

Analytical expressions for the eigenvalues, demographic quantities, and extinction criteria arising from a three-stage wildlife population matrix

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Funding information

University of Idaho Bioinformatics and Computational Biology Fellowship; College of Graduate Studies; College of Science and Bioinformatics; Computational Biology Fellowship

Abstract

We used the symbolic solution for the roots of a cubic polynomial to derive expressions for the eigenvalues of a three-stage population projection matrix. As well, we obtained expressions for eigenvectors, moduli, damping ratios, sensitivities, and elasticities. The equations reveal the existence of “superparameters;” natural groupings of vital rates that drive population dynamics. We show that growth rates can be calculated using (at most) three superparameters in place of as many as nine original vital rates, potentially simplifying data collection. Necessary and sufficient conditions for extinction can be summarized equivalently by three superparameter inequalities. For a common life history (Noon & Biles, 1990, *J Wildl Manag*, 54, 18–27) four vital rate parameters are reduced to two superparameters. The results are applicable to population viability and recovery analysis and harvest planning.

Two recommendations for resource managers:

- Superparameters can be estimated to determine population growth rates.
- Superparameters can be used to conduct rapid assessments of extinction risk.

KEYWORDS

dominant eigenvalue, finite rate of population growth, Lefkovich matrix, Leslie matrix, parameter reduction, population viability analysis, stage-structured population, subdominant eigenvalue



1 | INTRODUCTION

The population matrix model is a foundational mathematical concept in wildlife ecology (Caswell, 2001). The matrix model is used to project stage abundances of age or stage-structured populations in discrete time (Groenendael, Kroon, & Caswell, 1988). The model plays a key role in demography, evolutionary theory, life history theory, population dynamics, and conservation biology (Morris & Doak, 2002). In addition, the model has become an indispensable tool in wildlife management (Dinsmore & Johnson, 2012). Inputs for the matrix model are “vital rates,” including age or stage class fertilities and stage transition or survival probabilities (see Caswell, 2001; van Groenendael et al., 1988). The demographic quantities arising from the vital rates include the eigenvalues and eigenvectors of the matrix, from which one finds the asymptotic population growth rate, stable stage distribution, net reproductive values, matrix element sensitivities and elasticities, and the magnitudes, known as damping ratios, of transient population oscillations (Caswell, 2001). The model has been used to understand asymptotic (stable) population trends (e.g., Caswell, 2001), transient (oscillatory) population trends (e.g., Ezard et al., 2010), and stochastic population trends (e.g., Tuljapurkar, 1989).

Our broad focus here is on the parameterization, assumptions, and use of population matrix models. Our particular focus is on obtaining and studying symbolic formulas for how eigenvalues and eigenvectors depend on vital rates. The relative lack of such formulas has hindered our understanding of how the vital rates contribute to and combine to produce a population’s dynamical behavior. Obtaining eigenvalues and eigenvectors from a given matrix is in general a numerically intensive task. Algorithms for calculating eigenvalues and eigenvectors are readily implemented on modern computers, and software packages for such calculations have been widely available for some decades. Numerical experiments on how the changing of vital rates affect growth rates are easy to perform. However, the vast quantity of possible numerical experiments suggests that important vital rate interactions might be easy to miss. Stage-structured models have always held out the prospect of helping ecologists disentangle the varied ways births and deaths in subpopulations contribute to population growth, and symbolic relationships can aid in that study.

Sensitivities and elasticities (per-unit sensitivities) quantify the changes in the dominant eigenvalue in response to changes in individual vital rates (Caswell, 2001). A sensitivity or elasticity is defined in terms of the partial derivative of the dominant eigenvalue with respect to an individual vital rate. Sensitivities and elasticities can help managers identify which vital rates are influential in growth and require more precise estimation (Morris & Doak, 2002). A problem is that numerical value of a sensitivity conceals its functional dependence on the values of the other vital rates. Rates combine and interact nonlinearly toward producing population growth, and a given sensitivity can change substantially in response to the change in another vital rate (e.g., de Kroon, van Groenendael, & Ehrlén, 2000; Shyu & Caswell, 2016). The usual formulas for sensitivities and elasticities involve eigenvectors (Caswell, 2001), which in turn must be calculated numerically for populations with more than three stages. To the contrary, symbolic formulas in terms of the vital rates themselves might help understanding of potential interactions among the rates in producing population growth. Such understanding is crucial toward avoiding unforeseen consequences of management actions, in that such actions often involve altering vital rates.

The subdominant eigenvalues have received far less attention in theoretical and applied ecology than the dominant eigenvalue. The dominant eigenvalue, as the finite population growth rate and the ultimate indicator of a population’s fate, is a focus of endangered species



management policy (McGowan, Allan, Servoss, Hedwall, & Wooldridge, 2017). As well, the dominant eigenvalue is accompanied by an entourage of important quantities in the form of the stable stage proportions (right eigenvector) and the net reproductive values (left eigenvector; Caswell, 2001). The subdominant eigenvalues, by contrast, are frequently complex valued and accompanied by eigenvectors with negative or complex elements, rendering ecological interpretation difficult. Although all the complex components of the trajectories of stage abundances (as in when the projection matrix is written in terms of its eigenvalues and eigenvectors) cancel each other out (stage abundances remain positive and real), the influence of the subdominant eigenvalues appears in the form of stage oscillations (Fox & Gurevitch, 2000). The subdominant eigenvalue with the largest magnitude appears in the denominator of the damping ratio (e.g., Caswell, 2001), making this eigenvalue central for predicting the nature and severity of oscillations that occur during nonasymptotic population dynamics. The oscillations damp out provided the projection matrix is not pathological (i.e., produces sustained oscillations), but the initial amplitudes of the oscillations can be critically large, perhaps large enough to send the population into such low abundance levels that extinction vortex forces at the genetic and population levels take hold. Enhanced understanding of the role played by subdominant eigenvalues in stage-structured population dynamics will help ecological management (Fox & Gurevitch, 2000; Yearsley, 2004).

In general, a species with k life stages (where $k = 2, 3, \dots$) is modeled with a $k \times k$ population matrix containing up to $k \times k$ vital rates. The population matrix has a characteristic equation in the form of a k -degree polynomial (Cull & Vogt, 1973). The k eigenvalues of the matrix are roots of the characteristic polynomial (Beyer, 1978; Cull & Vogt, 1973), with one of the eigenvalues being the finite rate of population growth. Furthermore, the characteristic polynomial equation has up to k coefficients that are functions of the underlying vital rates. We suggest that these k “superparameters” represent combined demographic meta-events in the organism’s life history. The meta-events encapsulated in the superparameters are potentially interpretable and might be estimated directly with redesigned field studies, studies possibly involving a reduced number of stages. Because the empirical studies necessary for estimating vital rates are costly and, in some cases, risky to the animals, any such method of reducing the empirical requirements for estimating the finite growth rate might be a valuable addition to the tools of wildlife management.

Moreover, the demographic quantities that are calculated from eigenvalues, in particular sensitivities, elasticities, and damping ratio, also depend on the superparameters, opening the prospect that the superparameters might provide insights into how the demographic quantities vary with life history changes. Heppell, Caswell, and Crowder (2000) derived simplified estimates of elasticities in a general life table using eigenvector expressions, resulting in a condensation of the parameters necessary to obtain these demographic quantities. Representation in terms of superparameters offers potential for further condensation.

In the absence of stochastic forces, a population’s fate—recovery or extinction—is foretold by its finite rate of increase. The dominant eigenvalue is therefore a key focus, if not the determining factor, for studies and management policies regarding the viability of populations (Morris & Doak, 2002). Although a population with a finite growth rate greater than one might not persist long in a stochastic world and might even have a large chance of extinction (Dennis, Munholland, & Scott, 1991; Lewontin & Cohen, 1969), a finite growth rate less than one spell nearly certain doom. Because of the complexity of the relationships between vital rates and the finite rate of increase, the only way to determine whether the finite rate is less than one has



been to calculate it numerically from the projection matrix. It would be of interest to have criteria for extinction represented symbolically in terms of the vital rates.

Here, we examine some relationships between the vital rates and demographic quantities for a three-stage population matrix model. The projection matrix contains nine or less vital rates. We exploit the symbolic solution for the roots of a cubic polynomial to derive expressions for the dominant and subdominant eigenvalues of the three-stage projection matrix. The symbolic eigenvalue solutions further give rise to analytical expressions for matrix eigenvectors, complex moduli, damping ratios, sensitivities, and elasticities. In the characteristic equation, the nine demographic parameters (fertilities and stage transition probabilities) collapse into no more than three superparameters, giving rise to an expression for the growth rate containing the inputs of three superparameters only.

As well, we obtain necessary and sufficient criteria for extinction in the form of three inequalities that demonstrate when the dominant eigenvalue is less than 1. The three inequalities are represented in terms of the three superparameters. The inequalities reveal 511 possible structures of vital rate relationships which in turn are categorized into 40 structures involving superparameters. We provide a complete catalogue of superparameters and extinction criteria (Supporting Information S.1) for the various vital rate structures for the three-stage matrix model.

As an example, we study a particular three-stage life history with four vital rates that has been featured in wildlife studies, in which only members of the third stage (“adults”) contribute to the juvenile stage, and only adults can remain in their stage after one time unit. For the corresponding matrix model, the information in the vital rates condenses into two superparameters representing adult survival and adult recruitment. The condensation allows graphical portrayal of how interactions between the two superparameters can lead to high sensitivity (or in statistical terms, low estimability) of the finite rate of increase and other demographic quantities. Results are illustrated using data from the Northern Spotted Owl (*Strix occidentalis caurina*) study by Noon and Biles (1990). For this life history, the three criteria for extinction collapse into one simple inequality involving the two superparameters.

Analytical solution is, of course, possible for a four-stage matrix model, as the general quartic polynomial has a resolvent cubic equation (Beyer, 1978). We defer until later (and even to other investigators) an evaluation of whether the resulting enormous formulas can lend insights into population dynamics and resource management. Matrix models with five or more stages, in general, are not solvable, although special cases might exist that can be solved. For the present, the three-stage model practically beckons for such analytical attention, due to its widespread applicability in wildlife management.

2 | MATERIALS AND METHODS

The life history of a species determines the structure of its corresponding population matrix model. A common life history in wildlife populations contains three stages: a juvenile (newborn) stage ($j = 1$), a subadult stage ($j = 2$), and an adult stage ($j = 3$; e.g., Lande, 1988; Noon & Biles, 1990). We use the terms “juvenile,” “subadult,” and “adult” as they are in wide use but remark that the first two stages could represent reproductive stages by age but having different reproductive or survival rates than the third (“adult”) stage. The three-stage life history appearing in Figure 1 corresponds to the following population projection matrix \mathbf{L} :

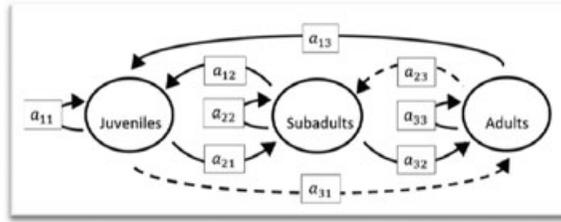


FIGURE 1 Three-stage population matrix model corresponding to Equation (1). The arrows represent the fertilities or transition probabilities within and across the three conventionally defined life stages; juveniles ($j = 1$), subadults ($j = 2$), and adults ($j = 3$). The vital rates a_{1j} represent the fertility at stage j , or the magnitude of reproduction that stage j contributes to the juvenile stage per time unit ($0 \leq a_{1j} < \infty$). The a_{ij} vital rate represents the probability ($0 \leq a_{ij} \leq 1$) that an individual will survive the discrete time unit and remain at stage j , or that they will neither die nor advance to the next stage. The $a_{(j+1),j}$ vital rates represent the probability ($0 \leq a_{(j+1),j} \leq 1$) that any individual will survive the discrete time unit and transition from stage j to stage $j + 1$. Less common (but plausible) vital rate a_{23} represents the fertility of adults replenishing the subadult cohort ($0 \leq a_{23} < \infty$), whereas vital rate a_{31} represents the probability that any given juvenile will survive and transition in one time unit to an adult ($0 \leq a_{31} \leq 1$)

$$\mathbf{L} = \begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix}. \tag{1}$$

Here, a_{ij} represents the vital rate in the i th row and j th column of \mathbf{L} . Each vital rate a_{1j} in the first row represents the fertility at stage j ($j = 1$ represents juvenile, $j = 2$ represents subadult, and $j = 3$ represents adult), or the average contribution of an individual in stage j into the juvenile stage at each time unit. The a_{ij} vital rate represents the probability that an individual will survive one time unit and remain at stage j , or the probability that an individual in stage j will neither die nor advance in each time unit. Notice that a_{11} can be interpreted as either fertility of the juvenile stage (with a positive real value), or the probability that a juvenile survives and remains a juvenile (with a value constrained between zero and one). The off-diagonal elements in the second and third rows represent the probability that any individual will survive the discrete time unit and transition into another stage (Figure 1).

Depending on the species, some vital rates may be negligible (demographic event happens too rarely to be of population-level consequence) or zero (biologically implausible). In these cases, the corresponding arrows in Figure 1 vanish, and the corresponding vital rate in Equation (1) becomes a zero. We note that plausible situations exist for any of the vital rates to be positive. For instance, if the second stage is not an age but rather a reduced-reproductive or nonreproductive adult stage, such as an adult without a territory, pack, or harem, then a_{23} represents the probability of a transition from the fully reproductive third stage to the reduced-reproductive second stage.

A leading purpose of a matrix model is to represent the life history of a species so that the dominant eigenvalue (finite rate of growth) can be estimated. Caswell (2001) provides a thorough summary of the various theorems (such as Perron–Frobenius) related to population projection matrices, the pertinent results for the dominant eigenvalue being as follows. Specifically, a system with k stages represented by a $k \times k$ matrix of nonnegative elements will have k eigenvalues, one of which, termed the dominant eigenvalue, is guaranteed to be real, nonnegative, and with modulus greater than or equal to the moduli of the other eigenvalues.



The dominant eigenvalue is the finite population growth rate characterizing the eventual geometric rate of population change once stage oscillations damp out and the stages approach stable proportions (in pathological cases, the stage oscillations can be permanent; Caswell, 2001). The dominant eigenvalue value has a simple interpretation: If the value is greater than one the population is ultimately increasing if the value is less than one the population is ultimately decreasing, and if the dominant eigenvalue is equal to one, the population will ultimately approach an unchanging abundance (Caswell, 2001). The magnitude of the dominant eigenvalue has been used as evidence to support managerial action in conservation and preservation applications (e.g., Doak, Kareiva, & Klepetka, 1994), making the dominant eigenvalue one of the most important and influential quantities arising from any mathematical population model.

The other $k - 1$ eigenvalues are those eigenvalues with moduli less than or equal in magnitude to the dominant (Fox & Gurevitch, 2000). These “subdominant eigenvalues” are typically complex valued, and appear as complex conjugates. Using these long-known facts n the context of our study, the system in Figure 1 has three stages, so the corresponding population matrix \mathbf{L} will (typically) have three distinct eigenvalues, a dominant, real-valued eigenvalue, and two complex conjugates.

The sensitivity for a vital rate in a population matrix model is defined as the change in the eigenvalue consequent to a change in the vital rate, whereas the elasticity is defined as the proportional change in the eigenvalue resulting from a proportional change in each vital rate (Caswell, 2001). Sensitivities and elasticities are utilized for management prescription in that the quantities can suggest to managers how to manipulate the system to obtain a desired dominant eigenvalue. Information about sensitivities and elasticities has guided managerial efforts and policy to produce desired future population effects (see studies in Salguero-Gómez et al., 2014, 2016).

2.1 | Eigenvalues and other demographic quantities

An eigenvalue of the matrix \mathbf{L} in Equation (1) is a solution, denoted λ , of a characteristic polynomial (Beyer, 1978)

$$\lambda^3 + p\lambda^2 + q\lambda + r = 0. \quad (2)$$

In Equation (2), the coefficients (p , q , and r) are natural groupings of the vital rates (a_{ij}) of \mathbf{L} , where

$$p = -(a_{11} + a_{22} + a_{33}), \quad (3)$$

$$q = (a_{11}a_{22} + a_{22}a_{33} + a_{11}a_{33} - a_{32}a_{23} - a_{21}a_{12} - a_{13}a_{31}), \quad (4)$$

and

$$r = (a_{11}a_{32}a_{23} + a_{12}a_{21}a_{33} + a_{31}a_{13}a_{22} - a_{11}a_{22}a_{33} - a_{21}a_{13}a_{32} - a_{31}a_{12}a_{23}). \quad (5)$$

Notice, in Equations 3–5, the quadratic coefficient (p) is the negative trace of \mathbf{L} , the linear coefficient (q) is the trace of the cofactor matrix of \mathbf{L} , and the constant coefficient (r) is the determinant of \mathbf{L} (Lax, 1997). We refer to the coefficient groupings p , q , and r as the “superparameters.” Knowledge of the values of the superparameters is sufficient for calculating the eigenvalues and any demographic quantities that depend only on eigenvalues.



The roots of a cubic polynomial have a well-known symbolic solution described in the 16th century by Cardano (Beyer, 1978; Hazewinkel, 1988). The result provides analytical expressions for each eigenvalue of a three-stage population matrix. Denoting the eigenvalues as λ_1 , λ_2 , and λ_3 , the roots of the characteristic equation of \mathbf{L} (Equation (2)) are

$$\lambda_1 = A + B + \frac{p}{3}, \quad (6)$$

$$\lambda_2 = -\frac{A+B}{2} + \frac{p}{3} + i\frac{A-B}{2}\sqrt{3}, \quad (7)$$

$$\lambda_3 = -\frac{A+B}{2} + \frac{p}{3} - i\frac{A-B}{2}\sqrt{3}, \quad (8)$$

where

$$a = \frac{(3q - p^2)}{3}, \quad (9)$$

$$b = \frac{(2p^3 - 9pq + 27r)}{27}, \quad (10)$$

$$A = \left\{ \left(-\frac{b}{2} \right) + \sqrt{\frac{b^2}{4} + \frac{a^3}{27}} \right\}^{1/3}, \quad (11)$$

and

$$B = \left\{ \left(-\frac{b}{2} \right) - \sqrt{\frac{b^2}{4} + \frac{a^3}{27}} \right\}^{1/3}. \quad (12)$$

With λ_1 being the dominant eigenvalue and λ_2 being the subdominant eigenvalue, the expression for the damping ratio is then

$$\rho = \frac{\lambda_1}{|\lambda_2|} = \frac{A + B + \frac{p}{3}}{\sqrt{\left(-\frac{A+B}{2} + \frac{p}{3} \right)^2 + \left(\frac{A-B}{2}\sqrt{3} \right)^2}}. \quad (13)$$

A low damping ratio (near 1) indicates that an unequilibrated system will exhibit wild oscillations, whereas a high ratio ($\gg 1$) indicates a fast return to geometric growth and stable stage structure.

Using Equation (2) in conjunction with the Implicit Differentiation Theorem (taking care to meet all assumptions; see Hadley, 1961), sensitivities for the superparameters are then written as

$$\frac{\partial \lambda}{\partial p} = -\frac{\lambda^2}{3\lambda^2 + 2p\lambda + q}, \quad (14)$$



$$\frac{\partial \lambda}{\partial q} = -\frac{\lambda}{3\lambda^2 + 2p\lambda + q}, \quad (15)$$

and

$$\frac{\partial \lambda}{\partial r} = -\frac{1}{3\lambda^2 + 2p\lambda + q}. \quad (16)$$

Letting i indicate the i th row of \mathbf{L} , and j indicate the j th column of \mathbf{L} , by the chain rule (Thomas, 2008), the sensitivity of the k th eigenvalue by the a_{ij} th vital rate is then

$$\frac{\partial \lambda_k}{\partial a_{ij}} = \frac{\partial p}{\partial a_{ij}} \frac{\partial \lambda_k}{\partial p} + \frac{\partial q}{\partial a_{ij}} \frac{\partial \lambda_k}{\partial q} + \frac{\partial r}{\partial a_{ij}} \frac{\partial \lambda_k}{\partial r}. \quad (17)$$

The sensitivities calculations using Equation (17) will arrive at the same conclusion to the sensitivities calculated using the numeric method in Caswell (2001) and Fox and Gurevitch (2000). The derivatives of the superparameters with respect to vital rates in Equation (17) are easy to calculate from Equations 3–5.

Superparameters reflect overall, integrated demographic forces (such as adult-to-adult recruitment). Whether superparameter sensitivities will aid management decisions akin to traditional individualized vital rate sensitivities is not yet clear. The usefulness of superparameter sensitivities will depend on the structure of the 3×3 matrix. In general, each vital rate appears in at least two superparameters (Equations 3–5), producing dependencies between the superparameters that complicate the interpretations of the sensitivities. However, in some cases such as that of a model of the Northern Spotted Owl (see below), each vital rate appears in only one superparameter, and the superparameters have straightforward demographic interpretations.

Using Equations 14–16, the elasticities of the dominant eigenvalue with respect to the superparameters are

$$e_p = -\frac{p\lambda^2}{3\lambda^3 + 2p\lambda^2 + q\lambda}, \quad (18)$$

$$e_q = -\frac{\lambda q}{3\lambda^3 + 2p\lambda^2 + q\lambda}, \quad (19)$$

and

$$e_r = -\frac{r}{3\lambda^3 + 2p\lambda^2 + q\lambda}. \quad (20)$$

By the chain rule (Thomas, 2008), the elasticity of the k th eigenvalue by the a_{ij} th vital rate is

$$e_{ij} = \frac{\partial p}{\partial a_{ij}} e_p + \frac{\partial q}{\partial a_{ij}} e_q + \frac{\partial r}{\partial a_{ij}} e_r. \quad (21)$$

The Supporting Information S.2 of this study contains derivations and expressions of Equations 2–21, in addition to individual vital rate sensitivities and elasticities (expansions of



Equations 17 and 21). As well, the Supporting Information S.2 contains derivations and expressions for the traditional dominant and subdominant eigenvectors but in this context, plus novel derivations for the sensitivities and elasticities of the subdominant eigenvalues with respect to the superparameters.

Some demographic quantities require only the values of the superparameters, whereas others require the values of the vital rates. As seen above, we discover that dominant and subdominant eigenvalues, damping ratio, and sensitivities and elasticities of the dominant eigenvalue with respect to the superparameters require only the superparameter values. However, the stable stage distribution and reproductive value vector (dominant right and left eigenvectors), along with sensitivities and elasticities of the dominant eigenvalue with respect to the individual vital rates require values of the individual vital rates.

2.2 | Extinction criteria

Whether or not the dominant eigenvalue is less than one can be determined, for a given set of vital rates, with some simple calculations and without having to calculate the eigenvalue itself. The criteria for the dominant eigenvalue to be less than one are contained within Samuelson's (1941) criteria for all the roots of a polynomial to lie within the unit circle. The Samuelson criteria were originally motivated by the problem of ascertaining whether a linear autoregressive time series model is stationary. The criteria arise as a simple transformation of the eigenvalues into roots of another polynomial for which the Routh–Hurwitz criteria (e.g., Pielou, 1977) for local stability in a differential equation model can be applied. The Routh–Hurwitz criteria are the necessary and sufficient conditions for all the roots of a polynomial equation to have negative real parts. As such, in theoretical ecology, they are much featured in “local stability theory” for equilibria of systems of differential equations (May, 1974; Pielou, 1977).

We provide a brief explanation of Samuelson's (1941) criteria in the novel context of the superparameters of the three-stage model. The characteristic polynomial for the three-stage model is given by $P(\lambda) = \lambda^3 + p\lambda^2 + q\lambda + r$, where p , q , and r are the superparameters (Equations 3–5). The eigenvalues are roots to $P(\lambda) = 0$. Consider the complex transformation $z = (\lambda + 1)/(\lambda - 1)$, which reverses to $\lambda = (z + 1)/(z - 1)$. Write z as some complex number $z = a + ib$. It is straightforward to show that $a < 0 \Leftrightarrow |z| < 1$, that is, if the real part of z is negative, then λ must lie within the unit circle on the complex plane, and vice versa. Now, $P(\lambda) = 0$ is the same as

$$\left(\frac{z+1}{z-1}\right)^3 + p\left(\frac{z+1}{z-1}\right)^2 + q\left(\frac{z+1}{z-1}\right) + r = 0. \quad (22)$$

Multiply both sides by $(z - 1)^3$ and then multiply out all the products and collect like powers of z together to represent z as a root of a new polynomial equation

$$z^3 + c_2z^2 + c_1z + c_0 = 0, \quad (23)$$

where

$$c_0 = \frac{1 - p + q - r}{1 + p + q + r}, \quad (24)$$



$$c_1 = \frac{3 - p - q + 3r}{1 + p + q + r}, \quad (25)$$

$$c_2 = \frac{3 + p - q - 3r}{1 + p + q + r}. \quad (26)$$

Applied to the cubic Equation (23), the Routh–Hurwitz criteria becomes

$$c_0 > 0, \quad (27)$$

$$c_2 > 0, \quad (28)$$

$$c_2 c_1 > c_0. \quad (29)$$

It follows that these superparameter inequalities are the Samuelson criteria for all roots of $P(\lambda) = 0$ to lie within the unit circle. Thus, Equations 27–29 are the extinction criteria for the three-stage matrix model; when all three inequalities are satisfied, the dominant eigenvalue is less than one. The criteria have various algebraic variants (see Farebrother, 1973; May, 1974; Okuguchi & Irie, 1990), a useful version of which is the set

$$1 + p + q + r > 0, \quad (30)$$

$$3 + p - q - 3r > 0, \quad (31)$$

$$1 - r^2 - pr - q > 0. \quad (32)$$

Derivations for Equations 22–32 appear in Supporting Information S.3.

3 | RESULTS

3.1 | Northern Spotted Owl Model

In a three-stage life history common in wildlife, only adults reproduce, adult stage members face a common annual survival probability, and both juveniles and subadults advance each time unit according to their own survival probabilities (Figure 2). The life history adequately describes many avian, reptilian, and amphibian species (Deevey, 1947; Salguero-Gómez et al., 2016) and formed the basis of a well-known model of the Northern Spotted Owl (Noon & Biles, 1990). We term this the “generic” life history for wildlife species. The projection matrix for the corresponding population matrix model is

$$\mathbf{L} = \begin{bmatrix} 0 & 0 & a_{13} \\ a_{21} & 0 & 0 \\ 0 & a_{32} & a_{33} \end{bmatrix}. \quad (33)$$

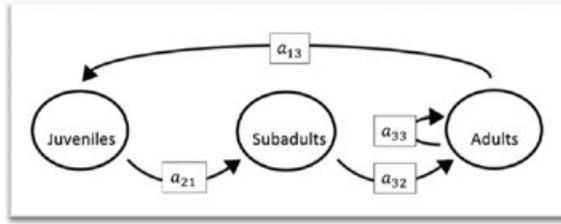


FIGURE 2 A species with this life history is modeled by matrix \mathbf{L} (Equation (34)). Specifically, juveniles survive and advance to subadults with probability a_{21} , subadults survive and advance to adults with survival probability a_{32} , whereas adults survive with probability a_{33} , and reproduce with fertility a_{13} . The Spotted Owl (Noon & Biles, 1990), and many avian, reptilian and amphibian species (e.g., Deevey, 1947, and many species found in the archived material for Heppell et al., 2000) adequately satisfy this representation

The vital rates represent the four important transitions in this life history; juveniles survive and advance to subadults with probability a_{21} , subadults survive and advance to adults with survival probability a_{32} , while adults survive with probability a_{33} , and reproduce with fertility a_{13} . Further common characteristics of this life table are: (a) the time intervals an individual spends in the juvenile and subadult stages are approximately equal, (b) subadult reproduction is negligible, and (c) surviving adults reproduce each time period.

For the generic life history, the superparameter $q = 0$, and so the characteristic equation of \mathbf{L} is

$$\lambda^3 + p\lambda^2 + r = 0, \tag{34}$$

in which the four vital rates have collapsed into two superparameters

$$p = -a_{33} \tag{35}$$

and

$$r = -a_{13}a_{21}a_{32}. \tag{36}$$

We point out that the quadratic equations displayed in Noon and Biles (1990) and Noon and Sauer (1992) do not correspond to the generic life history as defined here.

The formulas given by Equations 6–21 represent the various matrix quantities for the Northern Spotted Owl life history when the value $q = 0$ is substituted. The eigenvalues of \mathbf{L} are then identical to Equations 6–12, whereas the damping ratio of \mathbf{L} takes on the same form as Equation (13). The sensitivities of \mathbf{L} with respect to the superparameters and individual vital rates can be found with Equations 14, 16, and 17, whereas the elasticities of \mathbf{L} with respect to the superparameters and vital rates are given by Equations 18, 20, and 21, respectively. Noon and Biles (1990) give estimated vital rates as $a_{21} = 0.11$, $a_{32} = 0.71$, $a_{33} = 0.942$, and $a_{13} = 0.24$, giving a characteristic equation of $\lambda^3 - 0.942\lambda^2 - 0.0187 = 0$. The eigenvalues are $\lambda_1 = 0.962$, $\lambda_2 = -0.010 + 0.139i$, and $\lambda_3 = -0.010 - 0.139i$. The damping ratio of \mathbf{L} is $\rho = 6.894$, which is much greater than one, meaning that oscillations in the population caused by perturbations or imbalances in the stage distribution will damp out quickly to recover the stable stage distribution (and asymptotic growth rate). The sensitivity of the dominant eigenvalue to the superparameters of \mathbf{L} are: $\partial\lambda/\partial p = 0.201$, and $\partial\lambda/\partial r = 0.217$, while the elasticity of the dominant eigenvalue to the superparameters of \mathbf{L} are $e_p = 0.197$, and $e_r = 0.004$.



In the Northern Spotted Owl example, the elasticities and sensitivities with respect to superparameters have straightforward and important interpretations. The superparameter p is (minus) adult survival, while the superparameter r , being proportional to the product of adult fertility (a_{13}), juvenile survival (a_{21}), and subadult survival (a_{32}), is adult recruitment. The elasticities indicate, for example, that an increase in adult survival alone will cause a greater change to the dominant eigenvalue than the same *relative* increase in adult recruitment. The interpretation is consistent with, but provides even more information than the conclusion of Noon and Biles (1990): Mortality of an adult Northern Spotted Owl has a much graver impact on the population any other vital rate. The sensitivities indicate that the dominant eigenvalue responds about the same to small changes in p and r as measured in their original units.

The extinction criteria for the generic life history, found by substituting $q = 0$ in Equations 30–32, boil down into a single inequality

$$1 - a_{33} > a_{13}a_{21}a_{32}. \quad (37)$$

In words, extinction is certain if adult mortality is greater than adult recruitment. For the Northern Spotted Owl model of Noon and Biles (1990), the inequality is estimated as $0.058 > 0.0187$, so that the model predicts that the population is not viable.

The superparameters in the Northern Spotted Owl model appear in a univariate version of the stage-structured model, thereby lending more insights into growth dynamics and the extinction criteria (Equations 30–32 and 37). The system of three difference equations represented by $\mathbf{n}_{t+1} = \mathbf{L}\mathbf{n}_t$, where \mathbf{L} is the matrix in Equation (33) and \mathbf{n}_t is the column vector of the three-stage abundances, by substitution reduces to a single scalar equation for the adult stage

$$A_{t+1} = a_{33}A_t + a_{13}a_{21}a_{32}A_{t-2} = -pA_t - rA_{t-2}. \quad (38)$$

The characteristic equation of this third-order linear difference equation is the same as the characteristic equation of \mathbf{L} (Equation 34). Zero is an equilibrium of the difference equation, and for all the roots to be within the unit circle implies that zero will be a stable attractor of the trajectories of the difference equation, or in other words, certain extinction results. The difference equation for the adult stage also opens the possibility that estimation of characteristic roots and population viability analysis for the generic life history might be accomplished with ordinary time series analysis of abundances of just the adult stage.

3.2 | Other three-stage life histories

For all 3×3 matrix models, the nine vital rates combine into no more than three superparameters, with extinction criteria in the form of three superparameter inequalities. The Supporting Information S.1 contains the p , q , and r expressions and extinction criteria for all histories containing all nine vital rates, any eight vital rates (i.e., one rate is zero), any seven vital rates (two rates are zero), any six vital rates, any five vital rates, any four vital rates, any three vital rates, any two vital rates, and any one vital rate, for a total of 511 possible three-stage life histories ($\binom{9}{9} + \binom{9}{8} + \binom{9}{7} + \binom{9}{6} + \binom{9}{5} + \binom{9}{4} + \binom{9}{3} + \binom{9}{2} + \binom{9}{1} = 511$). Embedded in this



set are the 15 possible $(\binom{4}{4} + \binom{4}{3} + \binom{4}{2} + \binom{4}{1} = 15)$ two-stage life histories (e.g., Sibly, Hansen, & Forbes, 2000), and their corresponding p , q , and r superparameters and extinction criteria.

Matrix models with different vital rates can have identical superparameters. Any two matrices having identical superparameters will have identical dominant eigenvalues, subdominant eigenvalues, and damping ratios. As a result, the two population models will display similar degrees of transient reactivity and identical asymptotic growth rates. Model trajectories themselves depend on the eigenvectors as well as eigenvalues (via spectral decomposition of L) and therefore are in general different in models with identical superparameters.

There are classes of model behaviors defined by unique p , q , and r magnitudes. Furthermore, the combination of the life history structure (superparameter expressions) and the actual values for each vital rate determine the superparameter magnitudes and therefore to which behavior class that model belongs. An extensive analysis cataloguing superparameter patterns for all 511 possible 3×3 matrix structures appears in Supporting Information S.1.

4 | DISCUSSION

The superparameters represent the complicated cycles in the life history by which stages are replaced and in general are not likely to be readily interpretable, but some exceptions exist for particular life histories. In the generic life history model, the superparameters are adult per-individual survival probability and adult per-individual recruitment. For the general Leslie–Lewis matrix model with $k = 3$ age classes (i.e., generic life history except with $a_{33} = 0$), the characteristic equation is the discrete form of Lotka’s integral equation for the instantaneous growth rate and is represented by Caswell (2001; equation 4.42, adapted to our notation)

$$1 = a_{11}\lambda^{-1} + a_{21}a_{12}\lambda^{-2} + a_{21}a_{32}a_{13}\lambda^{-3}, \quad (36)$$

Multiplying both sides by λ^k produces the k -degree polynomial form, or in this case, the cubic. The coefficients for the powers of λ are the superparameters. Each superparameter here is the average number of offspring of an individual in the j th age class that will survive to reenter the j th age class.

When the superparameters have straightforward biological interpretations, managers might be able to estimate the superparameters with redesigned field studies. Potentially the estimation of no more than three superparameters would be needed to estimate the finite rate of increase for three-stage populations, and therefore extinction assessments. The eigenvalues, elasticities, and sensitivities for the generic life history (e.g., Northern Spotted Owl) depend functionally on just two superparameters involving adult demographics, suggesting that the tagging of juvenile or subadult individuals to obtain individualized survival probabilities might not be necessary. Along with altering the natural behaviors of tagged animals, there exist demographic costs associated with carrying tags in some species (Jones et al., 2013). Additionally, due in part to detectability challenges for smaller age classes (Gilroy, Virzi, Boulton, & Lockwood, 2012; Pike, Pizzatto, Pike, & Shine, 2008), sampling younger age classes to obtain estimates of survivability can be difficult (e.g., Doak et al., 1994). The superparameter results presented here could help reduce scientific visiting



and handling impact on entire cohorts of wildlife populations, resulting in potential cost savings for managers and lessened hazards for juveniles.

Any population projections using results presented here are obtained under the assumption that the vital rates do not change. Although significant research has been published on the use of matrix models in varied environments (e.g. Ezard et al., 2010; Tuljapurkar, 1989), the results and interpretation of this study currently require the assumption that static population dynamics arise over long periods of stable environments.

Population matrix models are central to contemporary wildlife management, as they enhance understanding of the dynamics, structure, and demographic consequences to changes within populations (Caswell, 2001). Improved understanding of how vital rates contribute to the finite growth rate and other demographic quantities is critical for the management of our wildlife legacy.

ACKNOWLEDGMENTS

The authors wish to thank Hal Caswell and three anonymous reviewers for their helpful comments. Funding was provided by the College of Graduate Studies, provided by the College of Graduate Studies, College of Science, and the Bioinformatics and Computational Biology Fellowship (University of Idaho, Moscow, ID).

CONFLICTS OF INTEREST

The authors declare that there are no conflicts of interest.

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SUPPORTING INFORMATION

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How to cite this article: Hanley B, Dennis B. Analytical expressions for the eigenvalues, demographic quantities, and extinction criteria arising from a three-stage wildlife population matrix. *Natural Resource Modeling*. 2019;e:12207. <https://doi.org/10.1111/nrm.12207>