TRANSIENT POPULATION DYNAMICS AND POPULATION MOMENTUM IN VERTEBRATES

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DISSERTATION ABSTRACT

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Maintenance of sustainable wildlife populations is one of the primary purposes of wildlife management. Thus, it is important to monitor and manage population growth and size over time. Population structure (i.e., age, stage, or size distribution) can affect both population size and growth over time; however, the effects of population structure on vertebrate population dynamics are poorly studied. Here, I examine and compare the effects of population structure on short- (i.e., transient) and long-term (i.e., asymptotic) population dynamics across selected vertebrate taxa.

A general formula for relating sensitivity of transient population growth rate to changes in life history parameters was developed. Using this tool and others, I found that variation in transient growth rates and their sensitivities to changes in life history parameters were largely dependent upon a population's initial net reproductive value. Furthermore, transient population dynamics of long-lived, slow reproducing species were more variable and different than asymptotic dynamics when compared to short-lived, fast reproducing species.

Management actions have strong potential to change population structure, which can produce strong residual effects on population size, commonly known as population momentum. I examined management actions targeted at halting the growth or decline of hypothetical populations and measured the effects of instantaneous changes in fertility or survival on short-term transient dynamics and population momentum. Population momentum following changes in fertility actually reduced population size in growing populations and increased population size in declining populations. Changes in survival rarely reversed the direction of short-term population growth, and resulting population momentum was generally in the direction of historical population growth.

Because population momentum has not been well studied across vertebrates, novel formulas and hypotheses relating the dynamics of population momentum to life history parameters were developed. Using algebra, calculus and computer simulation, I compared the dynamical relationship between life history and population momentum across a variety of bird, mammal, turtle, lizard, snake, and bony fish life histories. Population momentum was related to age at maturity within each taxon, and was largest in late maturing bony fishes. Lastly, I provide examples that illustrate how studies of population momentum can be used to better understand life histories, source-sink metapopulation dynamics, and management actions.

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I dedicate this work to my parents, Robert and Lorrie Koons for their continual love and support. To my mom, whose bout with cancer has put life in perspective. Her displays of strength and courage help one realize that work is work, life is about living it and sharing it with others.

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Computer software used: Microsoft Word XP, MathType 5.2, SigmaPlot 8.0.2, SAS 8.2, Matlab 7.0.1, Maple 9.5.

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I. GENERAL INTRODUCTION

In wildlife management, agency and stakeholder goals are often centered on the population, its size, and changes in size over time. To meet these goals, biologists often direct management at the population growth rate because it can be manipulated to increase population size in the case of conservation (e.g., Fujiwara and Caswell 2001) or decrease size in the case of control (e.g., Rockwell et al. 1997, Merrill et al. 2003).

Because population structure (i.e., the age, stage, size, or state distribution) is rarely known, it is usually assumed that the population is in a stable population structure. This assumption allows use of the stable-state metrics of population growth (e.g., λ_1, r, λ_S, and *a*), which are known as long-term, or asymptotic dynamics. All else being equal, theory suggests that convergence to asymptotic conditions will occur in most populations (Lopez 1961, Cull and Vogt 1973, Cohen 1976, 1977a, b, 1979, Tuljapurkar 1982, 1990).

Yet, environmental catastrophes, natural disturbances, selective harvest regimes, and animal release and relocation programs can disrupt the stability of population structure. If given enough time between perturbations, an unstable population structure will undergo damped fluctuations until the stable population structure is reached. Meanwhile, the population dynamics are 'transient' because they change according to the fluctuating population structure.

Empirical evidence has shown that stable population structures rarely exist in nature (Bierzychudek 1999, Clutton-Brock and Coulson 2002), probably because environments are so variable. Thus, the assumption of asymptotic population dynamics in the wild may be unwarranted in most cases, and more attention should be given to the transient dynamics (Hastings and Higgins 1994, Fox and Gurevitch 2000, Hastings 2001, 2004).

Much is known about the duration and oscillatory behavior of transient dynamics (Coale 1972, Keyfitz 1972, Trussell 1977, Tuljapurkar 1982); however, few have focused on the demographic causes of transient change in population size or growth rate. Even in the transient case, population size and growth rate describe the population’s status. Thus, it would be useful to understand the demographic mechanisms controlling change in transient dynamics.

Sensitivity analysis can be used to determine the functional relationship between population size or growth rate and the constituent vital rates (e.g., fecundity, survival, growth, maturation, recruitment, movement), and to project changes in population growth rate and size as vital rates change. Such analyses usually assume a stable population structure and focus on long-term population dynamics. However, new tools allow one to examine the sensitivity of transient population size and structure (Fox and Gurevitch 2000) or growth rate (Yearsley 2004) to changes in initial population structure or vital rates. These new tools are important because transient sensitivities may be very different from asymptotic sensitivities, and could be very useful in developing management plans or examining natural selection in highly perturbed environments.

In Chapter 2, my aim was to elucidate the biological correlates of intraspecific variation in transient dynamics across all possible population structures. My secondary objective was to explain variation in transient dynamics across life histories. To accomplish these objectives, I calculated the transient population growth rate, and its sensitivity to changes in vital rates, across the complete range of possible population structures for 6 bird and mammal species. Long-lived birds and mammals tend to have longer generation lengths and larger disparity in reproductive value across age classes. Thus, I hypothesized that these properties would cause the transient dynamics in long-lived species to be more variable and different than asymptotic dynamics when compared to short-lived, fast reproducing species.

Management actions also have strong potential to change vital rates by large enough amounts to disrupt population structure. Before population structure begins its approach to a stable-state following a perturbation, the population size can change rapidly and influence the ultimate abundance (Neubert et al. 2002). For example, when examining the potential benefit of turtle-excluder devices on shrimp trawls to loggerhead sea turtle (*Caretta caretta*) populations, Crowder et al. (1994) found that sudden improvements in survival rates caused instability in the age structure. The ensuing transient dynamics resulted in a population size much different than that predicted by asymptotic projections, which is the phenomenon that is better known as ‘population momentum’ (Keyfitz 1971). The classical description of population momentum in demography is as follows. If per capita fertility rates were high, creating an abundance of young individuals with high likelihood of surviving to maturity, and then suddenly dropped to the stationary level (i.e., $\lambda_1 = 1$, the level of lifetime individual replacement), a population would keep growing because overabundance of young individuals would ensure high net fertility rates long after the transition to stationary per capita fertility (sensu Keyfitz 1971).

In demography, studies of population momentum have influenced international policy (e.g., Bos et al. 1992, Bos et al. 1994, United Nations 2003); however, population biologists have paid very little attention to population momentum. Even though population momentum could occur in fish and wildlife populations when management or large environmental perturbations (e.g., hurricanes, floods, fires, epidemics) cause any vital rate to change by a large enough amount to alter the population structure, the phenomenon has not been explicitly examined.

In Chapter 3, I used computer simulation to measure the transient dynamics and population momentum resulting from the control or conservation of hypothetical wildlife populations. To simulate management practices focused on population growth rate, I halted population growth or decline by changing survival or fertility rates, which often have very different elasticities (i.e., sensitivities measured on a proportional scale; Heppell et al. 2000, Sæther and Bakke 2000). It is often suggested that management should focus on the vital rate with the highest elasticity to get the best return in population growth per unit of management effort (Caswell 2000). Yet, I show that short-term population growth and eventual size following some virtual management experiments are so different from the expectations of asymptotic elasticity analysis, that my findings could modify how we manage populations for control and conservation.

Understanding population momentum and its effect on population dynamics could increase the efficacy of conservation, natural resource management, and pest control practices. Further, it could help us better understand evolution and the invasion of new strategies in unstable or nonlinear environments. Chapter 3 is the first study of population momentum for non-human life cycles. Theory describing the behavior of population momentum across species is non-existent.

To partially fill this void, in Chapter 4 I used traditional methods for calculating population momentum, and used computer simulation and theoretical experiments (i.e., thought experiments) to examine population momentum across vertebrate life history strategies. As stated above, changes in vital rates will alter population structure, causing transient dynamics that can ultimately result in population momentum (Caswell 2001). Because transient dynamics of long-lived, slow reproducing vertebrates with delayed maturity are more reactive to changes in population structure than they are for short-lived, fast reproducing vertebrates with early maturity (Chapter 2), I predicted that the magnitude of population momentum would increase with age at maturity.

In Chapter 4, I used thought experiments where every population began on the same trajectory (i.e., growing or declining at the same rate). I then forced each population to transition to the long-term stationary population growth rate. Because the functional relationship between vital rates and population growth rate depends on life history (Heppell et al. 2000, Sæther and Bakke 2000, Oli and Dobson 2003), I had to change vital rates by different amounts for each life history in order to achieve stationary growth. This invoked a new question: how does population momentum respond to equal unit-changes across organisms? More generally, can we analytically measure the 'change' in population momentum caused by a 'unit change' in a single vital rate or the initial population structure?

I know of no general formula that relates unit changes in vital rates or population structure to changes in population momentum. Therefore, in Chapter 5 I derived analytical formulas for the sensitivity of population momentum to unit changes in any vital rate or the initial population structure. I then compared the sensitivity of population momentum to an assortment of vital rates across a wide variety of life histories, and examined population momentum in a simple source-sink metapopulation. Furthermore, I examined the effects of direct management of population structure on population momentum. These examples illustrate an entirely new set of questions for demographers, population biologists, and mathematicians to explore.

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II. TRANSIENT POPULATION DYNAMICS: RELATIONS TO LIFE HISTORY AND INITIAL POPULATION STATE

Abstract

Most environments are variable with disturbances (e.g., hurricanes, fires) that can lead to substantial changes in a population's state (i.e., age, stage, or size distribution). In these situations, the long-term (i.e., asymptotic) measure of population growth rate (λ_1) may inaccurately represent population growth in the short-term. Thus, I calculated the short-term (i.e., transient) population growth rate and its sensitivity to changes in the life-cycle parameters for 3 bird and 3 mammal species with widely varying life histories. Further, I performed these calculations for initial population states that spanned the entire range of possibilities. Variation in a population's initial net reproductive value largely explained the variation in transient growth rates and their sensitivities to changes in life-cycle parameters (all $AIC_c \geq 6.67$ units better than the null model, all $R^2 \geq 0.55$). Additionally, the transient fertility and adult survival sensitivities tended to increase with the initial net reproductive value of the population, whereas the sub-adult survival sensitivity decreased. Transient population dynamics in long-lived, slow reproducing species were more variable and different than asymptotic dynamics when compared to short-lived, fast reproducing species. Because λ_1 can be a biased estimate of the actual growth rate in the short term (e.g., 19% difference), conservation and wildlife

biologists should consider transient dynamics when developing management plans that could affect a population's state, or whenever population state could be unstable.

1. Introduction

Sensitivity analysis has become popular in ecology (e.g., van Groenendael et al., 1988; Horvitz et al., 1997; Benton and Grant, 1999; Heppell et al., 2000a) and has been used to manage and conserve wild populations (e.g., Rockwell et al., 1997; Cooch et al., 2001; Fujiwara and Caswell, 2001). Such analyses usually assume that the population's state (i.e., age, stage, or size distributions) remains stable through time (i.e., the asymptotic stable state), and that populations grow according to a constant, or stable distribution of rate(s) (e.g., λ_1, r, λ_s, a). All else being equal, theory suggests that the stable state assumption in population biology is a safe one (Lopez, 1961; Cull and Vogt, 1973; Cohen, 1976, 1977a, b, 1979; Tuljapurkar, 1984, 1990).

Environmental catastrophes, natural disturbances, selective harvest regimes, and animal release and relocation programs can significantly alter a population, causing unstable states. When given enough time between environmental perturbations, population state will approach the stable state. Meanwhile, the population dynamics are 'transient' because they change according to the fluctuating population state until the asymptotic stable state is achieved. Empirical evidence suggests that stable populations rarely occur in nature (Bierzychudek, 1999; Clutton-Brock and Coulson, 2002). Thus, the assumption of asymptotic population dynamics in the wild may be unwarranted in many cases (Hastings and Higgins, 1994; Fox and Gurevitch, 2000; Hastings, 2001, 2004).

Although much is known about the mathematics of transient dynamics (Coale, 1972; Keyfitz, 1972; Trussell, 1977; Tuljapurkar, 1982), few have focused on demographic causes of transient change in population size or growth rate even though they are the unifying parameters of evolutionary and population biology (Sibly et al., 2002).

Sensitivity analysis can be used to determine the functional relationship between population size or growth rate and the constituent vital rates (e.g., fecundity, survival, growth, maturation, recruitment, movement), and to project changes in population growth rate and size as vital rates change. New tools allow one to examine the sensitivity of transient population size and structure (Fox and Gurevitch, 2000) or growth rate (Yearsley, 2004) to changes in the initial population state or the vital rates. These new tools are important because transient sensitivities may be very different from asymptotic sensitivities. For example, in *Coryphantha robbinsorum*, the asymptotic population growth rate was most sensitive to adult survival, but transient population growth rate and size were most sensitive to growth of juvenile stages (Fox and Gurevitch, 2000; Yearsley, 2004). Thus, asymptotic sensitivities might not be informative for guiding short-term management decisions.

I examined the sensitivity of 'transient population growth rate' to changes in vital rates for 6 bird and mammal species across all possible population states. My primary objective was to elucidate the biological correlates of intraspecific variation in transient dynamics across the possible population states. My secondary objective was to explain variation in transient dynamics across life histories. Long-lived birds and mammals tend to have longer generation lengths and larger disparity in reproductive value across age classes. I hypothesized that these properties would cause transient dynamics in long-lived species to be more variable and different than asymptotic dynamics when compared to short-lived, fast reproducing species.

2. Methods

2.1. Data sets and matrix projection models

To examine the magnitude of difference between transient dynamics and asymptotic dynamics across species, I chose 3 bird and 3 mammal species that have been extensively studied and were known to have widely varying life histories. Along the slow-fast continuum of bird and mammal life histories, the 'slowest' species are those that live a long life, mature late, and have low reproductive rates and long generation lengths. The 'fastest' species are short-lived, mature early, have high reproductive rates and short generation lengths (sensu Gaillard et al., 1989; Charnov, 1993).

I attained age-specific vital rate data from published long-term studies of blue tit *Parus caeruleus* (Dhondt, 1989 a, b), manatee *Trichechus manatus* (Eberhardt and O'Shea, 1995), red deer (Benton et al., 1995; Albon et al., 2000), snow goose *Chen caerulescens* (Cooke et al., 1995; Cooch et al., 2001), snowshoe hare *Lepus americanus* (Meslow and Keith, 1968), and wandering albatross *Diomedea exulans* (Weimerskirch, 1992; Weimerskirch et al., 1997) (App. A). Wandering albatross and manatee have slow life histories, snow goose and red deer have medium-slow life histories, and blue tit and snowshoe hare have fast life histories (Heppell et al., 2000b; Sæther and Bakke, 2000). I used age-specific vital rates where the authors reported age-specific differences. Meslow and Keith (1968) did not detect age-specific differences in vital rates during their long-term study. To examine the effects of age-structured vital rates on transient dynamics in a fast species, I used Meslow and Keith’s (1968) original data, and implemented hypothetical age structure by increasing fertility by 5% for age 2 and 10% for ages 3 and older (App. A).

For each species, I assumed birth-pulse reproduction and parameterized the vital-rate data into a life cycle projection matrix (**A**) assuming a pre-breeding census

$$\mathbf{A}=\begin{bmatrix} 0 & \cdots & F_{\alpha} & \cdots & F_{\alpha+n-1} & F_{\alpha+n} \\ P_1 & 0 & 0 & \cdots & 0 & 0 \\ 0 & \ddots & 0 & \cdots & 0 & 0 \\ 0 & 0 & P_{\alpha} & \cdots & 0 & 0 \\ \vdots & 0 & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & P_{\alpha+n-1} & P_{\alpha+n} \end{bmatrix} \tag{1}$$

where α was the average age of first breeding and $(\alpha+n)$ was the oldest known age group with unique vital rates. Because the dynamics of increasing and decreasing populations can be very different, even within a single population (Mertz 1971), I multiplied each matrix by a constant *K* (Appendix A) so that the dominant eigenvalue of each matrix would equal 1.00.

2.2. Transient sensitivity analysis

For a population at any state, the population growth rate (GR) can be defined as,

$$\mathrm{GR}=\frac{\sum_{k}\mathbf{n}_{t,k}}{\sum_{k}\mathbf{n}_{t-1,k}} \tag{2}$$

where $\mathbf{n}_{t,k}$ is the *k-th* element of the population state vector at time *t*. Thus, if the population is not in the asymptotic stable state, GR is the transient growth rate for a one time-step interval (see App. B for longer time steps). I sought a solution to the sensitivity of the transient GR to infinitely small changes in a vital rate ($\mathrm{TS_{ij}}$), which can be defined as,

$$\mathrm{TS_{ij}} = \frac{\partial\left(\sum_{k}\mathbf{n}_{t,k} \Big/ \sum_{k}\mathbf{n}_{t-1,k}\right)}{\partial a_{ij}}. \tag{3}$$

The solution of $\mathrm{TS_{ij}}$ is a two-part equation as follows,

$$\mathrm{TS_{ij}} = \begin{cases} \dfrac{\mathbf{e}'\boldsymbol{\Delta}_{ij}\mathbf{n}_0}{\mathbf{e}'\mathbf{n}_0} & \text{for } t = 1 \\[2ex] \dfrac{\sum\limits_{l=0}^{t-2}\mathbf{e}'\mathbf{A}^{l}\boldsymbol{\Delta}_{ij}\mathbf{A}^{t-l-2}\left(\mathbf{A}\mathbf{n}_0\mathbf{e}' - \mathbf{n}_0\mathbf{e}'\mathbf{A}\right)\mathbf{A}^{t-1}\mathbf{n}_0 + \mathbf{e}'\mathbf{A}^{t-1}\boldsymbol{\Delta}_{ij}\mathbf{n}_0\mathbf{e}'\mathbf{A}^{t-1}\mathbf{n}_0}{\left(\mathbf{e}'\mathbf{A}^{t-1}\mathbf{n}_0\right)^2} & \text{for } t = 2, 3, \ldots \end{cases}$$

and derivation of the solution can be found in appendix B, where I provide further explanation of notation and the similarities and differences of my derivation to Yearsley's (2004).

2.3. Simulations and projection analysis

For each life-cycle matrix, I attained the stable population state vector and systematically generated 1000 state vectors, each normalized to one (1200 for wandering albatross because of the larger state-vector dimension), by systematically drawing numbers from a random uniform distribution. To examine transient dynamics under stable population state and random initial conditions, I projected each life-cycle matrix 5 time steps (years) with each state vector using equation B-1 (i.e., 1201 initial-condition state vector projections for wandering albatross and 1001 for all other species). To calculate the distance between each initial-condition state vector and the stable population state vector, I used Keyfitz's Δ (1968),

$$\Delta\left(\mathrm{x}, \mathrm{w}_1\right) = \frac{1}{2}\sum_{\mathrm{k}}\left|\mathrm{x}_{\mathrm{k}} - \mathrm{w}_{1,\mathrm{k}}\right| \tag{4}$$

where x_{k} and $\mathrm{w}_{1,\mathrm{k}}$ were the *k-th* elements of the initial population state and stable state vectors, respectively. The maximum value of Keyfitz's Δ is 1 and its minimum is 0 when the population state vectors are identical. A population state vector that has proportionately more breeding adults than the stable-state vector and one that has proportionately more sub-adults could have the same Δ value. To rectify this important biological difference, I assigned (+) values to all Δs when vectors had proportionately more breeding adults than the stable-state vector and (–) values to all Δs when vectors had proportionately more sub-adults than the stable-state vector. Species that mature and breed at age 1 (i.e., blue tit and snowshoe hare), and are counted with a pre-breeding census, will not have sub-adults in the population state vector. Thus, the signed Keyfitz Δ can only vary between 0 and 1 for these species. I used the signed Keyfitz Δ as a predictor variable in statistical analyses, and linearly mapped Δ values from the region $\left[-1,1\right]$ to the region $\left[0,2\right]$ in order to examine models using the exponential distribution, which ranges from 0 to infinity. In addition, I calculated the initial net reproductive value (c_1) of a population for each population state vector as,

$$\mathrm{c}_1 = \mathbf{v}_1' \times \mathbf{n}_0 \tag{5}$$

where $\mathbf{v}_1$ is the dominant left eigenvector of the $\mathbf{A}$ matrix normalized to 1 and represents state-specific reproductive value (Goodman, 1968).

Furthermore, I estimated the transient growth rate at time steps 1-to-2 (GR2), 4-to-5 (GR5), and 0-to-5 (5YRGR). 5YRGR is not the usual measure of growth rate, but rather a measure of the % change in population size over 5 years. Additionally, I estimated the sensitivity of transient GR to small changes in the vital rates at time steps 1-to-2 and 4-to-5 according to equation B-7. I then summed the transient sensitivity estimates across relevant state classes to obtain transient fertility sensitivity (TFS), transient sub-adult-survival sensitivity (TSASS), and transient adult survival sensitivity (TASS) for the aforementioned time steps (e.g., Oli and Zinner, 2001: 383). For comparison, I also estimated the asymptotic growth rate ($\lambda_1 = 1$ in all cases after adjusting each life cycle with a constant *K*, Appendix A) and sensitivities (Caswell, 1978) for each life history.

2.4. Data Analysis

I used data from the 1001 projections (1201 for wandering albatross) described above for each species and considered a variety of null, linear, and nonlinear models to examine the form of the relationship between the initial net reproductive value and the response variables describing transient dynamics (GR, TFS, TSASS, and TASS at each of the aforementioned time steps). Because heteroscedasticity was present in the transient response variables across the initial population states, I used iteratively re-weighted least squares (IRLS) robust regression with the Huber weight function (Rousseeuw and Leroy, 1987; Carroll and Ruppert, 1988; Neter et al., 1996: 418) to estimate the intraspecific relationships. Analyses were conducted with Proc NLIN (SAS Institute, Inc. 2000).

I used Akaike's Information Criterion adjusted for sample size (AIC_c) and Akaike weights (Akaike, 1973; Burnham and Anderson, 1998: 51, 124) to evaluate the amount of support in my data for each model in my candidate list (see above). I considered the best approximating model to be that with the lowest AIC_c value and highest Akaike weight (W_i) (Burnham and Anderson, 1998).

To examine the magnitudes of differences between transient and asymptotic population dynamics for each of the 7 life histories, I first measured the difference between each transient dynamic (e.g., GR2, TFS2, etc.) and the respective asymptotic dynamic for all simulated projections. I then calculated the absolute value of the difference, and finally estimated the mean and variance of the absolute values across all simulated projections (1001, 1201 for wandering albatross) for each life history. I again used IRLS robust regression with the Huber weight function to estimate the linear relationship between the generation length of the life history (explanatory variable) and each of the aforementioned 'difference' estimates (response variable) (Rousseeuw and Leroy, 1987). I used F-tests to examine the support, or lack thereof, for the *a priori* hypothesis that mean and variance of each 'difference' estimate would increase with generation length of the life history (Neter et al., 1996).

3. Results

For each intraspecific analysis, I examined 9 models (i.e., the null, linear, and nonlinear models) to identify how departures away from the stable population state affect the initial net reproductive value of a population, and another 9 models to identify how the initial net reproductive value affects transient dynamics. Transient dynamics measured at the annual time scale did not exist in any of the simulations conducted for the snowshoe hare life cycle without age-structured vital rates, meaning that asymptotic dynamics always occurred. However, the results for all other life cycles and initial population states had important ecological and conservation implications.

In all cases, I found that the signed Keyfitz Δ between a population state vector and the stable state vector (i.e., the departure distance) caused nonlinear changes in c_1. For species that exhibited some senescence in survival and/or fertility (i.e., blue tit and red deer), I detected negative relationships between c_1 and the Keyfitz Δ but found positive relationships in all other species (Fig. 1). The resulting changes in c_1 caused by departure in initial conditions away from the stable state largely determined the direction and magnitude of transient population growth rate and its sensitivity to changes in the vital rates. In all but two cases, the relationships between c_1 and the transient population growth rates were positive. Across species, the slope of the c_1 versus GR relationships tended to increase with the generation length of the species examined; however, this generalization is not perfect (see Manatee results in Fig.2). Furthermore, within-species slopes were greatest for the c_1 and 5YRGR relationship (Fig.2), indicating that initial conditions had an additive effect on population size over 5 years.

Similar to the GR results for each species, I detected strong linear or nonlinear relationships between c_1 and the variation in each of the transient sensitivities. I found a positive relationship between c_1 and transient fertility and adult survival sensitivities for the slower species, but found relatively flat relationships for the fastest species (Figs. 3 and 4). Because sub-adult survival contributed less to population growth when a smaller segment of the population was comprised of sub-adults (e.g., population states with large signed Keyfitz Δs), I found a negative relationship between c_1 and transient sub-adult survival sensitivities for 3 of 4 species. However, I detected interesting curvilinear relationships between c_1 and all vital-rate sensitivities for red deer, which may be related to delayed maturity and senescence present in their life cycle (Figs. 3 and 4). Of further significance, rankings of the transient sensitivities shifted across initial conditions in 5 of 6 species, and the rank-intersection point shifted with the time step (Figs. 3 and 4). Moreover, slope of the relationships between c_1 and the transient sensitivities was much smaller for among fast species (Figs. 3 and 4).

Across species, mean and variance of the 'difference' measures between transient and asymptotic dynamics (see Methods) increased and were highly correlated with generation length ($P < 0.10$ except in 3 cases; Fig. 5). At the extremes (global max and min), early transient growth rates (GR2 and GR5) were as much as 19%, 9%, 9%, 18%, 3%, and 1% different than asymptotic growth rate for wandering albatross, manatee, snow goose, red deer, blue tit, and snowshoe hare (with age-structured vital rates) respectively. More strikingly, effects of initial conditions were strongest over the culmination of the five years of projection. 5YRGR differed from $(\lambda_1)^5$ by as much as 59%, 21%, 31%, 55%, 11%, and 8% for the corresponding list of species just mentioned. At time step 1-to-2, extreme transient sensitivities were as much as 248%, 335%, 155%, 249%, 5%, and 4% different from asymptotic estimates for the same list of species mentioned above. While transient estimates are expected to approach asymptotic estimates over time, differences at the extreme values were alarmingly large after 5 time steps, 134%, 200%, 69%, 82%, 3%, and 2% for the corresponding list of species.

4. Discussion

Asymptotic demographic analysis has had a long history of use in population ecology; however, my results indicated that the stable population state should not be assumed unless empirically justified. Multistate capture-mark-recapture analysis can be used to estimate a population's state (Nichols et al. 1994, Williams et al. 2002) but measuring the population state will be a challenging task in most studies. Still, my approach can elucidate the potential importance of transient dynamics relative to asymptotic dynamics for populations that could have unstable states at some point in time. I discuss several biological underpinnings of transient dynamics so that more biologists can comprehend and use transient dynamics in future population ecology and management studies.

4.1. Intraspecific Patterns in Transient Dynamics

Damping ratios (Tuljapurkar, 1986; Law and Edley, 1990), asymptotic convergence times (Taylor, 1979; DeAngelis et al., 1980; Hastings and Higgins, 1994), Argand diagrams (Horst, 1977; Rago and Goodyear, 1987), examination of oscillations in state-vector components (Tuljapurkar, 1983, 1985) and examination of unstable equilibrium (Cushing et al., 1998) have all been used to present transient dynamics. However, these approaches fail to explicitly incorporate measures of population growth rate, which is one of the unifying parameters of ecology and evolution (Sibly et al., 2002).

In my study, I found that transient population growth rates and sensitivities were highly dependent upon initial conditions. Initial net reproductive values usually increased with the signed Keyfitz Δ because large Δs represented population states with proportionately more breeding adults than the stable state, and adult age classes frequently had higher reproductive value than sub-adult age classes. However, initial net reproductive value decreased with the signed Keyfitz Δ when vital rates declined with age (e.g., blue tit and red deer; Fig. 1).

Across all of the tested initial population states for each species, transient fertility and adult survival sensitivities generally increased with c_1, whereas the transient sub-adult survival sensitivity decreased (Figs. 3 and 4, but see red deer results). Each occurred because initial population states with low c_1 values generally consisted of more sub adults or partially senescent old individuals than the stable state (see Fig. 1). Individuals must survive to maturity before they can contribute young to the population, which explains why early transient growth rates are generally most sensitive to sub-adult survival for initial population states with low c_1 values. Initial population states with high c_1 values largely consisted of individuals that were at or near their peak reproductive value (Fig.1), thus the continued survival and fertility output of prime-aged adults contributed most to transient population growth rates under these conditions.

Initial net reproductive value (c_1) is an omnibus measure that can be used to predict transient dynamics (e.g., GR, TS_{ij}) across initial state conditions, through time, and to examine shifts in rank-order of vital rate contributions to transient GR (see figs. 3 and 4). Thus, the net reproductive value of a population can help explain many properties of transient dynamics (Templeton, 1980) and it will be important to study the ecological forces that affect c_1.

4.2. Interspecific Patterns in Transient Dynamics

Tuljapurkar (1985) found that damping ratios and periods of oscillation in the population state vector increased with generation length. In 15 of my 18 interspecific comparisons, I found that either mean or variance of estimated ‘differences’ between transient and asymptotic dynamics increased with generation length as well.

Furthermore, slopes of the abovementioned intraspecific relationships were steepest among slow and medium-slow species (Figs. 2, 3, and 4).

Population dynamics in fast species were resilient to departures from stable state; however, slow species experienced early transient dynamics that were variable across the tested initial-state conditions, very different than asymptotic dynamics, and the dynamics changed slowly over time as they slowly converged to the asymptotic stable state. Moreover, unstable population states sometimes produced net decreases or net increases in population size, a phenomenon known as population momentum (Keyfitz, 1971; Lande and Orzack, 1988; Koons et al. unpublished data).

Compared to fast species, slow species mature late and live long lives, increasing the chances for high variability in survival rates and reproductive investment across age classes. These life history characteristics lead to high disparity in reproductive value across age classes (see rv:rv, appendix A). Long generation length increases the time required for transient dynamics to change (Tuljapurkar 1985), and disparate reproductive values can lead to large changes in net reproductive following changes in population state. Collectively, I believe these factors make the dynamics of slow species more responsive to changes in population state.

4.3. Ecological Implications

Transient population analysis can reveal the possible effects of initial age or stage structure (Fox and Gurevitch, 2000; this study), colonization (Caswell and Werner, 1978), life history (DeAngelis et al., 1980; this study), harvest, and especially pulse perturbations to the environment (e.g., catastrophic mortality) on population dynamics. Of immediate concern, my results indicate that λ_1 can be a biased estimate of short-term population growth rate when population state is unstable (e.g., 335% difference between transient and asymptotic estimates), especially among slow and medium-slow species.

Popular methods for managing and conserving populations include release of captive-reared animals into the wild, relocation of wild individuals (e.g., Starling, 1991; Wolf et al., 1996; Ostermann et al., 2001), and state-specific harvest management (Larkin, 1977; Holt and Talbot, 1978). All of these methods will perturb population state and produce transient dynamics. Attempts to identify the best animal propagation or harvest program with asymptotic projection models could lead to incorrect conclusions (Merrill et al., 2003) and even mismanagement of populations. Long ago, MacArthur (1960) showed that management programs that favor individuals with high reproductive value will lead to large net reproductive values, which in turn cause high population growth rates and abundance. Programs that favor individuals with low reproductive value will produce opposite results. Moreover, favoring few individuals of high reproductive value or many individuals of low reproductive value can result in similar net reproductive values and transient dynamics. Using my approach, I suggest that resource managers place a strong emphasis on estimation of population state and reproductive value to examine the consequences of their management actions on short-term population dynamics, which are often more relevant to agency goals than long-term dynamics. Such studies will help reduce uncertainty in decision-making and the likelihood of deleterious management in the future.

Furthermore, anthropogenic catastrophes (e.g., oil and toxin spills, nuclear disasters, mining, war, bioterrorism) are common in today's world and many biologists try to understand the impacts of anthropogenic catastrophes on population dynamics

(Brockwell et al., 1983; Brockwell, 1985; Lande, 1993; Mangel and Tier, 1993, 1994). However, the impact of catastrophes on population dynamics cannot be elucidated with asymptotic methods alone because catastrophes could severely perturb population state. I have shown that this can drastically alter short-term population dynamics, and Koons et al. (unpublished data) have shown that it can significantly affect long-term population size. When catastrophes have the potential to perturb population state, I suggest that risk assessments, such as population viability analyses (Gilpin and Soulé, 1986) and population recovery analyses, pay closer attention to transient dynamics and to effects of population state on extinction or recovery times and probabilities.

4.4. Caveats

The degree to which asymptotic dynamics are a poor proxy for actual dynamics depends on the population state, time, and life history. Like many transient analyses, my results are unique to the time scale and models under examination. Because the number of unique eigenvalues and eigenvectors can change with matrix dimension, the chosen matrix dimension may influence transient dynamics. Yet, I found that expanding small-dimension matrices (e.g., 3-by-3, etc.) into a large-dimension matrix (29-by-29) resulted in transient growth rates that were identical to four decimal places. Matrix dimension did affect net reproductive value and time required to converge to the asymptotic stable state (see Caswell 2001:97), however differences were ≤ 0.005 and ≤ 0.05 years, respectively (Koons et al. unpublished data). Thus, in this study I saw little reason to use matrices that were larger than necessary to incorporate the published age-specific differences in vital rates. Furthermore, I purposefully used a simplistic approach to elucidate some of the biological factors causing transient population growth and related dynamics in an otherwise deterministic environment. Long-term population size, growth rate, sensitivities, and extinction probability can be approximated in stochastic environments for any population state if the degree of environmental variability is small to moderate (Tuljapurkar, 1982; Lande and Orzack, 1988; Lande et al., 2003). In the real world, vital rates, as well as age, stage, or size structure may vary substantially across time and space (e.g., Clutton-Brock and Coulson, 2002). Questions concerning transient dynamics in highly stochastic and periodically catastrophic environments have not been examined, and offer an arena for much needed research in the future.

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Appendix A. Age-specific values of average age-at-maturity (denoted by α), fertility (F), and survival rates (P) in the standardized matrices for wandering albatross (Weimerskirch, 1992; Weimerskirch et al., 1997), manatee (Eberhardt and O'Shea, 1995), snow goose (Cooke et al., 1995; Cooch et al., 2001), red deer (Benton et al., 1995, Albon et al., 2000), blue tit (Dhondt, 1989 a, b), and snowshoe hare (Meslow and Keith, 1968). Also, original life-cycle matrices parameterized with vital rates attained from the literature were multiplied by standardizing constants (*K*). Generation lengths (T, the time required for the population to increase by a factor of R_0 [the net reproductive rate]), and disparity of reproductive value across age classes (rv:rv, the ratio of the highest age-specific reproductive value to the lowest) are also displayed.

	Wandering Albatross			Manatee			Snow Goose			Red Deer			Blue Tit			Snowshoe Hare[a]			Snowshoe Hare[b]		
K		0.97			0.95			0.91			0.94			0.88			0.91			0.92	
T		21.29			14.34			5.63			7.73			1.52			1.24			1.23	
rv:rv		3.10			1.32			1.77			2.92			1.15			1.09			1.00	
	α	F_i	P_i	α	F_i	P_i	α	F_i	P_i	α	F_i	P_i	α	F_i	P_i	α	F_i	P_i	α	F_i	P_i
Age[c]																					
1			0.81			0.91			0.74			0.85	α	0.65	0.34	α	0.81	0.18	α	0.82	0.18
2			0.81			0.91	α	0.17	0.74			0.91		0.69	0.34		0.85	0.18		0.82	0.18

3			0.81			0.91	0.33	0.74	α	0.08	0.90	0.69	0.34	0.89	0.18	0.82	0.18
4			0.81	α	0.12	0.91	0.40	0.74		0.19	0.90	0.59	0.34				
5			0.94		0.12	0.91	0.46	0.74		0.21	0.90	0.59	0.34				
6			0.94							0.21	0.90						
7			0.94							0.21	0.90						
8			0.94							0.21	0.86						
9			0.94							0.21	0.86						
10	α	0.22	0.94							0.21	0.86						
11		0.22	0.94							0.21	0.86						
12		0.22	0.94							0.21	0.86						
13		0.22	0.94							0.16	0.65						
⋮		0.22	0.94														
19		0.22	0.94														
20		0.20	0.94														
⋮		0.20	0.94														

28	0.20	0.94
29	0.20	0.90

a – Snowshoe hare life cycle with age-structured vital rates.

b – Snowshoe hare life cycle without age-structured vital rates.

c –Pseudo age class.

† – All numerical values in the table are rounded to the nearest 10^{-2} decimal place. In the projection analysis I used values with precision to the 10^{-6} decimal place.

†† – The division of the values in the table by *K* yields the original vital rate values.

Appendix B. An analytical solution to the sensitivity (TS_{ij}) of transient population growth rate (GR) to changes in a vital rate, with comparisons to Yearsley's (2004) solution.

Traditionally, populations have been modeled with matrix equations of the form

$$\mathbf{n}_t = \mathbf{A}^t \mathbf{n}_0 \tag{B-1}$$

where $\mathbf{n}_t$ and $\mathbf{n}_0$ are vectors describing the population state (i.e., age, stage, or size distribution) at times *t* and 0, respectively, and **A** is an *n-by-n* (deterministic) matrix whose entries are denoted by a_{ij} (I denote matrices and vectors in bold type with upper-case and lower-case notation respectively). Alternatively, equation B-1 can be decomposed and expressed with the eigenvalues and eigenvectors of the **A** matrix,

$$\mathbf{n}_t = \sum_i c_i \lambda_i^t \mathbf{w}_i \tag{B-2}$$

where the $\mathbf{w}_i$'s are the right eigenvectors of **A**, the λ_i's are the associated eigenvalues, and the c_i's are dependent on initial conditions and the complex conjugates of the left eigenvectors of **A** (Caswell, 2001). The dominant right eigenvector ($\mathbf{w}_1$) and the dominant scalar (c_1) describe the asymptotic stable state and net reproductive value of the initial population (Templeton, 1980), respectively. The biological definitions of the sub-dominant eigenvectors and scalars are less clear (Caswell, 2001). Still, B-2 can provide a deeper understanding of the dynamics of $\mathbf{n}_t$, but some may find it difficult to work with.

For these reasons, Yearsley (2004) begins with equation B-2 to project $\mathbf{n}_t$ and appends Fox and Gurevitch's (2000) pioneering work by deriving a complex but elegant solution to the sensitivity of 'transient population growth rate' to infinitely small changes in a vital rate. His method allows one to calculate sensitivity of average transient growth rate for specific age or stage classes, or for entire populations. If one does not need detailed information about class-specific dynamics, I derive a simpler solution to the sensitivity of transient population growth rate of the entire population to infinitely small changes in a vital rate that begins with equation B-1 rather than B-2.

As described in the text, the population growth rate of a population in any state (not assuming the stable state) can be defined according to equation 2. Because $\mathbf{n}_t$ in equation 2 is derived from the **A** matrix and the initial state vector, my definition of growth rate is quantitatively equivalent to Yearsley's (2004) calculation that uses the weighted average of the eigenvalue spectrum belonging to the **A** matrix (the individual state-vector components at time *t*-1 in my equation 2 operate as weights). For comparative purposes, population growth rates for the *k-th* element of the population state vector can simply be calculated by deleting summation symbols in my equation 2. Furthermore, to estimate population growth rate over any time step *m*, the denominator of equation 2 can be changed to $\mathbf{n}_{t-m,\,k}$.

Nevertheless, my goal was to find a simple analytical solution to sensitivity of the transient GR for the entire population to infinitesimally small changes in a vital rate (TS_{ij}, equation 3). To do this I begin with equation B-1 to project $\mathbf{n}_t$. I note that $\mathbf{A}^0$ is defined as the identity matrix. I denoted **e** as the vector whose components are all equal to 1 and Δ_{ij} as the n-by-n matrix whose entry in the *i-th* row and *j-th* column is 1 and 0 everywhere else. I make special note that for t = 1, 2, . . .

$$\frac{\partial}{\partial a_{ij}}\mathbf{A}^{t} = \sum_{l=0}^{t-1}\mathbf{A}^{l}\boldsymbol{\Delta}_{ij}\mathbf{A}^{t-l-1} \qquad \text{(B-3)}$$

where *l* simply operates as a dummy variable. I then use this definition of the partial derivative of the **A** matrix with respect to one of its entries to derive the sensitivity of transient growth rate to changes in the **A**-matrix entries. Thus, for t = 1

$$\frac{\partial\left(\sum_{\mathrm{k}}\mathbf{n}_{\mathrm{t,\,k}}\Big/\sum_{\mathrm{k}}\mathbf{n}_{\mathrm{t\,-1,\,k}}\right)}{\partial \mathrm{a}_{\mathrm{ij}}} = \frac{\partial}{\partial \mathrm{a}_{\mathrm{ij}}}\frac{\mathbf{e}'\mathbf{A}\mathbf{n}_0}{\mathbf{e}'\mathbf{n}_0} = \frac{\mathbf{e}'\mathbf{\Delta}_{\mathrm{ij}}\mathbf{n}_0}{\mathbf{e}'\mathbf{n}_0} \tag{B-4}$$

and for t = 2, 3, . . .

$$\begin{aligned}
\frac{\partial\left(\sum_{\mathrm{k}}\mathbf{n}_{\mathrm{t,\,k}}\Big/\sum_{\mathrm{k}}\mathbf{n}_{\mathrm{t\,-1,\,k}}\right)}{\partial \mathrm{a}_{\mathrm{ij}}} &= \frac{\partial}{\partial \mathrm{a}_{\mathrm{ij}}}\frac{\mathbf{e}'\mathbf{A}^{\mathrm{t}}\mathbf{n}_0}{\mathbf{e}'\mathbf{A}^{\mathrm{t\,-\,1}}\mathbf{n}_0} \\
&= \frac{\frac{\partial}{\partial \mathrm{a}_{\mathrm{ij}}}\left[\mathbf{e}'\mathbf{A}^{\mathrm{t}}\mathbf{n}_0\right]\mathbf{e}'\mathbf{A}^{\mathrm{t\,-\,1}}\mathbf{n}_0 - \mathbf{e}'\mathbf{A}^{\mathrm{t}}\mathbf{n}_0\frac{\partial}{\partial \mathrm{a}_{\mathrm{ij}}}\left[\mathbf{e}'\mathbf{A}^{\mathrm{t\,-\,1}}\mathbf{n}_0\right]}{\left(\mathbf{e}'\mathbf{A}^{\mathrm{t\,-\,1}}\mathbf{n}_0\right)^2} \\
&= \frac{\sum_{l=0}^{\mathrm{t\,-1}}\mathbf{e}'\mathbf{A}^{l}\mathbf{\Delta}_{\mathrm{ij}}\mathbf{A}^{\mathrm{t}-l-1}\mathbf{n}_0\mathbf{e}'\mathbf{A}^{\mathrm{t\,-\,1}}\mathbf{n}_0 - \mathbf{e}'\mathbf{A}^{\mathrm{t}}\mathbf{n}_0\sum_{l=0}^{\mathrm{t\,-2}}\mathbf{e}'\mathbf{A}^{l}\mathbf{\Delta}_{\mathrm{ij}}\mathbf{A}^{\mathrm{t}-l-2}\mathbf{n}_0}{\left(\mathbf{e}'\mathbf{A}^{\mathrm{t\,-\,1}}\mathbf{n}_0\right)^2}
\end{aligned} \tag{B-5}$$

where the last expression can also be written in the form,

$$\frac{\sum_{l=0}^{\mathrm{t\,-\,2}}\mathbf{e}'\mathbf{A}^{l}\mathbf{\Delta}_{\mathrm{ij}}\mathbf{A}^{\mathrm{t}-l-2}\left(\mathbf{A}\mathbf{n}_0\mathbf{e}' - \mathbf{n}_0\mathbf{e}'\mathbf{A}\right)\mathbf{A}^{\mathrm{t\,-\,1}}\mathbf{n}_0 + \mathbf{e}'\mathbf{A}^{\mathrm{t\,-\,1}}\mathbf{\Delta}_{\mathrm{ij}}\mathbf{n}_0\mathbf{e}'\mathbf{A}^{\mathrm{t\,-\,1}}\mathbf{n}_0}{\left(\mathbf{e}'\mathbf{A}^{\mathrm{t\,-\,1}}\mathbf{n}_0\right)^2} \tag{B-6}$$

Therefore, given equations B-5 and B-6,

$$\mathrm{TS}_{\mathrm{ij}} = \begin{cases} \dfrac{\mathbf{e}'\mathbf{\Delta}_{\mathrm{ij}}\mathbf{n}_0}{\mathbf{e}'\mathbf{n}_0} & \text{for t = 1} \\[2ex] \dfrac{\sum_{l=0}^{\mathrm{t\,-\,2}}\mathbf{e}'\mathbf{A}^{l}\mathbf{\Delta}_{\mathrm{ij}}\mathbf{A}^{\mathrm{t}-l-2}\left(\mathbf{A}\mathbf{n}_0\mathbf{e}' - \mathbf{n}_0\mathbf{e}'\mathbf{A}\right)\mathbf{A}^{\mathrm{t\,-\,1}}\mathbf{n}_0 + \mathbf{e}'\mathbf{A}^{\mathrm{t\,-\,1}}\mathbf{\Delta}_{\mathrm{ij}}\mathbf{n}_0\mathbf{e}'\mathbf{A}^{\mathrm{t\,-\,1}}\mathbf{n}_0}{\left(\mathbf{e}'\mathbf{A}^{\mathrm{t\,-\,1}}\mathbf{n}_0\right)^2} & \text{for t = 2, 3, . . .} \end{cases} \tag{B-7}$$

Figure 1. The top performing models of c_1 as a function of the signed Keyfitz Δ (mapped to the region [0, 2]) for wandering albatross (R^2 = 0.75; the initial dip in the fitted line is an artifact of the model fit to sparse data at the lower tail of Keyfitz Δ values; the raw data do not indicate an initial dip), manatee (R^2 = 0.65), snow goose (R^2 = 0.76), red deer (R^2 = 0.81), blue tit (R^2 = 0.44), and snowshoe hare (with age-structured vital rates, R^2 = 0.87). Generation lengths for these species were 21.29, 14.34, 5.63, 7.73, 1.52, and 1.24 years, respectively (Appendix A). Data points were omitted to permit viewing of the predicted relationship.

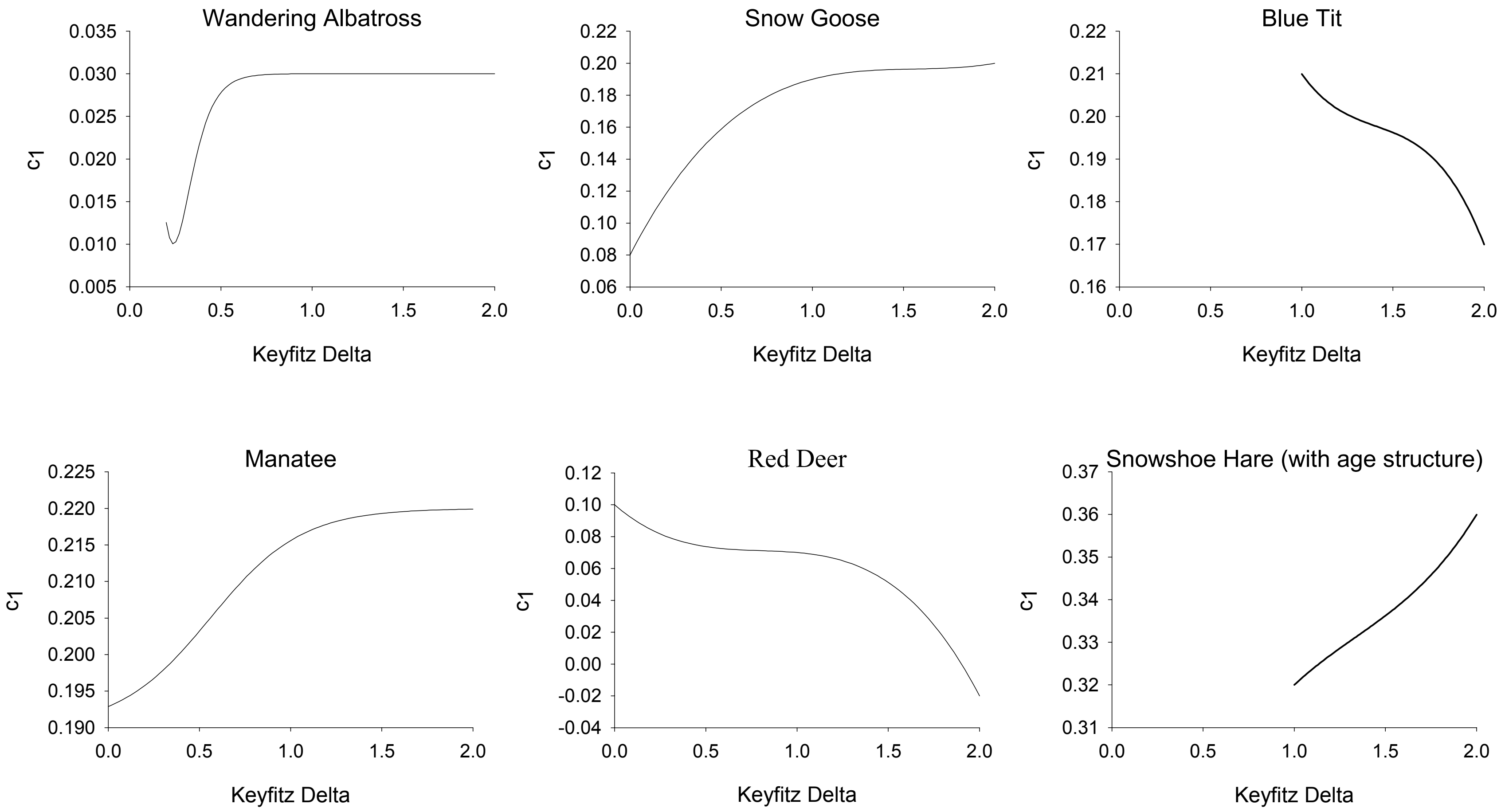

Wandering Albatross
c1
0.035
0.030
0.025
0.020
0.015
0.010
0.005
0.0
0.5
1.0
1.5
2.0
Keyfitz Delta
Snow Goose
c1
0.22
0.20
0.18
0.16
0.14
0.12
0.10
0.08
0.06
0.0
0.5
1.0
1.5
2.0
Keyfitz Delta
Blue Tit
c1
0.22
0.21
0.20
0.19
0.18
0.17
0.16
0.0
0.5
1.0
1.5
2.0
Keyfitz Delta
Manatee
c1
0.225
0.220
0.215
0.210
0.205
0.200
0.195
0.190
0.0
0.5
1.0
1.5
2.0
Keyfitz Delta
Red Deer
c1
0.12
0.10
0.08
0.06
0.04
0.02
0.00
-0.02
-0.04
0.0
0.5
1.0
1.5
2.0
Keyfitz Delta
Snowshoe Hare (with age structure)
c1
0.37
0.36
0.35
0.34
0.33
0.32
0.31
0.0
0.5
1.0
1.5
2.0
Keyfitz Delta

Figure 2. The top performing models of the transient growth rates at time steps 1-to-2 (····GR2), 4-to-5 (----GR5), and 0-to-5 (—5YRGR) as functions of c_1 for wandering albatross (R^2 values listed in order for GR2, GR5, and 5YRGR; $R^2 = 0.90, 0.86, 0.92$) manatee ($R^2 = 0.87, 0.91, 1.00$), snow goose ($R^2 = 0.95, 0.95, 1.00$), red deer ($R^2 = 0.89, 0.87, 0.98$), blue tit ($R^2 = 0.74, 0.68, 1.00$), and snowshoe hare (with age-structured vital rates; $R^2 = 0.87, 0.96, 1.00$). Data points were omitted to permit viewing of predicted relationships. For comparison, $\lambda_1 = 1$ in all cases.

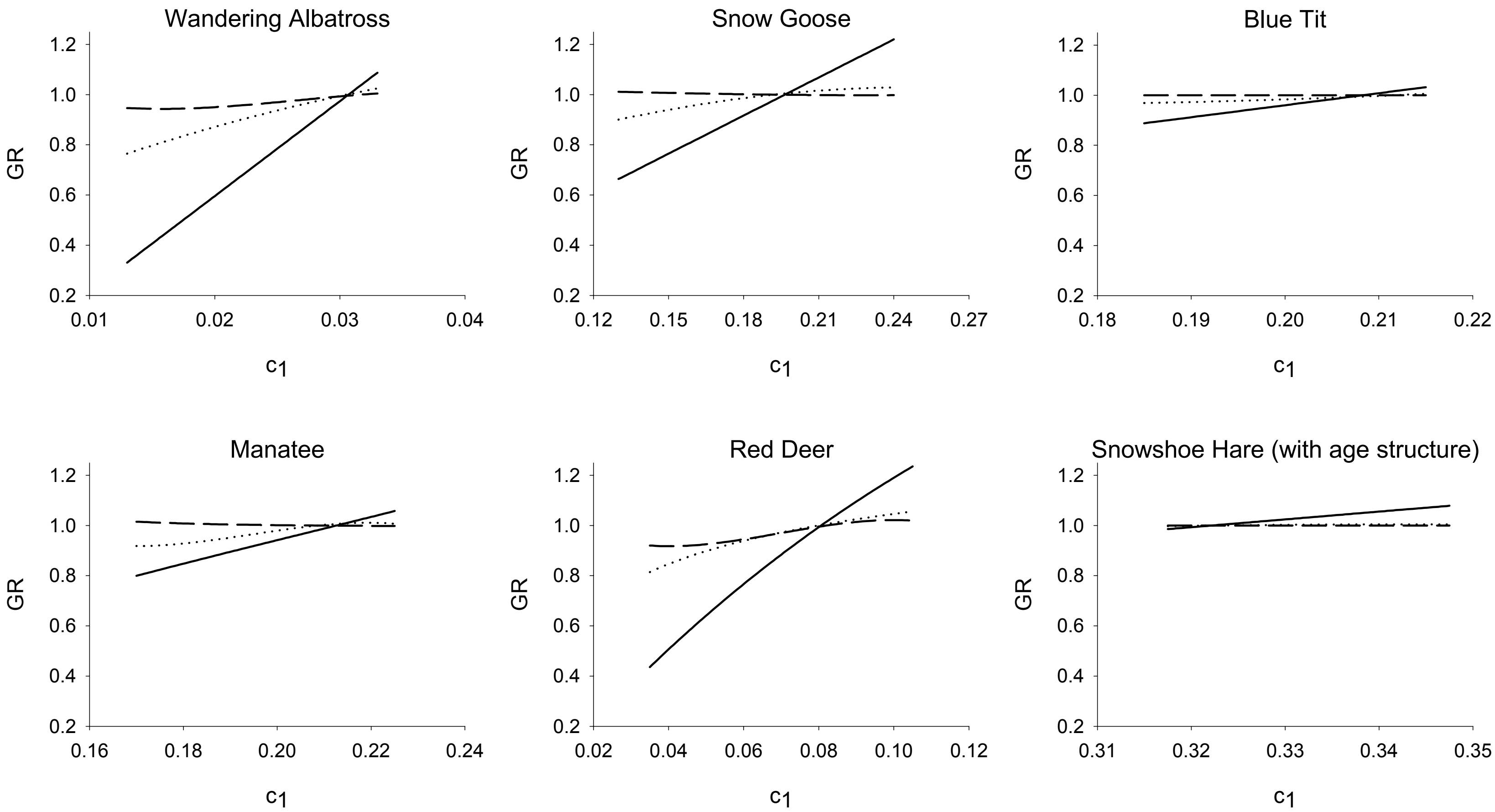

Wandering Albatross
GR
1.2
1.0
0.8
0.6
0.4
0.2
0.01
0.02
0.03
0.04
c_1
Snow Goose
GR
1.2
1.0
0.8
0.6
0.4
0.2
0.12
0.15
0.18
0.21
0.24
0.27
c_1
Blue Tit
GR
1.2
1.0
0.8
0.6
0.4
0.2
0.18
0.19
0.20
0.21
0.22
c_1
Manatee
GR
1.2
1.0
0.8
0.6
0.4
0.2
0.16
0.18
0.20
0.22
0.24
c_1
Red Deer
GR
1.2
1.0
0.8
0.6
0.4
0.2
0.02
0.04
0.06
0.08
0.10
0.12
c_1
Snowshoe Hare (with age structure)
GR
1.2
1.0
0.8
0.6
0.4
0.2
0.31
0.32
0.33
0.34
0.35
c_1

Figure 3. The top performing models of the transient sensitivities [(····) fertility, (----) sub-adult survival, and (—) adult survival] at time step 1-to-2 as functions of c_1 for wandering albatross (R^2 values listed in order for fertility, sub-adult survival, and adult survival; $R^2 = 0.75, 0.73, 0.74$), manatee ($R^2 = 0.97, 0.97, 0.97$), snow goose ($R^2 = 0.63, 0.86, 0.76$), red deer ($R^2 = 0.71, 0.67, 0.66$), blue tit ($R^2 = 0.93$, --, 0.38), and snowshoe hare (with age-structured vital rates; $R^2 = 1.00$, --, 0.86). Data points were omitted to permit viewing of predicted relationships. For comparison, ● = asymptotic fertility sensitivity, ■ = asymptotic sub-adult survival sensitivity, ▲ = asymptotic adult survival sensitivity.

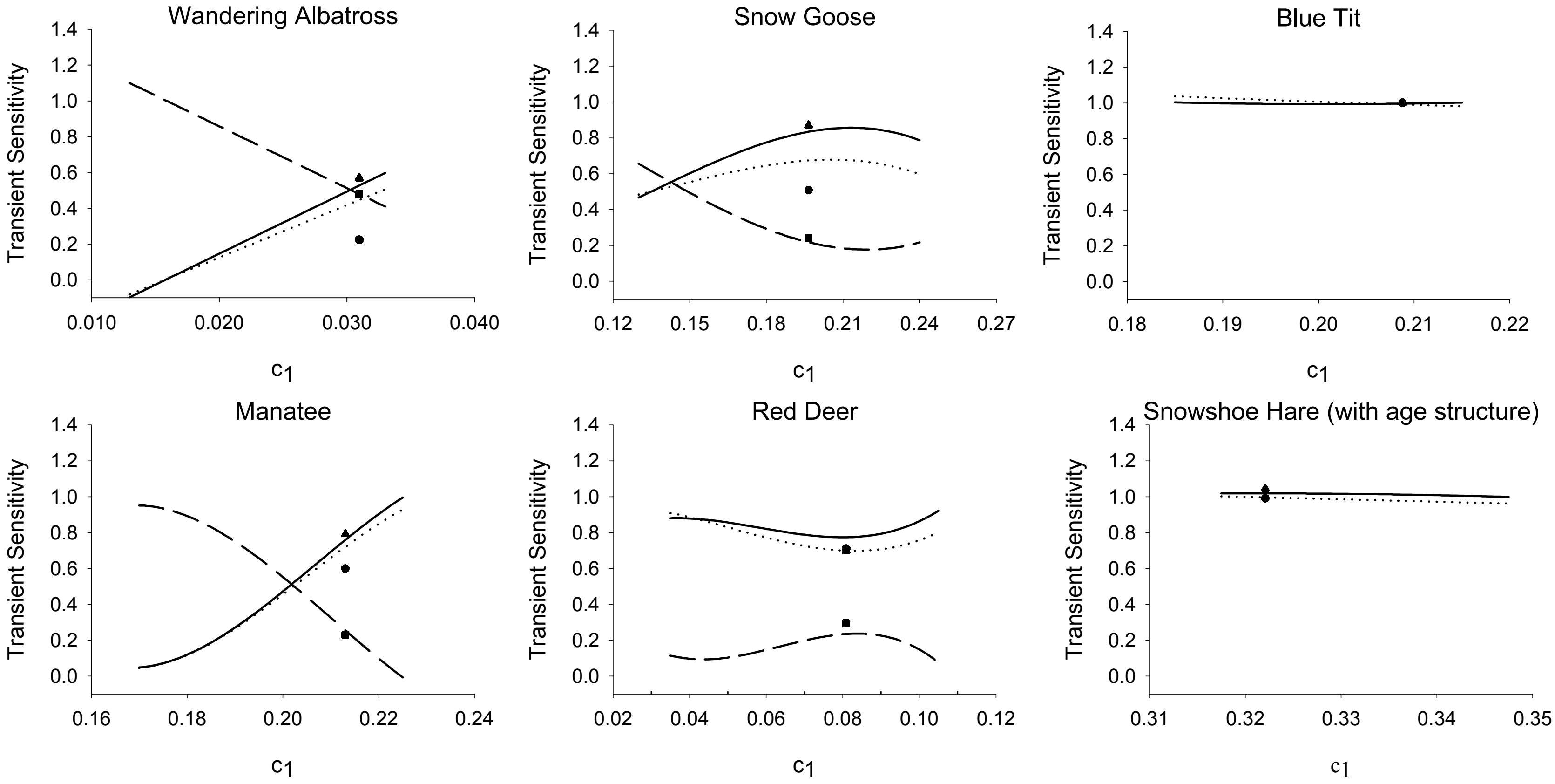

Wandering Albatross
Transient Sensitivity
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.010
0.020
0.030
0.040
c_1
Snow Goose
Transient Sensitivity
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.12
0.15
0.18
0.21
0.24
0.27
c_1
Blue Tit
Transient Sensitivity
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.18
0.19
0.20
0.21
0.22
c_1
Manatee
Transient Sensitivity
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.16
0.18
0.20
0.22
0.24
c_1
Red Deer
Transient Sensitivity
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.02
0.04
0.06
0.08
0.10
0.12
c_1
Snowshoe Hare (with age structure)
Transient Sensitivity
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.31
0.32
0.33
0.34
0.35
c_1

Figure 4. The top performing models of the transient sensitivities [(····) fertility, (----) sub-adult survival, and (—) adult survival] at time step 4-to-5 as functions of c_1 for wandering albatross (R^2 values listed in order for fertility, sub-adult survival, and adult survival; $R^2 = 0.88, 0.86, 0.86$), manatee ($R^2 = 1.00, 1.00, 1.00$), snow goose ($R^2 = 0.64, 0.87, 0.72$), red deer ($R^2 = 0.93, 0.64, 0.62$), blue tit ($R^2 = 0.97$, --, 0.55), and snowshoe hare (with age-structured vital rates; $R^2 = 1.00$, --, 0.96). Data points were omitted to permit viewing of predicted relationships. For comparison, ● = asymptotic fertility sensitivity, ■ = asymptotic sub-adult survival sensitivity, ▲ = asymptotic adult survival sensitivity.

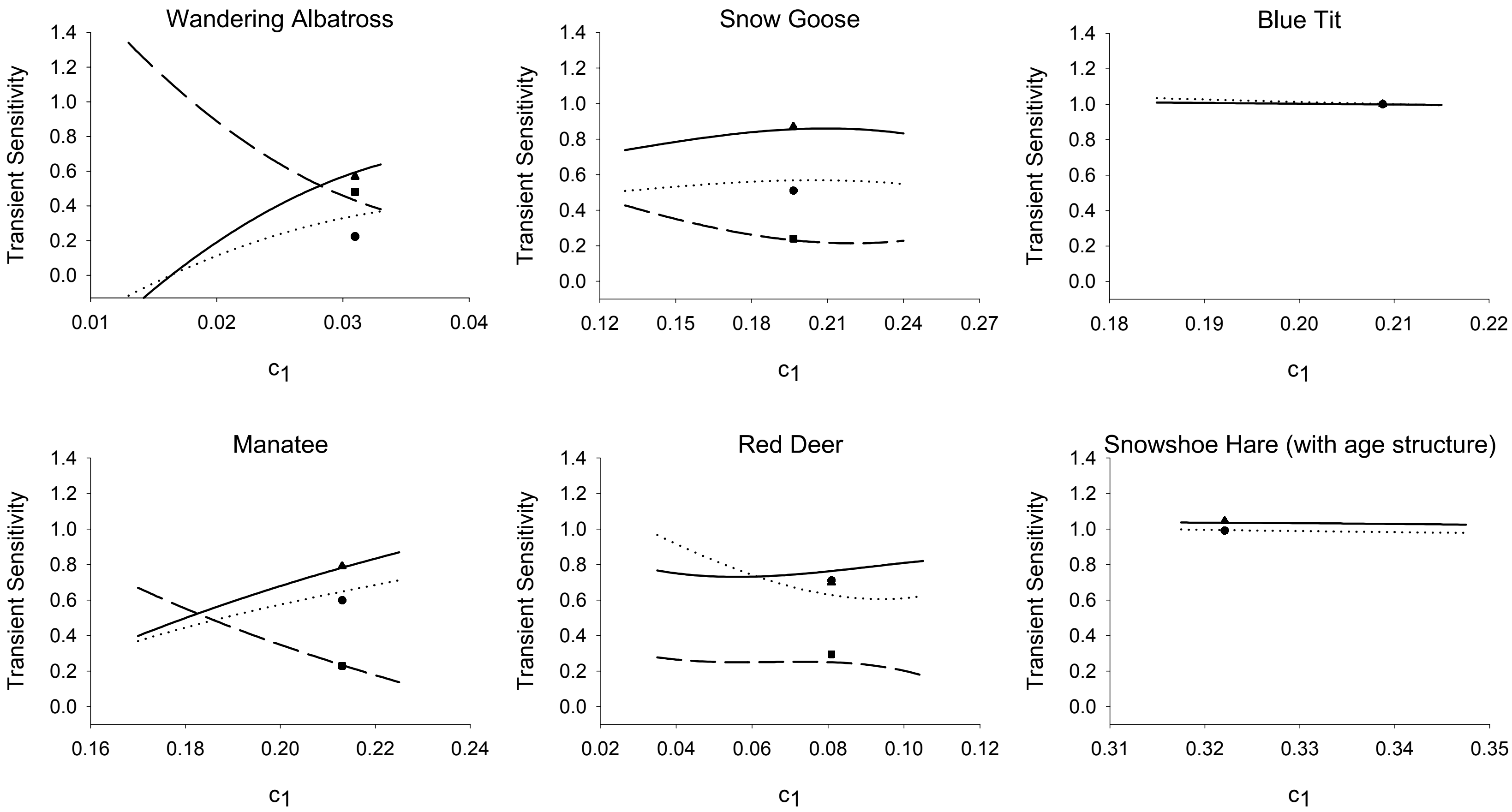
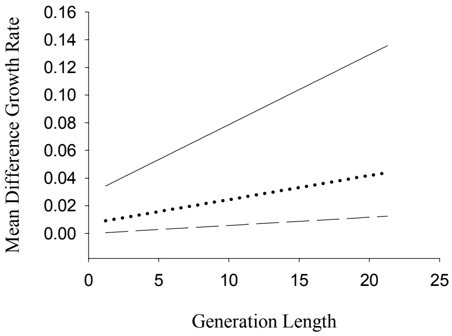
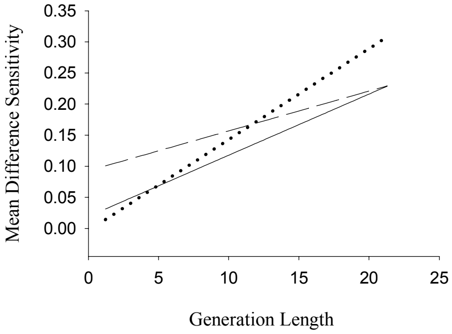

Wandering Albatross
Transient Sensitivity
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0.01
0.02
0.03
0.04
c1
Snow Goose
Transient Sensitivity
0.12
0.15
0.18
0.21
0.24
0.27
c1
Blue Tit
Transient Sensitivity
0.18
0.19
0.20
0.21
0.22
c1
Manatee
Transient Sensitivity
0.16
0.18
0.20
0.22
0.24
c1
Red Deer
Transient Sensitivity
0.02
0.04
0.06
0.08
0.10
0.12
c1
Snowshoe Hare (with age structure)
Transient Sensitivity
0.31
0.32
0.33
0.34
0.35
c1

Figure 5. The interspecific relationship between generation length and estimated differences between transient and asymptotic population dynamics (across all simulations for each species). (a) Correlations between generation length and species-specific means of, GR2 - λ_1(····) ($R^2 = 0.80$, $n = 7$, $P = 0.006$), GR5 - λ_1(----) ($R^2 = 0.64$, $n = 7$, $P = 0.080$), and 5YRGR - $(\lambda_1)^5$ (—) ($R^2 = 0.71$, $n = 7$, $P = 0.018$). (b) Correlations between generation length and species-specific means of, TFS2 - FS (····) ($R^2 = 0.95$, $n = 7$, $P < 0.001$), TSASS2 - SASS (----) ($R^2 = 0.18$, $n = 4$, $P = 0.57$), and TASS2 - ASS (—) ($R^2 = 0.71$, $n = 7$, $P = 0.045$). (c) Correlations between generation length and species-specific means of, TFS5 - FS (····) ($R^2 = 0.86$, $n = 7$, $P = 0.003$), TSASS5 - SASS (----) ($R^2 = 0.92$, $n = 4$, $P = 0.043$), and TASS5 - ASS (—) ($R^2 = 0.92$, $n = 7$, $P = 0.001$). (d) Correlations between generation length and species-specific variances of, GR2 - λ_1 ($R^2 = 0.77$, $n = 7$, $P = 0.010$), GR5 - λ_1 ($R^2 = 0.54$, $n = 7$, $P = 0.267$), and 5YRGR - $(\lambda_1)^5$ ($R^2 = 0.67$, $n = 7$, $P = 0.028$). (e) Correlations between generation length and species-specific variances of, TFS2 - FS ($R^2 = 0.73$, $n = 7$, $P = 0.025$), TSASS2 - SASS ($R^2 = 0.46$, $n = 4$, $P = 0.321$), and TASS2 - ASS ($R^2 = 0.81$, $n = 7$, $P = 0.026$). (f) Correlations between generation length and species-specific variances of, TFS5 - FS ($R^2 = 0.76$, $n = 7$, $P = 0.011$), TSASS5 - SASS ($R^2 = 0.99$, $n = 4$, $P = 0.007$), and TASS5 - ASS ($R^2 = 0.90$, $n = 7$, $P = 0.001$). Data points were omitted to permit viewing of predicted relationships.

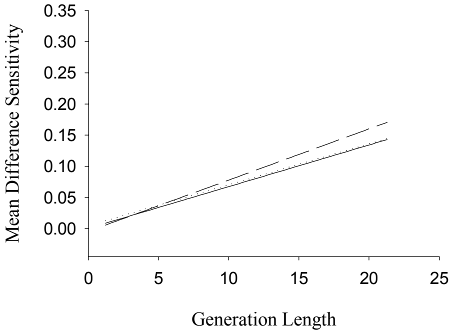
a)


Mean Difference Growth Rate
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
0
5
10
15
20
25
Generation Length

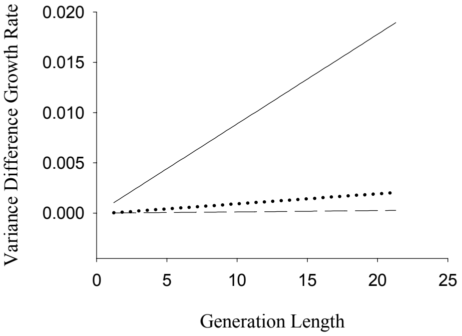
b)


Mean Difference Sensitivity
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0
5
10
15
20
25
Generation Length

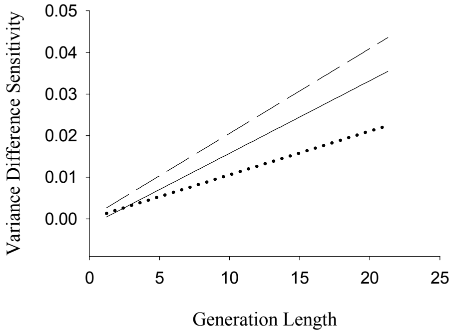
c)


Mean Difference Sensitivity
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
0
5
10
15
20
25
Generation Length

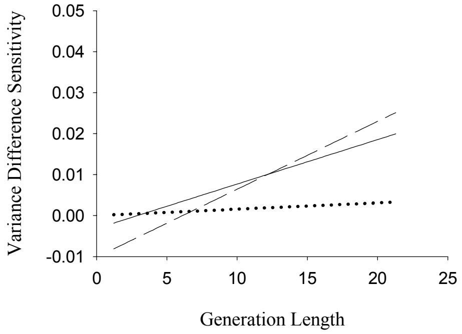
d)


Variance Difference Growth Rate
0.020
0.015
0.010
0.005
0.000
0
5
10
15
20
25
Generation Length

e)


Variance Difference Sensitivity
0.05
0.04
0.03
0.02
0.01
0.00
0
5
10
15
20
25
Generation Length

f)


Variance Difference Sensitivity
0.05
0.04
0.03
0.02
0.01
0.00
-0.01
0
5
10
15
20
25
Generation Length

III. POPULATION MOMENTUM: IMPLICATIONS FOR WILDLIFE MANAGEMENT

Abstract: Maintenance of sustainable wildlife populations is one of the primary purposes of wildlife management. Thus, it is important to monitor and manage population growth over time. Sensitivity analysis of long-term (i.e., asymptotic) population growth rate to changes in vital rates is commonly used in management to identify the vital rates that contribute most to population growth. Yet, dynamics associated with long-term population growth rate only pertain to the special case when there is a stable age (or stage) distribution of individuals in the population. Frequently, this assumption is necessary because age structure is rarely estimated. However, management actions themselves have strong potential to change the age distribution of a population. For initially growing and declining populations, I instituted hypothetical management targeted at halting the growth or decline of the population, and measured the effects of a changing age structure on population dynamics. When I changed vital rates, age structure became unstable and population momentum caused populations to grow in a much different fashion than that predicted from the long-term population growth rate. Interestingly, changes in fertility actually reversed the direction of short-term population growth. Population momentum can significantly affect population dynamics, and will be important to consider in the use of population models for management.

INTRODUCTION

In wildlife management, agency and stakeholder goals are often centered on the population, its size, and the change in size over time. To meet these goals, managers often direct management at population growth rate because it can be manipulated to increase population size in the case of conservation (e.g., Fujiwara and Caswell 2001) or decrease size in the case of control (e.g., Rockwell et al. 1997, Merrill et al. 2003).

Studies of population growth rate sensitivity to changes in underlying vital rates (e.g., fecundity, survival, growth, maturation, recruitment, movement) has become popular in wildlife and conservation to prioritize management actions aimed at producing change in population growth rate (e.g., Brault and Caswell 1993, Crowder et al. 1994, Doak et al 1994, Heppell 1998). Sensitivity analysis can help answer important life history and ecology questions as well (e.g., papers within Heppell et al. 2000a, Dobson and Oli 2001, Oli and Dobson 2003).

Nonetheless, predictions made from analytical sensitivity analyses can be poor when vital rates change simultaneously by different amounts, as they do in the real world (Citta and Mills 1999, Mills et al. 1999, 2001). Furthermore, analytical sensitivity analyses inherently assume existence of a stable age distribution, which means that calculations depend on the long-term (i.e., asymptotic) population dynamics (de Kroon et al. 2000, Caswell 2001, Ehrlén et al. 2001, Mills and Lindberg 2002). Methods that are used to examine contributions of stochastically fluctuating vital rates to population growth rate typically focus on asymptotic dynamics as well (e.g., life table response experiments [Horvitz et al. 1997], and life stage simulation analysis [Wisdom et al. 2000]). Simulation-based sensitivity analyses do not need to assume a stable age distribution but often do because age distributions are rarely known. When changing a vital rate in a sensitivity analysis, we assume that the change would not perturb the population out of a stable age distribution (Mills and Lindberg 2002). It remains to be seen how robust this assumption is in wildlife populations (Citta and Mills 1999, Mills and Lindberg 2002).

Management actions themselves have strong potential to change vital rates by amounts large enough to disrupt the age structure. Before the age distribution begins its approach to the stable age distribution after a perturbation, the population size can change rapidly (Neubert et al. 2002). These dynamical responses to an unstable age structure are known as transient dynamics (see Fig.1), and do occur in nature. Cessation of red deer (*Cervus elaphus*) culling on the Isle of Rum, Scotland caused large changes in the red deer age structure, with transient population dynamics persisting since culling stopped (Clutton-Brock and Coulson 2002, Coulson et al. 2004). In addition, when examining the potential benefit of turtle-excluder devices on shrimp trawls to loggerhead sea turtle (*Caretta caretta*) populations, Crowder et al. (1994) found that sudden improvements in survival rates caused instability in the age structure. The ensuing transient dynamics resulted in a population size much different than that predicted by asymptotic projections, which essentially is the phenomenon that is better known as 'population momentum' (Keyfitz 1971) (see Fig.1). Population momentum could occur in wildlife populations when management or large environmental perturbations (e.g., hurricanes, floods, fires, epidemics) cause any vital rate to change by an amount large enough to alter the age structure, but it has not been explicitly examined.

If wildlife populations do experience population momentum, estimating the effects of momentum on population size should be taken into account when developing conservation and management plans. Here, I used computer simulation to examine control and conservation of hypothetical wildlife populations. To simulate management practices focused on population growth rate, I halted population growth or decline by changing survival or fertility rates which often have very different elasticity values (Heppell et al. 2000b, Sæther and Bakke 2000). It is often suggested that management of the vital rate with the highest elasticity will produce the best returns in population growth (Caswell 2000). Yet, I show that short-term population growth and eventual size following some virtual management experiments are so different from the expectations of asymptotic analysis that my findings could influence the way we manage populations for control and conservation.

METHODS

Data Simulation

To examine population momentum following management actions, I created 3 life histories with stationary asymptotic growth rates ($\lambda_1 = 1$) that mature at 1, 2, and 3 year(s) of age. I designed life histories where survival rates to age *i* (P_i) increase with age of maturity (α) and fecundity (*m*, average number of daughters born to a reproductively mature female) decreases which is the pattern observed across birds and mammals (Sæther 1988, Gaillard et al. 1989, Promislow and Harvey 1990).

In my population model I calculated fertility (F) assuming a pre-breeding census ($F = P_1 * m$), with birth occurring at one time of the year. Fertility and the age-specific survival rates for each life history were parameterized into a population projection matrix (**A**).

$$\mathbf{A} = \begin{bmatrix} F & F & F \\ P_2 & 0 & 0 \\ 0 & P_{3+} & P_{3+} \end{bmatrix} \tag{1}$$

This model assumes geographic closure of a population and density independent growth. Although density dependence is ultimately a necessity for all populations, my focus was on rapidly growing or declining populations (see below) where density feedback on survival or fertility is often negligible.

To set up virtual management experiments, I used projection matrices with stationary growth:

$$\mathbf{A}_{\alpha_1} = \begin{pmatrix} 0.555 & 0.555 & 0.555 \\ 0.4 & 0 & 0 \\ 0 & 0.5 & 0.5 \end{pmatrix}; \mathbf{A}_{\alpha_2} = \begin{pmatrix} 0 & 0.286 & 0.286 \\ 0.7 & 0 & 0 \\ 0 & 0.8 & 0.8 \end{pmatrix}; \mathbf{A}_{\alpha_3} = \begin{pmatrix} 0 & 0 & 0.139 \\ 0.8 & 0 & 0 \\ 0 & 0.9 & 0.9 \end{pmatrix}$$

(fertility values in the top row of each matrix are rounded to the 3rd decimal place), and created growing ($\lambda_1 = 1.2$) populations by multiplying the matrix parameters by 1.2. For the $\alpha = 3$ life history, multiplication of matrix parameters by 1.2 yielded survival rates > 1; thus, fertility had to be increased by a greater amount than survival to achieve the desired population growth rate. Hence, I multiplied survival rates by a constant C, and fertility by C^x, then solved for C (solution = 1.104) and x (solution = 9) simultaneously. Similarly, for each life history I created declining ($\lambda_1 = 0.8$) populations by multiplying the matrix parameters by 0.8. For the $\alpha = 3$ life history, I also created populations that were initially growing ($\lambda_1 = 1.35$ and 1.05) or declining ($\lambda_1 = 0.65$ and 0.95) by greater and lesser amounts in 'supplemental experiments' using a similar application of constants.

Virtual Management Experiments

Here, I considered populations that were growing so rapidly that they could cause environmental damage and populations that are declining at a rate that could yield extinction (i.e., the growing and declining populations defined above). For the $\alpha = 3$ life history, I also consider populations that are growing and declining at rates within the common bounds of long-term environmental variation (i.e., $\lambda_1 = 1.05$ and 0.95).

Depending on the bird or mammal life history, the functional contribution of survival or fertility to asymptotic population growth will vary (Heppell et al. 2000b, Sæther and Bakke 2000). I focused my experiments on changing adult survival or fertility. In the first set of experiments for each life history, I started with a growing population as the initial condition and then decremented survival rate of adult age classes by the amount necessary to attain stationary asymptotic growth (i.e., the amount required to change λ_1 from 1.2 to 1). I performed a similar experiment by decrementing fertility. In the second set of experiments for each life history, I started with a declining population as the initial condition and then augmented survival rate of adult age classes by the amount necessary to achieve stationary asymptotic growth, and then performed similar experiments by augmenting fertility.

To elucidate the effects of managing the asymptotic population growth rate, I assumed that populations initially had a stable age distribution. I then projected the actual dynamics caused by an unstable age structure following perturbations to a vital rate. Population momentum (M) was calculated according to Keyfitz (1971):

$$\mathrm{M} = \lim_{t \to \infty} \frac{\|\mathbf{n}_t\|}{\|\mathbf{n}_0\|} \tag{2}$$

where $\|\mathbf{n}\|$ is the total population size. This is simply the ratio of the ultimate population size following a perturbation to population size immediately before the perturbation. To attain exact analytical estimates of population momentum, equation 2 was adjusted to birth-pulse vector form:

$$\mathrm{M} = \frac{\mathbf{e}^{\mathrm{T}}\left(\mathbf{v}_1^{(\mathrm{new})} * \mathbf{w}_1^{(\mathrm{initial})}\right)\mathbf{w}_1^{(\mathrm{new})}}{\mathbf{e}^{\mathrm{T}} * \mathbf{w}_1^{(\mathrm{initial})}} \tag{3}$$

where $\mathbf{e}$ is a vector of ones, $\mathbf{v}_1$ is the dominant left eigenvector of the projection matrix $\mathbf{A}$ (i.e., the non-scaled age-specific reproductive values), $\mathbf{w}_1$ is the dominant right eigenvector of the projection matrix (i.e., the non-scaled stable age distribution), 'initial' refers to the projection matrix for the initial conditions (growing or declining population), and 'new' refers to the projection matrix following changes in adult survival rates or fertility (Caswell 2001:104). Population momentum is measured on a percentage scale centered on 1, thus a momentum of 1.25 means that the population will grow by 25% before eventually reaching the new stable age distribution. Further, a momentum of 1 has zero magnitude. To evaluate the relative importance of momentum, I compared momentum across management experiments, and across three life histories. Because it was necessary to change vital rates by different amounts to attain the fixed management goal ($\lambda_1 = 1$) in my experiments, I also examined the influence of proportional change in a vital rate on population momentum.

To compare results from my experiments to predictions from an asymptotic elasticity analysis, I first calculated elasticities (Elasticity = $\partial \log \lambda_1 / \partial \log \text{vital rate}$; de Kroon et al. 1986) for the initially growing and declining populations. Elasticities may provide a better means for comparing the functional contributions of different vital rates to λ_1 than sensitivities (Sensitivity = $\partial\lambda_1/\partial$ vital rate ; Caswell 1978) because elasticities are measured on a relative scale (de Kroon et al. 1986, Benton and Grant 1999, but see Link and Doherty 2002). I then used elasticities to predict the impact of each management experiment on asymptotic population growth rate for the time step immediately following the vital rate perturbation ($t \rightarrow t+1$) (Heppell 1998, Caswell 2001).

$$\textit{Predicted proportional change in } \lambda_1 \approx \textit{Proportional change in vital rate} \times \textit{Elasticity} \quad (4)$$

Next, I measured the observed proportional change in the actual population growth rate ($\mathbf{N}_{t+1}/\mathbf{N}_t$) for the same time step in a way similar to Mills et al. (1999); however, they measured the observed proportional change in λ_1, rather than the observed proportional change in $\mathbf{N}_{t+1}/\mathbf{N}_t$.

$$\textit{Observed proportional change in actual growth rate} = \frac{\left(\mathbf{N}_{\mathrm{t+1}}/\mathbf{N}_{\mathrm{t}} - \mathbf{N}_{\mathrm{t}}/\mathbf{N}_{\mathrm{t-1}}\right)}{\mathbf{N}_{\mathrm{t}}/\mathbf{N}_{\mathrm{t-1}}} \quad (5)$$

I then calculated the bias of the elasticity prediction, which assumes a stable age distribution following a vital rate perturbation.

$$\textit{Bias of elasticity prediction} = \textit{Predicted proportional change in } \boldsymbol{\lambda}_1 \textit{ - Observed proportional change in actual growth rate} \quad (6)$$

Finally, I examined the influence of proportional change in a vital rate on bias of the elasticity prediction.

RESULTS

Using Keyfitz's measurement of population momentum, I estimated the actual effect of instantaneous vital rate changes on age structure, short-term population growth, and long-term population size. The initially increasing populations with $\alpha = 1,2$, and 3 life histories had 52%, 17%, and 10% more adults in the last age class, respectively, relative to the stable age distribution following the decrement in adult survival. The initially decreasing populations had 30%, 12%, and 5% fewer adults in the last age class relative to the stable age distribution following augmentation of adult survival. As a result, the direction of population momentum for each life history was consistent with the historical pattern of growth (Fig. 2), and was small in magnitude (absolute magnitude ≤ 0.045). Moreover, the actual population growth rate rapidly stabilized to an asymptotic stationary rate (e.g., see Fig. 2) for life histories that had high adult survival elasticities (Table 1). I also detected a small negative relationship between age at maturity and magnitude of population momentum for the increasing population experiment, and a small positive relationship for the decreasing population experiment (Fig. 3).

Effects of changing fertility contrasted with the findings for changes in adult survival (Figs. 2 and 3). Surprisingly, initially increasing populations with $\alpha = 1,2$, and 3 life histories all had 32% fewer adults in the last age class relative to the stable age distribution following the decrement in fertility. The initially decreasing populations all had 60% more adults in the last age class relative to the stable age distribution following augmentation of fertility. As a result, the initially growing populations decreased and the initially declining populations increased (Fig. 2). Thus, changes in fertility, which had the lowest asymptotic elasticity for the $\alpha = 2$ and 3 life histories (Table 1), caused population size to change in a direction that would be considered more desirable for control and conservation purposes. Furthermore, in experiments with decreasing populations, the magnitude of momentum resulting from changes in fertility increased with age at maturity (Fig. 3). Population size responded more to changes in fertility than to changes in adult survival rates. As a result, magnitudes of momentum in the experiments were much larger (as much as 0.17) than those produced by changes in adult survival (Fig. 3), except in the increasing population experiment for the $\alpha = 1$ life history.

Because fertility often exhibited a small elasticity value, it had to be changed by large amounts to achieve stationary population growth. Large changes in a vital rate cause large perturbations to the age structure (see above), which then causes the magnitude of population momentum to increase. This explains why the magnitude of momentum was larger following changes in fertility versus changes in adult survival (Fig. 4).

When I considered the supplemental population experiments for the $\alpha = 3$ life history, magnitude of population momentum increased as the difference between the initial population growth rate and the management objective ($\lambda_1 = 1.00$) increased. This relationship was most pronounced when fertility was decremented in the decreasing population experiments (Fig. 5). Once again, these results were influenced by proportional change in a vital rate that was required to achieve the management objective ($\lambda_1 = 1.00$) (Fig. 4).

Additionally, I detected substantial bias when using elasticity values to predict proportional change in population growth rate following a given proportional change in a vital rate. As the proportional change in adult survival rate increased, the absolute values of the bias in the elasticity prediction also increased. Furthermore, the bias was high for increases in adult survival and low for decreases in adult survival (Fig. 6). Thus, the direction of bias was consistent with the direction of change in adult survival. When the proportional change in fertility increased, the absolute value of the bias in the elasticity prediction also increased, similar to the results for changes in adult survival. However, the bias was low for decreases in fertility and high for increases in fertility (Fig. 6), which occurred because the unstable age structure caused the direction of population growth to change following perturbations to fertility.

DISCUSSION

Maintenance of sustainable wildlife populations is one of the primary purposes of wildlife management. Thus, understanding the true nature of management actions on population dynamics should be of fundamental importance to wildlife biologists. Asymptotic sensitivity analysis has become a popular tool in wildlife biology because it has the potential to elucidate efficient means of managing vital rates for optimal returns in population growth rate and size (e.g., Doak et al. 1994, Rockwell et al. 1997, Wisdom and Mills 1997, Hoekman et al. 2002). However, empirical evidence indicates that asymptotic measures do not always capture the actual dynamics that occur in nature (Bierzychudek 1999, Clutton-Brock and Coulson 2002, Coulson et al. 2004, Franklin et al. 2004).

Management actions themselves can affect a population's age structure (Crowder et al. 1994, Coulson et al. 2004). In my population experiments, changes in vital rates did perturb populations away from the stable age distribution. As a result, I found that asymptotic elasticity values did not accurately predict the proportional change in population growth rate following a given proportional change in a vital rate (Fig. 6). Thus, I conclude that predictions made from asymptotic elasticities are not robust to the inherent assumption of a stable age distribution. Analytical solutions for examining the sensitivity of the transient population growth rate (Yearsley 2004, Koons et al. unpublished data) and size (Fox and Gurevitch 2000) now exist for cases when age structure is unstable, but known. Age structure is rarely known, but if it is, my results support use of these methods to address ecological questions and to guide management practices.

For stable age-structured populations that were growing or declining, I used matrix models to demonstrate that suddenly changing a vital rate can result in population momentum. Similarly, management actions that attempt to change the direction of long-term population growth (e.g., changing λ_1 from 1.2 to 0.97, or from 0.8 to 1.03) result in population momentum values that are quite similar to those presented in my paper (< 0.016 units of difference; Koons unpublished data). Population momentum has lasting effects on population size in ways that are not revealed by asymptotic analyses, and I show that momentum varies with life history, depends on the specific vital rate that is changed, and depends on the proportional change that is made to a vital rate.

Population momentum is a complicated process that proximately depends on how changes in a vital rate affect the age structure (Eqn. 3). In the virtual management experiments, the number of adults in the initial population relative to the stable age distribution that was eventually attained depended on the vital rate that was changed (i.e., adult survival or fertility). Populations that initially had a surplus of older adults experienced positive population growth and positive (> 1) population momentum, and populations that initially had deficits of older adults experienced negative population growth and negative (< 1) population momentum. Caswell (2001:106) also found that the direction of population momentum depended on initial surplus or deficit of adults in a stage-structured model. Thus, it seems clear that initial age (or stage) structure relative to that following changes in a vital rate, will dictate the direction of short-term population growth and momentum.

While the direction of population momentum is determined by the specific vital rate that is changed, the magnitude of population momentum must be influenced by the magnitude of change in the vital rate. Large changes in a vital rate will produce large changes in the age structure and thus the equilibrium population size.

Still, population momentum was related to life history (Fig. 3). Perturbations to the age distribution of populations with short generation lengths are assuaged quickly because of rapid population turnover, and the converse is true for animals with long generation lengths (Tuljapurkar 1985). Still, oscillations in the age structure (see Fig. 1) may take a long time to converge to the stable age distribution, but cause little change in the net population size. Recently, Koons et al. (unpublished data) have found that transient population growth rates amongst late-maturing, long-lived birds and mammals are initially very reactive to direct changes in age structure, but less so for early-maturing, short-lived species. This initial reaction to a perturbation can have a lasting effect on the long-term population size (Figs. 1 and 2; Neubert et al. 2002). Thus, I believe that the 'reactivity' of a population to perturbations is the primary factor driving patterns of population momentum across life histories, and that the time required for a population to return to a stable age distribution plays a secondary role. Nevertheless, more work will be required to quantitatively establish the connection between life history and population momentum.

My studies considered population momentum following one-time perturbations to life histories with exponential growth, in otherwise constant environments. In addition, my goal was to examine population dynamics following vital rate perturbations in a fashion that is one step closer to reality than that assumed under asymptotic sensitivity analysis. The virtual management experiments were not meant to represent reality. Fertility in my models was the product of fecundity and survival to the first birthday. Thus, it would be interesting to examine the response of population momentum to changes in these lower-level life history parameters as well as the seasonal components of survival (e.g., survival of young to fledging, winter survival, etc.). In some populations, density dependence may cause vital rates to change more slowly over time than the instantaneous changes considered here. Li and Tuljapurkar (1999) found that momentum increases with the time it takes to attain the vital rate goal. Thus, momentum could have strong effects on populations regulated by density dependence and future management studies should build on my findings by examining population momentum in these environments and others (e.g., stochastic and periodic environments).

RESEARCH AND MANAGEMENT IMPLICATIONS

Population momentum could push populations far past an environmental carrying capacity or even to extinction, depending on the direction of momentum. By affecting the long-term population trajectory, momentum could shorten or lengthen the time for a population to go extinct or recover from a perturbation, relative to that projected with an asymptotic analysis (e.g., Merrill et al. 2003). Thus, population momentum should be considered in population viability analyses (sensu Gilpin and Soulé 1986).

These matters, as well as others, should be of concern to wildlife managers when the management goals are centered on both population size and growth rate (e.g., North American Waterfowl Management Plan). If population size is already too large or too small, managing the asymptotic population growth rate may be inefficient. For example, I might prefer a management action that can initially reduce or increase the population size, and at the same time produce the desired population growth rate in the future. It is conceivable that managers could actually use population momentum to their advantage in order to achieve such a goal. For example, even if fertility has a low elasticity value, it may be more feasible to change fertility than adult survival. My results indicate that changing fertility produces short-term population growth and momentum that is consistently in a 'desirable' direction for population control or conservation, but changing adult survival does not. In my pre-breeding census models, fertility was the product of fecundity and survival to the first birthday. Depending on the organism, managers may find it easier to manipulate fecundity (e.g., releasing hatchery-reared young) or survival to the first birthday (e.g., improving fawn survival or chick survival).

Animal harvest can also affect vital rates like survival (e.g., additive harvest), and it can alter the structure of a population (e.g., slot limits in fisheries, trophy management of ungulates). Thus, it seems highly probable that harvest management could cause population momentum, and in turn affect population size and the sustainability of harvest itself. Yet, population dynamics operating under the pressures of harvest are thought to follow density-dependent processes. My results only pertain to density-independent population growth. Thus, more work will be required to elucidate the possible effects of harvest on population momentum in density-dependent systems.

In order to more accurately examine the actual effects of vital rate management on the population dynamics, it will be necessary for field biologists to collect data on population age distributions (e.g., Coulson et al. 2004). Knowledge of age distributions could alleviate the reliance of management actions based on asymptotic population analysis. If age distributions can be estimated, one would be able to determine if wild populations are close to their stable age distributions. If they are, then asymptotic sensitivity analysis might be very useful to wildlife managers; however, if they are not, the tools presented here and by others (Fox and Gurevitch 2000, Yearsley 2004, Koons et al. unpublished data) will be more useful. Lastly, incorporation of age distribution estimates into population models will allow me to more accurately examine past and future population dynamics. For example, it is largely believed that fluctuations in population growth rate and size in wild populations are caused by stochastic fluctuations in the vital rates. However, observed fluctuations in population growth rate and size are partially caused deterministically by unstable age structures (e.g., the transient dynamics and population momentum). Understanding the actual influence of age structure on population dynamics in the wild will improve our knowledge about population dynamics as a whole (Clutton-Brock and Coulson 2002, Coulson et al. 2004).

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Table 1. Vital rate elasticity values for populations that were initially growing (λ_1 = 1.2) and declining (λ_1 =0.8) across the three life histories (α = 1, 2, 3).

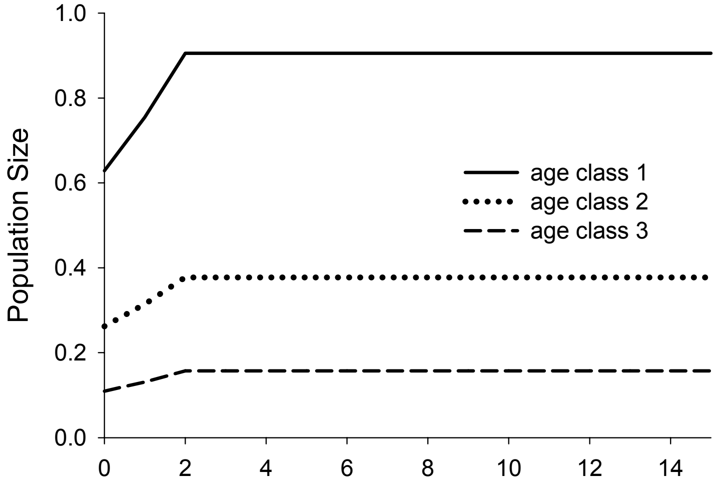
	Elasticity Values[a]					
	Growing Populations			Declining Populations		
α	Fertility	Sub-adult Survival	Adult Survival	Fertility	Sub-adult Survival	Adult Survival
1	0.53		0.47	0.53		0.47
2	0.16	0.17	0.67	0.16	0.17	0.67
3	0.13	0.25	0.62	0.08	0.17	0.75
3[b]	0.17	0.34	0.49	0.08	0.17	0.75
3[c]	0.08	0.17	0.75	0.08	0.17	0.75

a – Elasticities are summed across the relevant age classes and rounded to two decimal places.

b – Additional results for populations of the α = 3 life history that were initially growing (λ_1 = 1.35) or declining (λ_1 = 0.65) at a greater rate than in the standard experiments. Whenever a matrix is multiplied by a constant (C), the eigenvalues are simply scaled by the constant and the eigenvector structure does not change. Thus, elasticity values do not change.

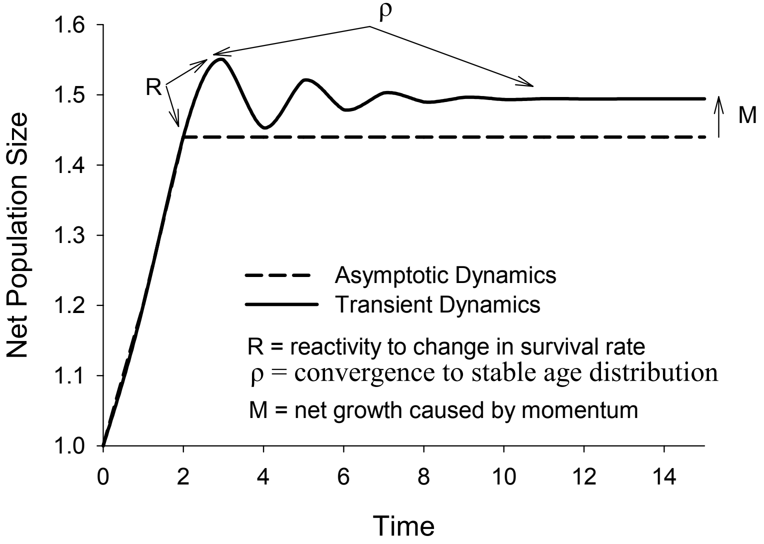
c – Additional results for populations of the α = 3 life history that were initially growing (λ_1 = 1.05) or declining (λ_1 = 0.95) at a lesser rate than in the standard experiments.

Figure 1. An example of a population with 3 age classes growing at the rate of $\lambda_1 = 1.2$ until the second time step, when survival rate is changed to produce stationary asymptotic growth ($\lambda_1 = 1$). In (a) I show continual asymptotic growth following the changed survival rate, which can only happen if the population somehow transitions automatically to the new stable age distribution. In (b) I show the oscillating transient dynamics that would actually occur (barring direct manipulation of the age distribution by managers) after the survival rate is changed. In (c) the age classes are summed together to depict the projected net population size for each scenario (**a** and **b**), and I show how the population initially reacts (reactivity R) to the changed survival rate, how long it takes the population to reach a stable age distribution (convergence ρ), and the net increase in size caused by population momentum (momentum M).



a) Asymptotic Population Dynamics

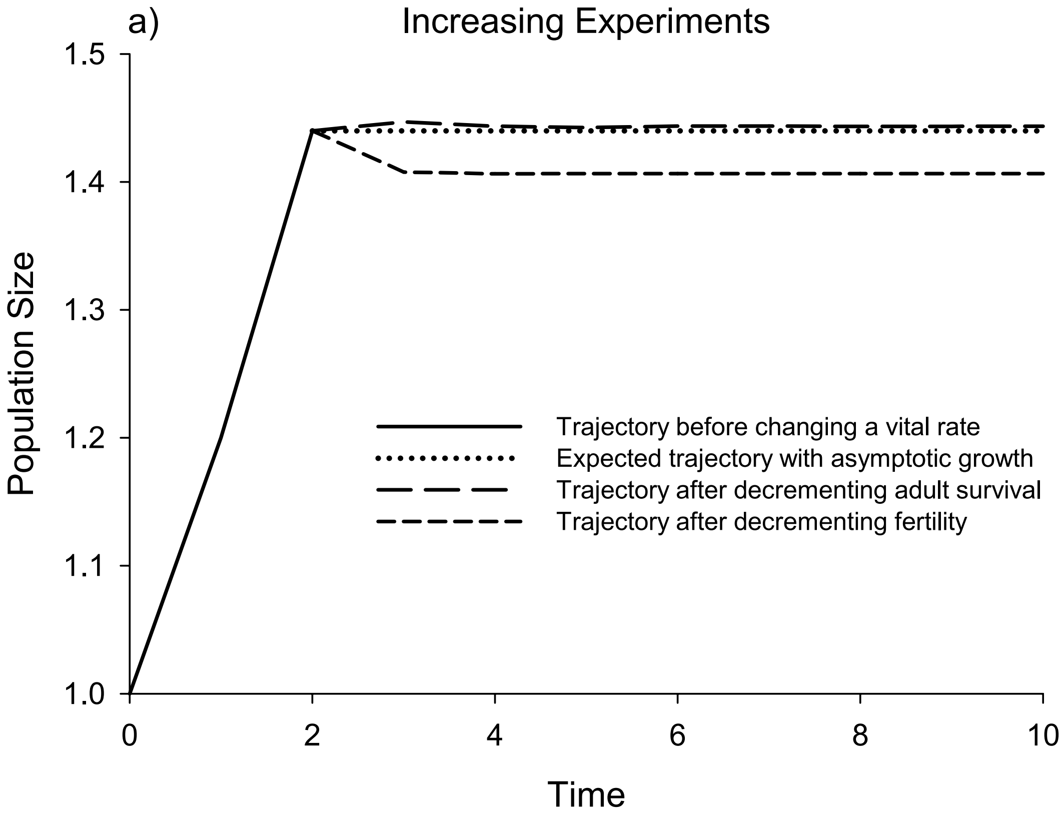
b) Transient Population Dynamics



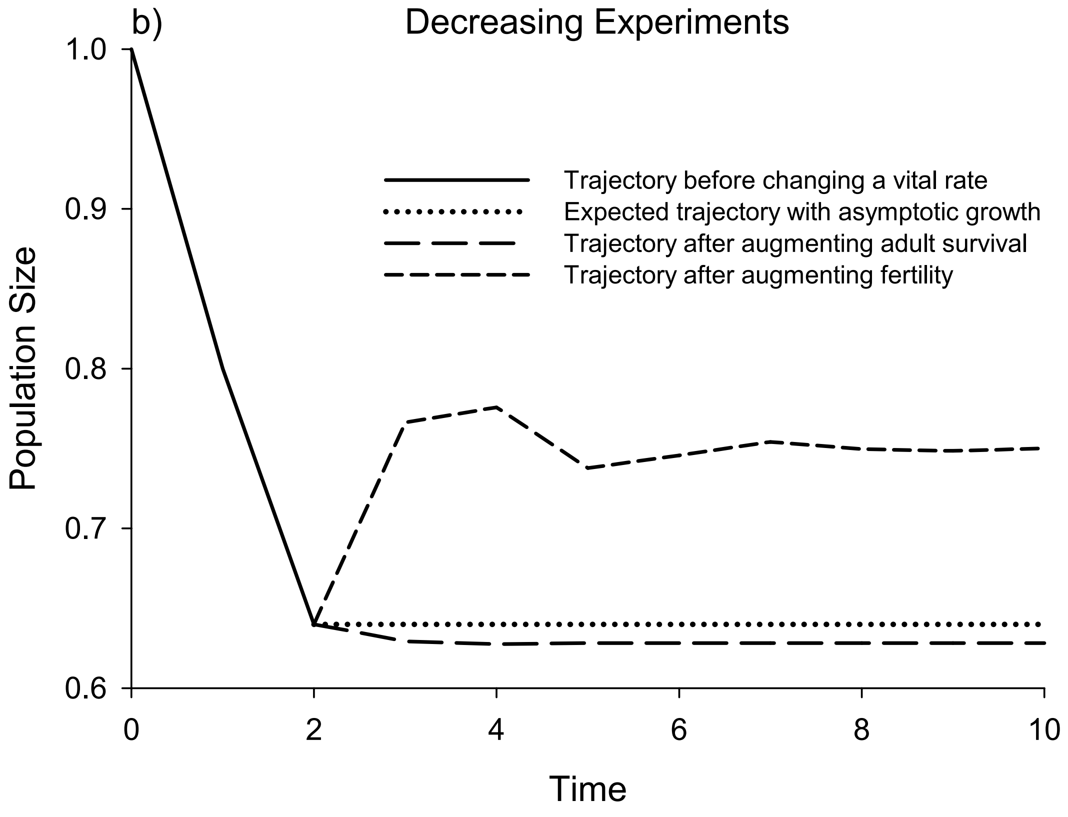
c) Net Asymptotic and Transient Population Dynamics

R = reactivity to change in survival rate
ρ = convergence to stable age distribution
M = net growth caused by momentum

Figure 2. Population projections of the $\alpha = 3$ life history for the standard increasing (a; $\lambda_1 = 1.2$) and decreasing (b; $\lambda_1 = 0.8$) population experiments. Across experiments, either adult survival rate or fertility was changed at the second time step to achieve stationary asymptotic growth ($\lambda_1 = 1.0$). Results were similar for the other life histories except the transient dynamics and resulting population momentum values were generally of lesser magnitude.



a) Increasing Experiments



b) Decreasing Experiments

Figure 3. Population momentum values across all life histories ($\alpha = 1, 2, 3$) for the standard increasing (a; $\lambda_1 = 1.2$) and decreasing (b; $\lambda_1 = 0.8$) population experiments where adult survival or fertility was manipulated. The scaling of the y-axis differs between (a) and (b).

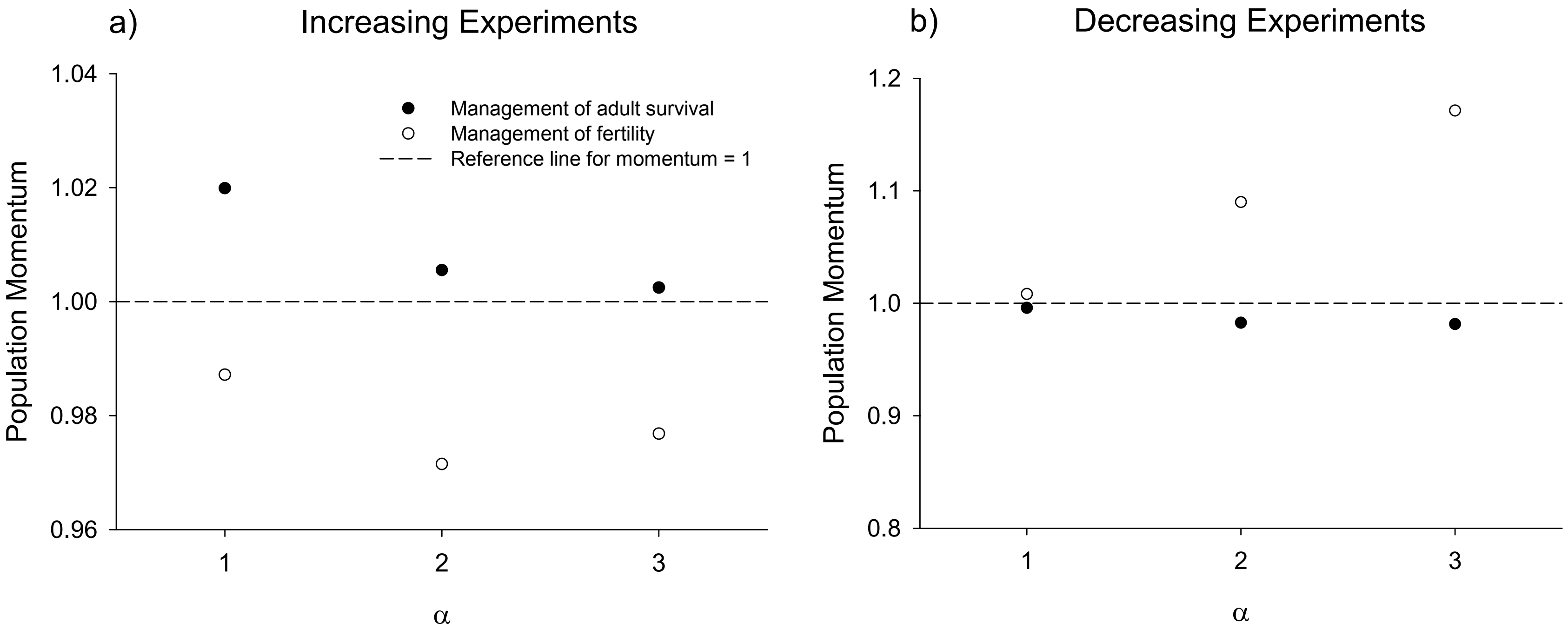

a)
Increasing Experiments
Population Momentum
1.04
1.02
1.00
0.98
0.96
1
2
3
α
● Management of adult survival
○ Management of fertility
Reference line for momentum = 1
b)
Decreasing Experiments
Population Momentum
1.2
1.1
1.0
0.9
0.8
1
2
3
α

Figure 4. The magnitude of population momentum as it relates to the proportional change made to a vital rate across all the population experiments and life histories.

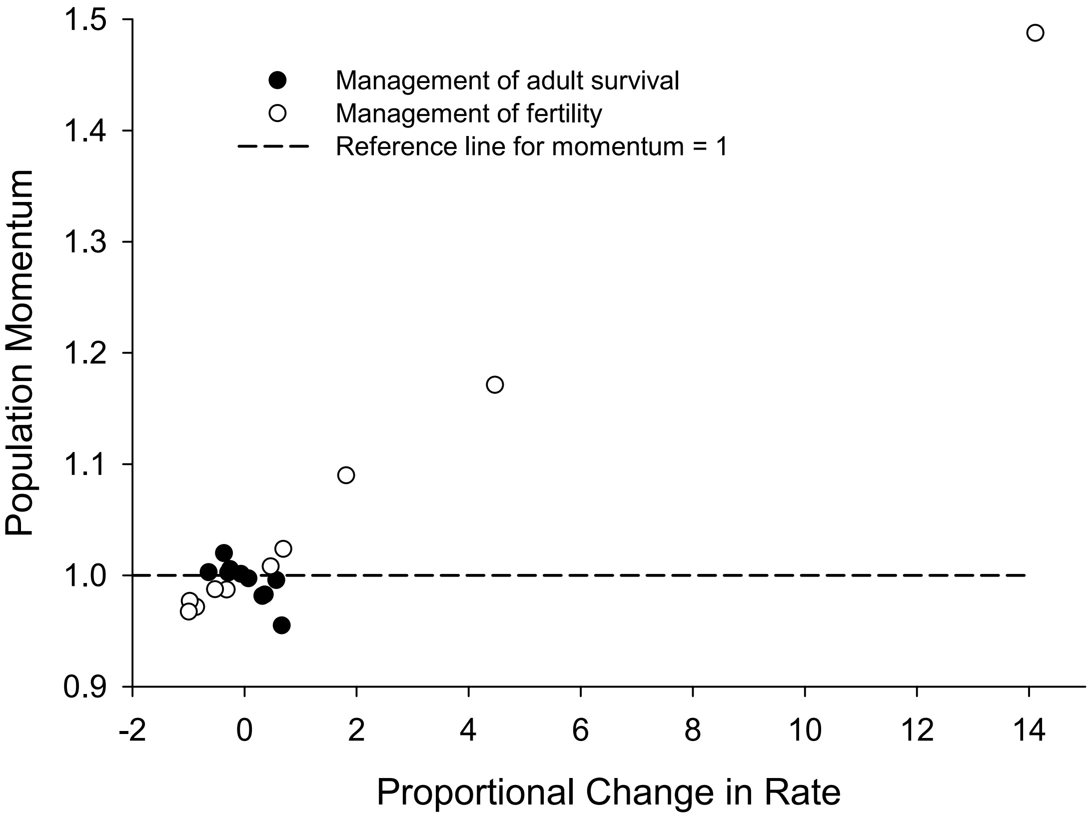

1.5
1.4
1.3
1.2
1.1
1.0
0.9
Population Momentum
● Management of adult survival
○ Management of fertility
Reference line for momentum = 1
-2
0
2
4
6
8
10
12
14
Proportional Change in Rate

Figure 5. Population momentum values across all population experiments for the $\alpha = 3$ life history where adult survival or fertility was manipulated.

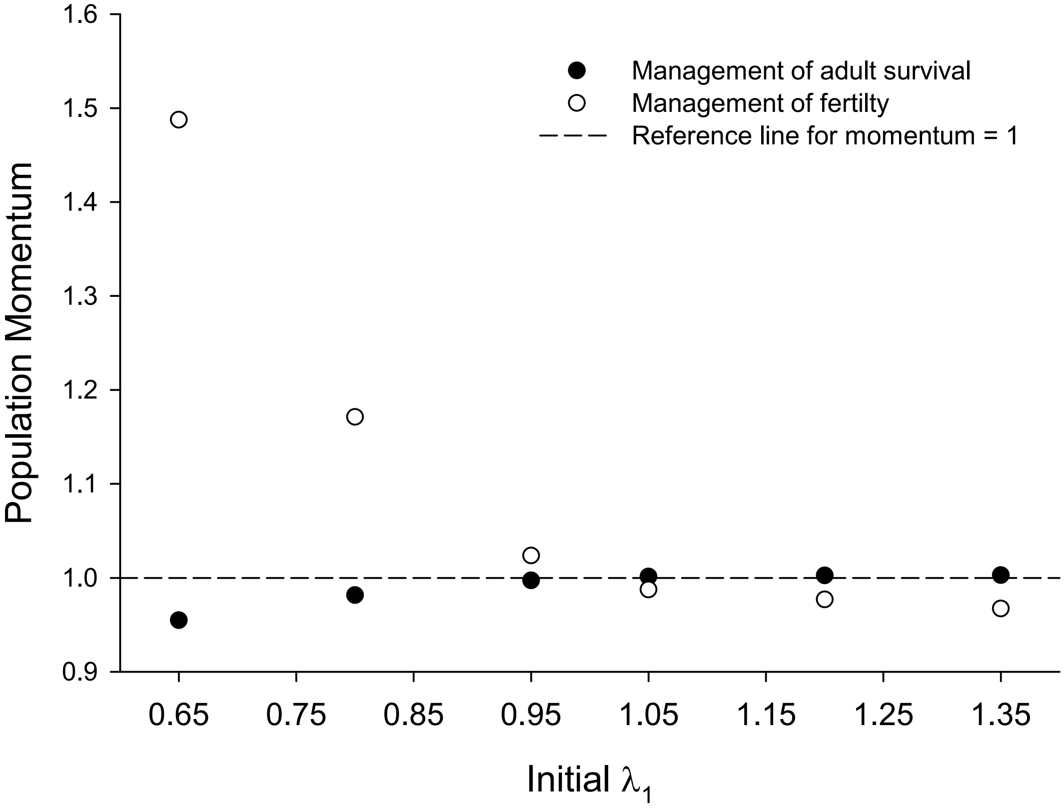
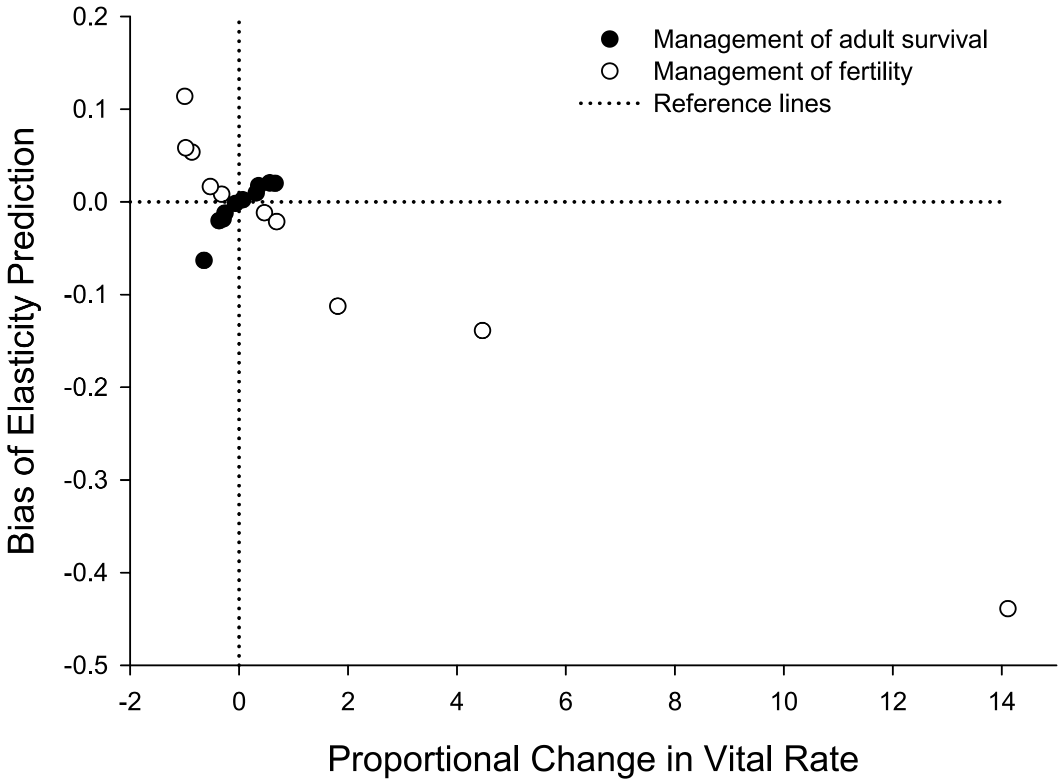

1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
Population Momentum
0.65
0.75
0.85
0.95
1.05
1.15
1.25
1.35
Initial λ_1
Management of adult survival
Management of fertilty
Reference line for momentum = 1

Figure 6. The relationship between the bias produced by the predicted proportional change in population growth rate (based on elasticity of each vital rate in the initial-condition matrices; Table 1) relative to the observed proportional change in population growth rate (y-axis), and the proportional change made to each vital rate (x-axis) across all the population experiments and life histories. The x-axis is measured on a proportional scale; thus, a value of 4 indicates a fourfold increase. The y-axis measures the difference between two proportional measures.



Management of adult survival
Management of fertility
Reference lines
Bias of Elasticity Prediction
Proportional Change in Vital Rate
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-2
0
2
4
6
8
10
12
14

IV. POPULATION MOMENTUM ACROSS VERTEBRATE LIFE HISTORY STRATEGIES

Abstract. Population momentum is a measure of the relative change in ultimate population size following change in a vital rate or population structure. Population dynamics vary across vertebrates, but population momentum across this group of organisms has not been examined. To help fill this void, I simulated iteroparous and semelparous life histories that represent a wide variety of vertebrates. In a series of theoretical experiments, I demonstrated that population momentum is related to age at maturity in different ways across vertebrates. During gradual vital rate changes (e.g., a change that takes 5 years to complete), I controlled for the effects of per capita vital rates on population growth and found that population momentum was generally similar to that following an instantaneous change. In many cases, population momentum significantly affected short-term population growth and long-term population size; thus, momentum will be important to consider in natural resource management as well as studies of life history evolution.

INTRODUCTION

A central aspect of biology is the population, its size and changes in size over time. Population size and growth rate are commonly modeled with tools that inherently assume stability of population structure (i.e., age, stage, or size structure) through time (e.g., see papers within Heppell et al. 2000, Sibly et al. 2002). Yet, ecologists realize that this assumption may rarely be met in nature (Bierzychudek 1999, Clutton-Brock and Coulson 2002, Nichols and Hines 2002, Hastings 2004). An unstable population structure can have a strong residual effect on future population size, which is known as population momentum. In demography, studies of population momentum have influenced international policy (e.g., Bos et al. 1992, Bos et al. 1994, United Nations 2003); however, population ecologists have paid very little attention to population momentum.

Some ecologists might wonder how population momentum occurs. As an example, if per capita fertility rates were high, creating an abundance of young individuals with high likelihood of surviving to maturity, and then suddenly dropped to the stationary level (i.e., $\lambda_1 = 1$, the level of lifetime individual replacement), a population would keep growing because overabundance of young individuals would ensure high net fertility rates long after the transition to stationary per capita fertility (sensu Keyfitz 1971). In general, momentum could occur whenever any vital rate changes, or when activities like commercial fishing alter population structure (Hall 1999). Understanding population momentum and its effect on population dynamics could increase the efficacy of conservation, natural resource management, and pest control practices. Yet, only one study of population momentum has been conducted on non-human populations (Koons et al. 2005), and theory describing the behavior of population momentum across species is lacking.

To partially fill this void, I used conventional methods to calculate population momentum, and used computer simulation and theoretical experiments (i.e., thought experiments) to examine population momentum across vertebrate life history strategies. In a structured population, changes in vital rates will alter population structure, causing transient dynamics (i.e., short-term dynamics of a population with unstable population structure), and ultimately, population momentum (Caswell 2001). Because transient dynamics of long-lived, slow reproducing vertebrates with delayed maturity are more reactive to changes in population structure than they are for short-lived, fast reproducing vertebrates with early maturity (Koons et al. 2005b), I predicted that the magnitude of population momentum would increase with age at maturity.

METHODS

Data Simulation

To find a theoretical relationship between population momentum and life history, I explored 3 strategies where reproduction can occur several times within a lifetime (i.e., iteroparous), and 2 where reproduction occurs once and is followed by death (i.e., semelparous). Life histories were based on theory (Stearns 1992, Charnov 1993) and generally representative of iteroparous 1) birds and mammals, 2) turtles, lizards, and snakes, 3) bony fishes, and semelparous 4) large-bodied bony fishes, 5) small-bodied bony fishes. To generate life histories for 1-3, I simulated age at maturity (α), fecundity (*m*; average number of daughters born to a mature female), and survival for age-classes 2 and older (P_{2+}) according to the equations and corresponding curves shown in Appendix

1. Then, I set long-term growth rate (i.e., λ_1: the asymptotic growth rate) to 1 and numerically solved for age-class 1 survival (P_1). To generate life histories for each semelparous strategy, I simulated α and *m* according to equations and corresponding curves shown in Appendix 1, set asymptotic growth rate to 1, assumed P_{2+} to be 36 times greater than P_1 (Kareiva et al. 2000, Wilson 2003), and numerically solved for P_1. Population momentum was examined at regular intervals across the range of simulated α values for each life history strategy.

I parameterized the life history variables into pseudo age-structured (**A**), (Lefkovitch 1965) and age-structured (**B**) projection matrices (Leslie 1945, 1948) for iteroparous and semelparous strategies, respectively. I assumed birth-pulse reproduction and used a pre-birth census, where fertility equaled the product of fecundity and age-class 1 survival ($F = m * P_1$) (Caswell 2001), and α represents the age at maturity.

$$\mathbf{A} = \begin{bmatrix} 0 & 0 & \cdots & F_\alpha & F_{\alpha+1} \\ P_{2+} & 0 & \cdots & 0 & 0 \\ 0 & P_{2+} & \cdots & 0 & 0 \\ 0 & 0 & \ddots & 0 & 0 \\ 0 & 0 & \cdots & P_{2+} & P_{2+} \end{bmatrix} \qquad \mathbf{B} = \begin{bmatrix} 0 & 0 & \cdots & F_\alpha & 0 \\ P_{2+} & 0 & \cdots & 0 & 0 \\ 0 & P_{2+} & \cdots & 0 & 0 \\ 0 & 0 & \ddots & 0 & 0 \\ 0 & 0 & \cdots & P_{2+} & 0 \end{bmatrix}$$

I used projection matrices with stationary asymptotic growth ($\lambda_1 = 1$) as the starting point in my theoretical experiments. Because quickly growing populations are often caused by high fertility rates, I created growing ($\lambda_1 = 1.1$) populations by numerically changing fertility. Because quickly declining populations are often caused by suppressed survival rates, I created declining ($\lambda_1 = 0.9$) populations by changing survival rates for adult age classes and the age class immediately preceding maturity. For simplicity, I limited my study to these special cases of growing and declining populations, but acknowledge that fertility or survival could cause populations to change in either direction.

Theoretical experiments

Here, I consider populations that are growing so rapidly that they could cause environmental damage and populations that are declining at a rate that could yield extinction (i.e., the growing and declining populations defined above). My objective was to examine population size following changes in the vital rates that would, all else being equal, eventually halt the growth or decline. Hypothetically, changes in vital rates could be caused by the environment or anthropogenic manipulation. In the first group of experiments, I started with a growing population ($\lambda_1 = 1.1$) as the initial condition and then decremented fertility by the necessary amount to attain stationary growth ($\lambda_1 = 1$). I considered an instantaneous decrement in fertility and a gradual change of equal amounts over 5 years. A 5-year transition was used because our empirical understanding of population dynamics often comes from ecological studies and experiments that are short term, and because management plans and objectives are often short term as well.

In the second group of experiments, I started with a declining population ($\lambda_1 = 0.9$) as the initial condition and then augmented survival rates for adult age classes and the age class immediately preceding maturity by the amount necessary to attain stationary growth. I considered both an instantaneous augmentation of survival and a gradual change of equal amounts over 5 years.

I measured population momentum (M) following instantaneous changes in vital rates according Caswell's (2001:104) discrete-time formula:

$$\mathrm{M} = \frac{\mathbf{e}^{\mathrm{T}}\left(\mathbf{v}_1^{(\text{new})} * \mathbf{w}_1^{(\text{initial})}\right)\mathbf{w}_1^{(\text{new})}}{\mathbf{e}^{\mathrm{T}} * \mathbf{w}_1^{(\text{initial})}}. \tag{1}$$

Here, $\mathbf{e}$ is a vector of ones, $\mathbf{v}_1$ is the dominant left eigenvector of the projection matrix **A** or **B** that describes reproductive value (it is not normalized into a unit vector), $\mathbf{w}_1$ is the dominant right eigenvector of the projection matrix and describes the stable population structure (here, it is not normalized into a unit vector), 'initial' refers to the projection matrix for the initial conditions (growing or declining population), and 'new' refers to the projection matrix following changes in adult survival rates or fertility. The left and right eigenvectors of a projection matrix satisfy $\langle \mathbf{v}_i, \mathbf{w}_i \rangle = 1$ and $\langle \mathbf{v}_i, \mathbf{w}_j \rangle = 0$ for $i \neq j$ where $\langle \ \rangle$ is the scalar product. Equation 1 describes the ultimate population size that is actually attained following a vital-rate change, relative to the size of an otherwise equivalent population that experiences the same vital-rate change but always grows according to a stable population structure (i.e., the Stable Equivalent Population). Because the term "population momentum" is reserved by some demographers for the special case where per capita fertility transitions to the stationary level, Tuljapurkar and Lee (1997) called the ratio of the ultimate population size to that in a Stable Equivalent Population, the Stable Equivalent Ratio. Yet, population momentum can be measured following change in any vital rate (Li and Tuljapurkar 1999).

Because iteroparous organisms can successfully reproduce in successive time steps, positive fertilities exist in ≥ 2 adjacent columns in the projection matrix. Thus, projection matrices for iteroparous life histories are primitive, meaning that there exists one dominant eigenvalue and the asymptotic dynamics approach a stable point.

However, semelparous organisms have positive fertility in only one age class; therefore, projection matrices for semelparous life histories are imprimitive and have co-dominant eigenvalues. Thus, unless the population begins in a stable population structure, the asymptotic population size and (st)age distribution of semelparous organisms are cyclic with a period equal to the number of eigenvalues that share the largest size (*d*) (Caswell 2001). Still, a running average of the (st)age distribution over *d* converges to $\mathbf{w}_1$ and grows at the rate λ_1 (Cull and Vogt 1973). For semelparous life histories, I measured population momentum with the limit of these running average values.

To measure population momentum for gradual changes in fertility or survival, I began with Keyfitz's original formula (1971):

$$\mathrm{M}_{key} = \lim_{t\to\infty} \frac{\|\mathbf{n}_t\|}{\|\mathbf{n}_0\|} \tag{2}$$

where $\|\mathbf{n}\| = \sum_i n_i$ is the total population size. This is simply the ratio of the ultimate population size following a transition to the stationary level, to that immediately before the transition. Then, I calculated the numerator of equation 2 with a Markov chain of gradually changing vital rates:

$$\mathbf{n}_t = \mathbf{A}_{t-1}\mathbf{A}_{t-2}\cdots\mathbf{A}_1\mathbf{A}_0\mathbf{n}_0, \tag{3}$$

and denoted this measure of population momentum as M_2 (e.g., Schoen and Kim 1998, Li and Tuljapurkar 1999, 2000, Goldstein 2002). Here, $\mathbf{A}_t$ is the time-specific projection matrix of vital rates, and $\mathbf{n}_0 = \mathbf{w}_{0,nor.}$, which is the dominant right eigenvector of $\mathbf{A}_0$ normalized to 1. When changes in a vital rate occur gradually, two factors cause population momentum. First, the population structure that acts on each new set of vital rates is not stable, which can produce a residual effect on population size. Second, gradually changing vital rates will continue to cause population growth or decline regardless of population structure (Tuljapurkar and Lee 1997, Schoen and Jonsson 2003). This measurement of net population growth following gradual changes is not directly comparable to that following an instantaneous change, in which only the first factor causes momentum (Keyfitz 1971). To explicitly understand population momentum for gradual vital rate changes, I also calculated a measure of population momentum that controls for the effects of gradually changing per-capita vital rates on the population size M_3:

$$M_3 = \lim_{t \to \infty} \frac{\left\| \mathbf{n}_t \right\|}{\left\| \mathbf{n}_{t,asymptotic} \right\|} \tag{4}$$

Here, $\mathbf{n}_t$ was projected with equation 3 and $\mathbf{n}_{t,asymptotic}$ was projected with the following Markov chain:

$$\mathbf{n}_{t,asymptotic} = \mathbf{A}_{t-1}\mathbf{w}_{t-1,nor.} \left\| \mathbf{A}_{t-2}\mathbf{w}_{t-2,nor.} \right\| \cdots \left\| \mathbf{A}_1\mathbf{w}_{1,nor.} \right\| \left\| \mathbf{A}_0\mathbf{w}_{0,nor.} \right\| \tag{5}$$

where $\mathbf{w}_{t,nor.}$ is the dominant right eigenvector of $\mathbf{A}_t$ normalized to 1 (i.e., the stable age distribution). This is simply the ratio of the ultimate population size that is attained following a gradual vital rate change to the size that would be expected if population structure were stable throughout time with respect to $\mathbf{A}_0, \mathbf{A}_1, ..., \mathbf{A}_{t-1}$ (i.e., the Stable Equivalent Ratio; Lee and Tuljapurkar 1997). Hence, equation 4 controls for changes in population size directly caused by vital rates during the gradual change.

All measures of population momentum are centered on 1. Values of momentum above 1 indicate that the population will grow beyond that expected under asymptotic conditions, and values below 1 indicate that the population size will be less than that expected under asymptotic conditions.

I characterized each life history with the age at maturity. Age at maturity is a life history invariant that has a large influence on mean fitness (Cole 1954, Lewontin 1965), is highly correlated with other life history variables (Stearns 1992, Charnov 1993), and provides a consistent means for comparison across iteroparous and semelparous vertebrates.

RESULTS

For the first time in population biology, I calculate and make interspecific comparisons of population momentum for iteroparous ($n = 30$) and semelparous ($n = 10$) life histories. For each experiment, all 3 measures of population momentum (M, M_2, M_3, eqns. 1-5) exhibited the same pattern across life histories within a vertebrate life history strategy. However, the relationship between population momentum and age-at-maturity differed among the 5 life history strategies that I examined (Figs. 1 and 2).

Following instantaneous decrements in fertility to growing populations, the historical population structure reversed the direction of population growth ($M < 1$, and M_3 also < 1; Fig. 1, solid and open circles). Population momentum generally decreased with age at maturity, and the distance between both M and M_3 and 1, generally increased. However, the relationship was concave for bird and mammal life histories (Fig. 1 a), indicating that the earliest and latest maturing life histories were more resistant to forces of population momentum. As age at maturity increased, gradual transitions in fertility had a greater effect on population momentum (M_3) relative to instantaneous transitions (M) for bird and mammal, as well as turtle, lizard, and snake life history strategies, but not for other strategies (Fig. 1, comparison of solid and open circles). Despite the effects of population structure ($M_3 < 1$), net increases in population size usually occurred ($M_2 >$

1; Fig. 1, triangles). Nevertheless, actual population structure restricted populations from growing as large as they would have if population structure were stable throughout time, especially for life histories with delayed maturation (intermediate age at maturity in birds and mammals). In fact, the effect of population structure was so strong (indicated by M_3) for iteroparous bony fishes that it caused a net decline in population size ($M_2 < 1$) for life histories that mature at ≥ 10 years of age (Fig. 1 c).

After augmenting the survival rate (for age classes described in the methods) in declining populations, historical population structure had a small effect on population momentum for all bird and mammal, as well as turtle, lizard, and snake life histories (Fig. 2 a-b, solid and open circles). As a result, a net reduction in population size occurred (M and $M_2 < 1$), which was largely dictated by the low per capita survival rates during the gradual change (Fig. 2 a-b, triangles). To the contrary, bony fish life histories were not resistant to the effects of historical population structure following changes in survival. Historical population structure usually reversed the direction of population growth following instantaneous changes in survival ($M > 1$). In fact, M and M_3 increased with age at maturity for all bony fish life history strategies (Fig. 3 c-e, solid and open circles). However, gradual changes in survival still resulted in net reductions in population size ($M_2 < 1$) for all bony fish life histories (Fig. 3 c-e, triangles). Nonetheless, population size did not decline as much as it would have had population structure remained stable throughout time, especially for bony fish life histories with delayed maturity.

Because the functional contributions of fertility and survival to λ_1 (measured with elasticities) vary with life history, I generally had to perturb the vital rates by different proportionate amounts across life histories in order to achieve stationary population growth in my experiments (Figs. 1 and 2, right axes). The population structure of the growing populations ($\lambda_1 = 1.1$) had a surplus of young immature individuals, and a deficit of mature adults, relative to the asymptotic population structure for stationary vital rates ($\lambda_1 = 1$). The decrease in fertility also shifted some of the reproductive value toward younger age classes (Fig. 3). As a result, populations for each life history experienced transient dynamics with greater net mortality and lesser net fertility than would have occurred in a Stable Equivalent Population. This caused a reversal in the direction of population growth following instantaneous change in fertility ($M < 1$, Fig. 1; M_3 also < 1).

To varying degrees across the 5 life history strategies, population structures of declining populations ($\lambda_1 = 0.9$) had a deficit of mature adults and individuals in the youngest immature age classes, but a surplus of the middle-aged immature individuals, relative to the asymptotic population structure for stationary vital rates. The increase in survival shifted bird and mammal, as well as turtle, lizard, and snake reproductive values towards the oldest age classes but shifted bony fish reproductive values towards the older sub-adults rather than adults (Fig. 4). This led to transient population dynamics that had little effect on long-term population size in birds and mammals, as well as turtles, lizards, and snakes, but often led to a reversal in the direction of population growth amongst bony fish life histories (M and $M_3 > 1$; Fig. 2 c-e).

DISCUSSION

Our understanding of population momentum is limited because it has not been examined for most animals. Recently, Koons et al. (2005) examined three animal life histories and found that population momentum varied according to the vital rate that was changed, the magnitude of that change, and life history. I used theoretically derived life histories to examine this latter finding in greater depth, and describe how population momentum varies across vertebrate life histories for instantaneous and gradual changes in vital rates.

Li and Tuljapurkar's (1999) measure of M_2 following gradual changes in fertility increased exponentially with the time over which the gradual transition occurred and was generally much larger than Keyfitz's momentum (M). However, M_2 is not comparable to M because M_2 can be caused by historical population structure as well as gradually changing per capita vital rates, whereas M is only caused by historical population structure (Bongaarts and Bulatao 1999, Schoen and Jonsson 2003). By controlling for effects of non-stationary vital rates during a gradual transition (M_3), I generally found little difference in population momentum between instantaneous and 5-year changes. The only differences I detected were for longer-lived bird and mammal, as well as turtle, lizard, and snake life histories (Figs. 1 and 2). Furthermore, patterns of net population growth following 5-year vital rate changes were caused by historical population structure (M_3), rather than non-stationary vital rates. Thus, I focus my discussion on the causes and consequences of life history variation in population momentum caused by the historical population structure (M and M_3).

Following changes in fertility or survival, M and M_3 generally moved further away from 1 as age at maturity increased, supporting my hypothesis. However, there were notable exceptions among the bird and mammal, as well as turtle, lizard, and snake life history strategies. For these two strategies, M and M_3 were negligible after augmentation of survival in the declining populations, suggesting that these strategies were resistant to population momentum (Fig. 2 a-b). Further, the earliest and latest maturing bird and mammal life histories, as well as the turtle, lizard, and snake life histories with intermediate age at maturity, exhibited signs of resistance to population momentum following decremented fertility in the increasing populations (Fig. 1 a-b). To the contrary, population momentum in bony fish life histories was very reactive to all vital-rate changes, especially for life histories with delayed maturity (Figs. 1 and 2, c-e).

Demographically, these patterns can be explained by population structure and reproductive value, which directly affect population momentum (e.g., see equation 1). In my experiments, vital rates of late-maturing life histories generally had to be changed by larger proportionate amounts than for early maturing life histories, especially amongst the bony fishes (Figs. 1 and 2). Larger changes in a vital rate will cause larger changes in asymptotic population structure, meaning that a historical population structure that acts on newly changed vital rates will have either a surplus or deficit of breeding adults. This produces transient population dynamics with greater or lesser net reproduction, recruitment, or both, than would occur under asymptotic conditions. Thus, variation in population momentum across life histories can often be explained by the amount that a vital rate is changed (Fig. 1 b-e, Fig. 2 c-e). However, this relationship is not universal. Changes in reproductive value of multiple age classes could potentially offset the abovementioned effect of historical age structure (Fig. 1a), sometimes resulting in little population momentum (Fig. 2 a-b).

Furthermore, the pattern between population momentum and age at maturity differed across life history strategies because stable population structures and the allocation of reproductive value across age classes are inherently different among vertebrate life history strategies. For example, the stable population structure in bony fishes is heavily skewed towards young and the distribution of reproductive value is heavily skewed toward adults. Among birds, mammals, turtles, lizards, and snakes these distributions are less skewed (e.g., Figs. 3 and 4), which makes these organisms more resistant to population momentum following changes in survival. Yet, to better understand the demographic connection between population momentum and population structure, reproductive value, and life history vital rates, a method for measuring the sensitivity of population momentum to equal unit or proportional changes in vital rates or initial population structure will be needed (presented in Chapter 5).

Population size is important in ecology, conservation, pest control, and harvest management. Thus, ecologists and resource managers should consider population momentum in population projections that are used to make management decisions or when quantifying the ecological causes of historical population dynamics (Caswell 2001). My results indicated that population momentum will have the strongest effect on population size of long-lived vertebrates with delayed maturity, especially amongst iteroparous bony fishes, which are often harvested for commercial or sport purposes. Recently, Hauser, Cooch, and Lebreton found that population momentum could limit the ability of managers to regulate populations with harvest techniques (unpublished data). Thus, I highly recommend implementation of population momentum into harvest-management models to better assess the effects of harvest on population dynamics.

The direction of population momentum (> 1 or < 1) will also be important to consider in pest control and conservation. Demographers have always found population momentum to follow the direction of historical population growth (e.g., Fischer and

Heilig 1997). Yet, population momentum for a stage-structured population of *Calathea ovandensis* was in the opposite direction of historical growth (Caswell 2001:106), and Koons et al. (2005) found similar results for pseudo age-structured animal populations. In Physics, momentum of an object that changes direction is known as an 'impulse' (Buckwalter and Riban 1987). Similar to the aforementioned studies, impulses occurred in my study, causing momentum in the opposite direction of historical population growth following decrements in fertility for increasing populations and following augmentations of survival in decreasing bony fish populations. On the other hand, population momentum following augmentation of survival in decreasing bird, mammal, turtle, lizard, and snake populations was small and sometimes in the same direction of historical population growth. Depending on the life history and vital rate that is changed, population momentum could be beneficial or detrimental for pest control and conservation (Koons et al. 2005). My results should provide guidance to population ecologists and resource managers that will have to carefully assess how population momentum could affect population size of the animals they monitor.

To conclude, I note that single, temporally isolated vital-rate changes seldom occur in nature. I purposefully ignored continual stochastic changes to clarify the effects of population momentum on population size. My theoretical findings should be used as a starting point to guide empirical studies, which will be needed to test my theoretical predictions and to gain an understanding of the ubiquity of population momentum in nature. Lastly, I recommend that studies of population viability (sensu Gilpin and Soulé 1986), and other subject matter of conservation and evolutionary concern, consider the contribution of population momentum to projected dynamics.

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Appendix 1. Theoretical generating functions and corresponding curves for fecundity (*m*), and survival rate for age classes ≥ 2 (P_{2+}; iteroparous life histories only) across the age at maturity (α) of vertebrate life histories. Figure *a* represents iteroparous birds and mammals where $m = 13 * e^{-0.3*\alpha}$, $P_{2+} = 1 - e^{-0.25*\alpha}$, and empirical estimates of fecundity (•) and adult survival (◦) are presented as examples for (from left to right on all figures): snowshoe hare (*Lepus americanus*), wandering albatross (*Diomedea exulans*), orca (*Orcinus orca*), and the U.S. human population (*Homo sapiens*). Figure *b* represents iteroparous turtles, lizards, and snakes where $m = 1.1 * \alpha$, $P_{2+} = 0.99\left(1 - e^{-0.39*\alpha}\right)$, and empirical estimates of fecundity (•) and adult survival (◦) are presented for Iguanidae lizards, painted turtle (*Chrysemys picta*), snapping turtle (*Chelydra serpentina*), and loggerhead sea turtle (*Caretta caretta*). Figure *c* represents iteroparous bony fishes where $m = -7830 + 7830 * e^{0.15*\alpha}$, $P_{2+} = 1 - e^{-0.1*\alpha}$, and empirical estimates of fecundity (•) and adult survival (◦) are presented for threespine stickleback (*Gasterosteus aculeatus*), hake (*Merluccius merluccius*), and charr (*Salvelinus alpinus*). Figure *d* represents semelparous large-bodied bony fishes where $m = 650 * \alpha$, and empirical estimates of fecundity (•) are presented for pink (*Oncorhynchus gorbuscha*), coho (*Oncorhynchus kisutch*), chum (*Oncorhynchus keta*), Chinook (*Oncorhynchus tshawytscha*), and sockeye (*Oncorhynchus nerka*) salmons. Figure *e* represents semelparous small-bodied bony fishes where $m = -9360 + 9360 * e^{0.55*\alpha}$, and empirical estimates of fecundity (•) are presented for eulachon (*Thaleichthys pacificu*) and alewife (*Alosa pseudoharengus*).

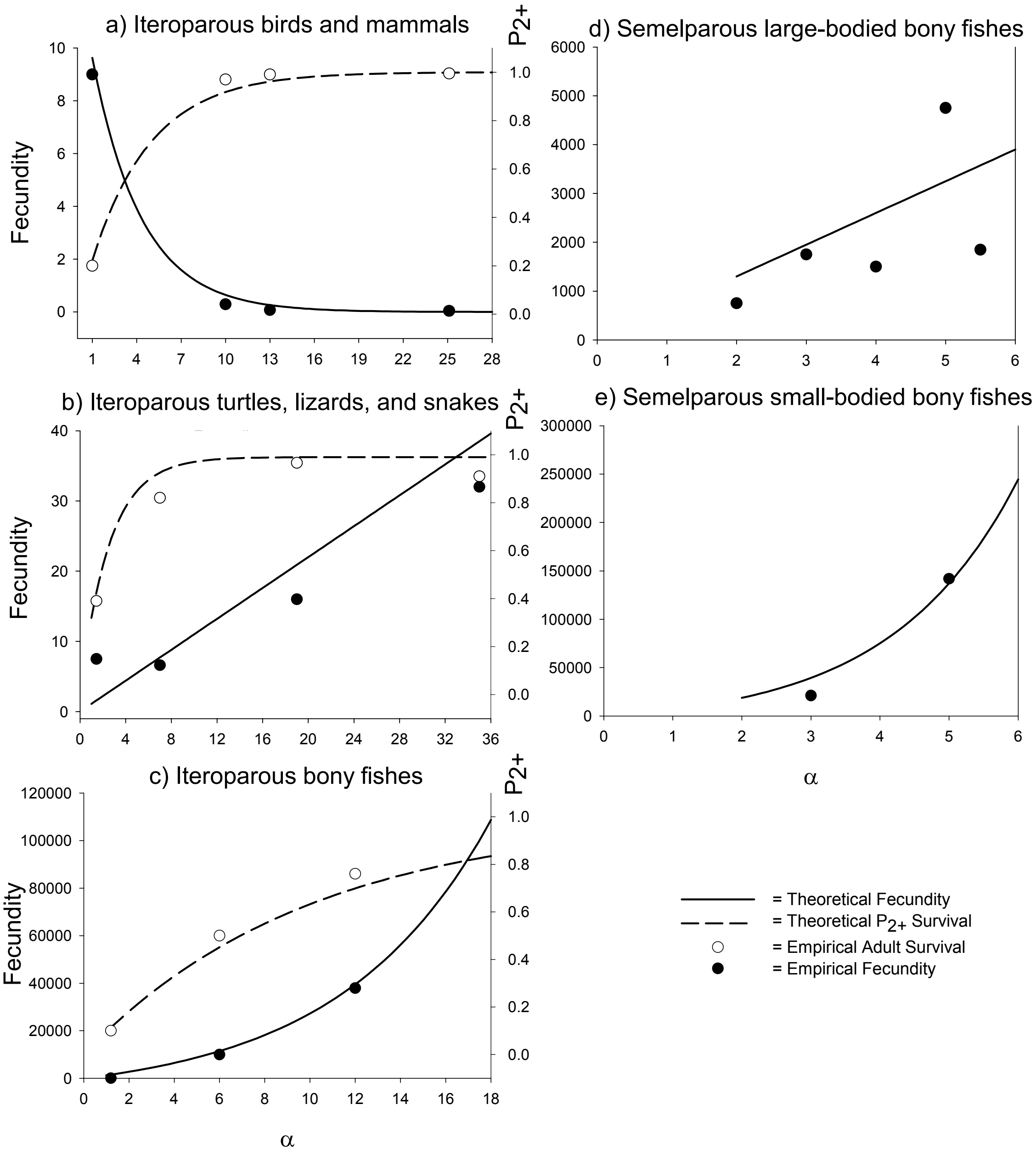

a) Iteroparous birds and mammals
Fecundity
P2+
0
2
4
6
8
10
0.0
0.2
0.4
0.6
0.8
1.0
1
4
7
10
13
16
19
22
25
28
b) Iteroparous turtles, lizards, and snakes
Fecundity
P2+
0
10
20
30
40
0.0
0.2
0.4
0.6
0.8
1.0
0
4
8
12
16
20
24
28
32
36
c) Iteroparous bony fishes
Fecundity
P2+
0
20000
40000
60000
80000
100000
120000
0.0
0.2
0.4
0.6
0.8
1.0
0
2
4
6
8
10
12
14
16
18
α
d) Semelparous large-bodied bony fishes
0
1000
2000
3000
4000
5000
6000
0
1
2
3
4
5
6
e) Semelparous small-bodied bony fishes
0
50000
100000
150000
200000
250000
300000
0
1
2
3
4
5
6
α
= Theoretical Fecundity
= Theoretical P2+ Survival
= Empirical Adult Survival
= Empirical Fecundity

Figure 1. Plots of population momentum (left axis), evaluated at regular intervals of α, for the growing population experiments ($\lambda_1 = 1.1$) where fertility was decremented to the stationary level across iteroparous a) birds and mammals, b) turtles, lizards, and snakes, c) bony fishes, and semelparous d) large-bodied bony fishes, e) small-bodied bony fishes. The right axis shows proportional change in fertility that was required to achieve the stationary level.

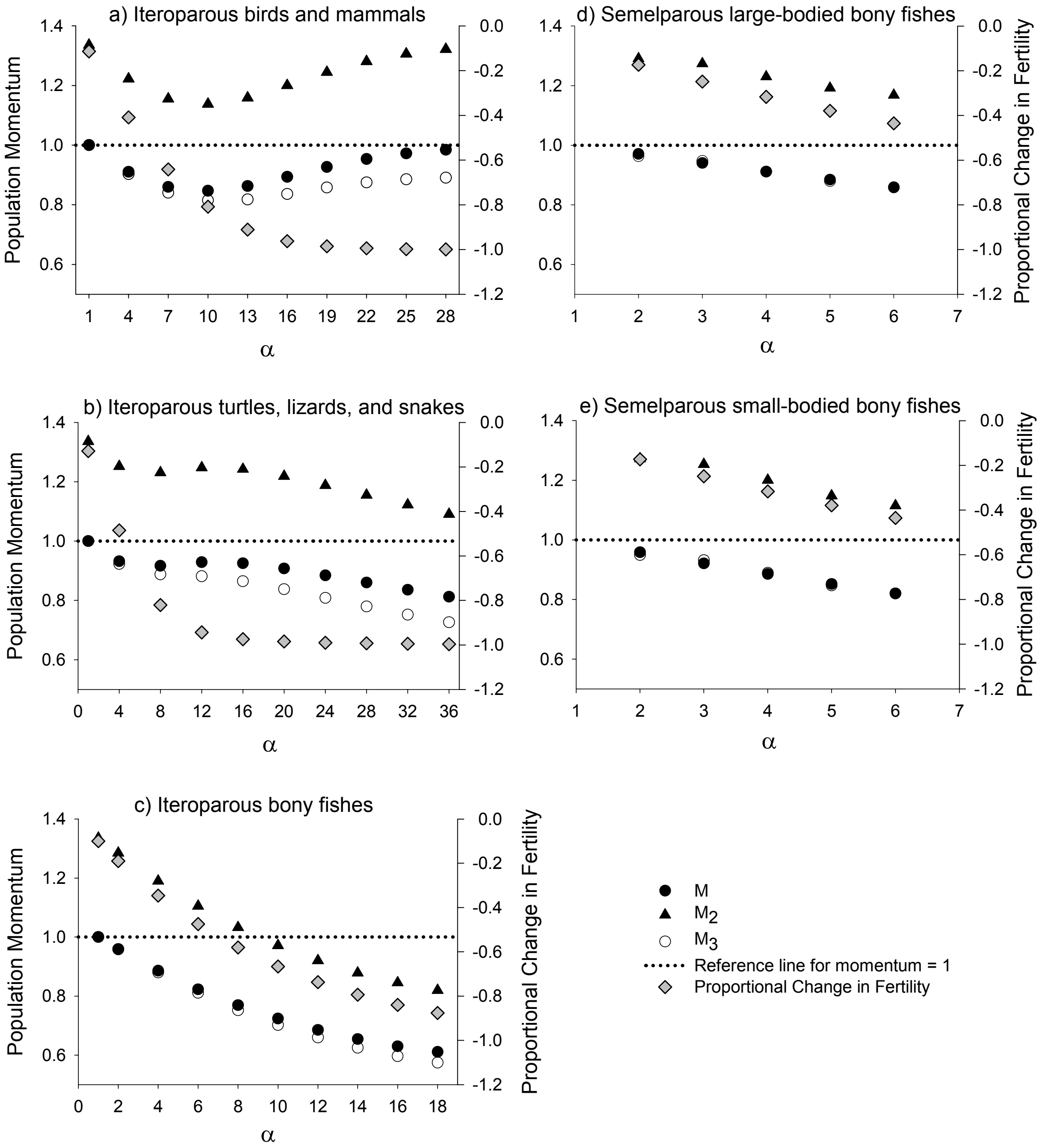

a) Iteroparous birds and mammals
b) Iteroparous turtles, lizards, and snakes
c) Iteroparous bony fishes
d) Semelparous large-bodied bony fishes
e) Semelparous small-bodied bony fishes
Population Momentum
Proportional Change in Fertility
α
1.4
1.2
1.0
0.8
0.6
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
-1.2
1 4 7 10 13 16 19 22 25 28
0 4 8 12 16 20 24 28 32 36
0 2 4 6 8 10 12 14 16 18
1 2 3 4 5 6 7
● M
▲ M_2
○ M_3
Reference line for momentum = 1
◆ Proportional Change in Fertility

Figure 2. Plots of population momentum (left axis), evaluated at regular intervals of α, for the declining population experiments ($\lambda_1 = 0.9$) where survival rates for adult age classes and the age class immediately preceding maturity were augmented to the stationary level across iteroparous a) birds and mammals, b) turtles, lizards, and snakes, c) bony fishes, and semelparous d) large-bodied bony fishes, e) small-bodied bony fishes. The right axis shows proportional change in survival that was required to achieve the stationary level (a > 8-fold increase in survival was required for the iteroparous bony fish life history with an age at maturity of 1).

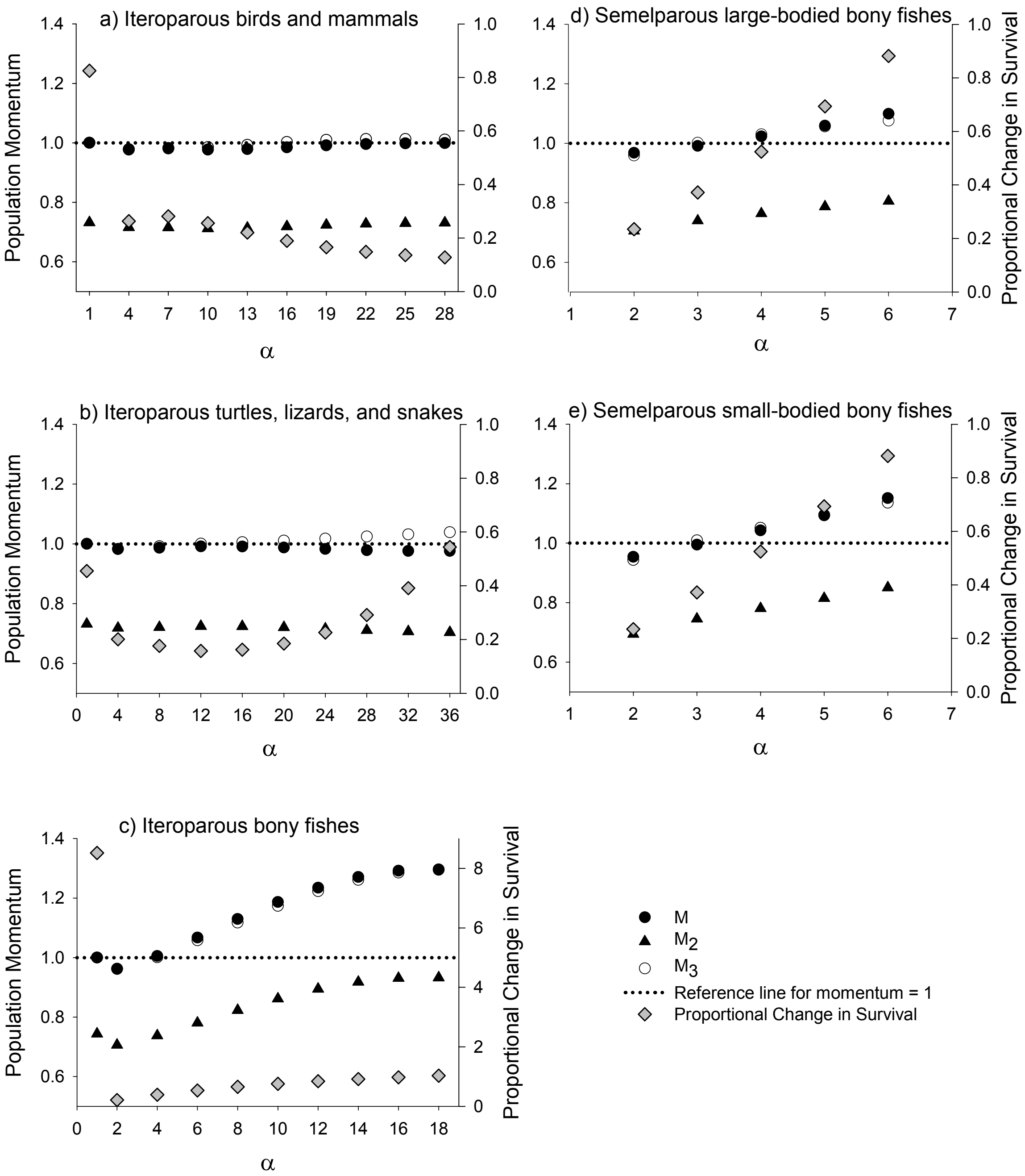
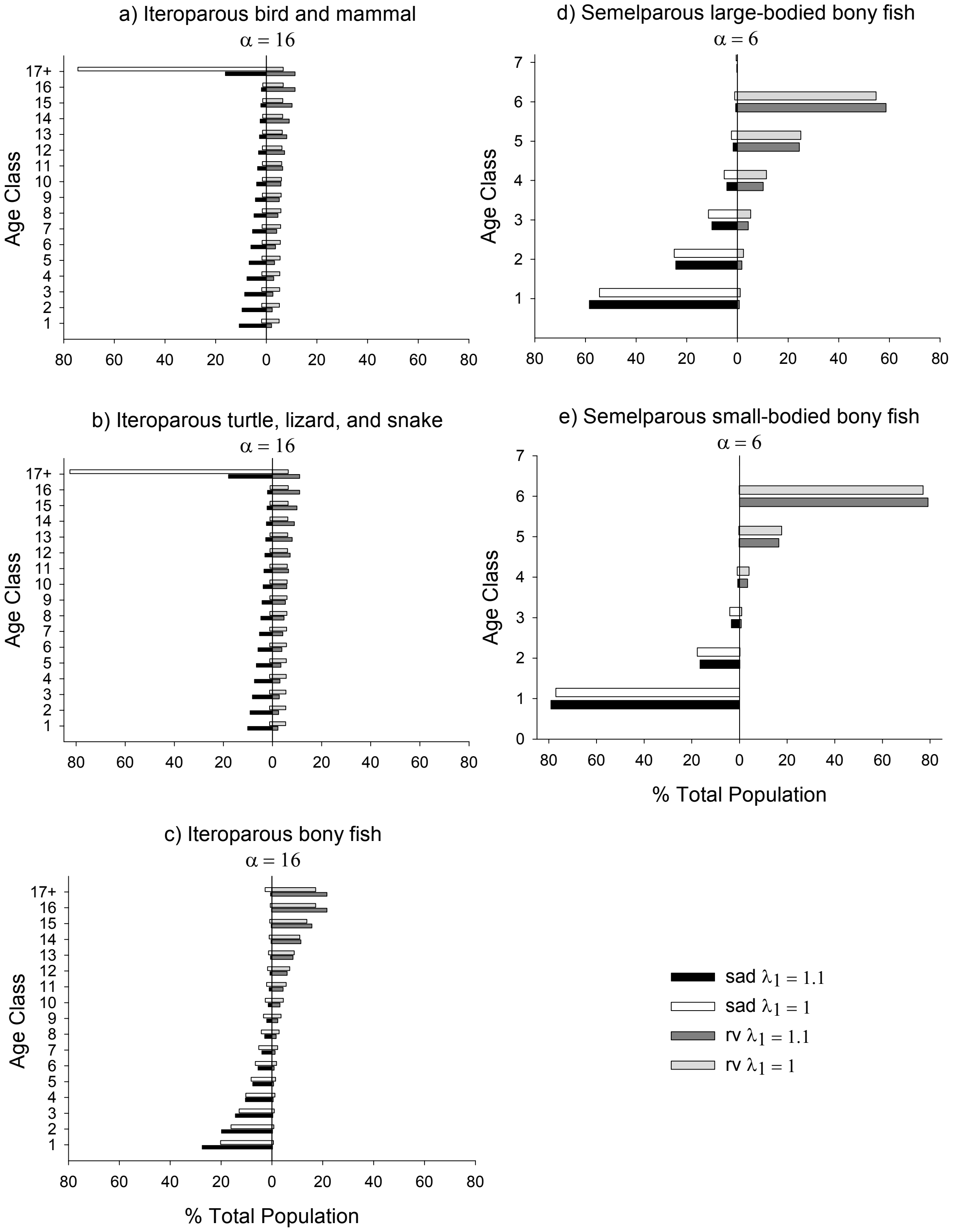

a) Iteroparous birds and mammals
b) Iteroparous turtles, lizards, and snakes
c) Iteroparous bony fishes
d) Semelparous large-bodied bony fishes
e) Semelparous small-bodied bony fishes
Population Momentum
Proportional Change in Survival
α
1.4
1.2
1.0
0.8
0.6
0.0
0.2
0.4
0.6
0.8
1.0
1 4 7 10 13 16 19 22 25 28
0 4 8 12 16 20 24 28 32 36
0 2 4 6 8 10 12 14 16 18
1 2 3 4 5 6 7
0
2
4
6
8
● M
▲ M2
○ M3
Reference line for momentum = 1
◆ Proportional Change in Survival

Figure 3. Example plots of the asymptotic stable age distributions (sad; left bars), and reproductive values (rv; right bars) for the experimental growing and stationary populations of selected life histories with an age at maturity of 16 for iteroparous strategies and 6 for semelparous strategies.



a) Iteroparous bird and mammal

$\alpha = 16$

d) Semelparous large-bodied bony fish

$\alpha = 6$

b) Iteroparous turtle, lizard, and snake

$\alpha = 16$

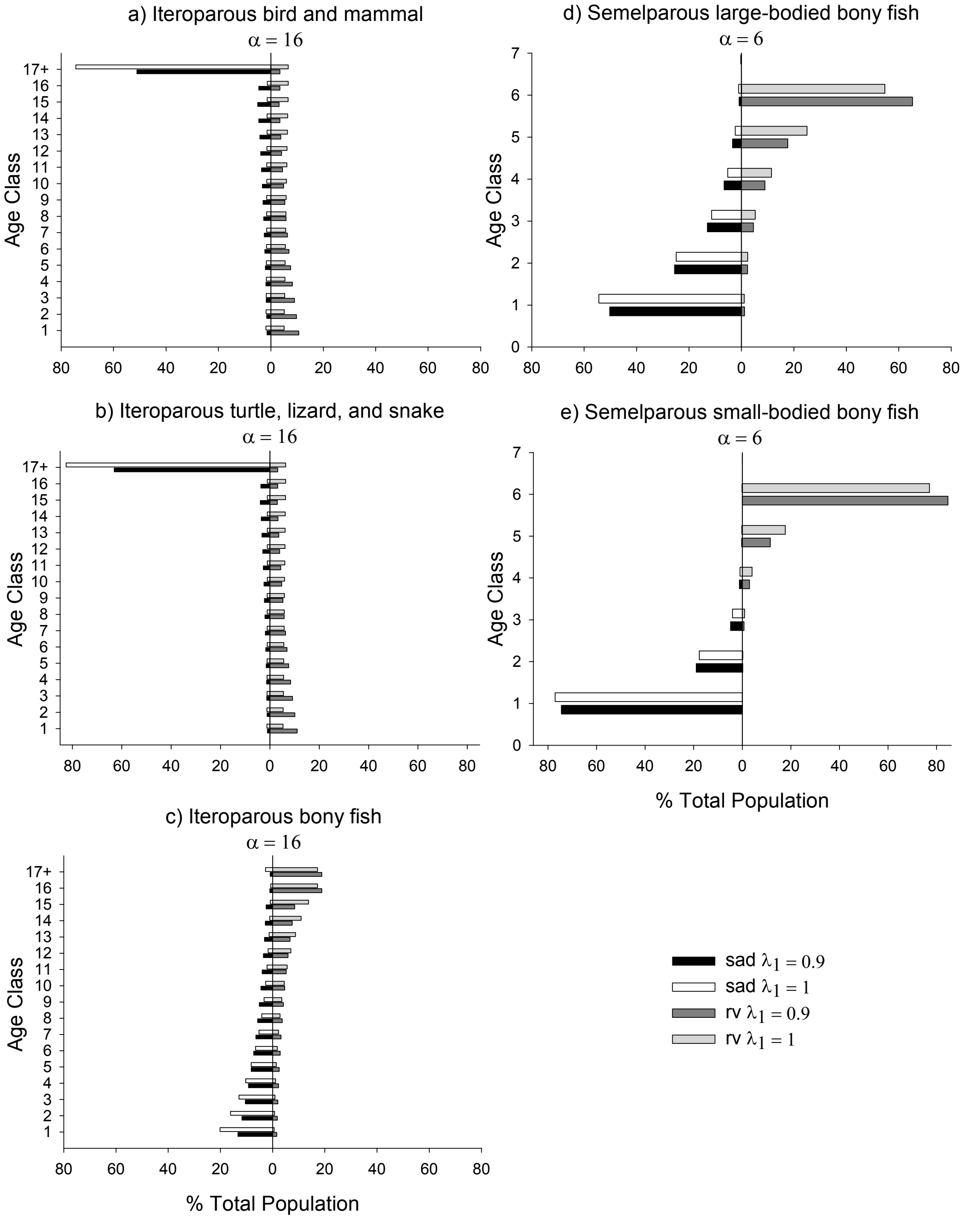
e) Semelparous small-bodied bony fish

$\alpha = 6$

c) Iteroparous bony fish

$\alpha = 16$

Figure 4. Example plots of the asymptotic stable age distributions (sad; left bars), and reproductive values (rv; right bars) for the experimental declining and stationary populations of selected life histories with an age at maturity of 16 for iteroparous strategies and 6 for semelparous strategies.


a) Iteroparous bird and mammal
α = 16
b) Iteroparous turtle, lizard, and snake
α = 16
c) Iteroparous bony fish
α = 16
d) Semelparous large-bodied bony fish
α = 6
e) Semelparous small-bodied bony fish
α = 6
Age Class
17+
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
80
60
40
20
0
20
40
60
80
% Total Population
sad λ1 = 0.9
sad λ1 = 1
rv λ1 = 0.9
rv λ1 = 1

V. GENERAL FORMULAS FOR THE SENSITIVITY OF POPULATION MOMENTUM TO CHANGES IN POPULATION VITAL RATES AND INITIAL CONDITIONS

Abstract. Population structure can produce strong residual effects on population size, commonly known as population momentum. Population momentum has a long history of study in demography, but has only recently received attention in the ecological literature. Prior to now, there has not been a general way to examine change in population momentum resulting from unit changes in population vital rates (e.g., birth rates, death rates, etc.) or population structure. I derive general formulas for the sensitivity of population momentum to changes in population vital rates or population structure. The sensitivity for changes in vital rates is similar to population growth rate sensitivity that is widely used in demography, ecology, evolution, conservation, and management. My formulas are readily computable, and I provide examples and applications that illustrate their use in studies of life history, ecology, and applied management.

1. Introduction

Population size is central to the fields of demography and population biology. Demographers often study population size because it can affect economies, policy, social dynamics, and even natural resource supplies (Bos et al. 1994, Fischer and Heilig 1997, United Nations 2003). Biologists pay special attention to population size when trying to keep small populations from going extinct, controlling pest populations, and in management of populations that provide hunting, fishing, and viewing opportunities (Caughley 1977). Additionally, the change in population size over time (i.e., population growth rate) describes the average fitness and performance of the population (Fisher 1930, Sibly et al. 2002), and is used in many theoretical studies of life history. Thus, population size is an important parameter for many reasons.

When population structure (i.e., the distribution of abundance across age, stage, size, or sex classes) is stable, population size is solely determined by the vital rates (i.e., fecundity, survival, age at maturity, immigration, emigration). However, it is fundamental to understand that when population structure is not stable, population structure can actually influence the long-term trajectory of population size (Tuljapurkar and Lee 1997). For example, if a population initially has an ‘over abundance’ of mature adults it will experience transient dynamics and might reach a larger population size than a population that initially has a stable population structure and grows according to the same vital rates. Alternatively, a population may have a stable population structure, but experience a systematic change in one or several vital rates, such that the new set of vital rates act on the old population structure. In either case, it is the historical population structure that affects the physical behavior of momentum in population size (Tuljapurkar and Lee 1997), which is commonly known as “population momentum” (sensu Keyfitz 1971a).

Because the study of population momentum can help us better understand increases and decreases in population size, it has been studied extensively in demography (e.g., Keyfitz 1971a, Frauenthal 1975, Mitra 1976, Wachter 1988, Fischer and Heilig 1997, Kim and Schoen 1997, Schoen and Kim 1998, Bongaarts and Bulatao 1999, Li and Tuljapurkar 1999, 2000, Schoen and Jonsson 2003), and has recently been examined in wildlife management (Koons et al. 2005; Hauser, Cooch, and Lebreton In Review) and population ecology (Koons et al. 2005b, Chapter 4).

I know of no general formulae that relate unit changes in vital rates or population structure to changes in population momentum. Here, I present analytical formulae for the sensitivity of population momentum to unit changes in any vital rate or initial conditions. I compute population momentum sensitivities across a wide variety of life histories, in a simple source-sink metapopulation, and for cases where applied management could directly affect population structure.

2. Derivation

2.1. Population model

I use bold-type capital letters to denote matrices and bold-type lower case letters to denote vectors. Italicized letters denote the entries of vectors and matrices. I use $\bar{x}$ to denote the conjugate of x, $\mathbf{x}^{\mathrm{T}}$ to denote the transpose of the vector $\mathbf{x}$ and $\mathbf{x}^*$ to denote the complex conjugate transpose.

Most studies of population momentum are conducted with continuous time models. However, the underlying mechanisms of population momentum are more easily seen in discrete form (Schoen and Jonsson 2003). Thus, my derivation is based on a linear, discrete, time-invariant population model

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t . \tag{1}$$

Here, $\mathbf{n}_t$ is an *n*-dimensional vector with $n_i(t)$ describing the number of individuals in the *i*th stage at time *t*. **A** is an $n \times n$ matrix with (i, j)-entry a_{ij} equal to the transition rate from the *j*th stage to the *i*th stage. Alternatively, the population vector at any time *t* can be expressed as:

$$\mathbf{n}_t = \sum_i c_i \lambda_i^t \mathbf{w}_i , \tag{2}$$

where the $\mathbf{w}_i$'s are right eigenvectors of **A**, the λ_i 's are the associated eigenvalues, and the c_i's are dependent on the initial conditions and left eigenvectors (Caswell 2001). The *i*th eigenvalues λ_i and corresponding right $\mathbf{w}_i$ and left $\mathbf{v}_i$ eigenvectors of **A** satisfy

$$\mathbf{A}\mathbf{w}_i = \lambda_i \mathbf{w}_i \tag{3}$$

$$\mathbf{v}_i^* \mathbf{A} = \lambda_i \mathbf{v}_i^* . \tag{4}$$

The indexing is chosen in such a way that λ_1 is the eigenvalue with largest modulus. For large *t*, this eigenvalue and its eigenvector dominate the expression for $\mathbf{n}_t$ given in equation 2, and so eventually, the population grows approximately geometrically at the rate λ_1. The dominant right $\mathbf{w}_1$ and left $\mathbf{v}_1$ eigenvectors describe the asymptotic population structure and reproductive values, respectively (Goodman 1968). Throughout, I assume that the eigenvectors have been scaled so that $\langle \mathbf{v}_i, \mathbf{w}_i \rangle = 1$ and $\langle \mathbf{v}_i, \mathbf{w}_j \rangle = 0$ for $i \neq j$. I further assume that the eigenvalues of **A** are distinct.

2.2. Measurement of population momentum

Keyfitz (1971a) originally calculated population momentum for a stable population that was originally growing at some rate g that underwent an instantaneous transition to stationary growth (i.e., $g = 1$; the level of lifetime individual replacement). He defined population momentum M as the ultimate size of the population relative to that immediately before the instantaneous change in the vital rate(s):

$$\mathrm{M} = \lim_{t \to \infty} \frac{\left\| \mathbf{n}_t \right\|}{\left\| \mathbf{n}_0 \right\|}, \tag{5}$$

where $\left\| \mathbf{n}_{\mathrm{t}} \right\| = \sum_i n_i(t)$ is the total population size. However, physical momentum in population size is not restricted to the special case described by Keyfitz. I seek a model that is general enough to calculate the phenomenon of momentum in populations for 1) Keyfitz's original thought experiment, 2) populations that are initially unstable and eventually grow according to an asymptotic growth rate g (not necessarily the stationary rate), 3) populations that initially have a stable structure and grow at a rate g, that undergo instantaneous change in population structure resulting in population momentum, and 4) populations that initially have a stable structure and grow at a rate g_1, that undergo instantaneous change in a vital rate resulting in a new asymptotic growth rate g_2 (not necessarily the stationary rate, e.g., a population that undergoes a vital-rate change that causes asymptotic growth rate to change from 1.05 to 0.98). Caswell's (2001:104) discrete formula for population momentum M happens to satisfy all of these conditions:

$$\mathrm{M} = \frac{\mathbf{e}^{\mathrm{T}} \left(\mathbf{v}_1^{*} \mathbf{n}_0 \right) \mathbf{w}_1}{\mathbf{e}^{\mathrm{T}} \mathbf{n}_0}, \tag{6}$$

where $\mathbf{e}$ is a vector of ones. In condition 2 above, $\mathbf{n}_0$ is a vector describing the initially unstable distribution of population size across stage classes, and all else being equal, the population eventually grows at the rate $g = \lambda_1$. In condition 3 above, $\mathbf{n}_0$ is a vector describing the initially stable population structure and the population grows at the rate $g = \lambda_1$, then $\mathbf{n}_0$ is perturbed and the population undergoes transient dynamics, which can cause population momentum. All else being equal, the population will eventually grow at the same rate $g = \lambda_1$. In conditions 1 and 4 above, $\mathbf{n}_0$ describes the stable distribution of population size before the vital rate(s) changes (change), and $\mathbf{v}_1$ and $\mathbf{w}_1$ are the left and right eigenvectors of the transition matrix following change in the vital rate(s) ($\mathbf{A}_{\text{new}}$). For projections from initial conditions and for instantaneous changes in vital rates or population structure, equation 6 essentially describes the ultimate population size of a population growing at any rate (g or g_2 above) as determined by the actual population structure, relative to the size of an otherwise equivalent population that always grows according to a stable population structure (i.e., the Stable Equivalent Population). Because the term "population momentum" is reserved by some demographers for the special case where per capita fertility transitions to the stationary level, Tuljapurkar and Lee (1997) call the ratio of the ultimate population size to that in the Stable Equivalent Population, the Stable Equivalent Ratio. Here, I do not restrict my use of "population momentum" to Keyfitz's special case (1971a) because momentum is a general physical phenomenon.

2.3. General formulas for the sensitivity of population momentum to unit changes in population vital rates

I wish to measure the sensitivity of population momentum to infinitesimal unit changes in the underlying vital rates (a_{ij}) of the transition matrix **A**. Perturbations of the vital rates will change the right and left eigenvectors; thus, sensitivities of these eigenvectors to change in a vital rate will also be needed. To develop general formulas, I used the product rule to differentiate equation 6 with respect to a single vital rate a_{ij}:

$$\begin{aligned}\frac{\partial \mathrm{M}}{\partial a_{ij}} &= \frac{\partial}{\partial a_{ij}}\left(\frac{\mathbf{e}^{\mathrm{T}}\left[\left(\overset{*}{\mathbf{v}}_1\mathbf{n}_0\right)\mathbf{w}_1\right]}{\mathbf{e}^{\mathrm{T}}\mathbf{n}_0}\right)\\ &= \frac{1}{\mathbf{e}^{\mathrm{T}}\mathbf{n}_0}\left[\mathbf{e}^{\mathrm{T}}\frac{\partial}{\partial a_{ij}}\left[\left(\overset{*}{\mathbf{v}}_1\mathbf{n}_0\right)\mathbf{w}_1\right]+0\right]\\ &= \frac{1}{\mathbf{e}^{\mathrm{T}}\mathbf{n}_0}\left[\mathbf{e}^{\mathrm{T}}\left[\left(\overset{*}{\mathbf{v}}_1\mathbf{n}_0\right)\frac{\partial \mathbf{w}_1}{\partial a_{ij}}+\left(\frac{\partial}{\partial a_{ij}}\left(\overset{*}{\mathbf{v}}_1\mathbf{n}_0\right)\right)\mathbf{w}_1\right]\right]\\ &= \frac{1}{\mathbf{e}^{\mathrm{T}}\mathbf{n}_0}\left[\mathbf{e}^{\mathrm{T}}\left[\left(\overset{*}{\mathbf{v}}_1\mathbf{n}_0\right)\frac{\partial \mathbf{w}_1}{\partial a_{ij}}+\left({\frac{\partial \mathbf{v}_1}{\partial a_{ij}}}^{*}\mathbf{n}_0\right)\mathbf{w}_1\right]\right]\end{aligned} \quad . \qquad (7)$$

Caswell (1980, 2001), developed solutions to the derivatives of the right $\mathbf{w}_1$ and left $\mathbf{v}_1$ eigenvectors with respect to change in a vital rate a_{ij}

$$\frac{\partial \mathbf{w}_1}{\partial a_{ij}} = w_j^{(1)}\sum_{m\neq 1}^{s}\frac{\bar{v}_i^{(m)}}{\lambda_1-\lambda_m}\mathbf{w}_m \,. \qquad (8)$$

$$\frac{\partial \mathbf{v}_1}{\partial a_{ij}} = v_i^{(1)}\sum_{m\neq 1}^{s}\frac{\bar{w}_j^{(m)}}{\bar{\lambda}_1-\bar{\lambda}_m}\mathbf{v}_m \,. \qquad (9)$$

where $w_j^{(m)}$ is the *j*th entry of $\mathbf{w}_m$. By incorporating Caswell's solutions (eq. 8 and 9) into equation 7, my general solution to the sensitivity of population momentum can be seen as

$$\frac{\partial \mathrm{M}}{\partial a_{ij}} = \frac{1}{\mathbf{e}^{\mathrm{T}}\mathbf{n}_0}\left[\mathbf{e}^{\mathrm{T}}\left[\left(\mathbf{v}_1^{*}\mathbf{n}_0\right)\left(w_j^{(1)}\sum_{m\neq 1}^{s}\frac{\overline{v}_i^{(m)}}{\lambda_1-\lambda_m}\mathbf{w}_m\right)+\left(\left(v_i^{(1)}\sum_{m\neq 1}^{s}\frac{\overline{w}_j^{(m)}}{\overline{\lambda}_1-\overline{\lambda}_m}\mathbf{v}_m\right)^{*}\mathbf{n}_0\right)\mathbf{w}_1\right]\right].(10)$$

Sometimes matrix-level entries are computed from multiple lower-level vital rates. For example, fertilities are the product of fecundity and some component of survival. To calculate the sensitivity of population momentum to lower-level parameters *x*, just use the chain rule

$$\frac{\partial \mathrm{M}}{\partial x} = \sum_{k,l}\frac{\partial \mathrm{M}}{\partial a_{kl}}\frac{\partial a_{kl}}{\partial x}. \tag{11}$$

The current definition of population momentum is asymptotic, and measured in the direction of the dominant left $\mathbf{v}_1$ and right $\mathbf{w}_1$ eigenvectors. Thus, equation 6 could also be written as $\mathrm{M}^{1,1} = \left(\mathbf{v}_1^{*}\mathbf{n}_0\right)\left(\mathbf{e}^{\mathrm{T}}\mathbf{w}_1\right)\big/\mathbf{e}^{\mathrm{T}}\mathbf{n}_0$, where the superscripts on M indicate direction with respect to (any *k,l*th pair of) the left and right eigenvectors. From equations 8 and 9, I can define

$$\mathrm{b}_m = \frac{w_j^{(1)}\overline{v}_i^{(m)}}{\lambda_1-\lambda_m}\text{, and} \tag{12}$$

$$\mathrm{c}_m = \frac{\overline{v}_i^{(1)}w_j^{(m)}}{\lambda_1-\lambda_m}. \tag{13}$$

Using these definitions, patterns in the abovementioned equations reveal that

$$\frac{\partial \mathrm{M}^{1,1}}{\partial a_{ij}} = \sum_{m \neq 1}^{s} \left(\mathrm{b}_m \, \mathrm{M}^{1,m} + \mathrm{c}_m \, \mathrm{M}^{m,1} \right). \tag{14}$$

Momentum is conserved in a system, and in the short term, portions of the population vector lie along each eigenvector (eq. 2). Thus, we could measure population momentum at any time *t*, in the direction of any *k,l*th pair of left and right eigenvectors. Additionally, equation 14 can be used to calculate the sensitivity of population momentum in the *k,l* direction to changes in a vital rate: $\frac{\partial \mathrm{M}^{k,l}}{\partial a_{ij}}$.

Population momentum sensitivities can also be calculated numerically

$$\frac{\partial \mathrm{M}}{\partial a_{ij}} \doteq \frac{\mathrm{M}_{post} - \mathrm{M}_{pre}}{\Delta_{ij}}. \tag{15}$$

Here, M_{pre} and M_{post} are the measurements of population momentum before and after the change Δ_{ij} in the vital rate a_{ij}. Although I have chosen to focus on the sensitivity of population momentum to unit changes in vital rates, the elasticity of population momentum to proportional changes in vital rates can easily be calculated from the analytical sensitivity or numerically,

$$\frac{\partial \log \mathrm{M}}{\partial \log a_{ij}} = \frac{\partial \mathrm{M}}{\partial a_{ij}} \frac{a_{ij}}{\mathrm{M}} \tag{16}$$

$$\frac{\partial \log \mathrm{M}}{\partial \log a_{ij}} \doteq \frac{\mathrm{M}_{post} - \mathrm{M}_{pre}}{\mathrm{M}_{pre}} \frac{1}{p_{ij}} \tag{17}$$

where p_{ij} is the proportional change in the vital rate a_{ij}. Population momentum is not a linear function of the a_{ij}, thus the elasticities do not sum to unity. Unfortunately, the elasticities do not quantify the contribution of the a_{ij} to M like they do for the geometric population growth rate (de Kroon et al. 1986). Nevertheless, elasticities are still useful for measuring the effect of relative change in a vital rate on population momentum.

2.4. General formulas for the sensitivity of population momentum to unit changes in population structure

Population momentum also depends on the initial population vector $\mathbf{n}_0$. Thus, I also seek to measure the sensitivity of population momentum to changes in the initial population structure. To develop general formulas for this sensitivity, I first used the quotient rule to differentiate equation 6 with respect to a single entry of the initial population vector $n_i(0)$:

$$\begin{aligned}
\frac{\partial \mathrm{M}}{\partial n_i(0)} &= \mathbf{e}^{\mathrm{T}}\mathbf{w}_1 \frac{\partial}{\partial n_i(0)}\left(\frac{\overset{*}{\mathbf{v}}_1\mathbf{n}_0}{\mathbf{e}^{\mathrm{T}}\mathbf{n}_0}\right) \\
&= \mathbf{e}^{\mathrm{T}}\mathbf{w}_1 \left[\frac{\mathbf{e}^{\mathrm{T}}\mathbf{n}_0 \dfrac{\partial}{\partial n_i(0)}\left(\overset{*}{\mathbf{v}}_1\mathbf{n}_0\right) - \overset{*}{\mathbf{v}}_1\mathbf{n}_0 \dfrac{\partial}{\partial n_i(0)}\mathbf{e}^{\mathrm{T}}\mathbf{n}_0}{\left(\mathbf{e}^{\mathrm{T}}\mathbf{n}_0\right)^2}\right]. \qquad (18) \\
&= \mathbf{e}^{\mathrm{T}}\mathbf{w}_1 \left[\frac{\mathbf{e}^{\mathrm{T}}\mathbf{n}_0\left(\bar{v}_i^{(1)}\right) - \overset{*}{\mathbf{v}}_1\mathbf{n}_0}{\left(\mathbf{e}^{\mathrm{T}}\mathbf{n}_0\right)^2}\right]
\end{aligned}$$

I note that the 'initial' point in time can be defined as the point in time from which the population will be studied forward. If one assumes that $\mathbf{e}^{\mathrm{T}}\mathbf{w}_1 = \|\mathbf{w}_1\| = 1,\ \mathbf{e}^{\mathrm{T}}\mathbf{n}_0 = \|\mathbf{n}_0\| = 1$, and $\mathbf{v}_1$ is real, then

$$\frac{\partial \mathrm{M}}{\partial n_i(0)} = v_i^{(1)} - \overset{*}{\mathbf{v}}_1\mathbf{n}_0 . \qquad (19)$$

In particular, if one examines the special case where $\mathbf{n}_0 = \mathbf{w}_1$, then

$$\left.\frac{\partial \mathrm{M}}{\partial n_i(0)}\right|_{\mathbf{w}_1} = v_i^{(1)} \text{-} 1. \tag{20}$$

Thus, knowledge of only the reproductive value and the initial population structure are needed to measure the sensitivity of population momentum to change in a single entry of the initial population structure. If it is safe to assume that the population structure is initially stable, then only reproductive value is needed, which is easily computed from **A**.

Now I consider perturbations that could affect multiple stage classes. To do this, let $\mathbf{u} = \left[u_1, \cdots, u_n\right]^{\mathrm{T}}$ be an arbitrary unit vector (i.e., $\|\mathbf{u}\| = 1$) to be regarded as a perturbation vector applied to $\mathbf{n}_0$. Furthermore, the directional derivative of M in the direction **u** is denoted $D_{\mathbf{u}}\mathrm{M}$, and is given by the formula

$$D_{\mathbf{u}}\mathrm{M} = \nabla \mathrm{M}^{\mathrm{T}} \mathbf{u}\,, \tag{21}$$

where $\nabla \mathrm{M} = \left[\partial \mathrm{M}/\partial n_1(0), \cdots, \partial \mathrm{M}/\partial n_n(0)\right]^{\mathrm{T}}$ is the gradient of M. The set of all vectors **x** for which $\nabla \mathrm{M}^{\mathrm{T}} \mathbf{x} = 0$ form a hyperplane in n-space. The directional derivative is positive, negative, or zero when **u** is on the positive side of the hyperplane, the negative side, or in the hyperplane itself, respectively. Furthermore, the directional derivative is maximized when **u** lies in the same direction as the gradient of M.

Considering the special case where $\mathbf{n}_0 = \mathbf{w}_1$ (with each being a unit vector),

$$\begin{aligned} \left. D_{\mathbf{u}}\mathrm{M}\right|_{\mathbf{w}_1} &= \nabla \mathrm{M}^{\mathrm{T}} \mathbf{u} \\ &= \left(\mathbf{v}_1 - \mathbf{e}\right)^{*} \mathbf{u} \end{aligned}\;. \tag{22}$$

When population structure is initially stable, population momentum equals 1. Therefore, the new value of M after perturbation is > 1, < 1, or = 1 when the directional derivative is

> 0, < 0, or = 0, respectively. If one only perturbs the *i*th entry of $\mathbf{w}_1$ (i.e., $\mathbf{u} = \left[0, \cdots, 0, 1, 0, \cdots, 0\right]^{\mathrm{T}}$), then the sign of the *i*th entry of $\mathbf{v}_1 - \mathbf{e}$ dictates the direction that M moves away from 1. In this case

$$D_{\mathbf{u}}\mathrm{M}\Big|_{\mathbf{w}_1} = \left.\frac{\partial \mathrm{M}}{\partial n_i(0)}\right|_{\mathbf{w}_1} = v_i^{(1)} - 1. \tag{23}$$

Thus, equation 20 is just a special case of the directional derivative (eq. 23). In addition, if $\mathbf{u} = \mathbf{w}_1$, then the distribution of individuals among stage classes does not change following the perturbation (**u**), so M is expected to remain at 1. This is indeed the case, since $D_{\mathbf{w}_1}\mathrm{M}\Big|_{\mathbf{w}_1} = \left(\mathbf{v}_1 - \mathbf{e}\right)^* \mathbf{w}_1 = \mathbf{v}_1^* \mathbf{w}_1 - \mathbf{e}^{\mathrm{T}} \mathbf{w}_1 = \mathbf{v}_1^* \mathbf{w}_1 - 1 = 0$.

3. Applications and examples

3.1. Sensitivity of population momentum across bird and mammal life histories

Here, I visit my study in Chapter 4. For increasing ($\lambda_1 = 1.1$) bird and mammal populations, I found that instantaneous decrements in fertility to the stationary level always decreased the net population size (M < 1), which contradicted patterns found in human populations (Fischer and Heilig 1997). Although of lesser magnitude, instantaneous augmentation of adult survival in decreasing ($\lambda_1 = 0.9$) bird and mammal populations also produced M < 1, and populations always stabilized at smaller sizes than the Stable Equivalent Population. Both experiments produced interesting patterns in M across life histories (Fig. 1).

Yet, I did not control for the size of the vital-rate perturbation in Chapter 4. Life history characteristics determine how much each vital rate has to be changed in order to achieve stationary growth (Fig. 1, right axis), which is problematic because the magnitude of change in a vital rate affects the magnitude of change in asymptotic population structure (eq. 8), and sometimes population momentum (eq. 10). I concluded that because the magnitude of population momentum did not always increase with the magnitude of change in a vital rate (Fig. 1, both axes), the earliest and latest maturing life histories must be more resistant to the forces of population momentum than others.

Examining the sensitivity of population momentum to equal changes in vital rates across life histories avoids the aforementioned problem in Chapter 4, and could shed more light on these findings. Using the data set in Chapter 4, I used equation 10 to examine patterns in population momentum sensitivities across bird and mammal life histories. Across populations that were initially increasing ($\lambda_1 = 1.1$), I found that the sensitivity of population momentum to unit changes in fertility (summed across relevant age classes) varied with age at maturity in a similar way (Fig. 2) as the actual values of population momentum in Chapter 4 (Fig. 1). The positive sensitivities of population momentum to unit changes in fertility indicate that increased fertility will increase population momentum. Likewise, decrements in fertility, like those applied in Chapter 4, will decrease population momentum, which explains why I observed $M < 1$ and net losses in population size in Chapter 4. Here, I found that different initial population growth rates (e.g., stationary growth) affected stable age structures and population-momentum sensitivity values, but not the general pattern in sensitivities across life histories. Thus, both Chapters 4 and 5 provide evidence that early and late maturing birds and mammals are more resistant to the forces of population momentum following changes in fertility than those with intermediate age at maturity.

Yet, across populations that were initially decreasing ($\lambda_1 = 0.9$), the relationship between age at maturity and sensitivity of population momentum to unit changes in adult survival was different (Fig. 3) than that for actual values of population momentum in Chapter 4 (Fig. 1). Life history patterns in the sensitivities were similar to my findings in Chapter 4 up until $\alpha = 10$. However, the actual sign of the sensitivities changed from negative to positive for $\alpha \geq 16$ (Fig. 3), indicating that small unit increases in adult survival can increase population momentum.

To examine why infinitesimally small increases in adult survival led to an increase in population momentum for certain life histories while large increases in adult survival led to a decrease in momentum, I used numerical simulation to examine how population momentum changed with increasing size of the adult survival perturbation. As predicted by the positive population momentum sensitivity for the $\alpha = 16$ life history, I found that small increases in adult survival produced $M > 1$, but that increases > 0.0687 produced $M < 1$, as found in Chapter 4. Interestingly, population momentum was maximized at a perturbation of 0.0384 (Fig. 4a). For the $\alpha = 28$ life history, population momentum was maximized (1.0255) at a perturbation of 0.0409. Still, perturbations $>$ 0.0951 produced $M < 1$, as found in Chapter 4 (Fig. 4b).

Compared to the initially declining populations ($\lambda_1 = 0.9$), asymptotic population structure and reproductive values of late-maturing life histories ($\alpha \geq 16$) changed substantially with increasing size of the perturbation applied to adult survival. The asymptotic distribution of abundance in the oldest adult age class and youngest sub-adult age classes increased with the size of perturbation applied to adult survival, while abundance in all other age classes decreased. Furthermore, the slopes of the relationship between adult survival perturbation size and asymptotic population structure were steepest in the oldest age classes (e.g., see Fig. 5). Conversely, reproductive value of the older sub-adult and adult age classes increased with the size of perturbation applied to adult survival, while that of the younger sub-adult age classes decreased. The slopes of the relationship between adult survival perturbation size and reproductive value were steepest in the oldest and youngest age classes (e.g., see Fig. 6). Long-lived, late-maturing life histories live a substantial amount of life as a sub-adult, which can create a complex population structure. Because of these life history properties of late-maturing birds and mammals, the nature of how a perturbation affects the disparity between actual population structure and the new asymptotic population structure and reproductive values following the perturbation can have a substantial impact on both the quantitative and qualitative aspects of population momentum (e.g., see Fig. 4).

3.2. Population momentum in a source-sink system

Here, I provide an example of population momentum and its sensitivity to changes in the dispersal of young produced in a source habitat that move to a sink habitat (Pulliam 1988). To illustrate my example, I use the following source-sink system

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & 2 & 0 & 0 & 0 \\ 0.25 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.50 & 0.75 & 0 & 0 & 0 \\ 0 & 0 & 0.10 & 0 & 0 & 1 \\ 0 & 0 & 0 & 0.25 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.50 & 0.75 \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \\ n_3 \\ n_4 \\ n_5 \\ n_6 \end{bmatrix}_{t} .$$

In my example, stages 1-3 belong to the sub-population in the source habitat, stages 4-6 belong to the sub-population in the sink habitat and represent the same stage classes as 1-3. All matrix entries represent local fertility or survival probabilities except $a_{4,3}$, which represents the number of offspring produced in the source habitat that successfully disperse and survive to the next census in the sink habitat (i.e., dispersants). The population in the source habitat is locally stationary ($\lambda_1 = 1$) and that in the sink habitat does not have self-sustaining fertility levels and would rapidly decline ($\lambda_1 = 0.9$) to extinction without connection to the source habitat. The asymptotic growth rate of the overall source-sink population is stationary ($\lambda_1 = 1$) because it is dictated by that in the source habitat. The source-sink population has asymptotic stage structure $\mathbf{w}_1 = \begin{bmatrix} 0.87 & 0.22 & 0.43 & 0.09 & 0.02 & 0.04 \end{bmatrix}^{\mathrm{T}}$, and a small number of successful dispersants (0.10). I used equation 10 to calculate the matrix of population momentum sensitivities (**MS**) to each non-zero a_{ij}, assuming stable stage structure:

$$\mathbf{MS} = \begin{bmatrix} 0 & 0 & 0.07 & 0 & 0 & 0 \\ -0.85 & 0 & 0 & 0 & 0 & 0 \\ 0 & -0.35 & -0.71 & 0 & 0 & 0 \\ 0 & 0 & \mathbf{0.91} & 0 & 0 & 0.09 \\ 0 & 0 & 0 & 0.52 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.23 & 0.47 \end{bmatrix}.$$

It is clear that population momentum of this particular source-sink system is highly sensitive to unit changes in the number of dispersants. Furthermore, the sign of this particular sensitivity value indicates that an increase in the number of dispersants should increase population momentum while a decrease should decrease population momentum.

Using this information, I examined how the population dynamics of a source-sink system would respond to an increase in the number of successful dispersants from 0.1 to 1. Such an event could occur if resources became abundant in the source habitat, allowing high fertility, but competition forced the extra offspring to disperse to the sink habitat.

Because the increase in dispersant offspring did not affect the population growth rate in the source habitat, asymptotic growth of the source-sink system remained stationary (λ_1 still = 1). However, increasing the number of successful dispersants did increase short-term growth of the source-sink system, which caused large population momentum (M = 1.82). All of the net growth in population size occurred in the sink habitat ($\mathbf{n}_\infty = \begin{bmatrix} 0.87 & 0.22 & 0.43 & 0.87 & 0.22 & 0.43 \end{bmatrix}^T$. Thus, change in the number of dispersants did not change the asymptotic growth of the source-sink system, but it did cause population momentum that equilibrated the number of individuals in each stage class across habitats. Depending on the organism, this result might be beneficial because it could provide more hunting and viewing opportunities, buffer the overall population from extinction in the event of stochastic events, or it could be deleterious if the organism is considered a pest. Although this is just one simple example, population momentum sensitivities could prove to be very useful for studying the dynamics of spatially-structured populations.

3.3. Effects of changing population structure

In many cases, managers might want to consider how different management strategies could change population momentum in their favor to keep population size within reasonable limits (Hauser, Cooch, and Lebreton In Review), or to decrease risks of extinction. Plant and animal release and relocation programs provide managers a variety of ways to directly 'add' individuals to specific age or stage classes of a population, while harvest, live-trapping, and other removal techniques allow managers to directly decrease abundance in specific age or stage classes. All of these management practices could change population momentum (eq. 6). Thus, I provide an example that illustrates how population momentum is affected by perturbations that add or remove individuals from specific age classes of a population. I use the following matrix **A**, which describes the mean vital rates of the lesser snow goose (*Chen caerulescens*) population at La Perouse Bay, Manitoba from 1973 to 1990 (Cooch et al. 2001).

$$\mathbf{A} = \begin{bmatrix} 0 & 0.12 & 0.26 & 0.38 & 0.41 \\ 0.83 & 0 & 0 & 0 & 0 \\ 0 & 0.83 & 0 & 0 & 0 \\ 0 & 0 & 0.83 & 0 & 0 \\ 0 & 0 & 0 & 0.83 & 0.83 \end{bmatrix}$$

In **A**, fertilities are represented on the top row and survival probabilities are on the sub-diagonal and bottom-right corner of the matrix. The 1st age class represents young and all other age classes represent aging adults.

To begin, I calculated the left $\mathbf{v}_1 = \begin{bmatrix} 0.34 & 0.44 & 0.52 & 0.56 & 0.57 \end{bmatrix}^{\mathrm{T}}$ and right $\mathbf{w}_1 = \begin{bmatrix} 0.46 & 0.36 & 0.28 & 0.21 & 0.73 \end{bmatrix}^{\mathrm{T}}$ eigenvectors of **A**. To simplify my scenario, I assumed that population structure was initially stable (i.e., $\mathbf{n}_0 = \mathbf{w}_1$), indicating M initially = 1. I also normalized $\mathbf{w}_1$ into a unit vector (i.e., $\left\|\mathbf{w}_{1,nor.}\right\| = 1$), and normalized $\mathbf{v}_1$, such that $\mathbf{v}_{1,nor.} = \mathbf{v}_1 \left\|\mathbf{w}_1\right\|$, which allowed me to use equations 22 and 23 to easily address my scenario. In addition, the normalized right and left eigenvectors are still eigenvectors of **A**, and the condition $\langle \mathbf{v}_i, \mathbf{w}_i \rangle = 1$ is maintained. Rounded to the second decimal, $\mathbf{w}_{1,nor.} = \begin{bmatrix} 0.23 & 0.17 & 0.14 & 0.10 & 0.36 \end{bmatrix}^{\mathrm{T}}$ and

$\mathbf{v}_{1,nor.} = \begin{bmatrix} 0.70 & 0.90 & 1.06 & 1.15 & 1.17 \end{bmatrix}^{\mathrm{T}}$.

Next, I used the directional derivative to measure the sensitivity of population momentum to a variety of perturbations to initial population structure (Table 1). It is readily seen that if only the *i*th entry of initial population structure is perturbed, then the direction M moves away from 1 is dictated by the sign of the *i*th entry of $\nabla \mathrm{M}$ or $v_i^{(1)}$ -1. For example, a unit increase in the 1st age class decreases population momentum (M < 1), a unit increase in an older adult age class increases population momentum (M > 1), and unit decreases produce opposite results (Table 1). Furthermore, a perturbation in the same direction as the gradient vector maximizes the response of population momentum to a unit change in the population structure, while a perturbation in the opposite direction of the gradient vector produces the exact opposite response. Perturbations equal to the stable age distribution ($\mathbf{w}_{1,nor.}$) do not change population momentum at all (M still = 1; Table 1).

Compared to the stable age structure of **A**, removing young (e.g., through clutch removal), releasing adults, or both, would allow a goose manager to quickly increase population momentum because each action shifts age structure towards reproducing adults. On the other hand, releasing young, removing adults (via harvest or live trapping), or both, would allow the manager to quickly decrease population momentum because these practices shift age structure towards offspring. However, it is important to remember that these results pertain only to the effects of directly changing population structure, not the effects of perturbing vital rates, which are presented above.

4. Discussion

The sensitivity of population growth rate to changes in population vital rates has a long history of use in demography, theoretical ecology, and evolution (Lewontin 1965, Hamilton 1966, Demetrius 1969, Emlen 1970, Goodman 1971, Keyfitz 1971b, and Mertz 1971). However, Caswell's (1978) discrete-form sensitivity formula, that simply requires the vectors describing reproductive value $\mathbf{v}_1$ and stable population structure $\mathbf{w}_1$, has made calculating this metric relatively simple. As a result, population growth rate sensitivity is now widely used in conservation, management, and applied ecology (e.g., van Groenendael et al. 1988, Horvitz et al. 1997, Benton and Grant 1999, papers within Heppell et al. 2000). Caswell also developed formulas for the sensitivities of reproductive value and stable population structure to examine the equivalence of maximizing reproductive value versus maximizing fitness (1980). These formulas have not been widely used; however, I have drawn upon this theory to develop my general formula for population momentum sensitivity.

Population momentum is a measure related to population size rather than population growth rate. All else being equal, population growth rate is ergodic, meaning that it forgets initial conditions. In contrast, population size is very responsive to initial conditions (Lee and Tuljapurkar 1997). Thus, I caution against confusing sensitivities calculated for the asymptotic population growth rate (e.g., λ_1) with those calculated for population momentum. Increased survival and fertility will always increase long-term growth rate, but this is not necessarily the case for population momentum.

The sensitivity of population size to changes in population vital rates or initial population structure can also be measured from eigenvectors of **A** (Fox and Gurevitch

2000, Caswell 2001). However, population momentum is the ratio of the population size that is ultimately attained following transient dynamics to the size of a hypothetical population that is always in an asymptotic stable state. Thus, those that are used to thinking about asymptotic population dynamics may find my momentum sensitivities very useful.

I have shown that unit increases in adult survival probabilities can often decrease population momentum, meaning that if population momentum is initially = 1, increased survival could decrease ultimate population size (Figs. 1 and 3). Interestingly, simultaneous changes in fertility and survival would have large effects on population growth rate; however, with regard to population momentum, simultaneous changes could offset each other and not change population momentum at all. Because reproductive value often depends on age or developmental stage, the nature of how perturbed vital rates affect age structure will dictate the direction and magnitude of population momentum. By studying the sensitivity of population momentum to direct changes in stable population structure, I was able to explicitly reveal the dependence of population momentum on reproductive value and population structure (Table 1). My simple formulas for the sensitivity of population momentum to perturbations away from the stable population structure (eq. 22, 23) can easily be used by demographers, managers, and conservation biologists to understand how changing population structure can affect population momentum.

Because the world is moving toward large-scale conservation planning, it is important to seek general patterns in life-cycle properties across species that could help guide conservation and management. Across several vertebrate groups, there are strong relationships between the population growth rate sensitivities (and elasticities) and simple life history characteristics (Heppell 1998, Heppell et al. 2000b, Sæther and Bakke 2000). In the bird, mammal, turtle, lizard, snake, and bony fish taxa, I have shown that population momentum also varies in predictable ways with life history (Chapter 4). In my first example, I used equation 10 to provide further evidence that particular life histories do indeed respond more to the forces of population momentum than others. General patterns in life-cycle properties and population dynamics do exist across vertebrate species. Thus, it may be possible to use life history characteristics of organisms to develop very general, but widespread conservation and management plans for many species.

For populations with stable or unstable population structures, my family of population momentum sensitivities can be used to examine how unit or proportional changes in vital rates or initial population structure will affect population momentum. This will be important in studies of demography, life history evolution, metapopulation and multi-region dynamics, conservation, pest control, and natural resource management.

Lastly, when comparing the results from small vital-rate perturbations to the large perturbations made in Chapter 4, I made an interesting discovery. Population momentum (M) can be maximized, and the size of a vital-rate perturbation can actually reverse the direction of population momentum in late-maturing organisms. These results seem to be related to the intricate differences between actual population structure and the asymptotic population structure associated with the changed set of vital rates, as well as the corresponding reproductive values (Figs. 5-6). I encourage further exploration of the behavior of population momentum across life history and perturbation space in linear and nonlinear systems. Hopefully, my discovery regarding the maximization of population momentum will generate new and exciting theoretical questions about the potential behavior of population momentum in nature.

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Table 1. The sensitivity of population momentum to unit changes **u** in the initial population structure of the lesser snow goose population at La Perouse Bay, Manitoba, indicated by the directional derivative $D_{\mathbf{u}}\mathrm{M}\big|_{\mathbf{w}_1}$, and the effect of the perturbation on population momentum M. Here, I used the normalized left eigenvector $\mathbf{v}_{1,nor.} = \begin{bmatrix}0.70 & 0.90 & 1.06 & 1.15 & 1.17\end{bmatrix}^{\mathrm{T}}$, and the following gradient of M: $\nabla\mathrm{M} = \begin{bmatrix}-0.30 & -0.10 & 0.06 & 0.15 & 0.17\end{bmatrix}^{\mathrm{T}}$, each rounded to the second decimal.

u[a]	$D_{\mathbf{u}}\mathrm{M}\big\|_{\mathbf{w}_1}$	Value of M after perturbation
$[1\ 0\ 0\ 0\ 0]^{\mathrm{T}}$	-0.30	< 1
$[0\ 0\ 1\ 0\ 0]^{\mathrm{T}}$	0.06	> 1
$[0\ 0\ 0\ 0\ 1]^{\mathrm{T}}$	0.17	> 1
$[-1\ 0\ 0\ 0\ 0]^{\mathrm{T}}$	0.30	> 1
$[0\ 0\ -1\ 0\ 0]^{\mathrm{T}}$	-0.06	< 1
$[0\ 0\ 0\ 0\ -1]^{\mathrm{T}}$	-0.17	< 1
$[0.2\ 0.2\ 0.2\ 0.2\ 0.2]^{\mathrm{T}}$	-0.003	< 1
$[-0.2\ -0.2\ -0.2\ -0.2\ -0.2]^{\mathrm{T}}$	0.003	> 1
$[-18.57\ -6.16\ 3.74\ 9.40\ 10.59]^{\mathrm{T}}$	9.80	>> 1
$[18.57\ 6.16\ -3.74\ -9.40\ -10.59]^{\mathrm{T}}$	-9.80	<< 1
$[0.23\ 0.17\ 0.14\ 0.10\ 0.36]^{\mathrm{T}}$ [b]	0	1

a – Rounded to the second decimal

b – The stable age distribution

Figure 1. Plots of population momentum (left axis), evaluated at regular intervals of age at maturity (α) for the thought experiments described by Koons and Grand (In Review) where fertility of growing populations ($\lambda_1 = 1.1$) was decremented to the stationary level across hypothetical bird and mammal life histories (●), and where adult survival of declining populations ($\lambda_1 = 0.9$) was augmented to the stationary level (▲). The right axis shows proportional change in each vital rate (open symbols) that was required to achieve the stationary level.

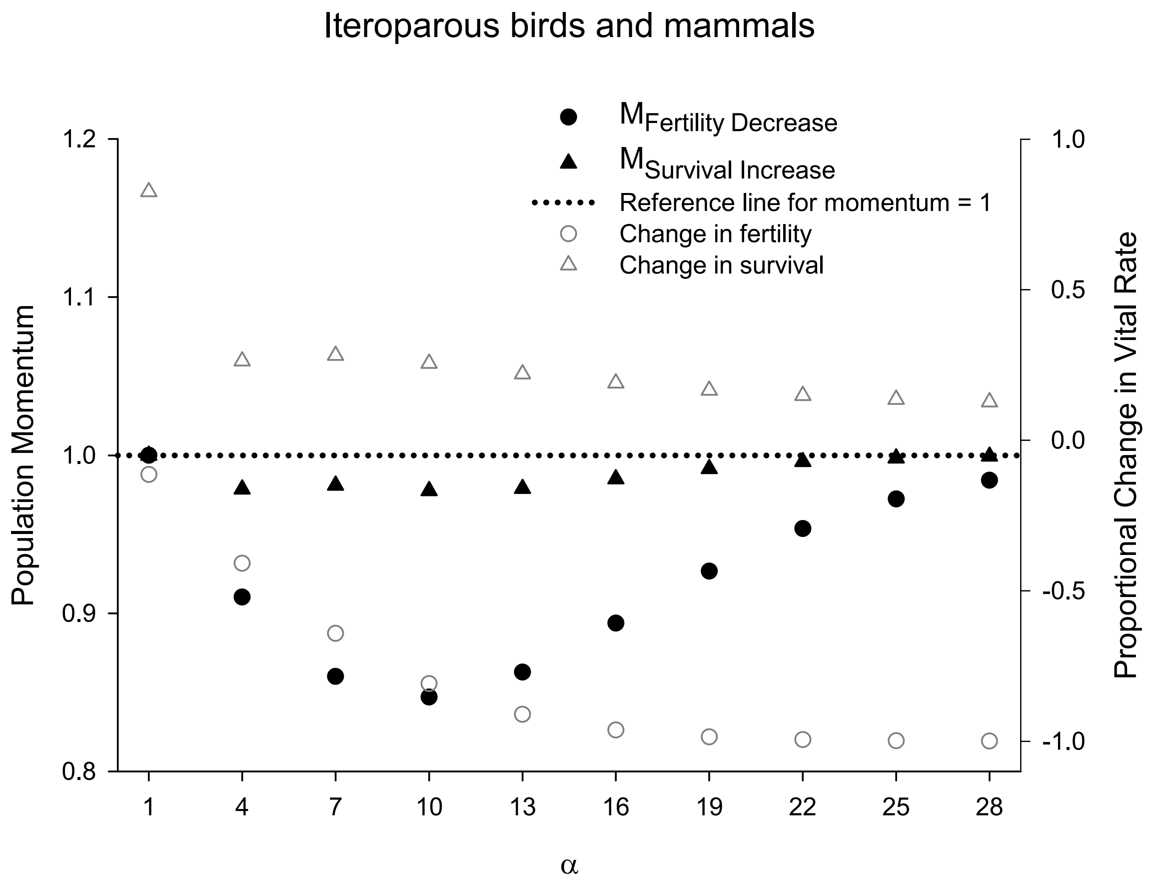

Iteroparous birds and mammals
$M_{Fertility\ Decrease}$
$M_{Survival\ Increase}$
Reference line for momentum = 1
Change in fertility
Change in survival
Population Momentum
Proportional Change in Vital Rate
1.2
1.1
1.0
0.9
0.8
1.0
0.5
0.0
-0.5
-1.0
1
4
7
10
13
16
19
22
25
28
α

Figure 2. The sensitivity of population momentum to infinitesimal unit changes in fertility (●) for increasing ($\lambda_1 = 1.1$) populations of bird and mammal life histories.

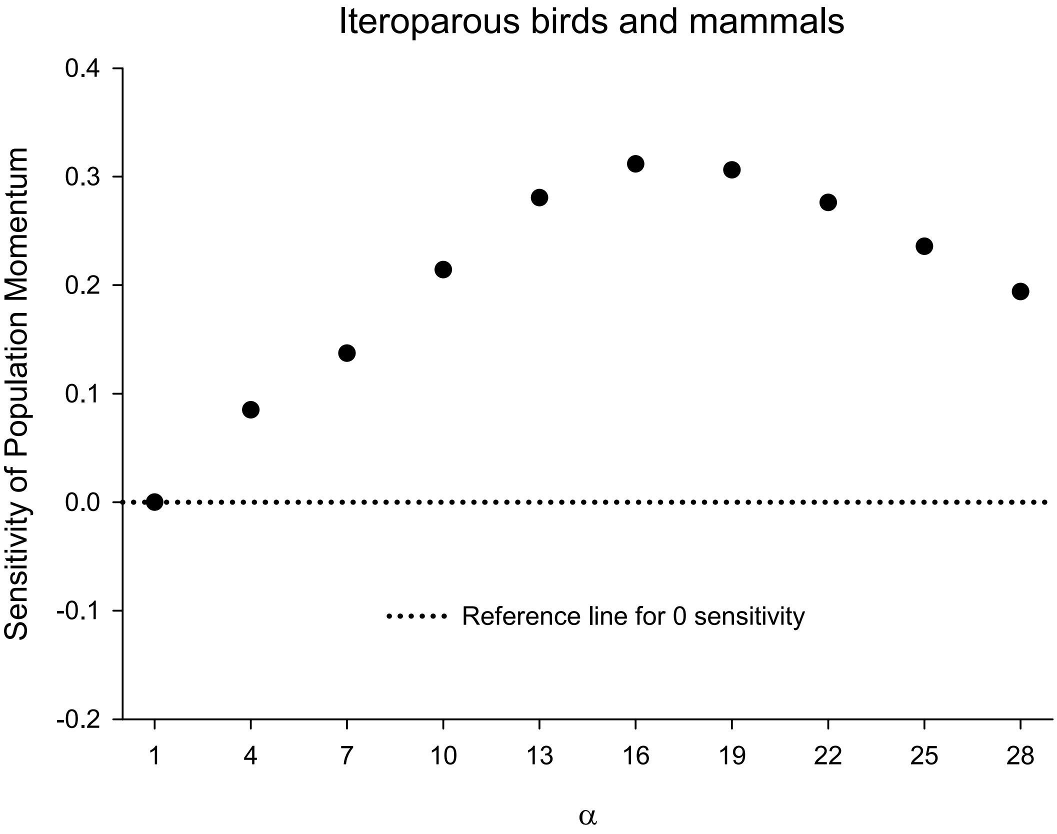

Iteroparous birds and mammals
Sensitivity of Population Momentum
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
1
4
7
10
13
16
19
22
25
28
α
Reference line for 0 sensitivity

Figure 3. The sensitivity of population momentum to infinitesimal unit changes in adult survival (▲) for decreasing ($\lambda_1 = 0.9$) populations of bird and mammal life histories.

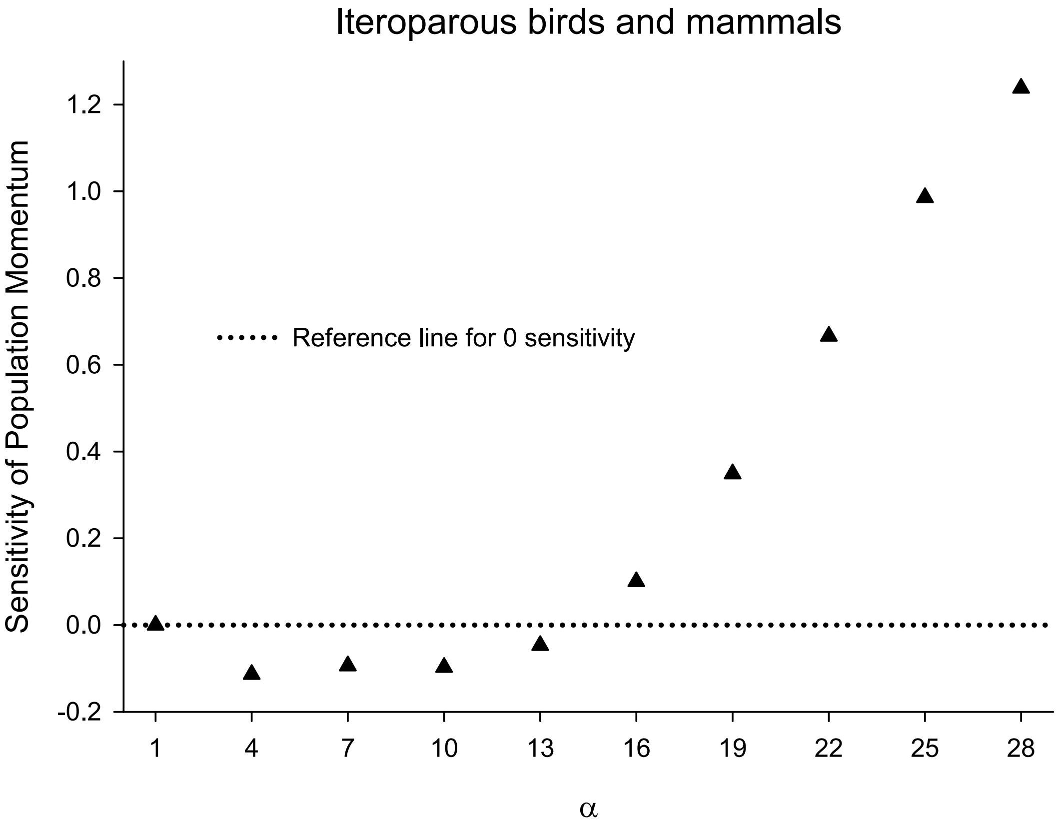
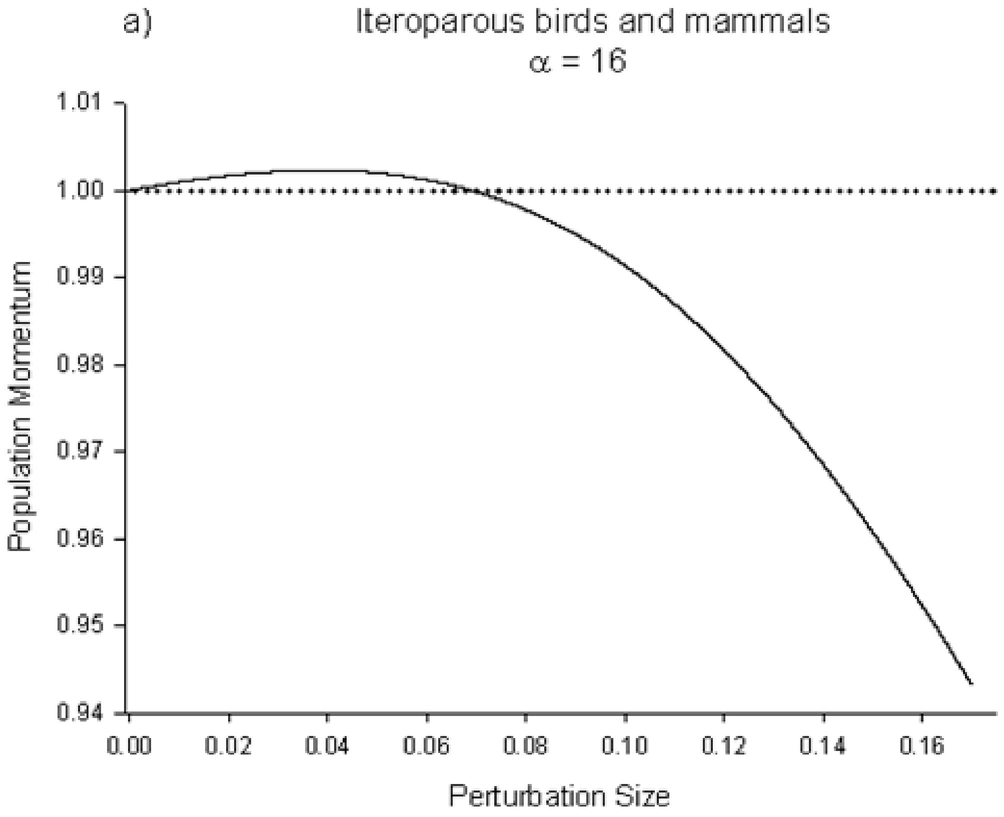

Iteroparous birds and mammals
Sensitivity of Population Momentum
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
Reference line for 0 sensitivity
1
4
7
10
13
16
19
22
25
28
α

Figure 4. The relationship between perturbation size of adult survival (x-axis) and population momentum (y-axis) for the α = 16 life history (a), and α = 28 life history (b).


a)
Iteroparous birds and mammals
$\alpha = 16$
1.01
1.00
0.99
0.98
0.97
0.96
0.95
0.94
Population Momentum
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
Perturbation Size

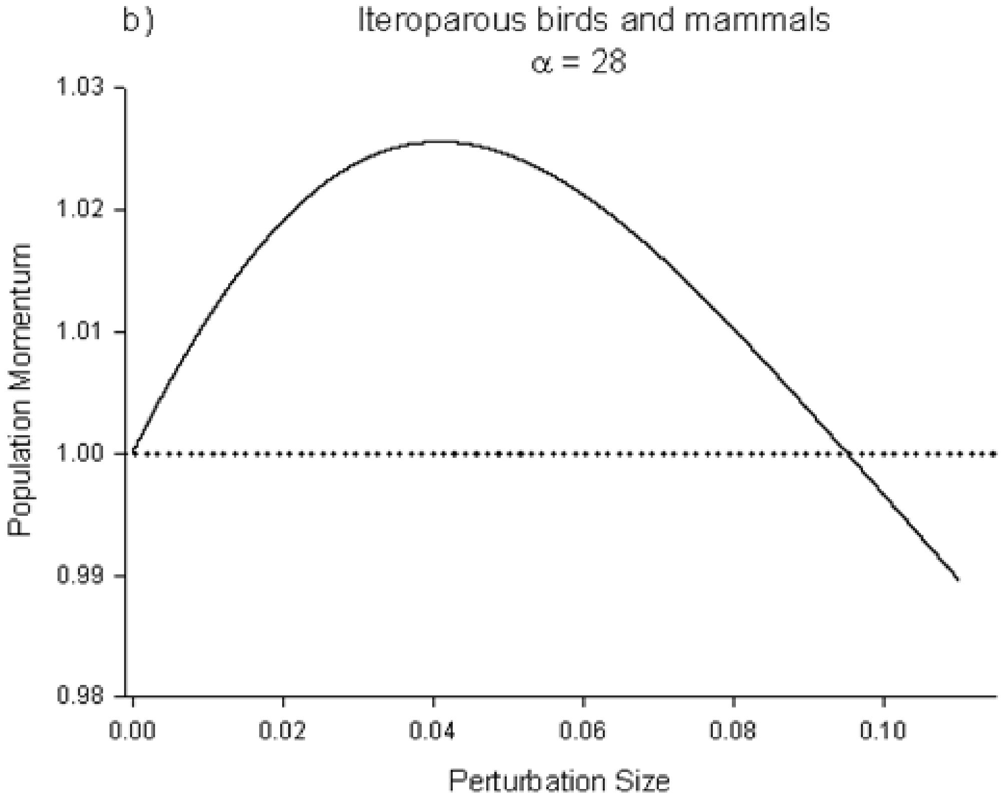

b)
Iteroparous birds and mammals
$\alpha = 28$
1.03
1.02
1.01
1.00
0.99
0.98
Population Momentum
0.00
0.02
0.04
0.06
0.08
0.10
Perturbation Size

Figure 5. The relationship between perturbation size of adult survival (x-axis) and the resulting asymptotic population structure (y-axis) for the α = 16 life history. Distribution of abundance in the oldest age classes is indicated by black and dark gray lines while distribution of abundance in the youngest age classes is indicated with light gray lines.

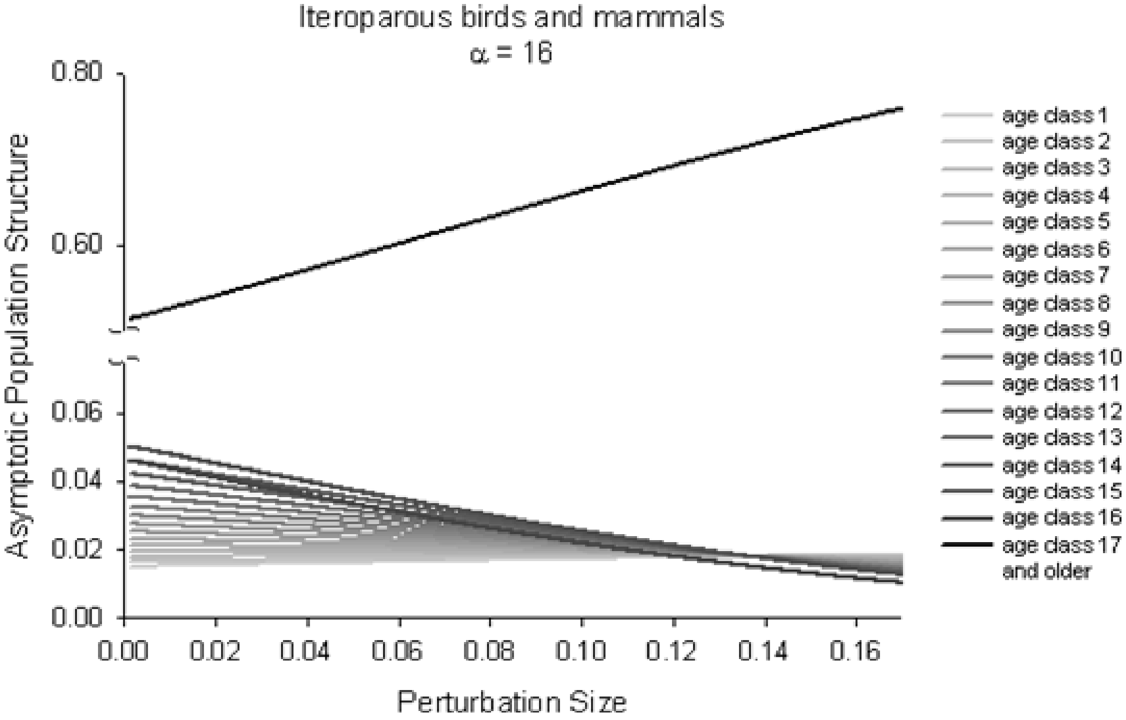
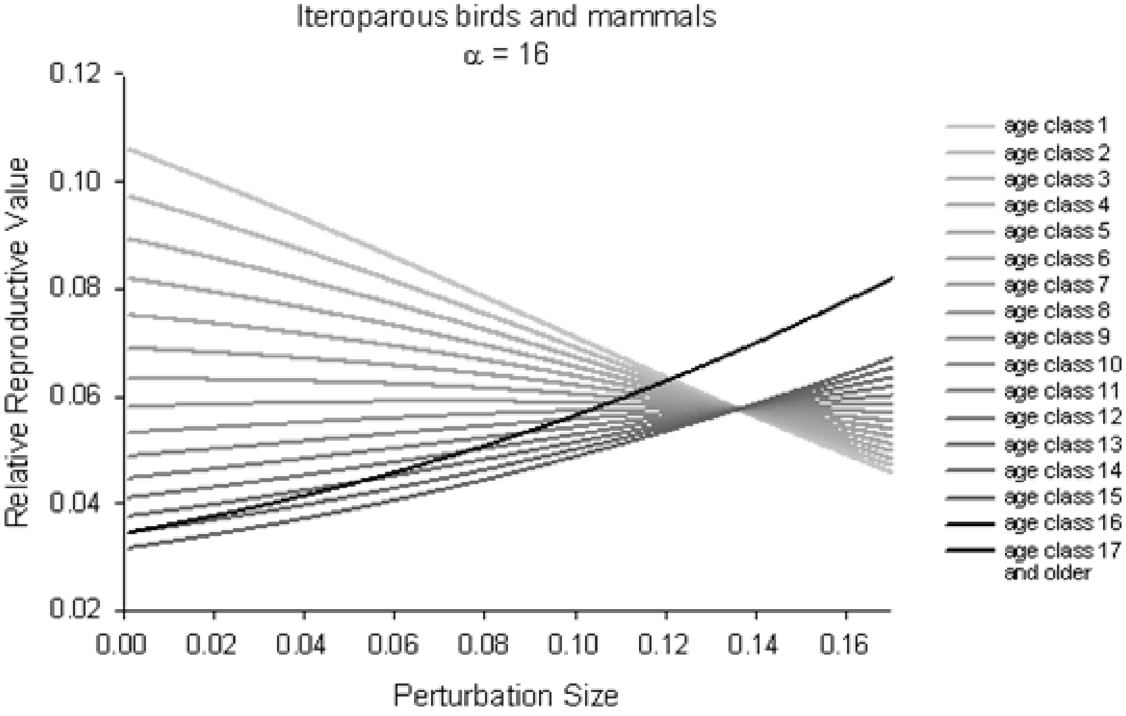

Iteroparous birds and mammals
$\alpha = 16$
Asymptotic Population Structure
0.80
0.60
0.06
0.04
0.02
0.00
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
Perturbation Size
age class 1
age class 2
age class 3
age class 4
age class 5
age class 6
age class 7
age class 8
age class 9
age class 10
age class 11
age class 12
age class 13
age class 14
age class 15
age class 16
age class 17 and older

Figure 6. The relationship between perturbation size of adult survival (x-axis) and the resulting relative reproductive values (i.e., reproductive value across age classes normalized to sum to 1; y-axis) for the $\alpha = 16$ life history. Relative reproductive value of the oldest age classes is indicated by black and dark gray lines while relative reproductive value of the youngest age classes is indicated with light gray lines.


Iteroparous birds and mammals
α = 16
Relative Reproductive Value
0.12
0.10
0.08
0.06
0.04
0.02
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
Perturbation Size
age class 1
age class 2
age class 3
age class 4
age class 5
age class 6
age class 7
age class 8
age class 9
age class 10
age class 11
age class 12
age class 13
age class 14
age class 15
age class 16
age class 17 and older

VI. GENERAL CONCLUSIONS

Asymptotic demographic analysis has a long history of use in population ecology; however, empirical studies suggest that conditions in nature might not justify this use in some cases (Bierzychudek 1999, Clutton-Brock and Coulson 2002, Coulson et al. 2004). For example, management actions can dramatically affect population structure (Crowder et al. 1994, Coulson et al. 2004). Therefore, the time has come for ecologists to pay stronger attention to population structure and its effect on population, community, and evolutionary dynamics (Hastings 2004).

Analysis of transient population dynamics and population momentum can reveal the possible effects of initial population structure (Fox and Gurevitch 2000, this study), colonization (Caswell and Werner 1978), life history (DeAngelis et al. 1980, this study), harvest, release of captive-reared animals into the wild, relocation of wild individuals, and environmental pulse perturbations (e.g., epidemics, catastrophic episodes) on population dynamics. If population structure is perturbed away from the stable state, asymptotic population analysis might not reveal the actual dynamics that could occur, and it could be misleading. For example, short-term transient growth can be highly erratic and set the population on a completely different long-term trajectory (i.e., population momentum). In effect, population momentum could push populations far past an environmental carrying capacity or even to extinction, depending on the direction of momentum. Relative to predictions from asymptotic dynamics, population momentum could shorten or lengthen the time it takes for a population to go extinct, recover from a perturbation, or explode to levels that become a nuisance (e.g., Merrill et al. 2003).

I suggest that resource managers place a stronger emphasis on estimation of population structure and reproductive value to examine the consequences of their actions on short-term population growth, and long-term population size. Such studies will help reduce uncertainty in decision-making and the likelihood of deleterious management in the future.

My dissertation is a theoretical starting point that could direct empirical studies and natural resource management. I largely used thought experiments in an attempt to elucidate patterns in transient population dynamics and population momentum across vertebrate life history strategies. By relaxing the classic assumption of stable population structure, I was able to explicitly explore the effect of unstable population structure on vertebrate population dynamics.

Many of my theoretical findings were novel. For example, I found that net reproductive value of the initial population could explain much of the intraspecific variation in transient population dynamics. Across species, long lifespan of slow reproducing species increases the chances for variability in somatic and reproductive investment across age classes (Charlesworth 1994). For this reason, transient dynamics of slow reproducing species were very responsive to changes in population structure, and slowly converged to the asymptotic stable state when compared to fast reproducing species.

Although seldom conveyed in the literature, transient dynamics dictate the behavior of long-term population momentum (Lande and Orzack 1988). Contrary to findings in human demography (Fischer and Heilig 1997), I found that large experimental changes in vital rates sometimes reversed the direction of population growth, resulting in large amounts of population momentum. In addition, population momentum varied with age at maturity in bird, mammal, turtle, lizard, snake, and bony fish life histories, but changed most abruptly with increasing maturity in bony fishes (Chapter 4, Figs 1 and 2) because of the underlying short-term transient dynamics. By using pyramid graphs to examine the distribution of abundance and reproductive values across (st)age classes of different life history strategies, it seemed that relative skew of each distribution determined how responsive populations in each vertebrate taxa were to the forces of population momentum.

However, it was not clear how changes in population structure, reproductive value, or both would affect population momentum. Much of my exploration into transient population dynamics and population momentum consisted of developing hypotheses about the effects of unstable population structure on transient population dynamics and momentum, and then testing these hypotheses with thought experiments. Yet, like empirical studies, thought experiments do not provide a general foundation for science to build upon. I needed to synthesize the myriad of ideas produced by the work in Chapters 2 – 4 with a general analytical tool that explicitly linked changes in vital rates to changes in population structure and reproductive value to change in population momentum. Therefore, in Chapter 5 I developed analytical formulas relating the sensitivity of population momentum to equal unit or proportional (elasticities) changes in vital rates or initial population structure. These formulas provide a consistent means for comparison of momentum across populations, life histories, initial conditions, or management practices Perhaps more importantly, the sensitivities presented in my dissertation provide a general theory relating transient population growth rate (Chapter 2) and population momentum (Chapter 5) to the underlying demographic parameters for scientists to build upon or reject outright.

My studies considered transient dynamics and population momentum following one-time perturbations to populations with density-independent population growth. The theoretical experiments were not meant to represent reality, but were developed to improve understanding of population dynamics in a way that is one step closer to reality than asymptotic analysis. Indeed, population density and species-interactions regulate many populations in nonlinear ways (Hixon et al. 2002). Under nonlinear population regulation, population dynamics can be very sensitive to initial conditions, and small changes in the initial conditions can even produce long-term chaos (May 1974, 1976, Cushing et al. 2002). Thus, transient dynamics and the physical force of momentum will be important to consider in nonlinear population models (Hastings 2004).

The frequent occurrence of long-lasting transient dynamics (e.g., thousands of years) in structured community models and spatially structured population models suggests that transients may be the norm over ecological times scales, rather than ‘short-term’ (Hastings and Higgins 1994, Hastings 2001, Chen and Cohen 2001). Not only should population ecologists pay more attention to transient dynamics and population momentum, but evolutionary biologists should as well. If transient dynamics can occur over long periods of time in nature, then natural selection could be operating on transient measures of fitness rather than asymptotic λ or r. Ultimately, if age-specific densities affect the fitness of a phenotype, then the physical forces of momentum could influence the permeation rate of specific newborn phenotypes into adulthood. Similarly, if nonlinear species interactions (i.e., competition, parasitism, mutualism, commensalism, amensalism, and predation) affect the fitness of a phenotype, momentum could influence the invasion rate and success of underlying mutant genotypes into wild types.

Studies of transient dynamics, chaos, and population momentum are slowly becoming more popular in ecology (e.g., Fox and Gurevitch 2000, Hastings 2004). Perhaps future studies on these topics will reveal that many components of variation in demographic parameters that we currently believe to be random noise are actually caused by the deterministic forces of transient growth, physical momentum, and chaos.

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