when vital rates co-vary with one another (Caswell 2000, van Tienderen 2000), all of which may apply to Lesser Scaup. By generating a life-cycle model, it is possible to more objectively develop and explore alternative hypotheses about which vital rates and age classes contribute most to population dynamics. Without a guiding population model, it is not obvious which management tool might be employed most effectively (e.g., habitat conservation, habitat manipulation, harvest regulation, predator management, or various combinations) to reverse population declines by targeting specific vital rates.

Prospective analysis of a life-cycle model developed from available life-history data can be used to estimate the effect of hypothetical changes in various vital rates on the short- or long-term rate of population growth in a constant environment (Caswell 1978, Yearsley 2004, Koons et al. 2005), a variable environment (Tuljapurkar 1990, Doak et al. 2005), as well as the effects of alterations to age structure on short- and long-term population size (Fox and Gurevitch 2000, Koons et al. 2006a,b). Such information provides insight as to which

aspects of the life cycle are the most appropriate targets for management (e.g., Akæakaya and Raphael 1998, Cooch et al. 2001, Clutton-Brock and Coulson 2002), with the confidence in inferences contingent on the quality of available data.

To provide a basis for understanding Lesser Scaup population dynamics, we summarize the available life-history data between 1934 and 2005 in the form of matrix life-cycle models (Caswell 2001) for Lesser Scaup breeding in the boreal forest, the prairie-parklands, and both regions combined using all available data. We used life-cycle perturbation analysis to evaluate the functional contribution of the various vital rates, variation in vital rates, and age structure to finite population growth rate and abundance. Using the model, we were able to identify important data limitations and prioritize vital rates for which future research is needed to guide management using a more biologically informed approach.

## METHODS

### Vital Rate Data

We developed a comprehensive vital-rate database for Lesser Scaup by extracting estimates from government reports and the peer-reviewed literature published between 1934 and 2005. We also included unpublished estimates from recent and ongoing studies (RGC, SS). For each study, we recorded years of study, vital rates estimated, estimated vital-rate statistics (mean, precision, and sample size), methods used, and region (boreal forest or prairie-parkland). When reported, age-specific variation in a vital rate was also recorded. If reported estimates were pooled across years (i.e., year-specific estimates were not provided), we used the pooled estimate for a given study location as a datum point. When estimates were provided for each year of study, we recorded the time-specific estimates for each study location as data points because we were interested in estimating variation in vital rates across time and location. If a particular pooled or time-specific estimate of a vital rate appeared in multiple publications, we only recorded the estimate once to avoid duplicates.

To develop data-based life-cycle models for Lesser Scaup, we calculated the weighted mean of each vital rate across all study locations and years for the boreal forest (eight study locations, 1951–2005),

prairie-parklands (16 study locations, 1934–2001), and for the composite of both regions (24 study locations, 1934–2005). We calculated weighted means using two different methods. For each region, we first calculated vital-rate means by weighting each datum point equally, and then by weighting each datum point by the reported sample size. For each vital rate, we then took the bi-average (i.e., the arithmetic mean) of the two weighted estimates and used this mean in the life-cycle models. For the two regions combined, we calculated the total variance of a vital rate across all study locations and years using standard methods. When ≥4 data points were available for a vital rate (all vital rates except juvenile survival), we estimated the vital-rate process variation ($\sigma^2_{process}$) using variance-decomposition methods described in Burnham et al. (1987). This method involves 1) estimating overall variance of mean estimates across studies, 2) using standard errors from each study to estimate the proportion of 1 that is due to sampling error, and 3) subtracting 2 from 1 to yield $\sigma^2_{process}$. We believed that existing vital-rate sample sizes within each of the boreal forest and prairie-parkland regions were generally too small to calculate process variation of the vital rates on a region-specific basis.

### Model Structure and Parameters

We approximated the annual life cycle of female scaup breeding in the boreal forest (BF), prairie-parklands (PP), and composite (CP) of all data using matrix models (**A**) with two stages indicative of age:

$$\mathbf{A}^k = \begin{bmatrix} F_{SY} & F_{ASY} \\ P_{SY} & P_{ASY} \end{bmatrix}, \qquad (1)$$

where $F_s$ and $P_s$ represent stage-specific fertilities and survival probabilities, respectively, and the superscript on **A** denotes the region that the model represents (Caswell 2001). The number of stage-specific vital rates appearing in our models was based on evidence of age-related variation reported in the published documents, primarily based on Afton . The two stage classes were 1) females entering their second calendar year of life (SY; i.e., individuals are just shy of their first birthday when

censused) and 2), older females, which we denote as "after second year" females (ASY). We focused our modeling efforts on females because sex ratio data indicate that they are the limiting sex (Afton and Anderson 2001). The matrix models were parameterized with a pre-breeding census (conducted in May) assuming birth-pulse reproduction (Caswell 2001). We used stage-specific values for a vital rate if available data indicated age-related variation in that rate.

We parameterized all life-cycle models using a set of vital rates that we believe are relevant to Lesser Scaup life history and meaningful to waterfowl management (Rockwell et al. 1997). Specifically, we calculated per capita fertility for females in stage class $s$ as:

$$F_s = 0.5 \times BP_s \times BS \times \left( CS_s \times NS + (1 - NS) \times RP_s \times CS_s \times NS \right) \times DS \times JS, \quad (2)$$

which assumes a maximum of two nesting attempts and allows renesting only if the first nesting attempt fails. In this equation, 0.5 accounts for the female offspring only (assuming a 50:50 sex ratio at birth), $BP_s$ is the breeding probability of females in stage $s$ (i.e., the proportion of mature females that nest in a given year); $BS$ represents breeding-season survival for both SY and ASY females; $CS_s$ is the clutch size of females in stage $s$; $NS$ is nesting success (i.e., the proportion of nests that hatch at least one egg); $RP_s$ represents the renesting probability for females in stage $s$ (i.e., the probability of producing a second clutch given total failure of the first clutch); $DS$ is duckling survival (i.e., the proportion of ducklings that survive to fledging); and $JS$ represents juvenile survival (the proportion of fledged ducklings that survive to the pre-breeding census in May). We converted Apparent $NS$ estimates to approximate Mayfield estimates using the Green conversion (Mayfield 1975, Green 1989, see especially Johnson 1991) so that all estimates were comparable. We calculated the probability of annual survival for females in each stage as:

$$P_s = BS \times NBS, \quad (3)$$

where $NBS$ represents the probability of surviving the non-breeding season for both SY and ASY females. In practice, $NBS$ was calculated as $NBS = P_s / BS$ (Rotella et al. 2003; RGC unpublished data).

The fertility equation presents the pathway through which individuals can be recruited into the SY stage during each time step. The complexities of the $F_s$ and $P_s$ transition equations were based on empirical data. We included $BS$ within the fertility equation because we believe that females must survive the breeding season to fledge young, and we were interested in evaluating the impact of female mortality during the breeding season on population dynamics. By its presence in the fertility equation, $BS$ accounted for nests that failed and ducklings that died due to mortality of breeding females. Available estimates of $NS$ and $DS$ were obtained from studies that did not distinguish nest or duckling losses due to female mortality from other sources. Thus, it was necessary to increase the mean $NS$ and $DS$ estimates in the models to avoid underestimating fertility (Hoekman et al. 2006). It was not necessary to adjust estimates of $RP_s$ because available estimates were derived from females that survived the breeding season (A. D. Afton, personal communication). The appropriate adjustments to $NS$ and $DS$ were achieved by dividing $NS$ by the probability of females surviving the nesting period and $DS$ by the probability of females surviving the brood-rearing period. To approximate these period-specific estimates of $BS$ for each region, we used a proportional hazards model (Agresti 1990, Cox 1972). The ratio of the hazard for the brood-rearing period relative to that for the nesting period was estimated from survival probabilities for these two periods reported in Koons and Rotella (2003b). The resulting mean values of $NS$ and $DS$ used in our models were 18%–19% and 6% greater, respectively, than the bi-averages estimated from available data (Table 1).

Based on published evidence of age-related variation in Lesser Scaup vital rates, we only used stage-specific values for $BP_s$, $CS_s$, and $RP_s$. We used composite estimates, pooled across ages, for the remaining demographic parameters (Table 1). The decision was straightforward for all rates except $NS$. Using Afton's (1984) data, we developed $NS$ estimates for SY (0.26, 95% CI = 0.13 to 0.42) and ASY females (0.33, 95% CI = 0.23 to 0.43). Given that these confidence intervals were largely overlapping, we did not believe that use of separate estimates was warranted, although we acknowledge

**Table 1.** Summary of vital rate estimates (θv) for female Lesser Scaup breeding in the boreal forest, prairie-parklands, and the two regions combined (composite model).

| $\theta_v$† | Boreal Forest | | Prairie-Parkland | | Composite | | | Data Sources |
|---|---|---|---|---|---|---|---|---|
| | mean | n § | mean | n § | mean | $\sigma_{process}$ | n § | |
| $BP_{SY}$ | 0.75 | 1 | 0.71 | 4 | 0.72 | 0.08 | 5 | a, b |
| $BP_{ASY}$ | 0.95‡ | – | 0.95 | 4 | 0.95 | 0.08 | 4 | a ¶ |
| $CS_{SY}$ | 7.88 | 20 | 8.82 | 28 | 8.37 | 0.75 | 48 | a, c, d, e, f, g, h, i, j, k, l, m, n, o, p, q, r, s, t, u, v |
| $CS_{ASY}$ | 9.74 | 20 | 10.68 | 28 | 10.22 | 0.75 | 48 | a, c, d, e, f, g, h, i, j, k, l, m, n, o, p, q, r, s, t, u, v |
| $RP_{SY}$ | 0.09‡ | – | 0.09 | 4 | 0.09 | 0.17 | 4 | a |
| $RP_{ASY}$ | 0.20‡ | – | 0.20 | 4 | 0.20 | 0.17 | 4 | a |
| $NS$ | 0.32 | 38 | 0.33 | 41 | 0.32 | 0.27 | 79 | a, c, d, e, f, g, h, j, k, l, m, n, o, q, s, u, v, w, x, y, z, ab, ac, ad, ae, af, ag, ah, ai, aj |
| $DS$ | 0.35 | 4 | 0.53 | 8 | 0.46 | 0.23 | 12 | a, m, n, o, t, u, ak, al, |
| $JS$ | 0.53 | 1 | 0.55 | 1 | 0.54 | 0.16 \| | 2 | am, an |
| $BS$ | 0.80 | 1 | 0.79 | 2 | 0.79 | 0.08 | 3 | m, n, o, am, ao |
| $NBS$ | 0.66 | 1 | 0.77 | 6 | 0.76 | 0.08 | 7 | am, an |

†Vital-rate abbreviations and definitions provided in the text.

‡Mean value of the vital rate assumed to be equal to that in the prairie-parklands because estimates do not exist for the boreal forest.

§ "n" is the number of year-specific and pooled (across time) estimates that were available for each region.

\| Assumed to be two times greater than that for *BS* and *NBS*.

¶ Note that Afton (1984) provided estimates of breeding probability and other vital rates for females of 1, 2, 3, or ≥4 years of age. Based on statistical evidence, we averaged the estimates for individuals of 2, 3, and ≥4 years of age, denoted as the "after second year" (ASY) stage class.

Data Sources: a) Afton 1984, b) McKnight and Buss 1962, c) Kalmbach 1937, d) Ellig 1955, e) Smith 1955, f) Keith 1961, g) Vermeer 1968, h) Long 1970, i) Stoudt 1971, j) Hammell 1973, k) Hines 1977, l) Brown 1987, m) Koons 2001, n) Koons and Rotella 2003b, o) Brook 2002, p) Nelson 1953, q) Townsend 1966, r) Petrula 1994, s) Fournier and Hines 2001, t) Walker and Lindberg 2005, u) Corcoran et al. 2006, v) SS unpublished data, w) Leitch 1952, x) Kiel 1953, y) Stoudt and Yeager 1955, z) Rogers 1964, ab) Vermeer 1970, ac) Smith 1971, ad) Giroux 1981, ae) Holm 1984, af) Aufforth et al. 1990, ag) Sankowski and Joynt 1992, ah) Koons and Rotella 2003a, ai) Walker et al. 2005, aj) Bellrose 1978, ak) Afton 1993, al) Dawson and Clark 1996, am) Rotella et al. 2003, an) RGC unpublished data, ao) Brook and Clark 2005.

that age-related variation may exist. To approximate stage-specific estimates of $CS_s$ for each region, we assumed that $CS_{ASY}$ was 1.86 eggs greater than $CS_{SY}$ as in Afton (1984).

## Analysis of Deterministic Life-Cycle Models

We developed deterministic matrix life-cycle models for each region, $\mathbf{A}^{BF}$, $\mathbf{A}^{PP}$, and $\mathbf{A}^{CP}$, by parameterizing each model with the relevant mean values of each vital rate (Table 1), and adjusted *NS* and *DS* according to the method described above. We assumed density-independent vital rates, a stable stage distribution, and no (co)variation among the vital rates over time (i.e., constant environments). For each model, we calculated $\lambda_1$, the population's finite rate of growth in a constant environment, as the dominant eigenvalue of each matrix model. The projected stable stage distribution and stage-specific reproductive values were calculated with the corresponding right $\mathbf{w}_1$ and left $\mathbf{v}_1$ eigenvectors, respectively (Lefkovitch 1965, Caswell 2001).

Although density-dependence should be incorporated into models designed for making long-term forecasts about population growth and abundance, empirical information about density regulation of Lesser Scaup vital rates is lacking (Boomer and Johnson 2005). Rather than attempting to make forecasts about Lesser Scaup population dynamics, our main objective was to estimate the functional relationship between vital rates and population growth rate with sensitivities and elasticities. Fortunately, density-independent population models can provide accurate estimates of vital-rate sensitivities and elasticities for both density-independent and density-regulated populations (Grant and Benton 2000, Caswell 2001).

To measure the effect of changes in each vital rate on $\lambda_1$, we calculated the sensitivity of $\lambda_1$ to unit changes in the lower-level vital rate means $\theta_v$ (e.g., *NS*) using chain-rule differentiation (Caswell 1978):

$$S_v = \frac{\partial \lambda_1}{\partial \theta_v} = \sum_{i,j} \frac{\partial \lambda_1}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial \theta_v}, \quad (4)$$

where $a_{ij}$ is the $i$, $j$th entry of $\mathbf{A}^k$ (e.g., $F_{ASY}$). Furthermore, we calculated "elasticities" as the sensitivity of $\lambda_1$ to proportional changes in the lower-level vital rates (Caswell et al. 1984, de Kroon et al. 1986):

$$E_v = \frac{\theta_v}{\lambda_1} \frac{\partial \lambda_1}{\partial \theta_v} = \frac{\theta_v}{\lambda_1} \sum_{i,j} \frac{\partial \lambda_1}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial \theta_v}. \quad (5)$$

Elasticities measure the proportional change in $\lambda_1$ resulting from a proportional change in $\theta_v$ and provide for a straightforward ranking of the functional contribution of the different vital rates to $\lambda_1$, given the data and modeling assumptions (de Kroon et al. 1986, 2000, Horvitz et al. 1997, but see Link and Doherty 2002). Nevertheless, sensitivities and elasticities are derivatives, and thus give the "local" slope of population growth rate as a function of a vital rate at its estimated mean value. Several of the vital rates used in our models were estimated from just a few studies (e.g., *BP* and *RP*) and others could be biased (e.g., annual survival probability). Because population growth rate is a nonlinear function of vital rates, sensitivities and elasticities could change if estimates of the underlying vital rates were substantially different. To test the robustness of sensitivities and elasticities to perturbation size and vital rate values, we examined the slope of population growth rate across a large range of absolute ($\pm 0.5$) and proportional ($\pm 50\%$) changes in the vital rates for the composite model (de Kroon et al. 2000).

Because (st)age structure is generally not expected to be stable to current vital rates if environmental conditions or harvest rates have recently changed (Hauser et al. 2006), we evaluated how unstable stage distributions might affect Lesser Scaup population dynamics. Using the same set of vital rates ($\mathbf{A}^{CP}$), we projected dynamics forward in time from initial stage distributions $\mathbf{n}$ ranging from all SY to all ASY individuals with the following equation:

$$\mathbf{n}(t) = \mathbf{A}^{CP^t}\mathbf{n}(0), \qquad (6)$$

where $\mathbf{n}(t)$ is a $2 \times 1$ vector representing abundance of SY and ASY females at time $t$, respectively. The total abundance in each of the initial populations was the same. For each projection, we numerically measured the time required for the stage distribution to converge to the stable stage distribution, after which $\lambda_1$ becomes the population growth rate (Caswell 2001). Before this time, an unstable stage distribution causes transient fluctuations in the population growth rate (see Koons et al. 2005). We also measured the relative effect of unstable stage distributions on long-term population size using Tuljapurkar and Lee's stable equivalent ratio (SER):

$$SER = \lim_{t \to \infty} \frac{\|\mathbf{n}(t)\|_1}{\|\mathbf{n}_{stable}(t)\|_1}, \qquad (7)$$

where $\| \ \|_1$ indicates the 1-norm (i.e., the vector sum) and the subscript *stable* denotes projection from the stable stage distribution. Thus, the SER measures the actual long-term population size projected from any stage distribution relative to that from an initially stable population (Tuljapurkar and Lee 1997), and is very similar to population momentum (Keyfitz 1971, Koons et al. 2006*a,b*).

## Analysis of a Stochastic Life-Cycle Model

Constant environments are not likely to occur in nature (Fox and Gurevitch 2000). Rather, vital rates and (st)age distribution fluctuate over time as environmental conditions change. To examine the consequence of temporally fluctuating vital rates and stage distribution on population dynamics, we developed a stochastic version of the composite model ($\mathbf{A}^{CP}(t)$). We did this by first generating probability distributions for each vital rate according to its estimated mean and process standard deviation: $\sigma_{process} = \sqrt{(\sigma^2_{process})}$. For modeling purposes, we assumed that process variation for both *BS* and *NBS* were equivalent to

that calculated from annual survival probabilities. We assumed equivalent process variation across the two stage classes for the stage-structured vital rates (i.e., $BP_s$, $CS_s$, and $RP_s$). Furthermore, because just two estimates of *JS* existed, we assumed that the process standard deviation of *JS* was twice that of the adult survival parameters. Because all vital rates except clutch size were probabilities bounded between 0 and 1, we assumed that they conform to a Beta distribution and that clutch size parameters conform to a stretched Beta distribution. We then generated a time sequence of 100 000 randomly selected values for each vital rate from its Beta or stretched-Beta distribution. Because information on correlation amongst the vital rates did not exist, values for each vital rate were selected independently.

Next, we generated a sequence of time-specific matrices composed of the randomly selected vital-rate values and projected the population forward in time from an arbitrary initial-stage-distribution:

$$\mathbf{n}(t) = \mathbf{A}^{CP}(t-1)\mathbf{A}^{CP}(t-2)\cdots\mathbf{A}^{CP}(1)\mathbf{A}^{CP}(0)\mathbf{n}(0). \quad (8)$$

We used this stochastic sequence of population dynamics and discarded the first 10 000 time steps to estimate the stochastic population growth rate (Heyde and Cohen 1985, Caswell 2001:396):

$$\lambda_s = \exp\left(\frac{1}{T - 10,000}\sum_{t=10,000}^{T-1} r(t)\right), \quad (9)$$

where $r(t) = \log(\|\mathbf{n}(t+1)\|_1 / \|\mathbf{n}(t)\|_1)$ and $T = 100\ 000$. We also estimated the variance of these $r(t)$ values. Ergodic theorems of random matrix products assure us that any stochastic projection of a Markovian model will approach $\lambda_s$ as $t \to \infty$ (Furstenberg and Kesten 1960, Oseledec 1968). We estimated the stochastic analogues of stable stage distribution and reproductive value using the procedure laid out in Caswell (2001:402–407; see also Tuljapurkar 1984, 1990).

In a stochastic environment, the sensitivity and elasticity of $\lambda_s$ to changes in the lower-level vital rates ($\theta_v$) cannot be found using chain-rule differentiation. Fortunately, Caswell recently derived formulas for these perturbation measures. Based on Caswell's formulas, we calculated the sensitivity of $\lambda_s$ to unit changes in the $\theta_v$ as:

$$S_{v,\,stochastic} = \frac{\partial \lambda_s}{\partial \theta_v} = \lambda_s \times \lim_{T \to \infty} \frac{1}{T} \sum_{t=0}^{T-1} \frac{\mathbf{v}'(t+1)\frac{\partial \mathbf{A}^{CP}(t)}{\partial \theta_v}\mathbf{w}(t)}{r(t)\mathbf{v}'(t+1)\mathbf{w}(t+1)}, \quad (10)$$

and the elasticity of $\lambda_s$ to proportional changes in the $\theta_v$ as:

$$E_{v,\,stochastic} = \frac{\theta_v}{\lambda_s}\frac{\partial \lambda_s}{\partial \theta_v} = \lim_{T \to \infty} \frac{1}{T}\sum_{t=0}^{T-1} \frac{\theta_v(t)\mathbf{v}'(t+1)\frac{\partial \mathbf{A}^{CP}(t)}{\partial \theta_v}\mathbf{w}(t)}{r(t)\mathbf{v}'(t+1)\mathbf{w}(t+1)}. \quad (11)$$

We also estimated the sensitivity of $\lambda_s$ to unit changes in the temporal variation of each vital rate using the process standard deviations and methods developed by Doak et al. :

$$S\sigma_{v,\,process} = \frac{\partial \lambda_s}{\partial \sigma_{v,\,process}} \approx \lambda_s \times \frac{-1}{(\lambda_1)^2}\left(S_v^2 \times \sigma_{v,\,process} + \sum_{x \neq v} S_v \times S_x \times \sigma_{x,\,process} \times \rho_{v,x}\right), (12)$$

where $\sigma_{v,\,process}$ is the process standard deviation of vital rate $v$ (i.e., of $\theta_v$), subscript $x$ denotes any other vital rate, and $\rho_{v,x}$ is the correlation coefficient between vital rates $v$ and $x$. In Eq. 12, $\lambda_1$, $S_v$, and $S_x$ are all measured from the deterministic life-cycle model $\mathbf{A}^{CP}$ (parameterized with mean vital-rate values) defined above. The elasticity analogue of Eq. 12 was approximated as:

$$E\sigma_{v,\,process} \approx \frac{-\sigma_{v,\,process} \times S_v}{(\lambda_1)^2}\left(S_v \times \sigma_{v,\,process} + \sum_{x \neq v} S_x \times \sigma_{x,\,process} \times \rho_{v,x}\right), (13)$$

and together, Eqs. 12 and 13 are useful for examining the effect of changes in the actual or estimated level of temporal variation in a vital rate on $\lambda_s$. Because we did not include correlation structure among vital rates in the stochastic model, the $\rho_{v,x}$ term equals 0 and cancels out the summation term on the far right-hand side of these equations (Doak et al. 2005).

## RESULTS

### Deterministic Life-Cycle Models

For many vital rates, only a single estimate was available within each region, whereas many estimates were available for other vital rates (e.g., prairie-parkland $NS$: $n = 41$; (Table 1)). Estimates of age-structured vital rates were largely derived from a single study within the prairie-parklands (Afton 1984). Too few estimates of $BP_s$, adult annual survival, $BS$, and thus $NBS$, were available to make robust comparisons across regions. In general, vital-rate estimates from studies conducted in the boreal forest were similar to those from the prairie-parklands, but mean values of $CS_s$, $DS$, and $NBS$ in the boreal forest were lower (Table 1).

The projected population growth rates for the boreal forest, prairie-parkland, and composite life-cycle models were vastly different ($\lambda_1 = 0.79$, 1.06, and 0.97 respectively), but each model was parameterized with data coming from a diverse spatial and temporal setting. Thus, these estimates of population growth rate are not representative of actual breeding populations. Nevertheless, the underlying dynamics related to population growth rate provided general insight into the demography of Lesser Scaup for each region. For example, the low population growth rate of the boreal forest model led to a stable stage distribution ($\mathbf{w}_1$) that was skewed more toward ASY individuals, $\mathbf{w}_1^{BF} = (0.33, 0.67)$, relative to estimates for the prairie-parkland and composite models: $\mathbf{w}_1^{PP} = (0.43, 0.57)$, $\mathbf{w}_1^{CP} = (0.38, 0.62)$ (note that each $\mathbf{w}_1$ should be a column vector). Estimated reproductive values ($\mathbf{v}_1$) were similar across the three models: $\mathbf{v}_1^{BF} = (0.46, 0.54)$, $\mathbf{v}_1^{PP} = (0.45, 0.55)$, and $\mathbf{v}_1^{CP} = (0.46, 0.54)$. Because each life-cycle model had a different $\lambda_1$, the sensitivity and elasticity values for each vital rate necessarily differed across models. The qualitative pattern (i.e., ranking) of vital-rate sensitivities was very similar across models, and the pattern of vital-rate elasticities was identical for all three models

(Table 2). For each life-cycle model, $\lambda_1$ was always most sensitive to unit and proportional (indicated by elasticities) change in *BS* followed by *NBS*, except in the prairie-parkland model where the sensitivity for *NBS* was ranked 3rd and that for *NS* was ranked 2nd. Except for the prairie-parkland model where $\lambda_1$ was highly sensitive to unit changes in *NS*, $\lambda_1$ was moderately sensitive to unit and proportional changes in the offspring survival vital rates (i.e., *NS*, *DS*, and *JS*). Although $\lambda_1$ was always more sensitive to unit and proportional changes in the fecundity vital rates ($BP_s$, $CS_s$, and $RP_s$) of the ASY stage relative to those for the SY stage, $\lambda_1$ was much less sensitive and elastic to changes in these vital rates compared with adult-survival and offspring-survival vital rates (Table 2). In addition, the slope of the relationship between population growth rate and each vital rate was nearly constant across a wide range of unit or proportional changes in each vital rate (Fig. 1), indicating that estimates of sensitivity and elasticity were quite robust to large deviations (e.g., bias) in vital-rate values (Fig. 1).

Projections from initially unstable stage distributions with the $\mathbf{A}^{CP}$ model indicated that even initial stage distributions consisting of all SY, or all ASY individuals would reach near-exact convergence by the 5th time step (equal to stable stage distribution in the 4th decimal place; (Fig. 2)). Therefore, the effect of an unstable stage distribution on future stage distribution and population growth rate is expected to be short lived. However, large deviations from the stable stage distribution could have a substantial effect on population size. For the $\mathbf{A}^{CP}$ model, initially unstable stage distributions led to long-term population sizes that were as much as 10.4% smaller (SER = 0.896) and 6.4% greater (SER = 1.064) than that for a population with an initially stable stage distribution (Fig. 3).

### Stochastic Life-Cycle Model

For some vital rates, process variation was estimated from just a few data points (e.g., $BP_s$ and $RP_s$), and for other vital rates it was estimated for many data points (e.g., $CS_s$ and *NS*; (Table 1)). The process variation of *JS* could not be estimated because just two estimates existed (see Methods for assumed value). Therefore, the stochastic life-cycle model for the composite of both regions ($\mathbf{A}^{CP}(t)$) was based on limited information about the process variation of several vital rates (Table 1).

As expected, the projected population growth rate in a temporally stochastic environment was lower ($\lambda_s = 0.906$, 95% CI: 0.903 to 0.908) than in a constant environment ($\lambda_1 = 0.97$). Yet, the large amount of process-variation in the underlying vital rates makes it difficult to actually predict future population growth rate (95% prediction interval: 0.45 to 1.81; see Neter et al. 1996 for definition of prediction interval). The stable stage distribution in a stochastic environment was skewed more toward ASY individuals (0.31, 0.69), and the reproductive values were similar (0.47, 0.53) to those for the deterministic model ($\mathbf{A}^{CP}$; see above).

In addition to reducing population growth rate, the introduction of temporally fluctuating vital rates into the composite model generally reduced the sensitivity and elasticity values as well. However, the *NS* and *NBS* stochastic sensitivity values, as well as the *NBS* stochastic elasticity value, were actually higher than the corresponding deterministic values (Table 2). Nevertheless, the qualitative patterns (i. e., ranking) of vital-rate sensitivities and elasticities were identical for the stochastic and deterministic life-cycle models (Table 2).

The sensitivities and elasticities of $\lambda_s$ to changes in $\sigma_{v,\,process}$ were all negative, indicating that increased $\sigma_{v,\,process}$ decreased $\lambda_s$ (and vice versa). Furthermore, the absolute value of these sensitivity and elasticity values was smaller than corresponding values for changes in $\theta_v$, indicating that change in $\sigma_{v,\,process}$ had a smaller functional effect on $\lambda_s$ than changes in $\theta_v$ (Table 2). Nevertheless, on top of the important effect that change in *NS* and *BS* had on $\lambda_s$, $\lambda_s$ was moderately sensitive to changes in temporal variation of *NS* and *BS* as well (Table 2).

### DISCUSSION

By summarizing available demographic vital rates, we identified gaps in our knowledge of Lesser Scaup life history and population dynamics, and estimated the potential impact of changes in demographic statistics on population growth rate and size. Our estimates of the sensitivity and elasticity of the projected population growth rate to changes in mean values of vital rates were similar across models (i. e., boreal forest, prairie-parkland, and composite), and were robust to large deviations in vital-rate values (Fig. 1) as well as the inclusion of temporal variability in the vital rates (Table 2). Sensitivities also indicated that including small amounts of

**Table 2.** Estimates of the sensitivity ($S_v$) and elasticity ($E_v$) of the finite rate of population growth in a constant environment, $\lambda_1$, to changes in the underlying vital rates ($\theta_v$) for the boreal forest, prairie-parklands, and the two regions combined (composite). In addition, estimates of the sensitivity and elasticity of the stochastic population growth rate ($\lambda_s$) to changes in the underlying vital-rate means ($S_{v,\,stochastic}$ and $E_{v,\,stochastic}$, respectively), and to changes in the temporal variation (measured with the process standard deviation) of each vital rate ($S\sigma_{v,\,process}$ and $E\sigma_{v,\,process}$, respectively) for the stochastic version of the composite model.

| $\theta_v$ | $S_v$ | | | | | $E_v$ | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Boreal Forest | Prairie-Parkland | Composite | $S_{v,\,stochastic}$ | $S\sigma_{v,\,process}$ | Boreal Forest | Prairie-Parkland | Composite | $E_{v,\,stochastic}$ | $E\sigma_{v,\,process}$ |
| $BP_{SY}$ | 0.073 | 0.170 | 0.119 | 0.077 | -0.0011 | 0.069 | 0.114 | 0.089 | 0.061 | -0.0001 |
| $BP_{ASY}$ | 0.193 | 0.295 | 0.254 | 0.214 | -0.0050 | 0.232 | 0.265 | 0.250 | 0.224 | -0.0004 |
| $CS_{SY}$ | 0.007 | 0.014 | 0.010 | 0.007 | -0.0001 | 0.069 | 0.114 | 0.089 | 0.061 | -0.0001 |
| $CS_{ASY}$ | 0.019 | 0.026 | 0.024 | 0.020 | -0.0004 | 0.232 | 0.265 | 0.250 | 0.224 | -0.0003 |
| $RP_{SY}$ | 0.033 | 0.070 | 0.050 | 0.025 | -0.0004 | 0.004 | 0.006 | 0.005 | 0.003 | -0.0001 |
| $RP_{ASY}$ | 0.103 | 0.153 | 0.133 | 0.089 | -0.0029 | 0.026 | 0.029 | 0.028 | 0.020 | -0.0005 |
| $NS$ | 0.606 | 0.969 | 0.810 | 0.814 | -0.1722 | 0.284 | 0.357 | 0.319 | 0.261 | -0.0508 |
| $DS$ | 0.643 | 0.704 | 0.667 | 0.589 | -0.0995 | 0.301 | 0.379 | 0.339 | 0.285 | -0.0250 |
| $JS$ | 0.449 | 0.730 | 0.606 | 0.498 | -0.0570 | 0.301 | 0.379 | 0.339 | 0.285 | -0.0100 |
| $BS$ | 0.988 | 1.342 | 1.222 | 1.161 | -0.1160 | 1.000 | 1.000 | 1.000 | 1.000 | -0.0102 |
| $NBS$ | 0.837 | 0.855 | 0.840 | 0.859 | -0.0548 | 0.699 | 0.621 | 0.661 | 0.715 | -0.0048 |

correlation structure among vital rates would have a negligible effect on stochastic growth rate (unpublished results; method described in Doak et al. [2005]). Therefore, even our simple deterministic models, where we assumed constant vital rates and no correlation among vital rates, can provide a great deal of insight into Lesser Scaup population dynamics. Nevertheless, large departures from a stable (st)age distribution could have an important impact on population abundance (Fig. 3), which cannot be predicted from vital rates alone (Keyfitz 1971). Thus, managers should develop ways to reduce uncertainty in age structure (e.g., harvest age ratios) and assess its potential impact on population dynamics (e.g., Hauser et al. 2006, Koons et al. 2006*a*).

Our sensitivity and elasticity analyses provided compelling evidence that changes in the mean value of both breeding- and non-breeding-season survival of adult females would have strong impacts on Lesser Scaup population growth (Table 2). Increased temporal variation of breeding-season survival would have a detrimental impact as well (Table 2) (temporal variation of a vital rate could be affected by global warming, change in habitat or predator community, etc.). Published capture-mark-recapture estimates of annual survival for adult female Lesser Scaup breeding in the Canadian parklands (Rotella et al. 2003) are 25% lower than capture-mark-recapture estimates for Greater Scaup breeding in Alaska (Flint et al. 2006). In addition, estimates of Lesser Scaup breeding-season survival

**Fig. 1.** Changes in the population growth rate $\lambda_1$ as a function of unit (sensitivity; boxes a and b) and proportional (elasticity; boxes c and d) changes in each vital rate of the deterministic composite model. The small degree of curvature in each line indicates that estimates of sensitivity (boxes a and b) and elasticity (boxes c and d) were quite robust to large deviations in vital-rate values. Probabilistic vital rates were simulated for biologically realistic values only ($0 \leq$ probability $\leq 1$); consequently, some of the lines do not span the entire range of perturbation shown on the x-axes.
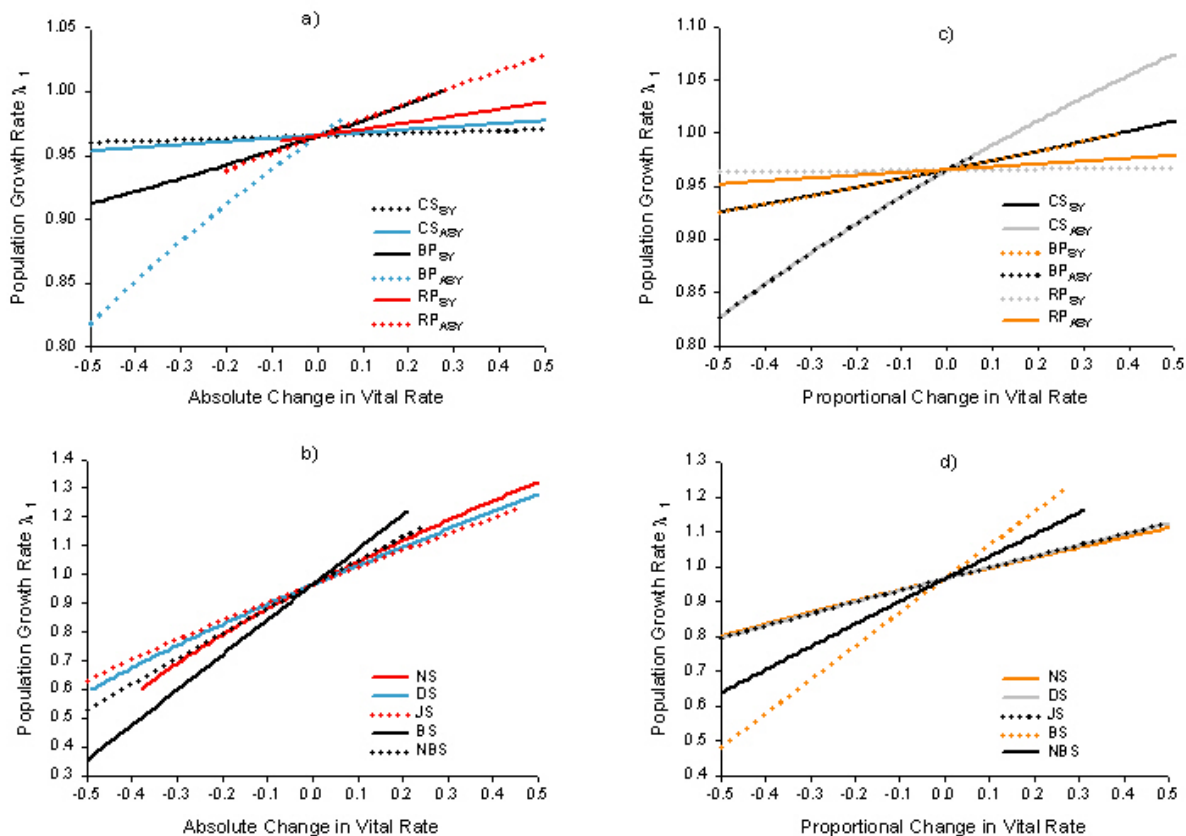


are low compared with other duck species (Koons and Rotella 2003b, Rotella et al. 2003, Brook and Clark 2005), and evidence from the parklands indicates that it is especially costly for females to attend nests where a number of predators pose a threat to their survival (Afton 1984, Koons and Rotella 2003b). During the non-breeding season Lesser Scaup must survive two migrations, hunting, and harsh weather conditions in order to breed again. Unfortunately, there is a great deal of uncertainty in estimates of Lesser Scaup survival at the continental

scale, and the effects of hunting on Lesser Scaup survival (i.e., additive vs. compensatory) are poorly understood (Boomer and Johnson 2005). Recent unpublished data, however, indicate no relationship between harvest rates and annual survival probabilities since the 1950s (C. A. Nicolai, J. S. Sedinger, A. D. Afton, and C. D. Ankney unpublished data). Nevertheless, increased banding efforts at several times of the year, and across a wide spatial scale, are needed to improve our ability to more precisely estimate seasonal survival of Lesser

**Fig. 2.** Projections of initially unstable stage distributions with the deterministic life-cycle model parameterized with data from both the boreal forest and prairie-parklands (composite model). The proportion of second-year (SY) individuals in the stage distribution is shown over time (the proportion of after-second-year individuals is simply 1 – proportion SY).
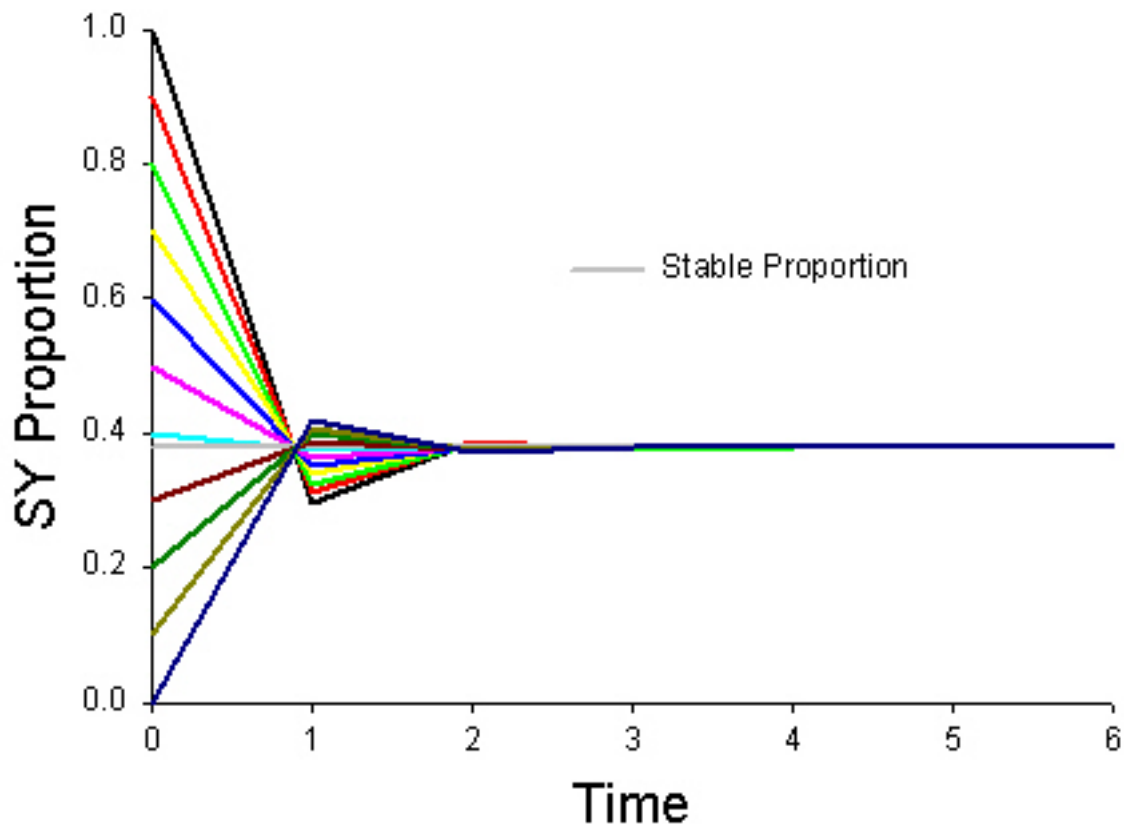


Scaup, and thus improve our knowledge of population dynamics.

Our sensitivity and elasticity analyses also indicated that changes in the mean value of nesting success, duckling survival, and juvenile survival would strongly affect Lesser Scaup population growth rate, and increased temporal variance of nesting success would have a deleterious impact (Table 2). The landscape that these birds use for breeding, migrating, and wintering has undergone considerable anthropogenic change, which may have altered vital rates. Climate and habitat change in the boreal forest, decreased quality of food resources on wintering and spring stopover areas, accumulation of contaminants, and harvest have all been proposed as possible factors contributing to the decline in Lesser Scaup numbers (Austin et al. 2000, Afton and Anderson 2001). However, we do not know how these factors affect the mean level, (co)variation, and density dependence of the aforementioned vital rates across space and time, especially those affecting adult females and eggs at the nest site. Therefore, if we are to understand factors limiting Lesser Scaup population growth, and design effective conservation actions to overcome these limitations, we must understand which of the vital rates are currently constrained and why.

**Fig. 3.** Stable equivalent ratios (SER) indicating the proportionate effect of initially unstable stage distributions on long-term population size. Stage distributions are represented by only the proportion of second-year (SY) individuals because the proportion of after-second-year individuals simply equals 1 – SY. The dotted line represents SER = 1, indicative of a stable population.
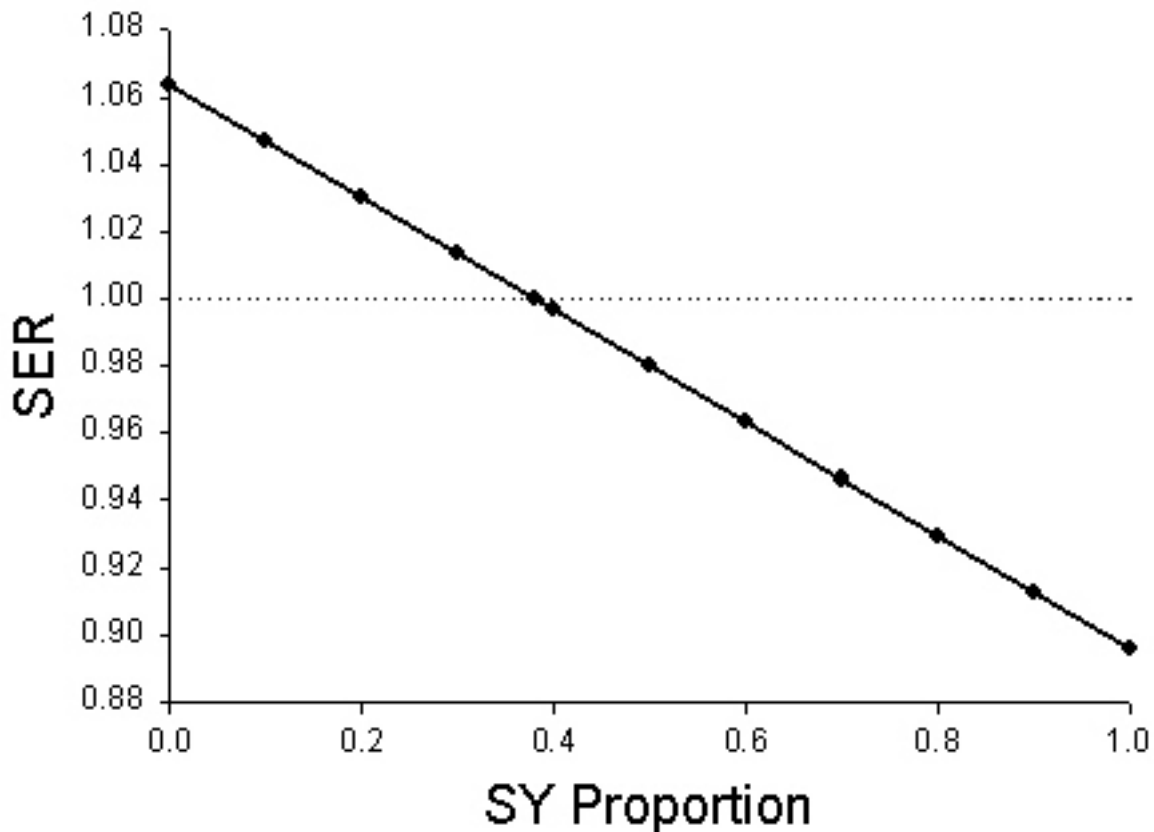


In addition to being a useful tool for examining population dynamics and guiding management, population models also serve as a powerful tool for learning about life-history evolution (Roff 1992, Stearns 1992). For example, the population growth rate of arctic-nesting geese is much more elastic to changes in adult survival than to changes in net fertility (Rockwell et al. 1997, Schmutz et al. 1997, Cooch et al. 2001), indicating that they have evolved a "slow" life history adapted to low rates of reproduction but long lifespan (see Sæther and Bakke 2000). The population growth rates of Northern Pintails (*Anas acuta*) and Greater Scaup breeding in Alaska are more elastic to changes in

adult survival than to changes in net fertility, but the difference between these elasticities is not as great as in the geese (Flint et al. 1998, 2006). At the other end of the spectrum, the population growth rate of Mallards breeding at lower latitudes is highly elastic to changes in net fertility, especially nesting success (Hoekman et al. 2002, 2006), indicating Mallards evolved a "faster" life history adapted to relatively rapid reproduction and shorter lifespan (Sæther and Bakke 2000). Our results for Lesser Scaup (all models) indicate that their life history is slightly slower than the Mallard but faster than Greater Scaup and pintails, and much faster than geese breeding at high latitudes. Nevertheless, Lesser

Scaup breeding propensity, and re-nesting intensity are poorly understood, especially in the boreal forest where these rates may be lower (Trauger 1971) than in the prairie-parklands region (where most estimates come from: Afton 1984). More data for these vital rates and others are needed for birds breeding in the boreal forest to determine whether or not their life-history strategy truly differs from their counterparts breeding in the prairie-parklands (where most existing vital-rate data come from (Table 1)). If so, Lesser Scaup breeding in the boreal forest may need to be managed in slightly different ways than those breeding in the prairie-parklands.

Although existing life-history data were too disconnected across space and time to determine which vital rates were responsible for historical declines in Lesser Scaup numbers, our models can serve as a template to be built upon for understanding scaup life history and to help create management plans aimed at reversing population declines. Herein, we identified vital rates most likely to affect scaup population dynamics if changed. However, at this time, the lack of long-term demographic studies prevents us from accurately predicting how particular management actions (e.g., changes in harvest regulation or land management) will affect Lesser Scaup population dynamics. So before management actions are implemented, we urge that long-term studies of Lesser Scaup breeding biology, seasonal survival, cross-seasonal habitat use, and foraging ecology be in place to test the effects of any management action on demographic vital rates and population dynamics. Only within this framework can models and management plans be updated adaptively (Williams et al. 2002).

*Responses to this article can be read online at:*
*http://www.ace-eco.org/vol1/iss3/art6/responses/*

## LITERATURE CITED

**Afton, A. D.** 1984. Influence of age and time on reproductive performance of female Lesser Scaup. *Auk* **101**:255–265.

———. 1993. Post-hatch brood amalgamation in Lesser Scaup: female behavior and return rates, and duckling survival. *Prairie Naturalist* **25**:227–235.

**Afton, A. D., and M. G. Anderson.** 2001. Declining scaup populations: a retrospective analysis of long-term population and harvest survey data. *Journal of Wildlife Management* **65**:781–796.

**Agresti, A.** 1990. *Categorical data analysis.* John Wiley and Sons, New York, New York, USA.

**Akçakaya, H. R., and M. G. Raphael.** 1998. Assessing human impact despite uncertainty: viability of the northern spotted owl metapopulation in the northwestern USA. *Biodiversity and Conservation* **7**:875–894.

**Aufforth, A. D., H. Goetz, and K. F. Higgins.** 1990. Duck nesting on islands at J. Clark Salyer Refuge in North Dakota, 1983–1984. *Prairie Naturalist* **22**:1–12.

**Austin, J. E., C. M. Custer, and A. D. Afton.** 1998. Lesser Scaup (*Aythya affinis*). *In* A. Poole and F. Gill, editors. *Birds of North America,* Number 338. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and American Ornithologists' Union, Washington, D.C., USA. [online] URL: http://bna.birds.cornell.edu/BNA/.

**Austin, J. E., A. D. Afton, M. G. Anderson, R. G. Clark, C. M. Custer, J. S. Lawrence, J. B. Pollard, and J. K. Ringelman.** 2000. Declining scaup populations: issues, hypotheses, and research needs. *Wildlife Society Bulletin* **28**:254–263.

**Austin, J. E., M. J. Anteau, J. S. Barclay, G. S. Boomer, F. C. Rohwer, and S. M. Slattery.** 2006. *Declining scaup populations: reassessment of the issues, hypotheses, and research directions.* Consensus report from the 2nd Scaup Workshop, U. S. Geological Survey, Bismarck, North Dakota, USA.

**Bellrose, F. C.** 1978. *Ducks, geese, and swans of North America.* Second edition. Stackpole Books, Harrisburg, Pennsylvania, USA.

**Boomer, G. S., and F. A. Johnson.** 2005. *An assessment of the harvest potential of the continental Scaup population.* Unpublished progress report. U.S. Fish and Wildlife Service, Laurel, Maryland, USA.

**Brook, R. W.** 2002. *Breeding ecology and local population dynamics of Lesser Scaup (*Aythya affinis*) in boreal forest of western Canada.* Thesis, University of Saskatchewan, Saskatoon, Saskatchewan, Canada.

**Brook, R. W., and R. G. Clark.** 2005. Breeding season survival of female Lesser Scaup in the northern boreal forest. *Arctic* **58**:16–20.

**Brown, P. W.** 1987. Influence of an unidentified epornitic on waterfowl nesting at Jessie Lake, Alberta. *Canadian Field Naturalist* **101**:454–456.

**Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock.** 1987. Design and analysis methods for fish survival experiments based on release–recapture. *American Fisheries Society Monograph* **5**:1–437.

**Caswell, H.** 1978. A general approach for the sensitivity of population growth rate to changes in life history parameters. *Theoretical Population Biology* **14**:215–230.

———. 2000. Prospective and retrospective perturbation analyses: their role in conservation biology. *Ecology* **81**:619–627.

———. 2001. *Matrix population models.* Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

———. 2005. Sensitivity analysis of the stochastic growth rate: three extensions. *Australian and New Zealand Journal of Statistics* **47**:75–85.

**Caswell, H., R. J. Naiman, and R. Morin.** 1984. Evaluating the consequences of reproduction in complex salmonid life cycles. *Aquaculture* **43**:123–134.

**Clutton-Brock, T. H., and T. Coulson.** 2002. Comparative ungulate dynamics: the devil is in the detail. *Philosophical Transactions of the Royal Society of London, B* **357**:1285–1298.

**Cooch, E. G., R. F. Rockwell, and S. Brault.** 2001.

Retrospective analysis of demographic responses to environmental change: an example in the lesser snow goose. *Ecological Monographs* **71**:377–400.

**Corcoran, R. M., J. R. Lovvorn, M. R. Bertram, and M. T. Vivion.** 2006. Lesser Scaup nest success and duckling survival on the Yukon Flats, Alaska. *Journal of Wildlife Management*: in press.

**Cox, D. R.** 1972. Regression models and life tables (with discussion). *Journal of the Royal Statistical Society* **74**:187–220.

**Dawson, R. D., and R. G. Clark.** 1996. Effects of variation in egg size and hatching date on survival of Lesser Scaup (*Aythya affinis*) ducklings. *Ibis* **138**:693–699.

**de Kroon, H., J., A. Plaisier, J. van Groenendael, and H. Caswell.** 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* **67**:1427–1431.

**de Kroon, H., J. van Groenendael, and J. Ehrlén.** 2000. Elasticities: a review of methods and model limitations. *Ecology* **81**:607–618.

**Doak, D. F., W. F. Morris, C. Pfister, B. E. Kendall, and E. M. Bruna.** 2005. Correctly estimating how environmental stochasticity influences fitness and population growth. *American Naturalist* **166**:E14–E21.

**Ellig, L. J.** 1955. *Waterfowl relationships to Greenfield Lake, Teton County, Montana.* Montana Fish and Game Department Technical Bulletin 1, Helena, Montana, USA.

**Flint, P. L., J. B. Grand, and R. F. Rockwell.** 1998. A model of Northern Pintail productivity and population growth rate. *Journal of Wildlife Management* **62**:1110–1118.

**Flint, P. L., J. B. Grand, T. F. Fondell, and J. A. Morse.** 2006. Population dynamics of Greater Scaup breeding on the Yukon-Kuskokwim Delta, Alaska. *Wildlife Monographs* **162**:1–22.

**Fournier, M. A., and J. E. Hines.** 2001. Breeding ecology of sympatric greater and Lesser Scaup (*Aythya marila* and *Aythya affinis*) in the subarctic Northwest Territories. *Arctic* **54**:444–456.

**Fox, G. A., and J. Gurevitch.** 2000. Population

numbers count: tools for near-term demographic analysis. *American Naturalist* **156**:242–256.

**Furstenberg, H., and H. Kesten.** 1960. Products of random matrices. *Annals of Mathematical Statistics* **31**:457–469.

**Giroux, J. F.** 1981. Ducks nesting on artificial islands during drought. *Journal of Wildlife Management* **45**:783–786.

**Grant, A., and T. G. Benton.** 2000. Elasticity analysis for density-dependent populations in stochastic environments. *Ecology* **81**:680–693.

**Green, R. E.** 1989. Transformation of crude proportions of nests that are successful for comparison with Mayfield estimates of nest success. *Ibis* **131**:305–306.

**Hammell, G. S.** 1973. *The ecology of the Lesser Scaup in southwestern Manitoba.* Thesis, University of Guelph, Guelph, Ontario, Canada.

**Hauser, C. E., E. G. Cooch, and J.-D. Lebreton.** 2006. Control of structured populations by harvest. *Ecological Modelling* **196**:462–470.

**Heyde, C. C., and J. E. Cohen.** 1985. Confidence intervals for demographic projections based on products of random matrices. *Theoretical Population Biology* **27**:120–153.

**Hines, J. E.** 1977. Nesting and brood ecology of Lesser Scaup at Waterhen Marsh, Saskatchewan. *Canadian Field Naturalist* **91**:248–255.

**Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball.** 2002. Sensitivity analyses of the life cycle of midcontinent Mallards. *Journal of Wildlife Management* **66**:883–900.

**Hoekman, S. T., T. S. Gabor, M. J. Petrie, R. Maher, H. R. Murkin, and M. S. Lindberg.** 2006. Population dynamics of Mallards breeding in agricultural environments in eastern Canada. *Journal of Wildlife Management* **70**:121–128.

**Holm, J. W.** 1984. *Nest success and cover relationships of upland-nesting ducks in northcentral Montana.* Thesis, University of Montana, Missoula, Montana, USA.

**Horvitz, C., D. W. Schemske, and H. Caswell.** 1997. The relative importance of life-history stages to population growth: prospective and retrospective analyses. Pages 247–272 *in* S. Tuljapurkar and H. Caswell, editors. *Structured-population models in marine, terrestrial, and freshwater systems.* Second edition. Chapman and Hall, New York, New York, USA.

**Johnson, D. H.** 1991. Further comments on estimating nesting success. *Ibis* **133**:205–207.

**Kalmbach, E. R.** 1937. *Crow–waterfowl relationships: based on preliminary studies on Canadian breeding grounds.* U.S. Department of Agriculture Circulation No. 433, Washington D.C., USA.

**Keith, L. B.** 1961. A study of waterfowl ecology on small impoundments in southeastern Alberta. *Wildlife Monograph* **6**.

**Kessel, B., D. Rocque, and J. S. Barclay.** 2002. Greater Scaup (*Aythya marila*). *In* A. Poole and F. Gill, editors. *Birds of North America*, Number 650. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA, and American Ornithologists' Union, Washington, D.C., USA. [online] URL: http://bna.birds.cornell.edu/BNA/.

**Keyfitz, N.** 1971. On the momentum of population growth. *Demography* **8**:71–80.

**Kiel, W. H. Jr.** 1953. Waterfowl breeding population and production in the Newdale-Erickson district of Manitoba—1953. Pages 81–85 *in* Anonymous. *Waterfowl populations and breeding conditions, summer 1953.* U.S. Fish and Wildlife Service, Special Scientific Report Wildlife No. 25, Washington, D.C., USA.

**Koons, D. N.** 2001. *Lesser Scaup breeding ecology in the Canadian parklands.* Thesis, Montana State University, Bozeman, Montana, USA.

**Koons, D. N., and J. J. Rotella.** 2003a. Comparative nesting success of sympatric Lesser Scaup and ring-necked ducks. *Journal of Field Ornithology* **74**:222–229.

**Koons, D. N., and J. J. Rotella.** 2003b. Have Lesser Scaup, *Aythya affinis,* reproductive rates declined in parkland Manitoba? *Canadian Field Naturalist* **117**:582–588.

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

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

**Koons, D. N., J. B Grand, and J. M. Arnold.** 2006*b*. Population momentum across vertebrate life histories strategies. *Ecological Modelling* **197**:418–430.

**Lefkovitch, L. P.** 1965. The study of population growth in organisms grouped by stages. *Biometrics* **21**:1–18.

**Leitch, W. G.** 1952. *Ecology of nesting waterfowl in the Missouri Coteau of southern Saskatchewan.* Thesis, University of Manitoba, Winnipeg, Manitoba, Canada.

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

**Long, R. J.** 1970. *A study of nest-site selection by island nesting anatids in central Alberta.* Thesis, University of Alberta, Edmonton, Alberta, Canada.

**Mayfield, H. F.** 1975. Suggestions for calculating nest success. *Wilson Bulletin* **87**:456–466.

**McKnight, D. E., and I. O. Buss.** 1962. Evidence of breeding in yearling female Lesser Scaup. *Journal of Wildlife Management* **26**:328–329.

**Mertz, D. B.** 1971. Life history phenomena in increasing and decreasing populations. Pages 361–399 *in* G. P. Patil, E. C. Pielou, and W. E. Waters, editors. *Statistical ecology. II. Sampling and modeling biological populations and population dynamics.* Pennsylvania State University Press, University Park, Pennsylvania, USA.

**Nelson, U. C.** 1953. Waterfowl breeding ground survey, 1953 in Alaska. Pages 1–6 *in* Anonymous. *Waterfowl populations and breeding conditions, summer 1953*. U.S. Fish and Wildlife Service, Special Scientific Report Wildlife No. 25, Washington, D.C., USA.

**Neter, J., M. H. Kutner, C. J. Nachsteim, and W.** **Wasserman.** 1996. *Applied linear statistical models.* Irwin, Chicago, Illinois, USA.

**Oseledec, V. I.** 1968. A multiplicative ergodic theorem: Ljapunov characteristic numbers for dynamical systems. *Transactions of the Moscow Mathematical Society* **19**:197–231.

**Petrula, M. J.** 1994. *Nesting ecology of ducks in interior Alaska*. Thesis, University of Alaska, Fairbanks, Alaska, USA.

**Rockwell, R. F., E. G. Cooch, and S. Brault.** 1997. Dynamics of the mid-continent population of lesser snow geese—projected impacts of reductions in survival and fertility on population growth rates. Pages 73–100 *in* B. D. J. Batt, editor. *Artic ecosystems in peril: report of the Arctic Goose Habitat Working Group.* Canadian Wildlife Service, Ottawa, Ontario, Canada, and U.S. Fish and Wildlife Service, Washington D.C., USA.

**Roff, D. A.** 1992. *The evolution of life histories: theory and analysis.* Chapman and Hall, New York, New York, USA.

**Rogers, J. P.** 1964. Effect of drought on reproduction of the Lesser Scaup. *Journal of Wildlife Management* **28**:213–222.

**Rotella, J. J., R. G. Clark, and A. D. Afton.** 2003. Survival of female Lesser Scaup: effects of body size, age, and reproductive effort. *Condor* **105**:336–347.

**Sæther, B.-E., and O. Bakke.** 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**:642–653.

**Sankowski, T. P., and B. L. Joynt.** 1992. *Completed project evaluation in the Peace River Region of northwestern Alberta, 1989–1991.* Unpublished Report, Institute of Wetland and Waterfowl Research, Ducks Unlimited-Canada, Winnipeg, Manitoba, Canada.

**Schmutz, J. A., R. F. Rockwell, and M. R. Petersen.** 1997. Relative effects of survival and reproduction on the population dynamics of emperor geese. *Journal of Wildlife Management* **61**:191–201.

**Smith, A. G.** 1955. Waterfowl breeding ground

surveys of special study areas in Alberta—1955. Pages 33–44 *in* Anonymous. *Waterfowl populations and breeding conditions, summer 1955.* U.S. Fish and Wildlife Service, Special Scientific Report No. 30, Washington, D.C., USA.

———. 1971. *Ecological factors affecting waterfowl production in the Alberta parklands.* U. S. Fish and Wildlife Service, Resource Publication 98, Washington, D.C., USA.

**Stearns, S. C.** 1992. *The evolution of life histories.* Oxford University Press, Oxford, UK.

**Stoudt, J. H.** 1971. *Ecological factors affecting waterfowl production in the Saskatchewan parklands.* U.S. Fish and Wildlife Service, Resource Publication 99, Washington, D.C., USA.

**Stoudt, J. H., and B. A. Yeager.** 1955. Waterfowl breeding ground survey of Redvers area, Saskatchewan, 1952–1955. Pages 63–72 *in* Anonymuos. *Waterfowl populations and breeding conditions, summer 1955*. U.S. Fish and Wildlife Service, Special Scientific Report No. 30, Washington, D.C., USA.

**Townsend, G. H.** 1966. A study of waterfowl nesting on the Saskatchewan River delta. *Canadian Field Naturalist* **80**:74–88.

**Trauger, D. L.** 1971. *Population ecology of Lesser Scaup in subarctic taiga.* Dissertation, Iowa State University, Ames, Iowa, USA.

**Tuljapurkar, S. D.** 1984. Demography in stochastic environments. I. Exact distributions of age structure. *Journal of Mathematical Biology* **19**:335–350.

———. 1990. *Population dynamics in variable environments.* Springer-Verlag, New York, New York, USA.

**Tuljapurkar, S., and R. Lee.** 1997. Demographic uncertainty and the stable equivalent population. *Mathematical and Computer Modelling* **26**:39–56.

**van Tienderen, P. H.** 2000. Elasticities and the link between demographic and evolutionary dynamics. *Ecology* **75**:2410–2415.

**Vermeer, K.** 1968. Ecological aspects of duck nesting in high densities among Larids. *Wilson Bulletin* **80**:78–83.

———. 1970. Some aspects of the nesting of ducks on islands in Lake Newell, Alberta. *Journal of Wildlife Management* **34**:126–129.

**Walker, J., M. S. Lindberg, M. C. MacCluskie, M. J. Petrula, and J. S. Sedinger.** 2005. Nest survival of scaup and other ducks in the boreal forest of Alaska. *Journal of Wildlife Management* **69**:582–591

**Walker, J., and M. S. Lindberg.** 2005. Survival of scaup ducklings in the boreal forest of Alaska. *Journal of Wildlife Management* **69**:592–600.

**Wilkins, K. A., M. C. Otto, and M. D. Koneff.** 2006. *Waterfowl population status, 2006.* U.S. Department of Interior Fish and Wildlife Service, Laurel, Maryland, USA.

**Williams, B. K., J. D. Nichols, and M. J. Conroy.** 2002. *Analysis and management of animal populations.* Academic Press, San Diego, California, USA.

**Yearsley, J. M.** 2004. Transient population dynamics and short-term sensitivity analysis of matrix population models. *Ecological Modelling* **177**:245–258.