

A GRAPH THEORY APPROACH TO DEMOGRAPHIC LOOP ANALYSIS

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Abstract. A demographic analysis of the life-cycle graph can be used to quantify the separate contributions of different life-history types to the population growth rate. Loop analysis has been proposed (van Groenendael et al. 1994) as the appropriate method for partitioning the elasticity matrix to determine these contributions. However, in the analysis of complex demographic models it is difficult to derive the loops by simple inspection of the life-cycle graph. I show how graph theory can be used to describe a general and systematic procedure for deriving the loops from the structure of the life-cycle graph. I demonstrate that the concept of nullity (from graph theory) can be applied in this context to correctly determine the number of loops for any graph. Using examples from *Campanula americana*, *Dipsacus sylvestris*, and *Caretta caretta*, I illustrate the relationship of the loops to biologically relevant life-history contrasts. This relationship is crucial for the application of loop analysis to life-history evolution for the purpose of partitioning the separate effects on the population growth rate among different life-history components.

Key words: *Campanula americana*; *Caretta caretta*; demographic loop analysis vs. summed elasticities; *Dipsacus sylvestris*; elasticity analysis; graph theory; life-cycle graphs; life history; loop analysis; population growth rate; projection matrices.

INTRODUCTION

The standard theory of life-history evolution invokes trade-offs between different components of fitness or modes of reproduction. Examples of trade-offs include survivorship vs. reproduction, present vs. future reproduction, and sexual vs. asexual reproduction (Roff 1992, Stearns 1992). Matrix projection models are commonly used to examine these fundamental contrasts in life-history evolution (van Groenendael et al. 1988, Caswell 1989). Typically, because population growth rate (λ) is a measure of fitness, demographic models have included perturbation analyses to determine elasticity, defined as the proportional sensitivity of λ to elements of the life-history matrix (de Kroon et al. 1986). This approach has been used to draw evolutionary inferences about the adaptive function of life-history features and the selective forces shaping life histories. However, the matrix elements (in stage-based models) are complex mixtures of life-history characters, such as survival and growth or survival and fecundity (van Groenendael et al. 1994), and the interpretation of the sensitivity of λ is not straightforward (Caswell and Trevisan 1994). For this reason, summing elements in the elasticity matrix (Silvertown et al. 1992, 1993) is not a useful method for contrasting one life-history type with another in comparative studies of life-history evolution (van Groenendael et al. 1994).

Models of life-history evolution compare different life histories with respect to fitness or, in this case, population growth rate. Because any one life history involves a suite of matrix elements, including birth, death, and stage transitions, a more appropriate method for comparing the relative contributions of different life-history morphs to the population growth rate is demographic loop analysis (van Groenendael et al. 1994). Loop analysis permits a morph-specific decomposition of the elasticity matrix, and thereby elucidates the total contributions of alternative life-history pathways to the population growth rate. However, loop analysis requires a complete listing of all possible loops for any life-cycle graph. It is not obvious how to generalize the examples of simple life-cycle graphs discussed by van Groenendael et al. (1994), each of which has relatively few stages and loops that are apparent by inspection. For more complex life histories, finding all possible loops by trial and error is nontrivial. In addition, because it is possible to construct more than one set of loops for demographic graphs with many stages and transitions, some guidelines are necessary for choosing among alternative sets of loops.

The analysis of demographic models has made extensive use of the projection matrix and the methods of linear algebra to calculate population growth rates and sensitivities (Caswell 1989). Alternative methods are based directly on the life-cycle graph (Caswell 1989). In particular, Lewis (1972, 1976) introduced z -transforms of the life-cycle graph to provide analytical expressions for the characteristic equation. In a simplification of Lewis' method for projecting the growth of a population with a heterogeneous life history, Hub-

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bell and Werner (1979) defined reproductive paths or loops and calculated the cumulative, overlapping contributions of each path to the population growth rate. Hubbell and Werner (1979:291) anticipated the recent application of graphs to population demography: "Finally, the method should aid in the study of the evolution of life-history patterns since it enables one to determine the efficacy of various mixed life-history strategies in raising the intrinsic rate of increase. It makes explicit how each life-history path contributes to the overall rate of population growth." Although the Hubbell and Werner method of finding reproductive loops is superficially similar to that of van Groenendael et al. (1994), elasticities were not described until de Kroon et al. (1986). The loop elasticities represent the relative contribution of the life-history types to fitness and are particularly important for the evolutionary interpretation.

Although both use a life-cycle graph, neither Hubbell and Werner (1979) nor van Groenendael et al. (1994) give a systematic method for deriving the loops. However, a general framework for deriving loops from an arbitrary graph has been given in the context of electrical circuits (e.g., Chen 1976, 1990), a literature probably not familiar to demographic researchers. In this paper, I explore the implications of graph theory for analyzing loops in demographic models and generalize the loop-analysis method to arbitrarily complex demographic models. First, I review the method of demographic loop-analysis proposed by van Groenendael et al. (1994). Second, I introduce necessary background from graph theory and discuss the concepts relevant to the analysis of demographic models. Last, I illustrate loop analysis for demographic models from the literature and from my own work on *Campanula americana*, a plant with populations containing both annuals and biennials. The conclusions from loop analysis are contrasted with interpretations drawn directly from the elasticities of each matrix element or from summing groups of elasticities. I show with these contrasts that loop analysis is an improved heuristic framework for studying life-history evolution.

LOOP ANALYSIS

A demographic model consists of stages and transitions between stages that describe the fates of individuals in terms of growth, survival, and reproduction at successive time intervals. The stages and the transitions are the nodes and edges of the life-cycle graph, respectively. A demographic life-cycle graph is "directed" in the sense that the transitions are the probability of an individual moving unidirectionally from one stage to another. For each edge in the life-cycle graph, the arrowhead defines the direction of the stage transition. The weight or value of the edge is the transition probability.

Loop analysis combines elements of both matrix and graph analysis. The loops are derived directly from the

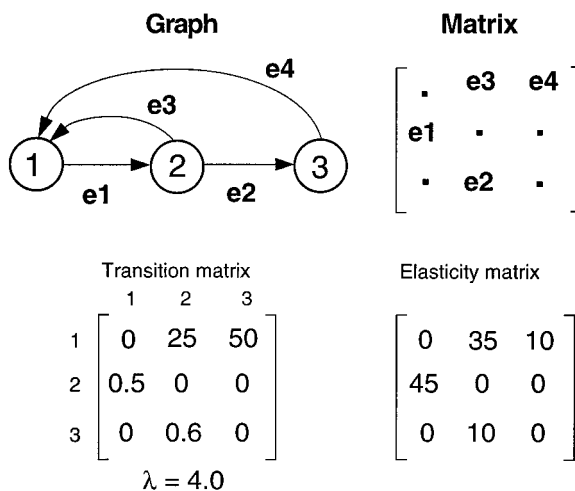
structure or connections of the nodes in the directed life-cycle graph. The structure of the model therefore determines the loops and delimits the potential comparisons among the life-history variables. A biological interpretation of the loops requires that the loops retain the same direction as the flow of individuals from one stage to the next through the life cycle.

Elasticities or proportional sensitivities (de Kroon et al. 1986) are calculated from the matrix of transition elements, and they become the weights on the edges of the directed graph of the elasticity matrix. The elasticities sum to 100% (de Kroon et al. 1986; Mesterton-Gibbons 1993). The sum of the elasticities for transitions entering a node is equivalent to the sum of the elasticities for transitions leaving a node (i.e., the row total equals the column total, of the elasticity matrix—see Table 2). This conservation of elasticity at a node implies that elasticities represent the flow of a conserved quantity through the graph. However, in the original matrix individuals are not conserved, because some of them die and leave the system. Therefore, because elasticities represent the contribution of the separate matrix elements to increasing the population growth rate, they must do so through the effects of individuals that actually complete the life cycle.

As a consequence of the conservation of elasticity at a node, each loop has a "characteristic elasticity," which is defined as the elasticity of the transition element that is unique to that loop. Furthermore, each element of the elasticity matrix is the sum of the characteristic elasticities that comprise that element. And lastly, the "loop elasticity" is the sum of the characteristic elasticities on each step in the loop (which is equivalent to the characteristic elasticity multiplied by the number of steps in the loop). For these reasons, the loop elasticities are additive and sum to 100% (van Groenendael et al. 1994). Therefore, the total elasticity can be decomposed into a set of loop elasticities representing the paths followed by individuals in the population. The loop elasticities can also be combined (e.g., in order to compare two life-history morphs each of which is age structured as in the *Campanula americana* example discussed below).

The general method of demographic loop analysis summarized from van Groenendael et al. (1994) involves four steps: (1) Construct a life-cycle graph and population transition matrix of the population under investigation. (2) Calculate the elasticity values of the matrix according to equations in, for example, Caswell (1989). (3) "Decompose the life cycle graph into *unbranched loops* in such a way that all transitions are incorporated *at least once* into some loop" (van Groenendael et al. 1994:2412 [italics in original]). The characteristic elasticity of the loop is equal to the elasticity of the element that is unique to the loop. (4) The loop elasticity is given by its characteristic elasticity multiplied by the number of transition elements that the

FIG. 1. Example of a graph with three nodes (numbers in circles) and four edges (e1, . . . , e4). It is a “directed graph” because the edges have an orientation (expressed by arrowheads). The position of each of the four edges is shown in the corresponding matrix. The transition matrix values are given and were used to calculate the population growth rate, $\lambda = 4.0$. Finally, the figure also presents the matrix of elasticities expressed as percentages.



loop contains. The elasticity summed over all loops = 1.

Graph theory provides a systematic procedure for constructing the loops at step (3) that avoids missing or incorrectly identifying loops, errors that can cause the sum of the loop elasticities to deviate from 1. In the next section, I first introduce some concepts from graph theory. I then show how to calculate the number of loops that are contained in an arbitrary life-cycle graph and how to determine a set of independent loops for any life-cycle graph.

GRAPH THEORY AND ITS APPLICATION TO LOOP ANALYSIS

An introduction to graph theory is provided by Wilson (1985). I first define several concepts from graph theory (Chen 1976, 1990). A *graph*, as used here, is a geometrical figure consisting of points (*nodes*) and lines (*edges*) that connect some of these points. In the case of a demographic model, the *stages* of the life cycle are the nodes, and the *transitions* among the stages are the edges of the graph. The edges have a direction from one node to the next indicated by the direction of the arrowhead on the graph (Fig. 1). A sequence of edges is defined as “open” if the initial node does not equal the final node and “closed” if the final node is the same as the initial node. A *path* is an open sequence of distinct edges and nodes, and a *loop* is a closed sequence of distinct edges. A *self-loop* (an edge returning to the same node) is a closed path of length 1.

A *component* is a connected subset of the graph containing the maximal number of edges. In general a graph may consist of several isolated components, but a demographic life-cycle graph, for which the corresponding matrix is irreducible (Caswell 1989), has only one component, because each stage of the life cycle can be reached from at least one other stage. A *spanning subgraph* is a subset of the graph that connects

each node. A *tree* is a spanning subgraph that contains no loops and is connected by $n - 1$ edges, where n = the number of nodes (Fig. 2). A *cotree* is the complement of a tree, that is the remaining edges of the graph that were not incorporated into the tree. An edge in a cotree is a *chord*. A tree and its cotree together comprise the entire graph.

Calculating the number of loops

The number of loops is equivalent to the *nullity*, L ,

$$L = b - n + c \tag{1}$$

where b is defined as the number of edges in the graph, n is the number of nodes, and c is the number of components (Chen 1976). As noted above, c is always 1 for demographic life-cycle graphs. For example, the graph of *Poa annua* (originally analyzed by Law et al. 1977) has five stages, eight transitions (or edges), and four loops (van Groenendael et al. 1994), in agreement with the nullity of the graph, $L = 8 - 5 + 1 = 4$. In *Hypochoeris radicata* (van Groenendael et al. 1994), which has three stages and seven transitions, the number of loops, $L = 7 - 3 + 1 = 5$, again in agreement with van Groenendael et al.’s enumeration of the loops. For examples with relatively few stages and transitions, it is not difficult to arrive at the number of loops by inspection. However, for larger models that are strongly connected (i.e., with many pairs of nodes that have transitions in both directions between them), the loops can be difficult to construct. It is helpful in these models to know the number of loops so that a set of unique loops can be determined, where each transition is included in at least one loop.

Obtaining the trees for a graph

In general, more than one tree is possible for each graph, and each tree will give a set of independent and unique loops. Algorithms are available for determining all possible trees for an arbitrary graph (Chen 1976:

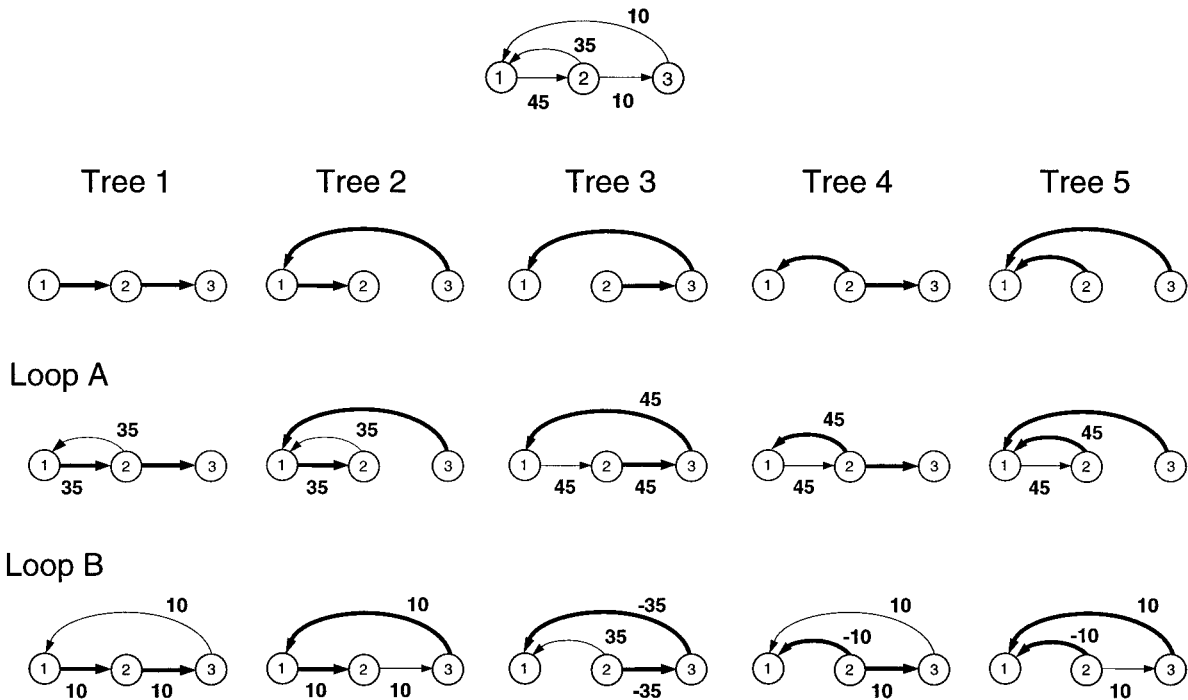


FIG. 2. The basic graph in the top panel is that of Fig. 1. The elasticity values (%) are shown as the weights on each of the edges in the graph. Shown below the basic graph are the five trees and the sets of two loops for each tree derived from this graph. The edges of the trees in loops A and B are shown as bold arrows; the chords are fine-line arrows. The tree and one of the chords from the cotree combine to form a loop. For example, using Tree 1, the A-loop (1-2-1) is formed by the edges of the tree + edge (e3), and the B-loop (1-2-3-1) is formed by Tree 1 + e4. The elasticities for each edge in the graph are given and are used to calculate the loop elasticities. In all cases the sum of the elasticities over all loops derived from a single tree is 100%. The edges of the B-loop for Tree 3, Tree 4, and Tree 5 do not all have the same orientation, and therefore the edges that are not in the same direction of the chord are assigned a negative value. The implications of this are discussed in the text (see *Graph Theory and its application . . . : Choosing alternative trees . . .*).

332 and Carre 1979: 163). The simplest way to generate trees of an n -node connected graph is to examine all possible combinations of $n - 1$ edges. This can be difficult because the number of operations in which trees are generated and checked against previously found trees varies exponentially with the number of nodes. A better approach is to generate the trees without duplication (Chen 1976). Fortunately, for the purposes of demographic loop analysis it is not necessary to obtain all trees of a graph. It is possible to start with a single tree and to construct a set of distinct loops directly from the tree. Biological reasons for choosing one set of loops over another are discussed below (see *Choosing among alternative trees . . .*).

A tree of a graph can be constructed by a systematic backtracking procedure (Read 1979). Each tree consists of $n - 1$ edges and must satisfy the requirement that all the nodes are connected by at least one edge, and there must be no loops in the tree. To obtain a tree start by drawing all the nodes. Choose any node to be the first active node, also known as the "reference node" or the "root of the tree." Next, add an edge that connects the active node to a second node. The node at the other end of the edge then becomes the active node. Add a second edge, not previously examined, that con-

nects the new active node to a further node, but that does not result in a loop in the tree. Repeat this procedure until all nodes are connected. Eventually all edges joined to the active node will be either in the tree or eliminated. The next step is to backtrack to the previous active node and choose, if possible, another potential edge that can be joined to this node. If no edges can be added to the tree from this node then backtrack again. The procedure ends when the backtracking has returned to the root of the tree, and there are no further edges to examine. For example, the graph in Fig. 1 has three nodes and therefore each tree will comprise $n - 1 = 2$ edges. Tree 1 (Fig. 2) was constructed by using node 1 as the reference node. The edge e1, was added to the tree, and node 2 became the active node. The edge e2 is added to the tree. The edge e4 is rejected because it would complete a circuit, so we backtrack to the previous active node 2. Edge e3 is also rejected because it would complete a circuit and so we backtrack to node 1, the root. The procedure stops because all edges have been examined, and all nodes are connected by the set of 2 edges, {e1, e2}, that comprise the tree. The five trees constructed by starting with different reference nodes are shown in Fig. 2. It is not possible to have a tree consisting of

the edges e_1 and e_3 , because node 3 will not be connected and the subgraph violates the requirement that it contain no loops.

Determining a set of independent loops for a life-cycle graph

The first step is to identify a tree for the graph using the procedure described above. Because there is a unique path between any two nodes in a tree, the addition of a chord to the tree produces a loop contained in the resulting graph. Thus, a loop is the result of a tree plus a chord from the corresponding cotree. Further, each of the chords in a cotree defines a loop (with respect to the tree) in a unique way. The number of loops will correspond to the number of chords in the cotree. Therefore, for any tree of a graph, it is possible to systematically construct the associated set of loops. As an example, if we consider the graph in Fig. 1 we can construct two loops for each tree (Fig. 2). The graph has four edges, $\{e_1, e_2, e_3, e_4\}$. Tree 1 (Fig. 2) consists of two edges $\{e_1$ and $e_2\}$. Loop A of Tree 1, consists of the tree and the chord $\{e_3\}$. This loop can also be described by the nodes it passes through, i.e., 1-2-1. Loop A has two steps, and the loop only includes one of the edges of the tree in the loop. The second loop (B) of Tree 1 consists of the edges $\{e_1, e_2\}$ from Tree 1 and the chord $\{e_4\}$, and so it has three steps and passes through the nodes 1-2-3-1. Notice that, although Loop B is derived from the same tree, $\{e_1, e_2\}$, it includes both of the edges of the tree in the loop.

Calculating loop elasticities

The hypothetical life-cycle graph (Fig. 1) is for a three-stage semelparous organism with two options for reproduction, early (at stage 2) or late (at stage 3) and is from van Groenendael et al. (1994). The transition matrix is used to calculate the population growth rate ($\lambda = 4.0$) and the elasticities (Fig. 1). The goal of loop analysis is to partition the elasticities into a set representing early reproduction (Loop A) and a set representing late reproduction (Loop B). The elasticity values are the weights on the edges in the graph, and the elasticity on the chord defines the characteristic elasticity of the loop. Because of the property of conservation of elasticity at a node it follows that the elasticity entering a node is the same as the elasticity leaving a node. Therefore, the characteristic elasticity also defines the elasticity for all edges in the loop. In our example the chord (defined as the edge that is not part of the tree) for Loop A has an elasticity of 35%, and there is one other edge in the loop that is then assigned this same elasticity (Fig. 2). The loop elasticity is obtained by summing the elasticity on each edge in the loop, i.e., 70% for Loop A. Similarly Loop B has a characteristic elasticity of 10% and a loop elasticity of 30%. The sum of the elasticity over all loops is 100% as required. The loop elasticities can then be interpreted to state that early reproduction contributes proportion-

ally more to the population growth rate than late reproduction in this life cycle. The loops from Tree 1 discussed here are the same as those presented for this model by van Groenendael et al. (1994). However, we now need to discuss the alternative sets of loops that can be constructed from this model (Fig. 2).

Choosing among alternative trees for a life-cycle graph

Other trees from the graph may produce the same loops as Tree 1, but this is not necessarily the case. For example, the loops for Tree 2 are identical to those from Tree 1, but those from the remaining Tree 3, Tree 4, and Tree 5 differ (Fig. 2) in either the structure of the loops, the loop elasticities, or both. What is now required are guidelines for choosing among the sets of loops.

The choice of tree depends first on the biological comparisons for which the model is designed and second on the desired property that the resulting loops are positive. The direction of the chord defines the direction of the loop, and a positive loop is one in which all edges of the loop have the same orientation as the chord. This is not problematic for an undirected graph, but for demographic loop analysis, if the directions do not agree, then the loop elasticities will fail to meet the requirement that the sum of the loop elasticities must be 100%.

Negative loops do not have the directions on the arrows flowing in a circular pattern (i.e., there will be a closed path or loop formed by the tree and the chord, but at least one of the edges will be in the opposite direction to the chord, and therefore two arrows will point to the same node). For example, in Fig. 2 Tree 5 has two loops, but the edges of the loop (B) do not have the same orientation. A negative loop, therefore, does not admit the biological interpretation of demographic loops as the paths that individuals follow in the life cycle. I have found that trees that contain either multiple edges entering (e.g., Tree 5) or leaving (e.g., Tree 4) a node often lead to negative loops and should therefore be avoided when constructing demographic loops. I also recommend that, when there are two edges connecting a pair of nodes, if possible, one of these edges be included in the tree. In the Fig. 2: top-panel example the edges e_1 and e_3 (defined in Fig. 1) both connect node 1 and node 2. When only one of these edges is included in the tree, as in Tree 1 and Tree 2, there are no negative loops. However, in the case of Tree 3, where neither is included, there are negative loops.

A possible solution to the problem of negative loops is to examine other trees of the graph until a tree with only positive loops is identified. This will not always be possible, however, as I have found that some demographic models do not have a set of loops that contain only forward flowing loops. An example of how

to deal with negative loops is discussed below for the model of teasel (*Dipsacus sylvestris*).

The "unique element" (or the chord) of the loop is important, because it is used to define the characteristic elasticity of a loop. From the definition of loops above we know that every loop will have a unique element, because each chord in the cotree is unique. Therefore, there is a slight difference in meaning between the strict definition of a loop above and that expressed by the following statement from van Groenendael et al. (1994: 2412): "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." Eq. 1 shows that this condition always holds because, for demographic models, $c = 1$, and the number of nodes $n \geq 1$. For example if $n = 1$, Eq. 1 implies that $L = b$ (that is, in a graph with only one node every edge would be a self loop), and if $n > 1$ then $L < b$, and the number of loops is less than the number of transition elements as required. It turns out, however, that the set of independent loops can be redefined to include loops that do not have a unique element. An example of this is discussed below for the teasel model in which the loops were redefined in response to the problem of a negative loop.

EXAMPLES

The following examples of demographic models of two herbaceous plants, *Campanula americana* and *Dipsacus sylvestris*, and the loggerhead sea turtle, *Caretta caretta*, will be used to illustrate the value and limitations of loop analysis. I emphasize the relationship of the loops to biologically relevant life-history contrasts. This relationship is crucial for the application of loop analysis within the context of life-history evolution, that is for partitioning the effects of different life-history pathways on the population growth rate.

The *C. americana* example is a relatively simple three-stage life-cycle graph that nevertheless embodies two important life-history contrasts, namely, delayed reproduction and the effect of a seed bank. I use this example to introduce the calculation of loop elasticities for a realistic biological model and to demonstrate an appropriate and straightforward application of the loop-elasticity methodology. This approach avoids the problems encountered by summing down rows and columns of the matrix of elasticities or of defining functional combinations of matrix elasticities as described by Silvertown et al. (1992). The model of *D. sylvestris* is a strongly connected life-cycle graph that further illustrates the utility of the graph-theory approach to demographic loop analysis, because the loops cannot be constructed by simple inspection. This teasel model also serves to motivate the discussion of a further refinement of the method of calculating loop elasticities

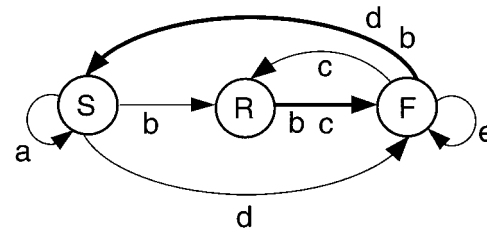


FIG. 3. The life-cycle graph of *Campanula americana*. There are three stages: S = dormant seeds, R = rosettes, and F = individuals that have flowered. The five demographic loops are labeled a–e. A loop consists of all the edges that are labeled with the same letter. For example, the b-loop begins at the F stage and then passes through the S and R stages before returning to the F stage. The edges of the tree are shown in bold, and each of the other edges is a chord in the cotree.

for loops. Both of these models lead to appropriate conclusions from the loop elasticities. In contrast, the third example of *C. caretta* illustrates the need for careful biological interpretation of loop elasticities. The published account of this model (Crouse et al. 1987) emphasizes the contribution of the vital rates at each stage to the population growth rate. The loop analysis however, focuses on multistage transitions and does not necessarily address changes that affect a single stage. However, the calculation of loop elasticities presented here does highlight the effect of vastly different stage durations in this model.

Campanula americana, a monocarpic herbaceous plant

This example compares the contribution of winter annual and biennial life-history types in the monocarpic herbaceous plant *C. americana*. The life-cycle graph (Fig. 3) has three nodes or stages: S = seeds in the seed bank, R = rosettes, F = individuals that have flowered. There are seven edges or transitions among the stages. Each transition represents the fate of an individual one year later in terms of growth, survivorship, or fecundity. The nodes are all connected by edges, and therefore there is only one component in this graph. From Eq. 1 we can calculate the nullity or number of loops as: $L = 7 - 3 + 1 = 5$. The elasticities are calculated from Wardle (1995). The important contrasts in this model are winter annual vs. biennial life histories and the role of age structure in terms of older winter annual and biennials emerging from the seed bank. The five demographic loops are shown in Fig. 3. The loop elasticities (Table 1) show that the biennials contribute more to the population growth rate than do winter annuals (75.4% > 4.3% and 16.8% > 2.5%). Dormancy (i.e., remaining in the seed bank) has a loop elasticity of 1%. The biennials emerging in the first year after dispersal have the highest loop elasticity (75.4%). Therefore, for this population with a $\lambda = 3.6$, the winter annuals and the seed bank are not contrib-

TABLE 1. Demographic loop characteristics of *Campanula americana*.

| Loop | Unique edge in loop† | No. of edges | Elasticity of unique edge (%) | Loop elasticity (%) |
|--------------------------|----------------------|--------------|-------------------------------|---------------------|
| a) Persistent seed bank | S-S | 1 | 1.0 | 1.0 |
| b) Biennial (older) | S-R | 3 | 5.5 | 16.5 |
| c) Biennial | F-R | 2 | 37.7 | 75.4 |
| d) Winter annual (older) | S-F | 2 | 1.4 | 2.8 |
| e) Winter annual | F-F | 1 | 4.3 | 4.3 |
| Total | | | | 100.0 |

Notes: There are five loops labeled a–e, and these are also shown in Fig. 3. The loops give the contribution of biennial and winter annual life-history types to the population growth rate ($\lambda = 3.6$). Older individuals are those that have spent time in the seed bank. The data are from the Allegan 1991–1992 population (Wardle 1995).

† The three stages (nodes) in the *C. americana* life cycle are: S = seeds in the seed bank, R = rosettes, and F = individuals that have flowered.

uting as much as the earlier-reproducing biennials to the growth rate of the population.

These types of comparisons would not be possible by summing the elasticities down the column of the matrix or by using functional definitions of the matrix elements as in Silvertown et al. (1992). The transitions in this model, such as the element representing the transition from stage “F” to stage “S,” are combinations of both winter annual and biennial seeds entering the seed bank. Loop analysis is the only method that provides a decomposition of the elasticity matrix into the contribution of each life-history type. Further analysis of this model including the statistical significance of the individual loops is presented elsewhere (Wardle 1995).

Dipsacus sylvestris, a monocarpic perennial plant

The second example is for a monocarpic perennial, *Dipsacus sylvestris*, or teasel, first described by Werner (1975), Werner and Caswell (1977), Caswell and Werner (1978), and then reanalyzed by Caswell (1989). The

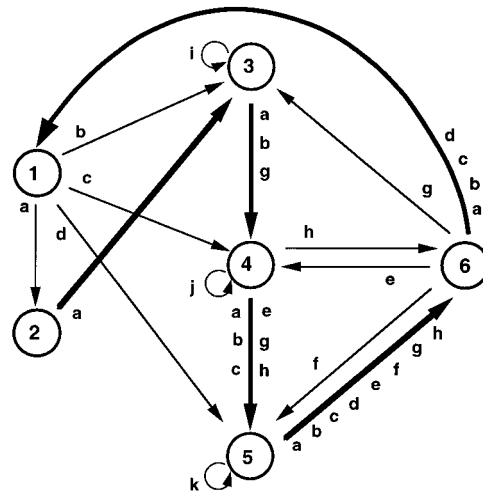


FIG. 4. The life-cycle graph of *Dipsacus sylvestris* redrawn from Caswell (1989:51: Fig. 4.3). Stages 1 and 2 are dormant seeds, stages 3–5 are small, medium, and large rosettes, and stage 6 is flowering individuals. The edges of the chosen tree are shown in bold, and each other transition is a chord in the corresponding cotree. The tree plus a chord completes a loop in the graph. There are 11 loops labeled a–k. Each edge is labeled with the letter of all the loops that pass along that edge. For example, the a-loop has six steps and follows the stages 1-2-3-4-5-6-1. Notice the edge that is the chord in each loop is unique to that loop. The edges that are part of the tree are traversed by more than one loop. The h-loop is the only loop in which the edges of the loop are reversed compared to the direction of the chord that defines the loop. See text (*Examples: Dipsacus sylvestris . . .*) for further explanation of this loop.

graph (Fig. 4) is modified from the Field A matrix of Werner and Caswell (1977:1106: Table 3), and only transitions measured in Field A are included. The transition interval is 1 yr. The elasticities for this matrix are given in Table 2. The graph has 6 stages and 16 transitions, and therefore $L = 16 - 6 + 1 = 11$. The loops were constructed from the tree shown as the bold edges in Fig. 4 and the 11 loops are labeled with the letters a–k. This example is used to explore the im-

TABLE 2. Elasticity matrix for *Dipsacus sylvestris*; data are elasticity values (%). Stages 1–6 are defined in the first column (e.g., stage 1 = dormant seeds, year 1). Note that the row total for any stage equals the corresponding column total, and the total elasticity (rounded) is 100%. Data are from Caswell (1989).

| Stage | Stages | | | | | | Row total |
|--------------------------|--------|-------|-------|--------|--------|--------|-----------|
| | 1 | 2 | 3 | 4 | 5 | 6 | |
| 1) Dormant seeds, year 1 | 0 | 0 | 0 | 0 | 0 | 6.594 | 6.594 |
| 2) Dormant seeds, year 2 | 0.025 | 0 | 0 | 0 | 0 | 0 | 0.025 |
| 3) Small rosettes | 0.079 | 0.025 | 0.015 | 0 | 0 | 0.151 | 0.270 |
| 4) Medium rosettes | 0.750 | 0 | 0.256 | 2.773 | 0 | 23.270 | 27.049 |
| 5) Large rosettes | 5.740 | 0 | 0 | 19.120 | 2.272 | 4.454 | 31.586 |
| 6) Flowering | 0 | 0 | 0 | 5.157 | 29.310 | 0 | 34.467 |
| Column total | 6.594 | 0.025 | 0.271 | 27.050 | 31.582 | 34.469 | 100 |

TABLE 3. Demographic loop characteristics of *Dipsacus sylvestris* (see Fig. 4 for depiction of loop details). Method A refers to the procedure that multiplies the elasticity of the unique step by the number of steps to obtain the loop elasticity. Method B, described in the text (see *Examples: Dipsacus sylvestris*. . .), accounts for the sign of edges in a loop, and in doing so the sum of the loop elasticities is 100% as required. Method C redefines the loops so that all edges are positive, however, the e-loop no longer has a unique element.

| Loop | Unique step in loop | No. of steps | Elasticity of unique step (%) | Loop elasticity | | |
|-------|---------------------|--------------|-------------------------------|-----------------|---------------|---------------|
| | | | | Method A (%) | Method B (%) | Method C (%) |
| a | 2-1† | 6 | 0.025 | 0.150 | 0.150 | 0.150 |
| b | 3-1 | 5 | 0.709 | 0.395 | 0.395 | 0.395 |
| c | 4-1 | 4 | 0.750 | 3.000 | 3.000 | 3.000 |
| d | 5-1 | 3 | 5.740 | 17.220 | 17.220 | 17.220 |
| e | 4-6 | 3 | 23.270 | 69.81 | 69.81 | ... |
| | 4-6‡ | 3 | 18.113‡ | ... | ... | 54.339 |
| f | 5-6 | 2 | 4.454 | 8.908 | 8.908 | 8.908 |
| g | 3-6 | 4 | 0.153 | 0.612 | 0.612 | 0.612 |
| h | 6-4 | 2 | 5.157 | ... | ... | 10.314 |
| | 6-4 | 3 | 5.157 | 15.471 | -5.157 | ... |
| i | 3-3 | 1 | 0.015 | 0.015 | 0.015 | 0.015 |
| j | 4-4 | 1 | 2.773 | 2.773 | 2.773 | 2.773 |
| k | 5-5 | 1 | 2.272 | 2.272 | 2.272 | 2.272 |
| Total | | | | 120.626 | 99.998 | 99.998 |

Notes: Numbers shown in boldface differ among the three methods of calculating loop elasticities; ellipses indicate that the alternative loop (“e” or “h” loop) is used in calculating the loop elasticity for that particular method.

† The transitions (edges) are defined as: to the first stage in the pair from the second stage of the pair.

‡ Not a unique step, so calculate loop elasticity as (23.270 – 5.157).

plications of reversed loop edges for demographic loop analysis.

In this teasel graph, all the chords, except h, form loops in which every other edge has the same orientation as the chord. The h-chord forms a loop in which the other two edges are in the opposite direction. I examined other trees for this model and all the trees produced at least one chord with reversed edges in the corresponding loop and some trees produced more negative loops. So we must decide how to calculate the loop elasticities for models with negative loops. The loop elasticity is usually calculated by multiplying the elasticity value of the unique element (or chord) by the sum of the number of edges in the loop. In the more

general method that includes negative loops, we first assign a value of +1 to edges in the same direction as the chord and a value of -1 to edges that are in the opposite direction of the chord. Next we assign the characteristic loop elasticity to each edge in the loop and multiply it by the value +1 or -1 as appropriate. The elasticity values on each edge in the loop are summed to give the overall loop elasticity. For example, the chord for the h-loop is the edge that runs from stage 4 to stage 6 and it has an elasticity of +5.157. The other two edges run in opposite direction to the chord so they are each assigned elasticities of -5.157. The total elasticity for the loop is +5.157 + 2(-5.157) = -5.157. The modified loop elasticities

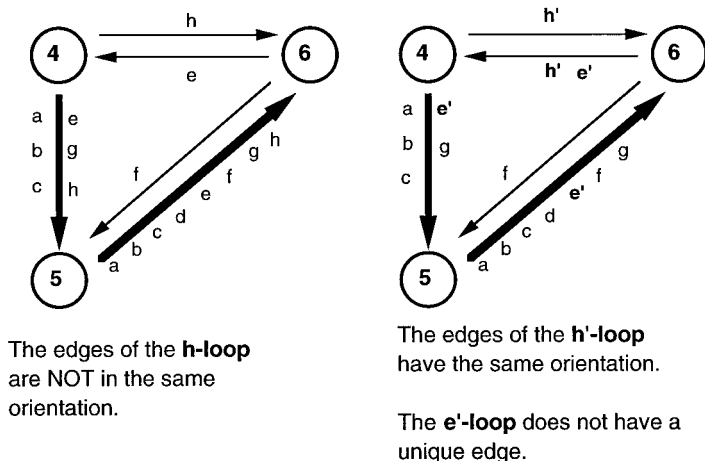


FIG. 5. Detail of stages 4, 5, and 6 from the Fig. 4 *Dipsacus sylvestris* life-cycle graph. The redefined h'-loop now goes from stage 6-4-6 in two steps. Note this loop now has all edges with the same orientation. The e'-loop still goes from stage 6-4-5-6 in three steps, but it does not have a unique edge in this figure.

TABLE 4. The summed loop elasticities for *Dipsacus sylvestris*. For details of the loops see Figs. 4 and 6 and the text (Examples: *Dipsacus sylvestris*. . .).

| | Loops | Loop elasticity (%) |
|--------------------|---------|---------------------|
| Biennials | h, f | 19.2 |
| Triennials | e | 54.3 |
| Quadrennials | g | 0.6 |
| Delay as a rosette | i, j, k | 5.1 |
| 1 yr in seed bank | b, c, d | 20.6 |
| 2 yr in seed bank | a | 0.15 |

sum to 100% as required (see Table 3: method B) rather than 121% (Table 3: method A) obtained using the standard method that does not include the sign of the edges in the loop.

Including the signs for the loops naturally leads to a set of equivalent loops that reflect the path of individuals in the life cycle. For example, the h-loop is redefined as the two-step loop (from stage 6-4-6; Fig. 5) and the e-loop can be redefined as the three-step loop (from stage 6-4-5-6; Fig. 5). This new e'-loop has no unique element, but the characteristic elasticity can be derived from the edge (stage 6 to stage 4) that is shared only by the h'-loop, and we know the value of the h'-loop elasticity from its unique element (stage 4 to stage 6). This is an example where the "lack of a unique element" (sensu van Groenendael et al. 1994) does not prevent the calculation of the loop elasticity as discussed earlier (*Graph theory . . . : Choosing among alternative trees . . .*). Therefore, the nullity provided us with the fact that there are 11 loops in this graph, and the signs of the loops indicated the location in the teasel graph where a loop without a unique element should be defined.

The biological interpretation of the loops may involve summing loop elasticities to present concise comparisons of alternative life-history types. The loop analysis of the teasel life cycle compares the contribution to the population growth rate of individuals of many ages. Teasel is a monocarpic perennial, and the youngest life history is a biennial (represented by loops h and f); there are also triennials (loop e), and quadrennials (loop g). The delay introduced by rosettes remaining in the same size class is represented by loops i, j, and k. The individuals that spend one year in the seed bank constitute loops b, c, and d and those spend-

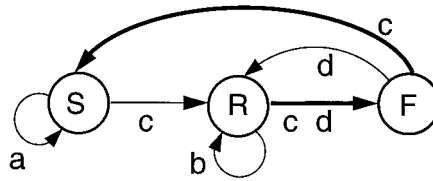


FIG. 6. The reduced life-cycle graph of *Dipsacus sylvestris*. There are now three stages, S = dormant seeds, R = rosettes, and F = individuals that have flowered. The four demographic loops are labeled a-d. The edges of the tree are shown in bold, and each of the other edges is a chord in the cotree.

ing two years in the seed bank constitute loop a. Table 4 shows the summed elasticities for these combined loops. Triennials have the highest elasticity (54%) followed by the loops for individuals that spent the first year in the seed bank (21%) and the biennials (19%).

Another approach to negative loops is to reduce the life-cycle graph so that some non-essential stages and transitions are regrouped into a simplified model. For example, the *D. sylvestris* matrix can be reduced to a three-stage model (Fig. 6). The three stages are dormant seeds, rosettes, and flowering individuals. There are four demographic loops: (a) the persistent seed bank, (b) biennials, (c) rosettes that delay reproduction, and (d) monocarps (>2 yr old) from the seed bank. Survivorship and fecundity data would be required to recalculate this new matrix and its loops.

The teasel graph is not atypical; other examples from the literature also have negative loops and require the generalized method that includes the signs of the loops. For instance, the model of the soft coral *Alcyonium* sp. (McFadden 1991) is a complicated size-structured matrix. The coral graph has 22 edges, 5 nodes, and 18 loops. In that model, four of the loops have reversed orientation, i.e., the direction on the chord is opposite of the direction on the remaining edges that, together with the chord, comprise the loop. However, it is possible to calculate the 18 independent loop elasticities that sum to 100% (G. M. Wardle, unpublished data).

Caretta caretta, an iteroparous long-lived turtle

The third example is a stage-classified matrix model for loggerhead sea turtles (*Caretta caretta*; Crouse et al. 1987). This model is widely known, because it was used to make recommendations regarding the conservation of a vulnerable species. It is included here to

FIG. 7. The life-cycle graph of loggerhead sea turtles, *Caretta caretta*. The stages are: (1) eggs, hatchlings, (2) small juveniles, (3) large juveniles, (4) subadults, (5) novice breeders, (6) 1st-yr remigrants, and (7) mature breeders. There are seven loops labeled a-g. The model is based on Crouse et al. (1987): Table 3).

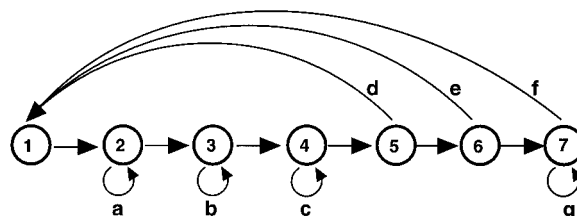


TABLE 5. Elasticity matrix for *Caretta caretta*; data are elasticity values (%). Stages 1–7 are defined in the first column. Note that the row total for any stage equals the corresponding column total, and the total elasticity (rounded) is 100%. The elasticities were calculated from the transition matrix in Crouse et al. (1987:1416). The population growth rate $\lambda = 0.945$.

| Stage | Stages | | | | | | | Row total |
|----------------------|--------|------|------|------|-----|------|------|-----------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | |
| 1) Eggs, hatchlings | 0 | 0 | 0 | 0 | 1.2 | 0.03 | 3.9 | 5.1 |
| 2) Small juveniles | 5.1 | 18.1 | 0 | 0 | 0 | 0 | 0 | 23.2 |
| 3) Large juveniles | 0 | 5.1 | 11.9 | 0 | 0 | 0 | 0 | 17.0 |
| 4) Subadults | 0 | 0 | 5.1 | 3.9 | 0 | 0 | 0 | 19.0 |
| 5) Novice breeders | 0 | 0 | 0 | 5.1 | 0 | 0 | 0 | 5.1 |
| 6) 1st-yr remigrants | 0 | 0 | 0 | 0 | 3.9 | 0 | 0 | 3.9 |
| 7) Mature breeders | 0 | 0 | 0 | 0 | 0 | 3.9 | 23.0 | 26.9 |
| Column total | 5.1 | 23.2 | 17.0 | 19.0 | 5.1 | 3.93 | 26.9 | 100.2 |

represent the many life-cycle models, either size structured or stage structured, that include a large number of self-loops or transitions in which individuals remain in the current stage rather than enter a different stage of the life cycle.

The life cycle graph of *C. caretta* has seven stages: (1) eggs, hatchlings, (2) small juveniles, (3) large juveniles, (4) subadults, (5) novice breeders, (6) 1st-yr remigrants, and (7) mature breeders (Fig. 7). The survivorship and fecundity data were compiled by Crouse et al. (1987) from published studies and used to calculate transitions for a 1-yr interval. The elasticities are given in Table 5. The model has seven loops ($L = 13 - 7 + 1 = 7$) (Fig. 7). The highest loop elasticity (27%) is for loop f, which represents individuals that have survived through all the juvenile stages and that reproduce at the mature adult stage. The next highest is loop g, representing the survivorship of mature adults (23%) (Table 6). The results of the loop analysis suggest that the loops that include the mature-adult stage are important in terms of increasing the population growth rate.

Here the emphasis on the mature stage from loop analysis differs from the conclusions of the original analysis of the individual stage elasticities by Crouse et al. (1987). The elasticities of the matrix elements led Crouse et al. (1987) to argue that changes in fecundity have only a small effect on λ , while changes in the probability of survival contribute most to λ . However, as noted by Crouse et al. (1987: 1418) the *P* values in their model are actually combinations of survival probabilities and stage-duration probabilities. When the elasticity associated with the survival part of these elements is calculated, they find a strong effect of the juvenile and subadult stages and a smaller effect of the mature adults. However, the juvenile and subadult stages have a stage duration of 7, 8, and 6 yr respectively. The stages of novice and 1st-yr breeders are only single-year stages (by definition), and the mature-adult stage spans up to 30 yr. The effect on the population growth rate of a proportional change in the survivorship of a stage that lasts a single year differs from that of stages lasting multiple years. Therefore,

the lower elasticities of the single-year stages may reflect a shorter stage duration.

Although loop analysis offers a different perspective on the interpretation of the demographic model, it is important to evaluate the conclusions of both approaches in terms of the biological questions the model was constructed to answer. The original motivation of the sea turtle model was to evaluate the demographic consequences of changes in the vital rates of the various stages. The loop analysis, however, focuses on multi-stage transitions and does not necessarily address changes that affect a single stage. The turtle model also differs from the previous two examples in that the turtles are iteroparous. Therefore the loops do not directly correspond to paths that individuals follow. For instance, if an individual is the offspring of a novice breeder (stage 5) and it passes through all previous developmental stages before reproducing as an adult, then the resulting sequence of 5-1-2-3-4-5-6-7-7 is not represented by a particular loop or combination of loops. A solution would be to collapse the stages 5 and 6 into stage 7 to make one reproductive stage. This example serves to illustrate that a method such as loop analysis should not be undertaken without an understanding of the demography of the biological system.

TABLE 6. Demographic loop characteristics of loggerhead sea turtles, *Caretta caretta*. There are seven loops labeled a–g, and these are also shown in Fig. 7. The loops give the contribution of the life-history types to the population growth rate, λ ($\lambda = 0.945$). The transition-matrix data are from Crouse et al. (1987).

| Loop | Unique step in loop | No. of steps† | Elasticity of unique step (%) | Loop elasticity (%) |
|-------|---------------------|---------------|-------------------------------|---------------------|
| a | 2-2 | 1 | 18.07 | 18.07 |
| b | 3-3 | 1 | 11.87 | 11.87 |
| c | 4-4 | 1 | 13.85 | 13.95 |
| d | 1-5 | 5 | 1.21 | 6.02 |
| e | 1-6 | 6 | 0.03 | 0.19 |
| f | 1-7 | 7 | 3.86 | 27.04 |
| g | 7-7 | 1 | 22.95 | 22.95 |
| Total | | | | 100.0 |

† No. of stages (edges). See Table 5 for stage descriptions.

CONCLUSION

Loop analysis is a powerful method for comparing the contributions of alternative life-history types (e.g., annual vs. biennial) to the population growth rate. The concepts from graph theory provide a systematic procedure for deriving the loops for any graph and particularly for complex life cycles. The generalized procedure for handling negative loops, illustrated with the teasel model, ensures that the sum of the loop elasticities will be unity. However, negative loops do not correspond to the flow of individuals in the life cycle, and thus a biological interpretation requires that these loops be redefined or that the graph be reduced to simplify comparisons. The appropriateness of loop analysis will depend on the motivation for constructing a particular demographic model. In the example of winter annual vs. biennial types of *Campanula americana*, the loops clearly reflect the alternative paths for individuals in the life history. This is not so apparent in the sea turtle model.

Loop analysis can be applied to the numerous demographic studies that have presented elasticities. From a comparative review of such results it will be possible to generalize the patterns of life histories and to relate them to the evolutionary processes that shape life histories, such as particular ecological conditions or spatial and temporal environmental variability.

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