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Transient population dynamics: Relations to life history and initial population state

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Abstract

Most environments are variable and disturbances (e.g., hurricanes, fires) 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, we calculated the short-term (i.e., transient) population growth rate and its sensitivity to changes in the life-cycle parameters for three bird and three mammal species with widely varying life histories. Further, we 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 of long-lived, slow reproducing species were more variable and more different than asymptotic dynamics than they were for 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.
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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 popula-

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tions (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., the age, stage, or size distribution) remains stable through time (i.e., the asymptotic stable state), and that the population grows 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's state, causing unstable states. When a population's state is not stable, it will change until the stable state is reached. Meanwhile, the population dynamics are 'transient' because they change according to the changing population state until the asymptotic stable state is achieved. Empirical evidence suggests that stable population states 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 the 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 than 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 making management prescriptions in the immediate future.

We examine the sensitivity of 'transient population growth rate' to changes in vital rates for six bird and mammal species across all possible population states. Our primary objective is to elucidate the biological correlates of intraspecific variation in transient dynamics across the possible population states. Our secondary objective is 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. We hypothesize that these properties will cause the transient dynamics in long-lived species to be more variable and different than asymptotic dynamics 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, we chose three bird and three mammal species that have been extensively studied and were known to have widely varying life histories across the slow–fast continuum. 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).

We attained age-specific vital-rate data from published long-term studies of blue tit *Parus caeruleus* (Dhondt, 1989a,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) (Appendix 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). We used age-specific vital

rates where the authors report 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, we used Meslow and Keith's (1968) original data, and implemented

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

hypothetical age structure by increasing fertility by 5% for age 2 and 10% for ages 3 and older (Appendix A).

For each species, we 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 is the average age of first breeding and $(\alpha + n)$ is 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), we multiplied each matrix by a constant K (Appendix A) so that the dominant eigenvalue of each matrix would be 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 Appendix B for longer time steps). We sought a solution to the sensitivity of

the transient GR to infinitely small changes in a vital-rate (TS_{ij}), which can be defined as,

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

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

and derivation of the solution can be found in Appendix B, where we further provide explanation of notation and the similarities and differences of our derivation to Yearsley (2004).

2.3. Simulations and projection analysis

For each life-cycle matrix, we 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, we projected each life-cycle matrix five-time steps (years) with each state vector using Eq. (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, we used Keyfitz's Δ (1968),

$$
\Delta(x, w_1) = \frac{1}{2} \sum_k |x_k - w_{1,k}| \tag{4}
$$

where x_k and $w_{1,k}$ are 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, we assigned (+) values to all Δ's when vectors had proportionately more breeding adults than the stable state vector and (−) values to all Δ's 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. We used the signed Keyfitz Δ as a predictor variable in statistical analyses, and linearly mapped Δ values from the region $[-1, 1]$ to the region $[0, 2]$ in order to examine models using the exponential distribution, which ranges from 0 to infinity. In addition, we calculated the initial net reproductive value (c_1) of a population for each population state vector as,

$$c_1 = \mathbf{v}'_1 \times \mathbf{n}_0 \qquad (5)$$

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, we 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 percentage change in population size over 5 years. Additionally, we 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 Eq. (B.7). We 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, we 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

We 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, we 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).

We 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 our data for each model in our candidate list (see above). We 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 magnitude of difference between transient and asymptotic population dynamics for each of the seven life histories, we first measured the difference between each transient dynamic (e.g., GR2, TFS2, etc.) and the respective asymptotic dynamic for all simulated projections. We then took 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. We 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). We used F-tests to examine the support, or lack thereof, for the a priori hypothesis that the mean and variance of each 'difference' estimate would increase with the generation length of the life history (Neter et al., 1996).

3. Results

For each intraspecific analysis, we examined nine 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 nine 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, we 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), we 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, we detected strong linear or nonlinear relationships between c_1 and the variation in each of the transient sensitivities. We found a positive relationship between c_1 and the 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), we found a negative relationship between c_1 and the transient sub-adult survival sensitivities for three of the four species. However, we detected interesting curvilinear relationships between c_1 and all of the vital-rate sensitivities for red deer, which may be related to the delayed maturity and senescence present in their life-cycle (Figs. 3 and 4). Of further significance, the rankings of the transient sensitivities shifted across initial conditions in five of the six species, and
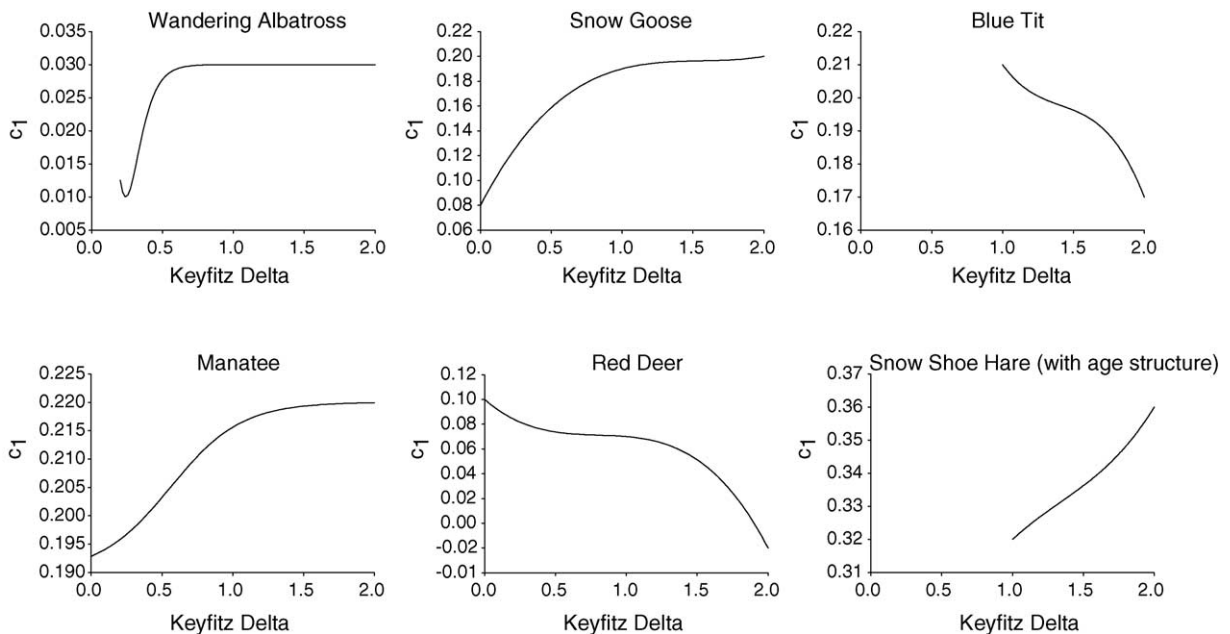

Fig. 1. The top performing models of c_1 as a function of the signed Keyfitz Δ (mapped to the region [0, 2]) for wandering albatross ($R^2 = 0.75$; the initial dip in the fitted line is an artifact of the model fit to sparse data at the lower tail of Keyfitz Δ values; the raw data does not indicate an 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, $R^2 = 0.87$). The 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 omitted to permit viewing of the predicted relationship.
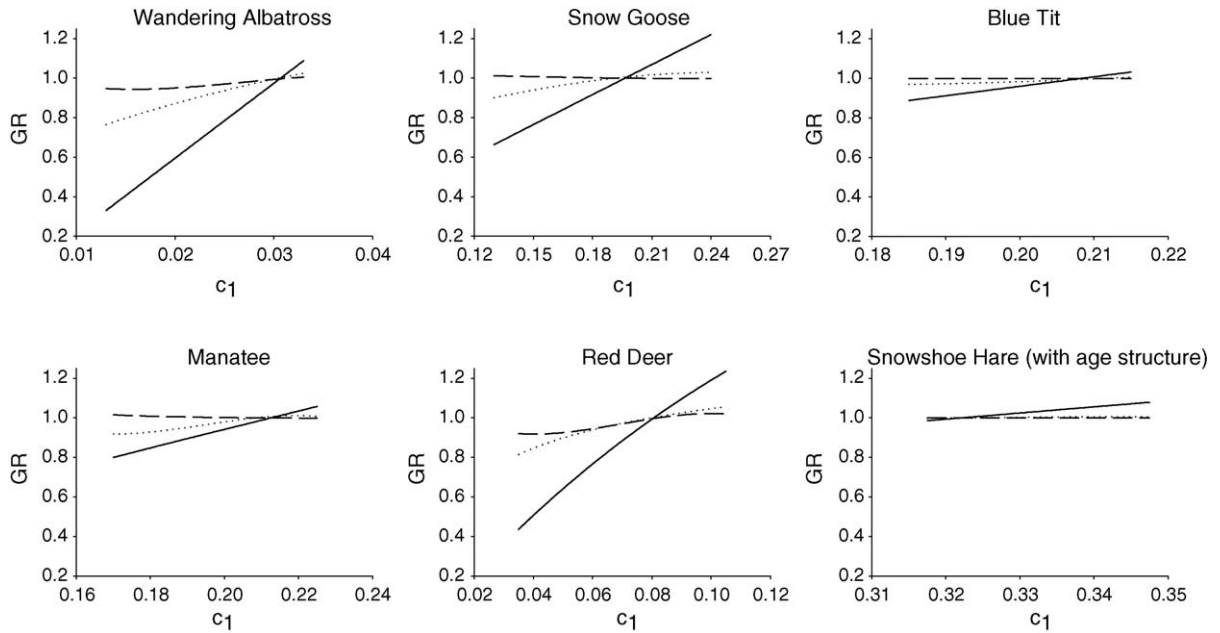
Fig. 2. The top performing models of the transient growth rates at time steps 1-to-2 ($\cdots$ GR2), 4-to-5 (- - -GR5), and 0-to-5 (—5YRGR) as functions of c_1 for wandering albatross (R^2 values listed in order for GR2, GR5, and 5YRGR; $R^2 = 0.90, 0.86, 0.92$) manatee ($R^2 = 0.87, 0.91, 1.00$), snow 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 omitted to permit viewing of the predicted relationship. For comparison, $\lambda_1 = 1$ in all cases.

the rank-intersection point shifted with the time step (Figs. 3 and 4). Moreover, the slope of the relationships between c_1 and the transient sensitivities was much smaller for the fast species (Figs. 3 and 4).

Across species, the mean and variance of the 'difference' measures between transient and asymptotic dynamics (see Section 2) increased and were highly correlated with generation length ($P < 0.10$ except in three cases; Fig. 5). At the extremes (global max and min), the early transient growth rates (GR2 and GR5) were as much as 19, 9, 9, 18, 3, and 1% different than the asymptotic growth rate for wandering albatross, manatee, snow goose, red deer, blue tit, and snowshoe hare (with age-structured vital rates), respectively. More strikingly, the effects of initial conditions were strongest over the culmination of the 5 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, the extreme transient sensitivities were as much as 248, 335, 155, 249, 5, and 4% different than asymptotic estimates for the same list of species mentioned above. While the transient estimates are expected to approach

the asymptotic estimates over time, the differences at the extreme values were alarmingly large after five 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, our results indicate 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, our 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. We discuss several biological underpinnings of transient dynamics so that more biologists can comprehend and use transient dynamics in future population ecology and management studies.
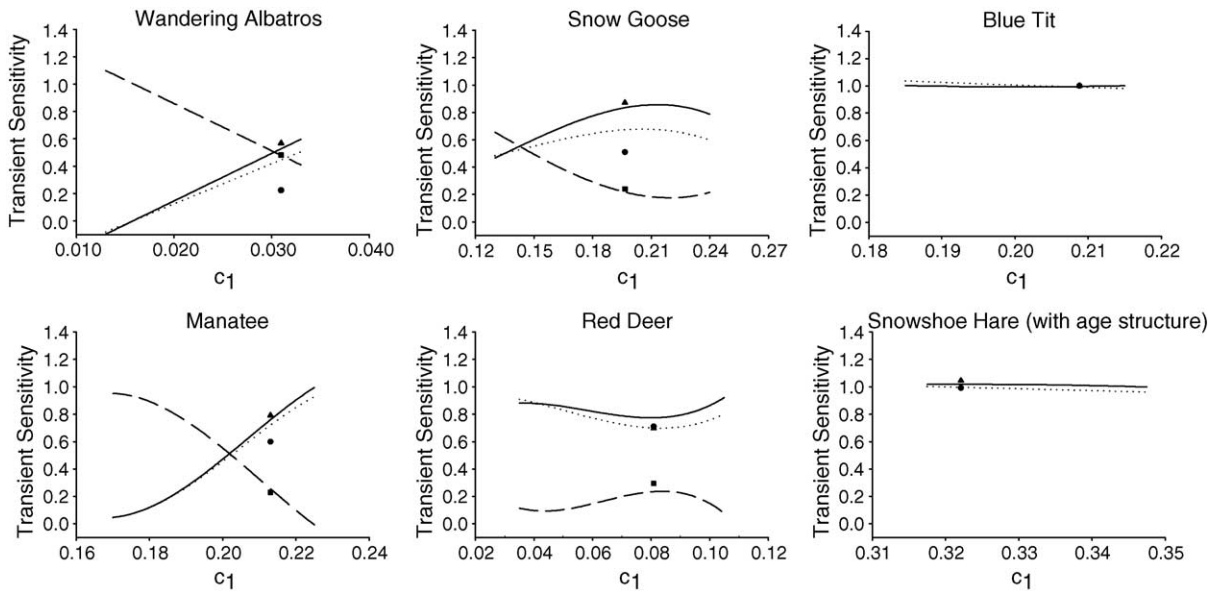
Fig. 3. The top performing models of the transient sensitivities [(· · ·) fertility, (- - -) sub-adult survival, and (—) adult survival] at time step 1-to-2 as functions of c_1 for wandering albatross (R^2 values listed in order for fertility, sub-adult survival, and adult survival; $R^2 = 0.75$, 0.73, 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 omitted to permit viewing of the predicted relationship. For comparison, (●): asymptotic fertility sensitivity; (■): asymptotic sub-adult survival sensitivity; (▲) asymptotic adult survival sensitivity.

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 our study, we found that transient population growth rates and sensitivities were highly dependent on initial conditions. The initial net reproductive value 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 possible 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). This 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.

The initial net reproductive value (c_1) is an omnibus measure that can be used to predict the transient dynamics (e.g., GR, TS_{ij}) across initial state
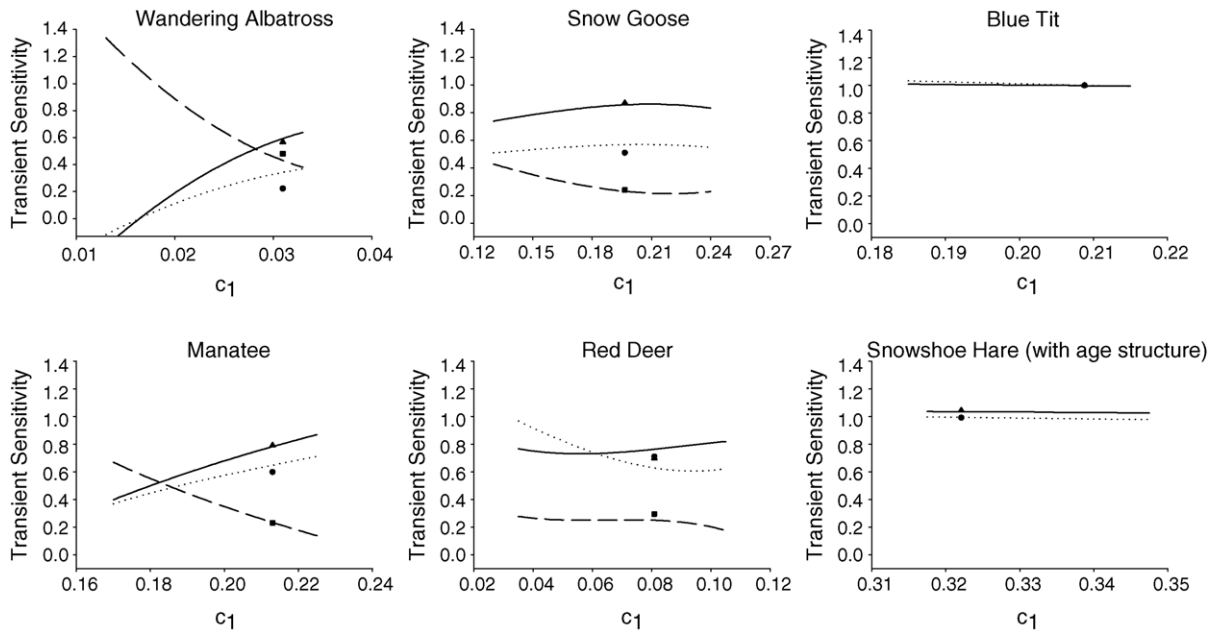
Fig. 4. The top performing models of the transient sensitivities [($\cdots$) fertility, (- - -) sub-adult survival, and (—) adult survival] at time step 4-to-5 as functions of c_1 for wandering albatross (R^2 values listed in order for fertility, sub-adult survival, and adult survival; $R^2 = 0.88, 0.86, 0.86$), 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 omitted to permit viewing of the predicted relationship. For comparison, (●): asymptotic fertility sensitivity, (■): asymptotic sub-adult survival sensitivity, (▲) asymptotic adult survival sensitivity.

conditions, through time, and to examine shifts in the 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 our 18 interspecific comparisons, we found that either the mean or variance of the 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. 2–4).

Population dynamics in fast species were resilient to departures from the stable state; however, slow species experienced early transient dynamics that were variable across the possible 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 the age classes. These life history characteristics lead to high disparity in reproductive value across age classes (see rv:rv, Appendix A). Long generation length will increase the time required for transient dynamics to change (Tuljapurkar, 1985), and disparate reproductive values could lead to large changes in net reproductive following changes in population state. Collectively, we believe these factors make the dynamics of slow species more responsive to changes in population state.
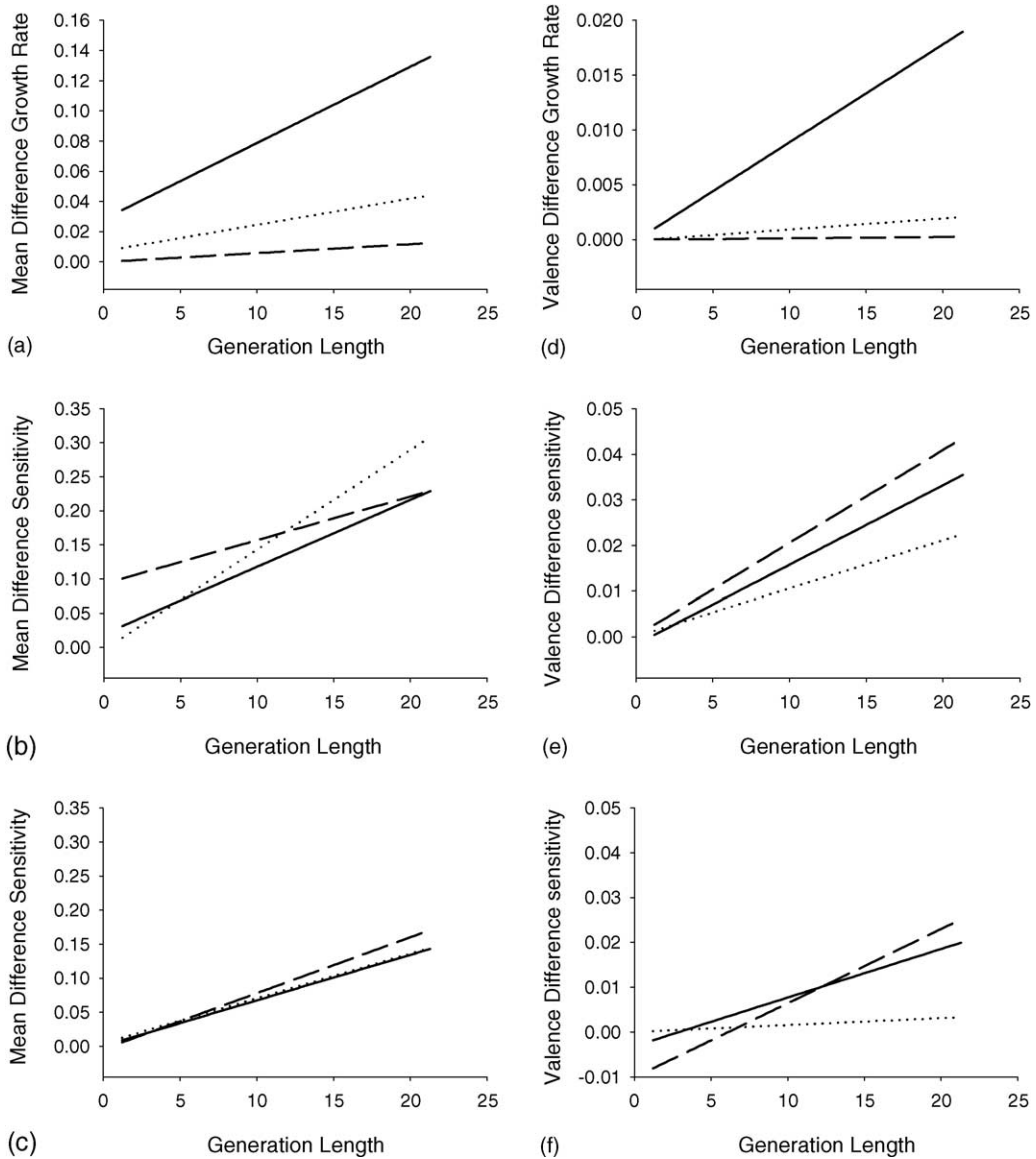
Fig. 5. The interspecific relationship between generation length of the life history and estimated differences between transient and asymptotic population dynamics (across all simulations for each species). (a) Correlations between generation length and the species-specific means of, GR2-λ_1 ($\cdots$) ($R^2 = 0.80$, $n = 7$, $P = 0.006$), 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 the species-specific means of, TFS2-FS ($\cdots$) ($R^2 = 0.95$, $n = 7$, $P < 0.001$), 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 the species-specific means of, TFS5-FS ($\cdots$) ($R^2 = 0.86$, $n = 7$, $P = 0.003$), 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 the 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 the 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 the 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 omitted to permit viewing of the predicted relationships.

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, our 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 our approach, we 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. We have shown that this can drastically alter the 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, we suggest that risk assessments, such as population viability analyses (Gilpin and Soulé, 1986) and population recovery analyses, pay closer attention to transient dynamics and the effects of population state on extinction or recovery times and probabilities.

4.4. Caveats

The degree to which asymptotic dynamics are a poor proxy to actual dynamics depends on the population state, time, and life history. Like many transient analyses, our 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, we 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 the net reproductive value and the 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 we saw little reason to use matrices that were larger than necessary to incorporate the published age-specific differences in vital rates. Furthermore, we purposefully took 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, the 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.

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, 1989a, b), and snowshoe hare (Meslow and Keith, 1968). Also, standardizing constants (K), which were multiplied to the original life-cycle matrices parameterized with vital rates attained from the literature, 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).

	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

	Wandering albatross			Manatee			Snow goose			Red deer			Blue tit			Snowshoe hare[a]			Snowshoe hare[b]		
Age[c]	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
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																		

(*Continued*)

Age[c]	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
19		0.22	0.94																		
20		0.20	0.94																		
⋮		0.20	0.94																		
28		0.20	0.94																		
29		0.20	0.90																		

[†] All numerical values in the table are rounded to the nearest 10^{-2} decimal place. In the projection analysis we 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.

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

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

  [c] Pseudo age class.

Appendix B

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

$$\mathbf{n}_t = \mathbf{A}^t \mathbf{n}_0 \qquad (B.1)$$

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 $\mathbf{A}$ is an $n \times n$ (deterministic) matrix whose entries are denoted by a_{ij} (we denote matrices and vectors in bold type with upper-case and lower-case notation, respectively). Alternatively, Eq. (B.1) can be decomposed and expressed with the eigenvalues and eigenvectors of the $\mathbf{A}$ matrix,

$$\mathbf{n}_t = \sum_i c_i \lambda_i^t \mathbf{w}_i \qquad (B.2)$$

where the $\mathbf{w}_i$'s are the right eigenvectors of $\mathbf{A}$, 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 $\mathbf{A}$ (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, Eq. (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 Eq. (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 the sensitivity of the average transient growth rate for specific age or stage classes, or for the entire population. If one does not need detailed information about class-specific dynamics, we 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 Eq. (B.1) rather than Eq. (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 Eq. (2). Because $\mathbf{n}_t$ in Eq. (2) is derived from the $\mathbf{A}$ matrix and the initial state vector, our definition of growth rate is quantitatively equivalent to Yearsley's (2004) calculation that uses the weighted average of the eigenvalue spectrum belonging to the $\mathbf{A}$ matrix (the individual state vector components at time $t-1$ in our Eq. (2) operate as the weights). For comparative purposes, population growth rates for the k-th element of the population state vector can simply be calculated by deleting the summation symbols in our Eq. (2). Furthermore, to estimate the population growth rate over any time step m, the denominator of Eq. (2) can be changed to $\mathbf{n}_{t-m, k}$.

Nevertheless, our goal was to find a simple analytical solution to the sensitivity of the transient GR for the entire population to infinitesimally small changes in a vital-rate (TS_{ij}, Eq. (3)). To do this we begin with Eq. (B.1) to project $\mathbf{n}_t$. We note that $\mathbf{A}^0$ is defined as the identity matrix. We denoted $\mathbf{e}$ as the vector whose

components are all equal to 1 and Δ_{ij} as the $n \times n$ matrix whose entry in the i-th row and j-th column is 1 and 0 everywhere else. We make special note that for $t = 1, 2, \ldots$

$$\frac{\partial}{\partial a_{ij}} \mathbf{A}^t = \sum_{l=0}^{t-1} \mathbf{A}^l \Delta_{ij} \mathbf{A}^{t-l-1} \tag{B.3}$$

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

$$\frac{\partial \left(\sum_k \mathbf{n}_{t,k} / \sum_k \mathbf{n}_{t-1,k} \right)}{\partial a_{ij}} = \frac{\partial}{\partial a_{ij}} \frac{\mathbf{e}' \mathbf{A} \mathbf{n}_0}{\mathbf{e}' \mathbf{n}_0} = \frac{\mathbf{e}' \Delta_{ij} \mathbf{n}_0}{\mathbf{e}' \mathbf{n}_0} \tag{B.4}$$

and for $t = 2, 3, \ldots$

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

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

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

Therefore, given Eqs. (B.5) and (B.6),

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

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