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Ecology, Vol. 75, No. 8 (Dec., 1994), 2410-2415.

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LOOP ANALYSIS: EVALUATING LIFE HISTORY PATHWAYS IN POPULATION PROJECTION MATRICES¹

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Abstract. A new way of analyzing life histories is presented, based on the use of elasticities as derived from the limit properties of population projection matrices. In general there is not a simple relation between life history traits and matrix elements and their corresponding elasticity values. By recognizing the fact that a life history trait always is part of a life history pathway that can be contrasted to other pathways, this problem can be overcome. The various life history pathways form loops within the life cycle graph, the graphical representation of the projection matrix. It is shown that one can calculate the elasticities of such loops from the single elasticity values in the matrix in an unequivocal way. This presents a new and meaningful decomposition of total elasticity in population projection matrices and provides a potentially powerful tool to evaluate the importance of alternative life history options in demographic studies. This point is demonstrated using two previously published sets of data.

Key words: *elasticity analysis; Hypochaeris radicata; life history; loop analysis; Poa annua; population dynamics; projection matrices; trade-off.*

INTRODUCTION

For a mathematical analysis of life cycles, and especially of complex life histories of structured populations, matrix models have proven particularly suitable (van Groenendael et al. 1988, Caswell 1989a). Since its introduction (Caswell et al. 1984, de Kroon et al. 1986), a measure of relative perturbation, called elasticity, has become a widely used tool in the analysis of population projection matrices (de Kroon et al. 1987, Carlsson and Callaghan 1991, Gotelli 1991, Åberg 1992, Kalisz and McPeck 1992, among many others). The elasticity of a transition in the life cycle quantifies the relative contribution of that particular element to the population growth rate. Its additivity and relative nature are the aspects of elasticity that make it useful in comparisons of the importance of transitions, or sets

of transitions, in life cycles between species or between different life histories within species (e.g., de Kroon et al. 1987, Kalisz and McPeck 1992, Silvertown et al. 1992, 1993). Variation in life history traits among individuals within populations is ubiquitous in both plants and animals. Examples of vegetative (clonal) vs. sexual reproductive morphs or variance in allocation to these functions in plants, zooplankton, and marine invertebrates, age to first reproduction and sexual morphs in several fish species, migratory vs. nonmigratory individuals within insect populations, and gender switching in plants have all been described. These arrays of life history pathways present within populations are the foundation for asking questions regarding trade-offs among life history traits (Caswell 1989b, Stearns 1992).

However, for the purpose of the analysis of different life history pathways in the context of life history studies, the value of elasticities alone is limited. The reason is that individual matrix elements often do not correspond directly to life history traits, and therefore do not quantify the relative contribution of such traits to overall fitness. For example, the different contributions of early vs. late reproduction to overall fitness are difficult to analyze with single elasticities because the timing of reproduction is a phenomenon of the life cycle

¹ Manuscript received 25 October 1993; revised 2 March 1994; accepted 30 March 1994.

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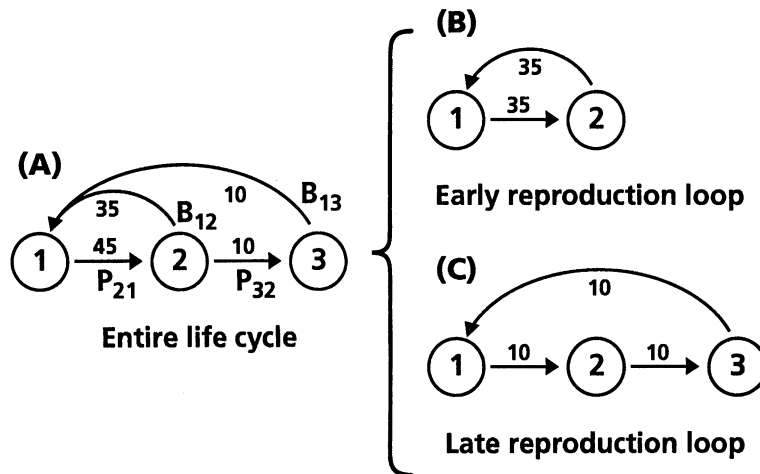


FIG. 1. (A) A hypothetical life cycle graph for a three-stage semelparous organism with two options for reproduction, early or late. The two loops that together form the life cycle are drawn separately. (B) Early reproduction loop; (C) late reproduction loop. Hypothetical elasticity values (percent) for all transitions are given. The characteristic elasticity values of the early and late reproduction loops are 35 and 10, and the combined elasticities of the loops sum to 70 and 30, respectively. The elasticity of the common transition between the two loops (P_{21}) equals the sum of the two characteristic elasticities.

as a whole. In such a case the objective should be to compare the importance of the entire life cycle of individuals that reproduce early with those that reproduce late. Grouping matrix elements and summing the corresponding elasticities, as carried out recently by Silvertown et al. (1993), does not contrast one life history option vs. the other, because many elements correspond to more than one pathway as we will show below. Since there is a general lack of correspondence between life history traits and transition elements for many organisms, a fundamental solution is necessary to quantify the effects of alternative life history traits.

The solution we suggest here is based on the recognition that a complex life cycle is composed of a number of more simple life history pathways that are the actual pathways used by the individuals in the population. Such pathways are denoted here by "loops," a term borrowed from community ecology where it is used in a comparable fashion in the analysis of community matrices (Yodzis 1989). The fundamental underlying principle is that each individual has only one pathway to pass through (Caswell and John 1992). This assumes that individuals can be usefully grouped into categories that follow one particular loop as opposed to or in preference of others. For the evaluation of the different pathways in a life history it is necessary to quantify the importance of the identified loops for overall fitness.

In this paper we develop a method, called loop analysis, that meets this goal. Loop analysis implies a calculation of the relative contribution of alternative life history loops to fitness, based on the elasticities of the transition elements of projection matrices. Directions to identify loops in the life cycle and to calculate their elasticity values are given and illustrated with two examples of actual life cycles.

LOOP ANALYSIS

The basic step in loop analysis is to consider elasticities in the context of the underlying life history structure as exemplified by the life cycle graph (Caswell 1989a). An important characteristic of this graph is the fact that it can be decomposed into a set of loops, each of which contributes to the dominant eigenvalue (the population growth rate λ) of the corresponding projection matrix in a simple additive way (de Kroon et al. 1987, Caswell 1989a). In a life history context the various loops represent the options for cohorts of individuals to complete their life cycle, making it possible to compare different life history pathways.

As an example, consider a simple life history of a semelparous organism consisting of three life cycle stages with reproduction possible only by stage 2 and 3 (Fig. 1). This life cycle contains one simple trade-off: early vs. late reproduction. It can be decomposed into two unbranched loops: a two-step loop (stage 1-2-1; Fig. 1B) representing early and a three-step loop (stages 1-2-3-1; Fig. 1C) representing late reproduction.

The mathematical basis for the calculation of the elasticities of the loops is rooted in the following two properties: (1) For each stage in the life cycle graph, the summed elasticity of incoming transitions equals the summed elasticity of outgoing transitions (see Appendix for proof). In our example: $e_{12} + e_{13} = e_{21}$ or $e_{21} = e_{12} + e_{32}$ (Fig. 1A). This property has two consequences. First, in each loop all transitions have the same elasticity value as can be seen in Fig. 1B and C. We term this value the "characteristic elasticity" of the loop. Second, the elasticity of each transition in the matrix can be thought of as being built up by the elasticities of loops passing through that transition, and consequently can be decomposed into the contributing

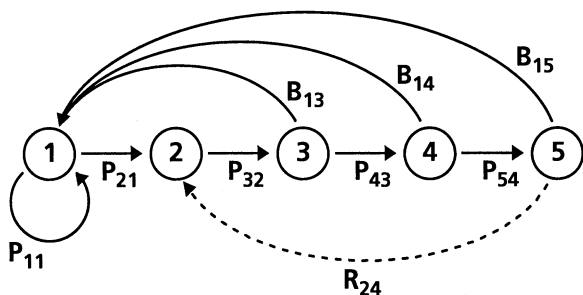


FIG. 2. Life cycle graph (solid arrows) for a structured population of *Poa annua* based on stage categories and on time steps of 3 mo, according to Law (1975). Numbers refer to life cycle stages: 1 = seeds in the seedbank; 2 = juveniles; 3 = young adults; 4 = adults; 5 = senescing adults. P transitions represent growth and survival, B transitions represent seed production. The dashed arrow (R_{24}) is a hypothetical transition used in the mathematical proof of the Appendix.

characteristic elasticities. Thus, e_{21} is the sum of the characteristic elasticities of the early and late reproduction loops. Some elements (such as B_{12} and B_{13} in our example) correspond to only a single loop and the elasticity values of these unique transitions equal the characteristic elasticity of the loop to which they correspond. (2) The elasticity of a loop is equal to the characteristic elasticity multiplied by the number of transitions of the loop. The elasticities of all loops in a matrix sum to one (see Appendix for proof). This is an important property because it shows that the relative nature of elasticities is maintained in loop analysis; loop analysis is just another way of decomposing the total response to relative perturbation. Consequently, loop elasticities quantify the relative contributions of alternative life history loops to λ and can thus be used for comparisons between alternative life history traits.

The following procedure contains the basic steps for performing loop analysis: (1) Construct a life cycle graph and population transition matrix of the population under investigation. The way in which the life cycle graph is constructed may influence the subsequent decomposition into loops (see point 3 below). Basic construction rules (van Groenendael et al. 1988, Caswell 1989a) can be used to obtain an optimal life cycle representation. (2) Calculate the elasticity values from the limit properties of the matrix according to equations in, for example, Caswell (1989a). (3) Decompose the life cycle graph into *unbranched loops* in such a way that all transitions are incorporated *at least once* into some loop. Each of the loops should contain at least one transition element that is unique to that loop, i.e., an element that corresponds only to one particular loop and not to others. The elasticity of this unique element equals the characteristic elasticity of the loop. (The condition that each loop should contain an element that is unique to that loop is not strict. If no unique element is present, the characteristic elasticity can be obtained by simple decomposition if the total number of loops in the population does not exceed the number

of transition elements [J. van Groenendael, *unpublished data*]. This is based on the property that the elasticity of each element is the sum of the characteristic elasticities of the loops passing through that transition.) Some life cycles may be decomposed into unbranched loops in more than one way. In such cases the loops can be chosen that reflect best the life history options of the species. (4) The loop elasticity is given by its characteristic elasticity multiplied by the number of transition elements that the loop contains. Summed over all loops the elasticity equals one.

EXAMPLES

Two examples are presented to demonstrate the merits of loop analysis when applied to the life cycle graphs of structured populations. The first example uses data for the annual grass *Poa annua* from Law (1975) as presented by Begon and Mortimer (1981). It addresses the issue of the variation in timing of reproduction in a monocarpic organism under increasing levels of density. The life cycle graph is presented as the solid lines in Fig. 2. Law (1975) formulated negative density-dependent relationships for seedling establishment (P_{32}) and seed production (the three B elements). Life cycle transitions that were density independent were given fixed transition probabilities. The density-dependent responses were evaluated by comparing five populations growing under increasing densities and the elasticity matrices for each of these populations are given

TABLE 1. Elasticity matrices for five populations (A to E) of *Poa annua* subjected to increasing density. Elasticity values are expressed as percent and the dominant eigenvalues (λ) are given as well. A is the population under the lowest density, E the population under the highest density.

Population	λ	Elasticity values (%)				
A	1.995	3.0	...	14.4	10.9	2.0
		27.3
		...	27.3
		12.9
		2.0	...
B	1.669	3.6	...	12.7	11.4	2.6
		26.6
		...	29.6
		13.9
		2.6	...
C	1.333	4.5	...	10.5	11.8	3.3
		25.7
		...	25.7
		15.2
		3.3	...
D	1.110	5.5	...	8.9	12.0	4.0
		24.8
		...	24.8
		16.0
		4.0	...
E	0.796	7.8	...	6.1	11.6	5.5
		23.2
		...	23.2
		17.1
		5.5	...

TABLE 2. Loop analysis for five populations (A to E) of *Poa annua* subjected to increasing density. The loops are: I = early reproduction; II = middle reproduction; III = delayed reproduction; IV = delayed germination. Note that the loop elasticities (given as percent) of a single matrix sum to one (except for rounding errors). The transition element containing the characteristic elasticity of the loop is given (see Fig. 2).

Popu- lation	Loop				Σ
	I	II	III	IV	
	Characteristic elasticity given by element				
	B_{13}	B_{14}	B_{15}	P_{11}	
A	43.2	43.6	10.0	3.1	99.9
B	38.1	45.6	13.0	3.6	100.3
C	31.5	47.2	16.5	4.5	99.7
D	26.7	48.0	20.0	5.5	100.2
E	18.3	46.4	27.5	7.8	100.0

in Table 1. Following the procedure outlined above, the life cycle graph of Fig. 2 can be decomposed into four loops: Loop I: early reproduction, transitions 3-1-2-3; Loop II: middle reproduction, transitions 4-1-2-3-4; Loop III: late reproduction, transitions 5-1-2-3-4-5; Loop IV: delayed germination, transition 1-1.

The result of the loop analysis readily shows the shift in importance between the various life history options in *Poa annua* (Table 2). As density increases, the importance of delayed reproduction and delayed germination increases at the expense of early reproduction. Such a shift is in accordance with expectations from life history theory. However, middle reproduction remains the most important life history pathway under all densities. While the top row elements in the elasticity matrix (Table 1) show similar shifts with increasing density as seen in the loop elasticities, they incorrectly represent the relative contributions to λ of each of the life history pathways. For instance, the elasticity values for late seed production (B_{15}) change from 2.0 to 5.5 from lowest to highest density (Table 1) and a similar relative shift can be seen in the loop elasticities for late reproduction (loop III, from 10.0 to 27.5, Table 2). However, the importance of late reproduction in comparison to other life history pathways increases dramatically from lowest to highest density, a phenomenon not obvious from the elasticity values of the single reproductive (B) elements as such. A correct assessment, therefore, of the effects of variation in life history traits is provided by the loop analysis.

A second more complicated example is given by *Hypochoeris radicata*, a perennial plant with rosettes capable of flowering as well as vegetative reproduction (ramification) resulting in the formation of side rosettes. A simplified life cycle graph for this species consists of three stages, juvenile rosettes, side rosettes, and mature rosettes (Fig. 3). Seeds take 2 yr to mature and juvenile rosettes are unable to ramify or flower. Side rosettes, however, may ramify or flower in the year following their formation. Projection matrices were

constructed for "colonizing" (establishing) roadside verge populations of *H. radicata*, subjected to three levels of artificial disturbance (mowing frequencies). In addition some of the elements in the transition matrix were made density dependent, and an iterative procedure resulted in the formation of matrices for "stable" populations in which there was no net change in population density (see de Kroon et al. 1987 for details).

Loop analysis applied to the life cycle of *H. radicata* as depicted in Fig. 3 results in the formation of five loops belonging to three categories: Loop I: survival (of mature rosettes), transition 3-3; Loop II: vegetative ramification, subdivided in IIa: ramification by side rosettes, transition 2-2 and IIb: ramification by mature rosettes, transitions 3-2-3; Loop III: sexual reproduction, subdivided in IIIa: seed production by side-rosettes, transitions 2-1-3-2 and IIIb: seed production by mature rosettes, transitions 3-1-3. This division allows an examination of the contribution of the different modes of reproduction (sexual vs. vegetative) to the life history of the species and of reproduction vs. survival. A preliminary analysis of life history pathways in *H. radicata* was presented in de Kroon et al. (1987).

The results show that in colonizing populations sexual reproduction is of overwhelming importance compared to the other life history options, especially when the population is subjected to the most intense disturbance regime (Fig. 4). The relative contributions of the vegetative ramification loops (IIa, IIb) are small, but it must be noted that the importance of sexual reproduction by side rosettes (Loop IIIa) may be considerable. Thus, in establishing populations of *H. radicata*, side rosette formation seems to serve the life history function of increasing the impact of sexual reproduction. Survival of rosettes plays a negligible role in the life history of *H. radicata*. Compared to colonizing populations, in stable populations of high density vegetative ramification increases in importance relative to

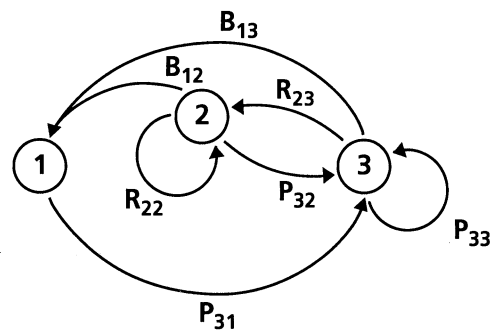


FIG. 3. Simplified life cycle graph for a population of *Hypochoeris radicata*. Stages are 1 = juvenile rosettes; 2 = side rosettes; 3 = mature rosettes. In the transition matrix the side and mature rosettes are subdivided in flowering and nonflowering categories as well as in size classes (see de Kroon et al. 1987), but for the sake of clarity this subdivision is omitted here. P transitions represent growth and survival, R transitions represent side rosette formation, and B transitions represent seed production.

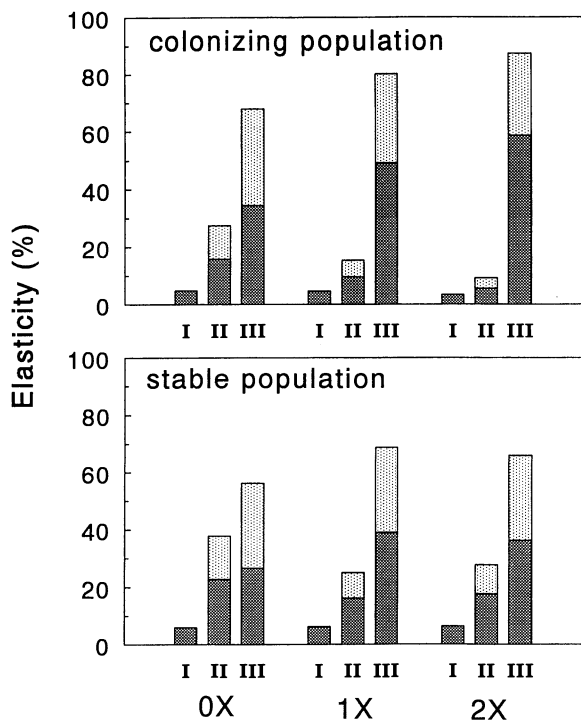


FIG. 4. The results of loop analysis for *Hypochaeris radicata*. The population is composed of five life history loops divided in three categories, survival (I), vegetative ramification (II), and sexual reproduction (III). Each of the latter two categories is divided into two loops representing contributions made by mature rosettes (dark shaded bars) and side rosettes (light shaded bars). Populations are compared that differ in age ("colonizing" populations that have recently established and "stable" populations growing under high density) and in the intensity of artificial disturbance (mowing frequency: 0 \times = no mowing, 1 \times = mowing once a year, 2 \times = mowing twice a year). Population growth rates λ for the colonizing populations are 1.27, 1.42, and 1.95 for mowing frequencies 0 \times , 1 \times , and 2 \times , respectively. For all three stable populations, λ equals one.

sexual reproduction (Fig. 4). However, sexual reproduction remains the most important life history pathway, and a major contribution is still made by the seed production of side rosettes. The impact of disturbance diminishes in stable compared to colonizing populations (Fig. 4).

These results of the loop analysis show how shifts in vegetative vs. sexual reproductive pathways occur in response to disturbance and density-dependent processes. They also point at the interaction between both modes of reproduction. Because vegetative side rosettes of *H. radicata* mature rapidly and are capable of flowering in the year after they are formed, their seed production is of major importance in the life history of the species.

CONCLUSION

We conclude that loop analysis clearly elucidates the contributions of alternative life history pathways to

population growth rate. Such contributions are not evident from single elasticity values for a particular life history transition or from the sum of elasticity values for a group of life history transitions. Loop analysis, therefore, presents a meaningful decomposition of the effects of relative perturbations of the elements of population projection matrices and provides a potentially powerful tool to evaluate the population dynamical consequences of alternative life history solutions in life history studies.

ACKNOWLEDGMENTS

We thank Glenda Wardle, Miguel Franco, Jonathan Silvertown, and Hans Metz for fruitful discussions on the topic of elasticities. Nick Gotelli and an anonymous referee gave valuable comments on the manuscript. H. de Kroon gratefully acknowledges the Royal Netherlands Academy of Sciences for financial support during the preparation of this paper. S. Kalisz gratefully acknowledges support from the National Science Foundation grant BSR-9006647 and NSF Research Training Group grant BSR-9113598. This is Kellogg Biological Station contribution number 776.

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APPENDIX

Consider the population matrix $A = (a_{ij})$, with stable state structure vector \mathbf{u} , a reproductive value vector \mathbf{v} , and a geometric growth rate λ . Letting superscript T indicate a transpose, these quantities satisfy

$$\begin{aligned} A\mathbf{u} &= \lambda\mathbf{u} \\ \mathbf{v}^T A &= \lambda\mathbf{v}^T. \end{aligned} \tag{A.1}$$

The relative impact of changes in the transition rate a_{ij} may be described by the elasticity

$$e_{ij} = \frac{\partial \log \lambda}{\partial \log a_{ij}} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} = \frac{a_{ij}}{\lambda} \frac{\mathbf{v}_i \mathbf{u}_j}{\langle \mathbf{v}, \mathbf{u} \rangle}. \tag{A.2}$$

Here we write $\langle \mathbf{v}, \mathbf{u} \rangle = \sum_i v_i u_i$ for the scalar product of the vectors $\mathbf{v} = (v_i)$ and $\mathbf{u} = (u_i)$. It is known (de Kroon et al. 1986, Messerton-Gibbons 1993) that using Eqs. A.1 and A.2, one has

$$\sum_i \sum_j e_{ij} = 1. \tag{A.3}$$

Property 1. Fix a particular life state i . Let the rates a_{ij} , for all j , be called the rates of *incoming* transitions, and the rates a_{ji} , for all j be called the rates of *outgoing* transitions. Then

$$\sum_{\text{incoming transitions}} e_{ij} = \sum_{\text{outgoing transitions}} e_{ji}. \tag{A.4}$$

Proof. From Eq. A.1 we have

$$\begin{aligned} \lambda u_i &= \sum_j a_{ij} u_j, \\ \lambda v_i &= \sum_j v_j a_{ji}. \end{aligned}$$

Multiply the first of these by v_i and the second of these by u_i , then divide each result by $\lambda \langle \mathbf{v}, \mathbf{u} \rangle$, to find

$$\frac{u_i v_i}{\langle \mathbf{v}, \mathbf{u} \rangle} = \sum_j \frac{a_{ij} v_i u_j}{\lambda \langle \mathbf{v}, \mathbf{u} \rangle} = \sum_j \frac{a_{ji} v_j u_i}{\lambda \langle \mathbf{v}, \mathbf{u} \rangle}.$$

From Eq. A.2 this is Eq. A.4.

Property 2A. Consider a life cycle whose transition matrix A has the structure of a Leslie matrix, but with the addition of self-loops, as shown by the solid lines in the life cycle graph of Fig. 2. In general notation we have $a_{i+1,i} > 0$ for $1 \leq i < k$; a set of (“reproductive”) states $J = (s_1, s_2, \dots, s_M)$ with $M \leq k$ and $1 \leq s_1 < s_2 < \dots < s_M \leq k$, such that $a_{i_i} > 0$ for every i in the set J ; for some indices i with $1 \leq i \leq k$ we have $a_{i_i} > 0$; and, all other $a_{ij} = 0$. Then

$$\sum_i e_{i,i} + \sum_{l \in J} l e_{l,l} = 1. \tag{A.5}$$

Proof. First consider the case where there are no self-loops for $i > 1$, so that all $a_{i,i} = 0$, for $i > 1$. In this case, notice that in this life cycle all loops pass through stage 1. Define the indicator function

$$I(l) = \begin{cases} 1, & \text{if } l \text{ is in set } J \\ 0, & \text{otherwise.} \end{cases}$$

Apply Eq. A.4 to state i with $2 \leq i \leq k - 1$, to find

$$e_{i,i-1} = e_{i+1,i} + I(i)e_{i,i}.$$

Applying Eq. A.4 to state k yields

$$e_{k,k-1} = I(k)e_{k,k}.$$

Using this last equation in the preceding one yields

$$e_{i,i-1} = \sum_{m \geq i} I(m)e_{1,m}, \quad \text{for } i \geq 2. \tag{A.6}$$

Now recall Eq. A.3, which for the life cycle of Fig. 2 may be written as

$$\begin{aligned} 1 &= \sum_i \sum_j e_{ij} \\ &= I(1)e_{11} + \sum_j I(j)e_{1j} + \sum_{i \geq 2} e_{i,i-1}. \end{aligned}$$

Using Eq. A.6 yields

$$1 = I(1)e_{11} + 2I(2)e_{12} + 3I(3)e_{13} + \dots,$$

which is the result (Eq. A.5) when only state 1 has a self-loop.

In the presence of other self-loops, note first that if we apply Property 1 to a node i that has a transition element $a_{i,i} > 0$, that self-loop contributes the same elasticity $e_{i,i}$ on both sides of Eq. A.4. Therefore the equations leading up to Eq. A.6 in the preceding discussion are unaffected by self-loops, and Eq. A.6 will continue to hold in the presence of self-loops. Applying Eq. A.3 to a life cycle with self-loops yields

$$\begin{aligned} 1 &= \sum_i \sum_j e_{ij} \\ &= \sum_i e_{i,i} + \sum_j I(j)e_{1j} + \sum_{i \geq 2} e_{i,i-1}. \end{aligned}$$

Now apply Eq. A.6 to get

$$1 = \sum_i e_{i,i} + 2I(2)e_{12} + 3I(3)e_{13} + \dots,$$

which is the desired result (Eq. A.5).

Property 2B. Suppose we add to the Leslie matrix life cycle of Fig. 2 a disjoint transition that connects states p and q with $1 < p < q$ and $a_{pq} > 0$, as shown by the dashed line in Fig. 2. Then Eq. A.5 is replaced by

$$(q - p + 1)e_{pq} + \sum_i e_{i,i} + \sum_{l \in J} l e_{l,l} = 1. \tag{A.7}$$

Proof. We prove this when there are no self-loops; the latter are handled in the same way as in the preceding proof. Adding the dashed line transition in Fig. 2 causes the following changes in the proof of Property 2A. Applying Eq. A.4 to state p we have

$$e_{p,p-1} = e_{p+1,p} - e_{pq} + I(p)e_{1p}, \quad \text{and}$$

applying Eq. A.4 to state q we have

$$e_{q,q-1} = e_{q+1,q} + I(q)e_{1q} + e_{pq},$$

while the application of Eq. A.4 to every other state yields the same result as in the proof of Property 2A. Therefore Eq. A.6 will remain valid for $i > (q + 1)$ and $i \leq p$, but

$$e_{i,i-1} = e_{pq} + \sum_{m \geq i} I(m)e_{1,m}, \quad \text{for } p < i \leq q.$$

Using these relationships in Eq. A.3 we get

$$(q - p + 1)e_{pq} + \sum_{l \in J} l e_{l,l} = 1.$$

Adding the self-loop contributions results in Eq. A.7.