

Semelparity versus iteroparity and the number of age groups

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ABSTRACT

The perennial question in life-history evolution is the difference in fitness to reproduce only once (semelparity, S) or more than once (iteroparity, I) per lifetime. It is frequently argued that semelparous individuals can achieve a higher reproductive output by trading off longevity for fecundity. Along the same lines, it could be stated that iteroparous breeders have lower reproductive output because they are allocating some of the resources to survival in the year(s) to come. To us, the classical life-history question is confounded by the number of age groups. In the evolutionary literature, semelparity is often equated with annual life history and iteroparity with perennial life history (in plants). Here, we disentangle the number of age groups from the life-history question by using a Leslie matrix approach. Invasion analyses show that, given equal numbers of age groups ($k_S = k_I$) and letting the geometric rates of increase λ_S and λ_I to range from 1 to 5, the parameter space is generous enough to allow either of the life histories to be an evolutionarily stable strategy, the two life histories can co-exist, or both may go extinct. Letting $k_S \neq k_I$ does not rescue the outcome.

Keywords: evolutionarily stable strategy, iteroparity, Leslie matrix, population dynamics, reproductive schedule, semelparity.

INTRODUCTION

Some organisms reproduce only once, while others have adopted the option to have several reproductive seasons during their lifetime. The most important question in life-history evolution is the relative fitness benefits of these two reproductive strategies, known as semelparity (S) and iteroparity (I) (Roff, 1992; Stearns, 1992). The problem has attracted considerable attention since Cole first addressed it (e.g. Cole, 1954; Murphy, 1968; Gadgil and Bossert, 1970; Bryant, 1971; Charnov and Schaffer, 1973; Goodman, 1974; Stearns, 1976, 1992; Horn, 1978; Emlen, 1984; Bulmer, 1985, 1994; Roff, 1992; Charlesworth, 1994; Ferrière and Fox, 1995; Ranta *et al.*, 2000a,b, 2001). In these studies, the terms ‘semelparity’

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and ‘iteroparity’ were often taken as synonyms for annual and perennial life histories of plants. In particular, Cole dealt explicitly with annuals when referring to semelparous reproduction.

To us, equating semelparity and iteroparity to annual and perennial life histories is a potential source of confusion. Here, we draw attention to the fact that many of the analyses of Cole’s paradox did not treat semelparity and iteroparity independently of the number of age groups. This is crystallized by saying that annuals produce a set of seeds once at age 1 and die subsequently, whereas perennials produce seeds every year in their life. To address the potential bias of different numbers of age groups, k , in semelparous and iteroparous breeders, we decided to use the Leslie matrix (Leslie, 1945, 1948) to model population renewal of semelparous and iteroparous strategies. This method enabled us to control both the number of age groups and the number of breeding occasions during a plant’s lifetime.

In our approach, we kept the number of age groups for semelparous and iteroparous breeders the same, $k_S = k_I$. The only difference allowed between the two breeding strategies was that semelparous breeders reproduce once only in the final year of their life, whereas iteroparous breeders have repeated reproductive bouts during their lifetime. We also allowed the option of matching the geometric rates of increase of the two breeding strategies, $\lambda_S = \lambda_I$. We take one reproductive strategy as the well-established resident strategy and then ask: ‘Is it possible for a rare mutant strategy to invade the population?’

In our invasion analysis, we wish to determine whether one of the two strategies, semelparity or iteroparity, is an unbeatable reproductive strategy. In essence, is semelparity or iteroparity, given $k_S = k_I$ and $\lambda_S = \lambda_I$, or $\lambda_S \neq \lambda_I$, an evolutionarily stable strategy (ESS; Maynard Smith, 1982)? Recall that a strategy or a type is referred to as an ESS when it is resident (common in the population) and is able to prevent an invasion by the other strategy. In the subsequent stages of our analysis, we let $k_S \neq k_I$ and search under which conditions the two reproductive strategies can co-exist.

LESLIE MATRIX APPROACH TO SEMELPARITY AND ITEROPARITY

Consider a species with k discrete age classes, $n_{x,t}$ being the number of females alive in the age group x at time t , while P_x is the probability that a female in the age group x at time t will be alive in the age group $x+1$ at time $t+1$. Finally, F_x is the number of female offspring born at time t per female aged x at time t that will be alive in the age group 1 at time $t+1$. Renewal of such a population can be written in matrix notation (Leslie, 1945; Caswell, 2001) as

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

where \mathbf{n} is a column vector giving the distribution of individuals in age groups at time t .

Matrix \mathbf{L} has the general form for a semelparous life history:

$$\mathbf{L}_S = \begin{bmatrix} 0 & 0 & \cdots & 0 & F_k \\ P_1 & 0 & \cdots & 0 & 0 \\ 0 & P_2 & \ddots & 0 & 0 \\ \vdots & & \ddots & & \vdots \\ 0 & 0 & \cdots & P_{k-1} & 0 \end{bmatrix} \quad (2a)$$

And, for an iteroparous life history:

$$\mathbf{L}_I = \begin{bmatrix} F_1 & F_2 & \cdots & F_{k-1} & F_k \\ P_1 & 0 & \cdots & 0 & 0 \\ 0 & P_2 & \ddots & 0 & 0 \\ \vdots & & \ddots & & \vdots \\ 0 & 0 & \cdots & P_{k-1} & 0 \end{bmatrix} \quad (2b)$$

Note that the subscripts S and I are not indicated with the F - and P -values in the two matrices. Everything else being equal, the semelparous breeding strategy differs from iteroparity in that $F_{1,S}, F_{2,S}, \dots, F_{k-1,S}$ are all zero, whereas $F_{k,S} > 0$, while for iteroparity all $F_{1,I}$ to $F_{k,I} \geq 0$. The dominant eigenvalue of the matrix \mathbf{L} is the geometric rate of increase, λ (Leslie, 1945, 1948; Caswell, 2001).

We first keep both the number of age groups and the rates of increase the same between the two breeding strategies ($k_S = k_I$ while varying λ_S and λ_I) and ask if one of the strategies is an ESS. We then continue with unequal numbers of age groups. As we wish to concentrate on the significance of age groups, we keep all $P_{x,S} = P_{x,I}$, and start our analyses with $k_S = k_I = 2$. Then, we gradually increase the number of age groups. The method for creating the \mathbf{L}_S and \mathbf{L}_I matrices with known λ_S and λ_I is given in the Appendix.

As is common in the evolutionary literature, to facilitate invasion analysis we prefer to work with models with limited growth instead of exponential growth (e.g. de Jong *et al.*, 1987). Thus, we set a density-dependent component to modify the fecundities as follows (Emlen, 1973):

$$F_{k,S}(N_S, N_I) = F_{k,S} \exp\left(1 - \frac{N_S(t) + N_I(t)}{K}\right)$$

$$F_{i,I}(N_S, N_I) = F_{i,I} \exp\left(1 - \frac{N_S(t) + N_I(t)}{K}\right) \quad (3)$$

where $i = 1, \dots, k$, K is the carrying capacity for the population size and $N = \sum n$, of course separate for semelparous and iteroparous life histories. Thus, we assume that individuals of the two life histories, when co-existing, compete with each other for common resources. It should be noted that the form of density dependence is the same for the two life-history types, allowing us to concentrate on the importance of the number of age classes.

Our approach is to use invasion analysis. In our analysis, one of the reproductive strategies is the resident common strategy (semelparity or iteroparity), having had ample time (5000 generations) to settle such that the effect of the initial conditions has been removed. In a stable population, this also means stabilizing the age distribution. Then, at one instant in time, the opposite strategy (iteroparity or semelparity) enters the system as a rare mutant (1×10^{-4} for the first age group). After 10,000 generations, we take a sample of 100 generations to assess whether the invasion was possible or not. For this period of time, we average (geometric mean) the population size \bar{N} separately for the two life histories and score persistence and success of invasion whenever $\bar{N} > 1 \times 10^{-4}$. We let λ range from 1 to 5 in steps of 0.14.

RESULTS

Our main result is straightforward, given $k_s = k_i$ anything goes: Depending on k , there are parameter combinations of λ_s and λ_i where (1) semelparity is an ESS, (2) iteroparity is an ESS, (3) both strategies are an ESS, (4) both strategies co-exist and (5) neither strategy persists (Fig. 1). The outcome is dependent not only on k and λ_s and λ_i , but also on the resident–invader sequence of the two life histories. We experimented with k ranging from 2 to 10 (always $k_s = k_i$), with the results as rich as in Fig. 1.

In the next step, we let $k_i < k_s$ and again allowed iteroparity (or semelparity) to be the resident life history, whereas semelparity (or iteroparity) was the rare mutant attempting to invade the system. We found that, for most of the parameter space explored (k and λ), semelparity was an ESS. However, even in these simulations, a small region was almost always detected where iteroparity was the ESS. This usually coincided with $\lambda_s < \lambda_i$ (Fig. 2). In this system, we also had λ_s, λ_i regions where both life histories were an ESS, or went extinct, coinciding with large values of λ_s .

Finally, when we had $k_i > k_s$, the outcome returned to a situation where either of the two life histories was an ESS in a part of the explored parameter region, iteroparity being an ESS when $\lambda_s < \lambda_i$ (Fig. 3A–D). However, depending on the asymmetry in age group numbers, we also found large regions of λ_s and λ_i where both iteroparity and semelparity co-existed for 10,000 generations after the invasion. Depending on the number of age groups and the geometric growth rates of the two life histories, the $k_i > k_s$ asymmetry results in fascinating patterns of ESS and co-existence. It is possible to have regions of λ_s where iteroparity is an ESS, followed by a range of λ_s where semelparity is an ESS, then co-existence and, finally, iteroparity again an ESS (Fig. 3E,F,K,L).

The simultaneous extinctions of iteroparity and semelparity in our simulations often coincide with $\lambda_s > 3$ and with a high number of age groups in the semelparous life history. This often results in violent fluctuations of the population size and eventually both the resident and the intruder go extinct. However, we lack a proper understanding of the causes of the simultaneous extinctions of iteroparity and semelparity.

DISCUSSION

Our starting point was to disentangle semelparity and iteroparity from the number of age groups. We did this because we felt that research on life histories has not always kept breeding strategies (iteroparity *vs* semelparity) distinct enough from life expectancy, here represented by the number of age groups. To avoid the potential bias of different numbers of age groups, k , in semelparous and iteroparous breeders, we used the Leslie matrix (Leslie, 1945, 1948) approach to model population renewal of semelparous and iteroparous strategies. This enabled us to control both the number of age groups and the number of breeding occasions during the lifetime.

We took one of the life histories as the established resident strategy and the other as the rare mutant strategy attempting to invade the system. Within reasonable limits, we used almost all possible permutations of the parameter values in our model. Our results can be summarized by saying that, depending on the number of age groups, age group asymmetry and geometric growth rates of the semelparous and iteroparous life histories, either iteroparity or semelparity is an ESS or both life histories can co-exist (and sometimes they can both go extinct).

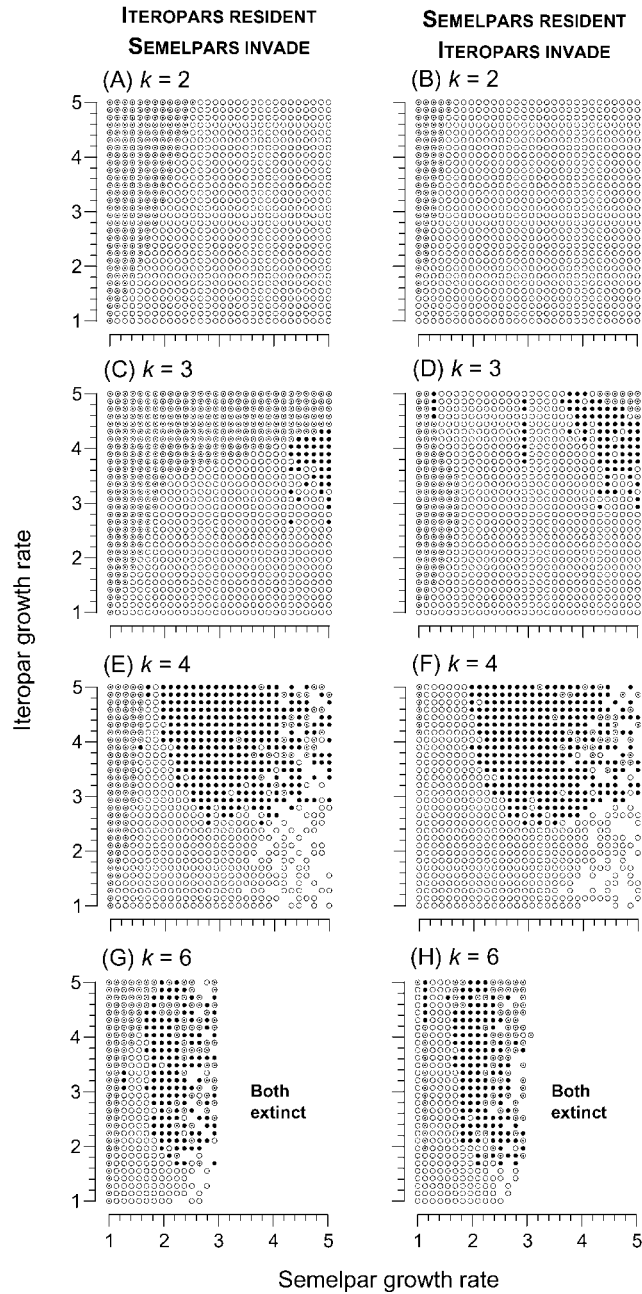


Fig. 1. Different shading in the parameter space delimited by geometric growth rate of semelparous and iteroparous life histories indicate regions where iteroparity wins (\odot), semelparity wins (\circ), both can co-exist (\bullet) or both go extinct (white). In the left-hand column, iteroparity is the resident strategy and semelparity is the invading strategy; the opposite cases are shown in the right-hand column. Here the number of age groups is matched for semelparity and iteroparity, $k_1 = k_s$. Each panel is a result of 900 parameter value combinations.

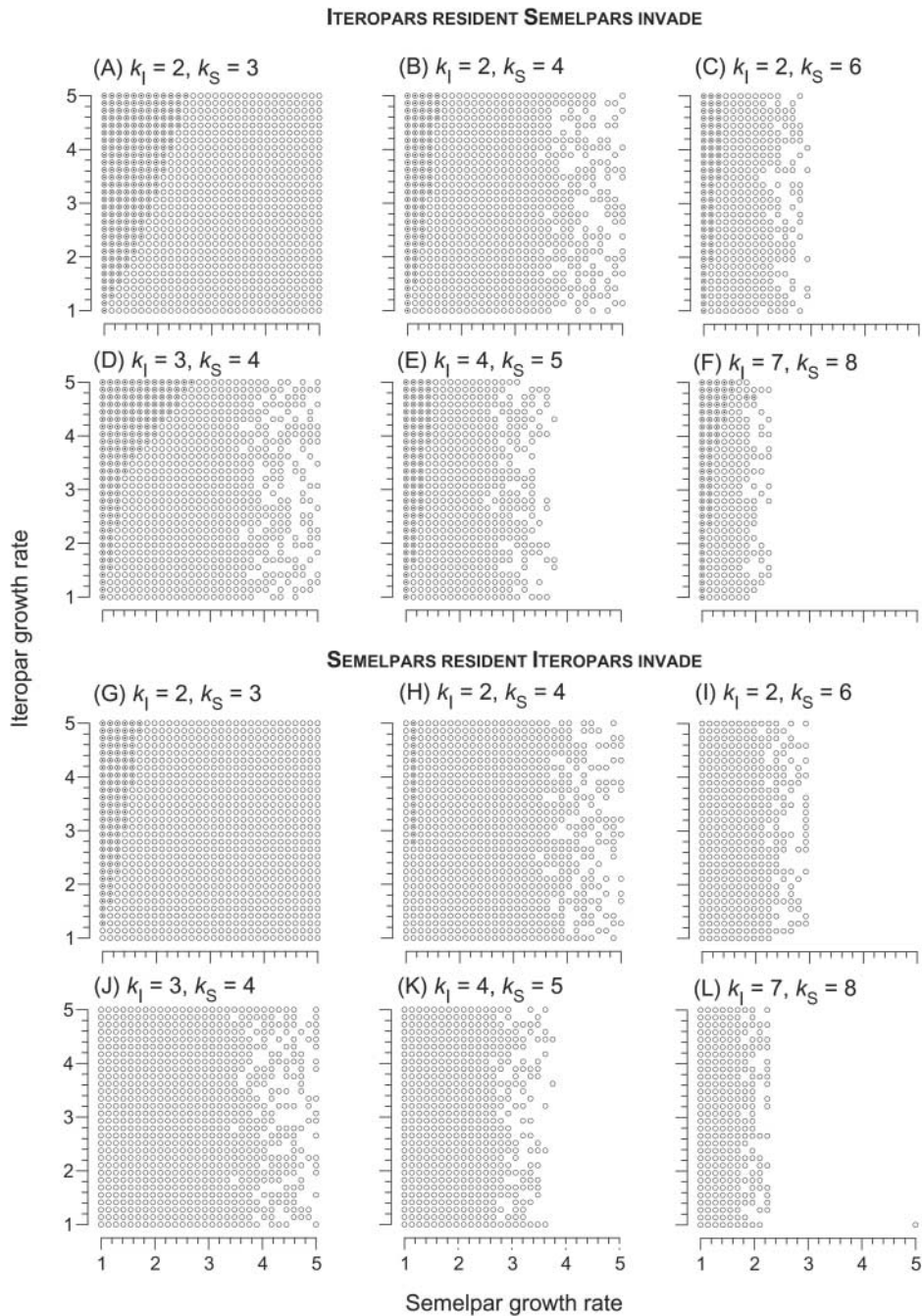


Fig. 2. As Fig. 1, but now $k_I < k_S$. In panels A–F, iteroparity is the resident strategy and semelparity is the invading strategy; the opposite cases are shown in panels G–L.

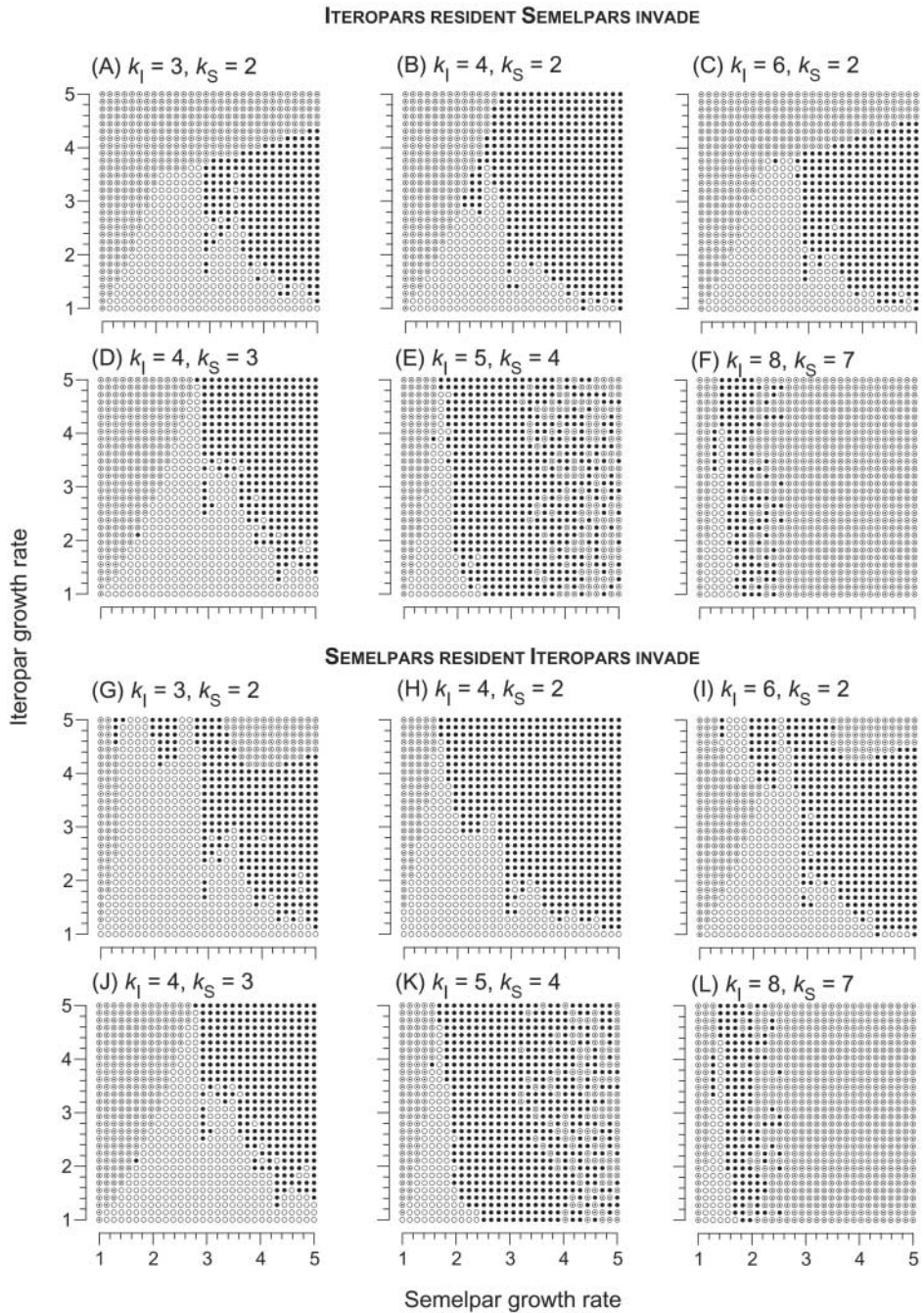


Fig. 3. As Fig. 2, but now $k_I > k_S$. In panels A–F, iteroparity is the resident strategy and semelparity is the invading strategy; the opposite cases are shown in panels G–L.

That different reproductive strategies occur simultaneously within a population is not a new observation. Schaffer (1974), who studied optimal reproductive strategies in age-structured population models, acknowledged that iteroparity and semelparity could occur simultaneously in a population. Schaffer's results were based on the assumption that fertility and post-breeding survival curves, as functions of reproductive effort, had a convex–concave or more complex shape.

In contrast to Schaffer's (1974) work, we took a demographic approach that highlights the dynamic aspect of evolution. Furthermore, we considered the possibility that semelparous organisms may reach high age. We believe that neglecting this possibility in the analysis of life histories may lead to an incomplete understanding of the fitness trade-offs between semelparity and iteroparity.

It has occasionally been argued that natural selection should favour early maturity because of the high risk to reproduction, which semelparous organisms face with increasing age. Nevertheless, we find semelparous perennials in nature, including some lobelias (Young, 1990), 13- and 17-year-old cicadas (Williams and Simon, 1995), several long-lived semelparous plants (Young and Augspurger, 1991) and salmon species (Schaffer, 1974), to mention a few.

Generally, any delay to maturity may lead to a reduction in fitness unless it is compensated by higher reproductive value at higher age, such as proportionately larger fecundity at higher age or size, as theory predicts (Stearns, 1992; Berrigan and Koella, 1994). Because of the higher risk to reproduction at higher age, semelparous organisms will generally not evolve to reach high ages. Biologically realistic age structures of semelparous and iteroparous populations will include, therefore, only a limited number of combinations. Consequently, we would expect that incorporating more than 10 age classes into our model would not change our basic conclusion.

Although the details of our analysis depend, to some extent, on the life histories of the resident and invading types, addressing the problem of semelparity and iteroparity – raised in the first place by Cole's paradox – using Leslie matrix modelling was relatively straightforward. The answer to our evolutionary problem is that both semelparity and iteroparity may be an ESS, both life histories can co-exist, or both iteroparous and semelparous breeders can sometimes go extinct simultaneously. The answer depends on life-history specific age group numbers and geometric growth rates of semelparous and iteroparous life histories.

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APPENDIX

We briefly outline the method with which we created the Leslie matrices for the semelparous as well as the iteroparous populations with given geometric growth rates λ_S and λ_I .

The creation of Leslie matrices from geometric growth rates involves eigenvalue problems, since λ_S and λ_I can be interpreted as the dominant eigenvalues of the $n \times n$ Leslie matrices \mathbf{A}_S and \mathbf{A}_I . Instead of calculating the actual eigenvalues, as is the case for conventional eigenvalue problems, we have to calculate the age-specific fecundity values in the Leslie matrices.

We begin with the characteristic equation for solving eigenvalue problems:

$$\mathbf{A}\mathbf{x} = \lambda\mathbf{x}; \quad \mathbf{x} = (x_1, x_2, x_3)^T \quad (1)$$

where \mathbf{A} is the Leslie matrix, λ is the eigenvalue of matrix \mathbf{A} and \mathbf{x} is the eigenvector of the operator \mathbf{A} belonging to λ . The eigenvector \mathbf{x} can be interpreted as the vector containing the age distribution in the population and λ as the population growth rate. Equation (1) can be rewritten as

$$\mathbf{A} - \lambda \mathbf{I} = 0 \quad (2)$$

where \mathbf{I} is the unit matrix of the same size as matrix \mathbf{A} . Thus, $\mathbf{A} - \lambda \mathbf{I}$ is a matrix of the same size as matrix \mathbf{A} . Solving equation (2) requires the calculation of the determinant of $\mathbf{A} - \lambda \mathbf{I}$, $\det(\mathbf{A} - \lambda \mathbf{I})$, providing us with a polynomial equation of n th degree in λ . For illustrative purposes, we calculate the determinant of $(\mathbf{A}_{33} - \lambda \mathbf{I})$, where \mathbf{A}_{33} is a 3×3 Leslie matrix with age-specific survival values, $p_{i+1,i}$, and age-specific fecundity values, $F_{1,i}$. From equation (2) we get

$$\det \left(\begin{bmatrix} F_{11} & F_{12} & F_{13} \\ p_{21} & 0 & 0 \\ 0 & p_{32} & 0 \end{bmatrix} - \lambda \mathbf{I} \right) = 0 \quad (4)$$

which can be rewritten as

$$\det \left(\begin{bmatrix} F_{11} - \lambda & F_{12} & F_{13} \\ p_{21} & -\lambda & 0 \\ 0 & p_{32} & -\lambda \end{bmatrix} \right) = 0 \quad (5)$$

Equation (5) can be expressed with smaller determinants as follows:

$$(F_{11} - \lambda) \times \det \left(\begin{bmatrix} -\lambda & 0 \\ p_{32} & -\lambda \end{bmatrix} \right) - p_{21} \times \det \left(\begin{bmatrix} F_{12} & F_{13} \\ p_{32} & -\lambda \end{bmatrix} \right) + 0 \times \det \left(\begin{bmatrix} F_{12} & F_{13} \\ -\lambda & 0 \end{bmatrix} \right) = 0$$

which can be rewritten as

$$-\lambda^3 + F_{11}\lambda^2 + F_{12}p_{21}\lambda + F_{13}p_{21}p_{32} = 0 \quad (6)$$

Recall that the unknown constants are the age-specific fecundity values F_{11} , F_{12} and F_{13} .

Proceeding further, we can make two simplifying assumptions with respect to the age-specific fecundity values of the semelparous population on the one hand and the iteroparous population on the other hand.

Next, for the semelparous population we assume that all fecundity values except the last one in the Leslie matrix should be zero. For the iteroparous population, we assume that all fecundity values are equal to each other and are positive. Thus, equation (6) can be presented for the semelparous population as

$$(-\lambda_s)^3 + p_{21}(p_{32}F_{13}) = 0 \quad (7a)$$

and for the iteroparous population as

$$(-\lambda_i)^3 + \lambda_i^2 F + \lambda_i p_{21} F + p_{21} p_{32} F = 0 \quad (7b)$$

from which we get

$$F_{13} = \frac{\lambda_s^3}{p_{21}p_{32}} \quad (8a)$$

and

$$F = \frac{\lambda_i^3}{\lambda_i^2 + p_{21}\lambda_i + p_{21}p_{32}} \quad (8b)$$

Equation (6) can be generally written as follows:

$$(-\lambda)^n - F_{11}(-\lambda)^{n-1} - p_{n-(n-1)}[F_{12}(-\lambda)^{n-2} - p_{n-(n-2)}[F_{13}(-\lambda)^{n-3} \dots - p_{n-1}[F_{1n}(-\lambda)^{n-n}]]] = 0 \quad (9)$$

Corresponding to equation (8a), the general solution for the semelparous population is given as:

$$F_{1,n} = \frac{\lambda^n}{\prod_{i=0}^{n-1} P_{(i+1),i}} \quad (10a)$$

Since we list only adult survival rates in the Leslie matrix, the juvenile survival rates enter the calculation as fecundity values, which are therefore corrected by being multiplied by the values of juvenile survival and appear in the Leslie matrix as modified fecundity values. For the special case of the annual type, we have a fecundity value in the Leslie matrix equal to λ .

Corresponding to equation (8b), we get the general solution for the age-specific fecundity values of an iteroparous population, under the assumption that all fecundity values are equal:

$$F = \frac{\lambda^n}{\sum_{k=0}^{n-1} \lambda^{n-(k+1)} \prod_{i=0}^k P_{(i+1),i}} \quad (10b)$$

