

AN IMPROVED FORMAL APPROACH TO DEMOGRAPHIC LOOP ANALYSIS

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Abstract. Loop analysis is introduced to demographic analysis as a tool to compare relative contributions of different life-history types to population growth rate. In 1998, G. M. Wardle brought in basic concepts of the graph theory to demographic loop analysis and proposed a methodology to determine the loops from any life-cycle graph based on these concepts. However, the mathematics behind Wardle's methodology cannot readily be used by most population ecologists. A new methodology that is also based on graph theory concepts but both makes ecological sense in its application and is simpler to implement is proposed. Three rules of thumb serve as the basis of the proposed methodology that brings a more systematic approach to loop selection: it identifies only those loops that are ecologically meaningful (i.e., loops that are forward-flowing and with positive elasticity values). Thus, it produces a loop set that is more amenable to answer questions on comparison of different life-history types. It is tested on several life-cycle graphs from the literature. Three of these are presented: *Vouacapoua americana*, *Dipsacus sylvestris*, and *Alcyonium* sp. In each case, the methodology successfully produced a loop set that makes sense in terms of the ecology of the species. The methodology is also implemented as a couple of open-source computer codes. It is hoped that the proposed methodology will lead to wider use of loop analysis in demographic population studies.

Key words: demographic loop analysis; elasticity analysis; graph theory; life-cycle graph; life history; loop analysis; population growth rate; population study; projection matrices.

INTRODUCTION

Elasticity analysis in matrix population models reveals the proportional change in population growth rate as a function of a proportional change in each different element in the projection matrix (de Kroon et al. 1986, 2000, Caswell 2001). However, individual elasticities have limited value in comparing different life-history pathways individuals of a particular species may follow in their life cycles. Loop analysis is an extension of elasticity analysis that allows for the explicit consideration of the underlying life-cycle structure (van Groenendael et al. 1994). In loop analysis, relative contributions of alternative life-history loops to population growth rate are calculated based on the elasticities of the transition elements of projection matrices. Various loops represent the alternatives for individuals to complete their life cycle. The basic steps of loop analysis are laid out in van Groenendael et al. according to which the decomposition of the life-cycle transitions

into unbranched loops is to be done with at least one transition element that is unique to each loop and in such a way that all transitions are included at least once in some loop. In addition, the elasticity properties of the identified loops should satisfy three conditions:

1) Condition 1 is the sum of elasticities entering a stage is equal to the sum of elasticities leaving that stage. The conservation of elasticity at a stage leads to two observations (van Groenendael et al. 1994, Wardle 1998). First, each loop has a "characteristic elasticity" that circulates through all transitions in that loop. In other words, in each loop, the elasticity of the growth rate to all transitions is the same. Second, elasticity of a particular transition is composed of the characteristic elasticities of loops that pass through that transition.

2) Condition 2 is the contribution of a loop to population growth rate (the elasticity of a loop, or "loop elasticity") is equal to the characteristic elasticity of the loop multiplied by the number of transitions of that loop.

3) Condition 3 is the sum of all elasticities equals one.

Because the elasticities of all loops in a matrix sum to one, loop elasticities quantify the relative contributions of alternative life cycles to population growth rate and therefore, they can be used in comparing different life-

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history traits. For more detailed discussions of the fundamentals and utility of demographic loop analysis in ecology, see van Groenendael et al. (1994) and Wardle (1998).

The examples used in van Groenendael et al. are simple enough to find the loops in their life cycles with simple visual inspection. For more complicated life-history patterns, however, it is not clear how this loop selection procedure would be carried out in a practical and efficient way. Wardle (1998) addresses this issue and proposes a tree-construction algorithm. Wardle's contribution is significant in introducing relevant concepts from the graph theory to demographic loop analysis and thus formalizing the loop selection procedure. Her algorithm allows for obtaining a set of loops from a single tree.

However, the tree-finding algorithm in Wardle (1998) may produce loop sets for which some loops do not follow the direction of the arrows on the arcs. Furthermore, a tree for which all loops are positive may not even exist for a particular life-cycle graph. Negative loops (i.e., undirected cycles) have no practical interpretation in life-history analysis as they are not representative of demographic loops as pathways that individuals follow in the life cycle. Wardle proposes three approaches to deal with negative loops so that the sum of loop elasticities adds up to one. First is assigning a value of +1 or -1 to transitions in a negative loop depending on their directions and then recalculating the loop elasticity. This, however, still may not lead to a loop set that is biologically interpretable. Second is redefining the set of independent loops so that negative loops are completely replaced by positive loops (i.e., directed cycles). The last one is reducing the life-cycle graph so that negative loops are eliminated. All three approaches necessitate laborious adjustments in the methodology and may even lead to potential information loss as in the third approach.

Indeed, any loop selection approach that exclusively makes use of graph theory concepts without regard to the knowledge on the ecology of the species under study will fail to guarantee producing ecologically relevant results. The approach presented in this note allows for a much simpler identification of loops and their elasticities. Yet, it incorporates the ecology of the species under study as an input for the loop selection process from the start. To this end, three new rules of thumb for loop construction in life-cycle studies are presented:

1) In selecting loops, only unidirectional (i.e., forward-flowing) loops are considered. Thus, the proposed methodology eliminates the negative loops phenomenon and its associated problems.

2) In processing the life-cycle graph into loops, one should start with the shortest loops (self-loops), proceed with the two-transition loops, and so on. The characteristic elasticity of the identified loop is determined by

the transition with the smallest elasticity value among all transitions incorporated in that loop. The characteristic elasticity thus computed is subtracted from the elasticities of the incorporated transitions. This process continues until no loop can be identified with the remaining elasticities of the transitions.

3) In selecting transitions to form new loops, priority is given to previously unselected ones if there are any. This ensures that all transitions are taken into account in forming loops.

The proposed methodology relies on these three rules of thumb and identifies only those loops that are ecologically meaningful. An ecologically relevant/meaningful loop is defined in this study as one that is forward-flowing with positive elasticity values; in demographic analysis, elasticities must be positive by definition because they represent the contributions of transitions or life-history traits to growth rate of the population. In addition, for loops to be proper representations of life-history traits that an individual may follow in its life cycle they have to be unidirectional.

The second rule of thumb is particularly helpful for demographic analysis as (1) it has the advantage of gradually building up the complexity of the life cycle and (2) in growing populations, population growth rate is, in general, stimulated mainly by loops of shorter delay (i.e., early reproduction; Charlesworth 1994, de Kroon et al. 2000). Another important asset of this approach is that it does not require each loop to incorporate at least one unique transition. In fact, Condition 1 suffices to calculate the characteristic elasticity of any loop as long as it is independent of others. The proposed methodology is illustrated on one simple and two fairly complicated life-cycle graphs from the literature. It was also coded in a popular computer environment (see Supplement) by making use of some more advanced graph-theoretic concepts. The codes can be used for complicated cases in which formal checking is desirable. The graph-theoretic details of the methodology are presented in Appendix A for interested readers.

METHODS

A life-cycle graph is composed of stages and transitions between them. In terms of graph theory, a life-cycle graph is a directed graph or digraph G where stages and transition are called nodes (or vertices) and edges, respectively. Thus, the structure of a life-history diagram can be represented as a digraph (Wardle 1998). The application of the proposed rules of thumb is straightforward for simple life-history graphs. For more complicated cases, manual tracking of all ecologically meaningful loops may become challenging and formal checking may be desirable. The codes provided in this study serve this purpose. Manual application of the proposed rules of thumb does not require knowledge of

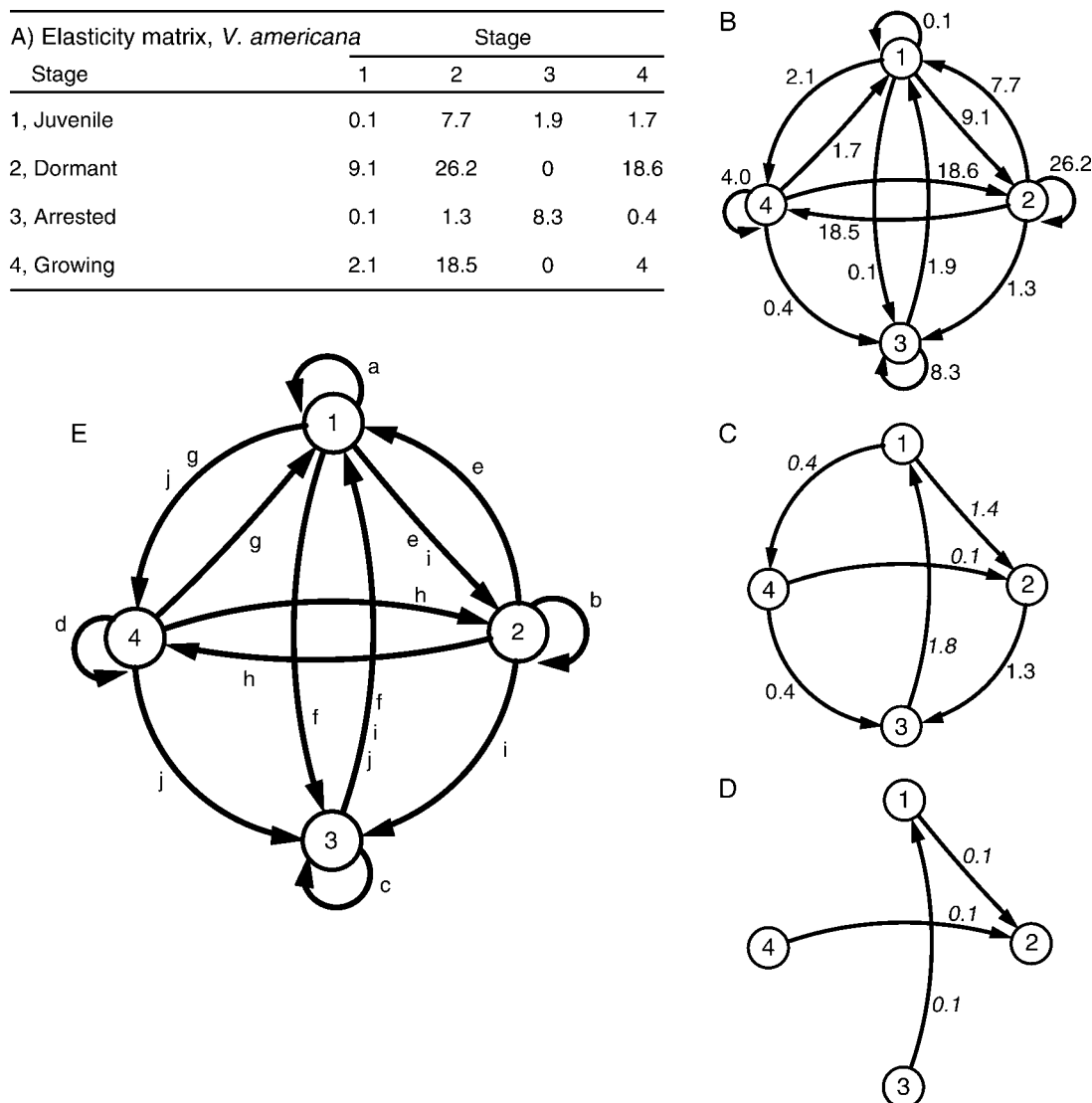


FIG. 1. (A) Elasticity matrix for *Vouacapoua americana*, with stages 1–4 being defined in the first column. Entries are elasticity values in percentages; data are from Sterck et al. (2003). (B) Life-cycle graph of *Vouacapoua americana* redrawn from Sterck et al. (2003: Fig. 2A). Stages 1–4 (outer circles) are juvenile, dormant, arrested, and growing modules of the tree species, respectively. (C) Transitions with nonzero remaining elasticity values after identifying the self- and two-transition loops. (D) Transitions with nonzero remaining elasticity values after identifying the three-transition loops. Remaining transitions do not form any directed loops so the search for loops ends (note that the elasticity values of already used transitions are in italics). (E) Ten loops identified by the methodology are labeled a–j on the graph. Each transition is labeled with the letters of all the loops that pass through that transition.

advanced graph-theoretic concepts. One of the codes, however, makes use of such concepts to the extent they are relevant to life-cycle graphs (see Supplement and Appendix A).

The methodology identifies only those loops that are forward-flowing. In other words, it considers only the directed cycles in a graph in selecting loops. In addition, the elasticity properties of the identified loops satisfy the three conditions stated previously. The upper bound for the identified ecologically meaningful loops is the

independent loop set, the size of which is given by the nullity (l) equation:

$$l = b - n + c \quad (1)$$

where b and n are defined as the number of transitions (edges) and stages (nodes), respectively and c is the number of components. For demographic life-cycle graphs, c is always 1.0 (Wardle 1998).

However, for the purposes of life-cycle population analyses, it may not be necessary to identify all of the

TABLE 1. Demographic loop characteristics of *Vouacapoua americana* as identified by the proposed methodology.

Loop	Loop composition†	Unique transition in loop†	No. transitions	Characteristic elasticity	Loop elasticity
a	1-1	1-1	1	0.1	0.1
b	2-2	2-2	1	26.2	26.2
c	3-3	3-3	1	8.3	8.3
d	4-4	4-4	1	4.0	4.0
e	1-2-1	2-1	2	7.7	15.4
f	1-3-1	1-3	2	0.1	0.2
g	1-4-1	4-1	2	1.7	3.4
h	2-4-2	2-4, 4-2	2	18.5	37.0
i	1-2-3-1	2-3	3	1.3	3.9
j	1-4-3-1	4-3	3	0.4	1.2
Total					99.7

† The transitions (edges) are defined as from the tail to the head of the transition.

independent loops in the life-cycle graph simply because there may not be as many ecologically meaningful loops in that life-cycle graph. For instance, in the *Vouacapoua americana* example in the next section, there are only 10 ecologically meaningful loops although the life-cycle graph has 11 independent loops. In this sense, the number of independent loops serves as an upper bound on the number of ecologically meaningful loops in a given life-cycle graph.

The most important aspect of the proposed approach is the introduction of the “shortest independent loop set” concept. The idea is that, in processing the life-cycle graph into loops, one should first start with the shortest loops (self-loops), then proceed with the two-transition loops, and so on until all the transitions are used. Although van Groenendaal et al. (1994) also implicitly adopt this approach, it is explicitly formalized with a clear underlying logic in this study. The underlying mechanism to form a shortest independent loop set (SILS) of a graph is accepting the shortest possible loop that can be formed using transitions with nonzero unaccounted/remaining elasticity values. Note that because elasticity of each transition in the matrix is assumed to be composed of elasticities of loops that pass through that transition, the remaining elasticities in a transition correspond to the sum of elasticities of those loops that pass through that transition but are not yet identified. The number of loops identified this way and their length are unique. The proposed methodology also determines the characteristic loop elasticities in accordance with the three conditions of demographic loop analysis.

This idea was implemented previously in the context of dynamic modeling (Oliva 2004, Güneralp 2006a, b). The methodology presented in this note extends its application to life-cycle graphs, which have their own distinct characteristics. In addition to the examples presented next, it is tested on life-cycle graphs of several other species including *Collinsia verna* (Kalisz and McPeck 1992), *Poa annua* (Law 1975, van Groenendaal et al. 1994), *Campanula americana* (Wardle 1998), and *Hypochaeris radicata* (de Kroon et al. 1987, 2000).

Illustration of the method

Vouacapoua americana, a shade-tolerant tropical canopy tree species.—This example involves a module life cycle of the tropical tree *Vouacapoua americana*. It is selected for two reasons. First, it has a relatively simple life-cycle graph and, therefore, serves as a good introductory example for the implementation of the proposed rules of thumb. Second, it serves as a case study where the number of ecologically meaningful loops in a life-cycle graph may be less than the number of independent loops of the graph.

A detailed study of the module dynamics of this species with a matrix model is in Sterck et al. (2003). The elasticity matrix and the life-cycle graph are given in Fig. 1A, B, respectively. The graph has four stages and 14 transitions. The size of its independent loop set is therefore $l = 14 - 4 + 1 = 11$. The implementation of the proposed rules of thumb, however, results in 10 ecologically meaningful loops as illustrated in Fig. 1B–D. The loops are listed in Table 1 together with the characteristic elasticities and loop elasticities. The calculated elasticities satisfy the three conditions. All identified loops are forward-flowing and thus the problem of having negative loops is automatically eliminated. The unique transitions in this and the following examples are listed for illustrative purposes only. The loops are also shown on Fig. 1E. Applying Wardle’s tree-finding algorithm, for comparison, produces as many loops as the nullity, namely 11 loops, one of which is not ecologically meaningful. This is illustrated in Appendix B as an example of how unrealistic loops can arise from life-cycle graphs together with a slightly modified version of Wardle’s approach, which eventually leads to the same 10 ecologically meaningful loops.

Dipsacus sylvestris teasel.—This monocarpic perennial plant was first described by Werner (1975), then reanalyzed by Caswell (2001). It is also used in Wardle (1998) for illustration of her loop analysis approach where it produces negative loops. Therefore, it is selected for illustration of the proposed method. The elasticity

A) Elasticity matrix, <i>D. sylvestris</i>						
Stage	Stage					
	1	2	3	4	5	6
1, Dormant seeds, year 1	0	0	0	0	0	6.594
2, Dormant seeds, year 2	0.025	0	0	0	0	0
3, Small rosettes	0.079	0.025	0.015	0	0	0.151
4, Medium rosette	0.750	0	0.256	2.773	0	23.27
5, Large rosettes	5.740	0	0	19.120	2.272	4.454
6, Flowering	0	0	0	5.157	29.310	0

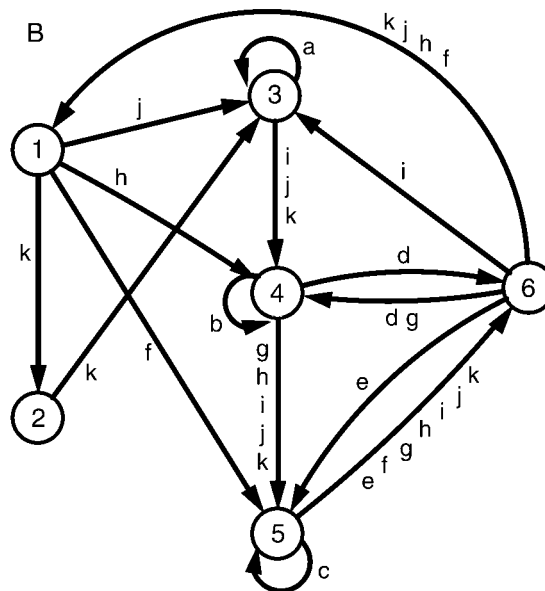


FIG. 2. (A) Elasticity matrix for *Dipsacus sylvestris*. Stages 1–6 are defined in the first column. Entries are elasticity values in percentages; data are from Wardle (1998:2545 [Table 2]). (B) Life-cycle graph of *Dipsacus sylvestris* redrawn from Caswell (2001: Fig. 4.4). Stages 1 and 2 are dormant seeds; stages 3–5 are small, medium, and large rosettes, respectively; and stage 6 is flowering individuals. Eleven loops that are identified are labeled a–k on the graph. Each transition is labeled with the letters of all the loops that pass through that transition.

TABLE 2. Demographic loop characteristics of *Dipsacus sylvestris* as identified by the proposed methodology.

Loop	Loop composition†	Unique transition in loop†	No. transitions	Characteristic elasticity	Loop elasticity
a	3–3	3–3	1	0.015	0.015
b	4–4	4–4	1	2.773	2.773
c	5–5	5–5	1	2.272	2.272
d	4–6–4	4–6	2	5.157	10.314
e	5–6–5	6–5	2	4.454	8.908
f	1–5–6–1	1–5	3	5.74	17.22
g	4–5–6–4	‡	3	18.113	54.339
h	1–4–5–6–1	1–4	4	0.75	3
i	3–4–5–6–3	6–3	4	0.151	0.604
j	1–3–4–5–6–1	1–3	5	0.079	0.395
k	1–2–3–4–5–6–1	1–2, 2–3§	6	0.023	0.138
Total					99.978

† The transitions (edges) are defined as from the tail to the head of the transition.

‡ Although loop g has no unique transitions, its elasticity is calculated based on Condition 1.

§ These two transitions have the same elasticity by Condition 1.

TABLE 3. Summed loop elasticities for *Dipsacus sylvestris*.

Life history types	Loops	Loop elasticity (%)
Biennials	d, e	19.222
Triennials	g	54.339
Quadrennials	i	0.604
Delay as a rosette	a, b, c	5.060
One year in seed bank	f, h, j	20.615
Two years in seed bank	k	0.138

matrix is given in Fig. 2A. The life-cycle graph (Fig. 2B) is modified from the Field A matrix of Werner and Caswell (1977: Table 3). Only transitions observed in Field A are included. The graph has six stages and 16

transitions. The size of its independent loop set is therefore $l = 16 - 6 + 1 = 11$. The number of loops that are identified by the proposed methodology is also 11 in this case, and they are listed in Table 2 as are the characteristic elasticities and loop elasticities. All identified loops are forward-flowing and the calculated elasticities satisfy the three conditions. The loops are also shown on Fig. 2B.

The comparison of alternative life-history types of teasel is presented in Table 3. The results of the comparison agree with Wardle (1998: Table 4): triennials have the highest elasticity (54.339%). The loops representing individuals that spend the first year in the

A) Elasticity matrix, <i>Alcyonium</i> sp.		Size class			
Size class	P	I	II	III	IV
P (planula larva)	0	0.05	0.12	0.2	0.22
I	0.44	2.47	4.81	3.14	1.21
II	0.15	4.68	13.8	10	4.46
III	0	3.07	10.2	10.7	7.83
IV	0	1.79	4.14	7.78	8.7

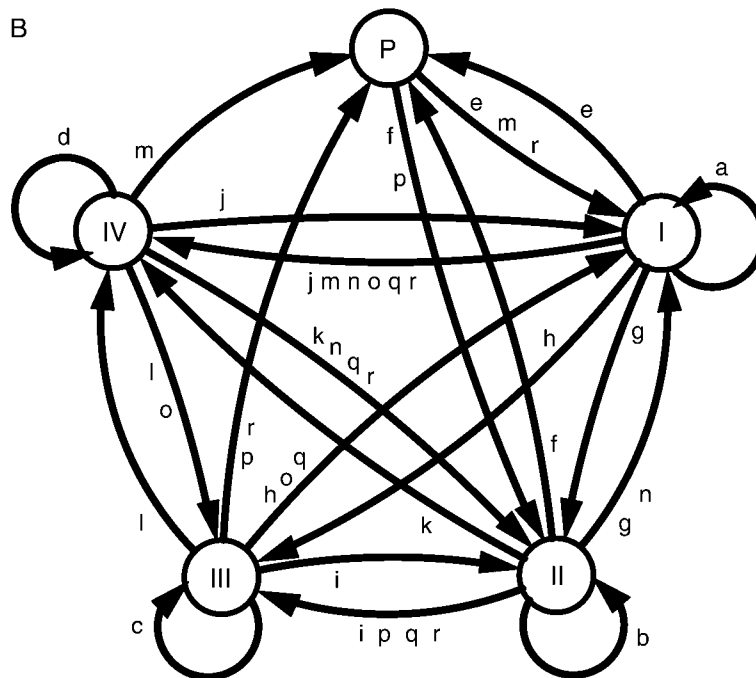


FIG. 3. (A) Elasticity matrix for *Alcyonium* sp. for size class transitions. Entries are elasticity values in percentages; data are from McFadden (1991: Table 6, Site T1). (B) Life-cycle graph of *Alcyonium* sp. drawn based on McFadden (1991: Table 6). Stage P is sexually produced planulae; stages I–IV are four size classes (<0.14 , 0.14 – 0.24 , 0.25 – 0.36 , and >0.36 cm², respectively). The 18 loops that are identified are labeled a–r on the graph. Each transition is labeled with the letters of all the loops that pass through that transition.

TABLE 4. Demographic loop characteristics of *Alcyonium* sp. as identified by the proposed methodology.

Loop	Loop composition†	Unique transition in loop†	No. transitions	Characteristic elasticity	Loop elasticity
a	I-I	I-I	1	2.47	2.47
b	II-II	II-II	1	13.8	13.8
c	III-III	III-III	1	10.7	10.7
d	IV-IV	IV-IV	1	8.7	8.7
e	P-I-P	I-P	2	0.05	0.1
f	P-II-P	II-P	2	0.12	0.24
g	I-II-I	I-II	2	4.68	9.36
h	I-III-I	I-III	2	3.07	6.14
i	II-III-II	III-II	2	10	20
j	I-IV-I	IV-I	2	1.21	2.42
k	II-IV-II	II-IV	2	4.14	8.28
l	III-IV-III	III-IV	2	7.78	15.56
m	P-I-IV-P	IV-P	3	0.22	0.66
n	II-I-IV-II	‡	3	0.13	0.39
o	III-I-IV-III	‡	3	0.05	0.15
p	P-II-III-P	‡	3	0.03	0.09
q	I-IV-II-III-I	‡	4	0.02	0.08
r	P-I-IV-II-III-P	‡	5	0.15	0.75
Total					99.89

† The transitions (edges) are defined as from the tail to the head of the transition.

‡ Although these loops have no unique links, their corresponding elasticities are calculated based on Condition 1.

seed bank have total elasticity of 20.615%, which is followed by biennials with 19.222%. The corresponding figures in Wardle are 54.3%, 20.6%, and 19.2%, respectively. The elasticities for the rest of the types agree as well.

Alcyonium sp., a soft coral species.—The model of this soft coral species is cited in Wardle as another example with a complicated size-structured matrix with negative loops. McFadden (1991) presents an in-depth demographic analysis of the species. The transition interval is one year. There are five size classes. The typical elasticity matrix of the species has 22 nonzero entries (McFadden 1991: Table 6). Hence, the coral graph has 22 transitions and five stages (Fig. 3).

The elasticity matrix for Site T1 in Table 6 of McFadden is used here (Fig. 3A). The loops of the life-cycle graph identified with the proposed approach are shown on Fig. 3B and listed in Table 4. The number of loops identified by the proposed methodology is equal to the size of the independent loop set for this example as well. The proposed approach is able to generate a loop set composed only of directed cycles even for this complicated life cycle and the loop elasticities sum to 100% (Table 4).

DISCUSSION

The proposed approach is applied to various other published life cycles as well. At each application, the approach identified a unique loop set that makes sense in terms of the ecology of the species. The proposed methodology based on the straightforward three rules of thumb correctly identified the ecologically meaningful loops in the *Vouacapoua* example as opposed to Wardle's approach, which would produce 11 loops

(Appendix B). The methodology also generated the same results as in Wardle in the *Dipsacus* and *Alcyonium* examples but without the complications associated with the presence of negative loops.

Note that the elasticity matrix has to be available for the proposed rules of thumb to be applicable because merely knowing that transitions exist is not enough to form an ecologically meaningful loop set. Such an approach as in Wardle (1998) will give as many independent loops as the nullity of the graph, but the resulting loop set is ultimately a product of a mathematical construct (i.e., the independent loop set concept, which focuses only on the overall structure composed of links and nodes of the graph without regard to the elasticity values taken on by those links) and not necessarily relevant to the ecology of the particular species under study. Therefore, it typically requires laborious adjustments, after an initial set is formed, to reach an ecologically meaningful result. The advantage of the proposed approach is that it combines the utility of graph theory with the knowledge on the ecology of the species under study by bringing the knowledge on the elasticity values of the life cycle into the loop identification process. An additional benefit of this approach is that it resolves the problem of arbitrarily forming an independent loop set among many possibilities if simply a graph-theoretical approach were to be used.

Loop analysis is an effective method for comparison of the contributions of alternative life histories to the population growth rate. The proposed loop-finding algorithm is biased toward shortest loops in the life cycle. In other words, it identifies a loop set that is the simplest and most granular depiction of the life cycle.

This is desirable as, in growing populations, shorter reproductive loops tend to make a larger contribution to population growth rate than longer loops (Charlesworth 1994). Likewise, in declining populations, self-loops (stasis) seem to attain the highest elasticities (de Kroon et al. 2000). More importantly, because the proposed approach implicitly takes the direction of arrows into account in selecting loops, it will always identify loops that are forward-flowing. In other words, the approach decomposes the life-cycle graph into the maximum possible number of independent loops that are ecologically meaningful while eliminating the confusion that is caused by the possible inclusion of loops formed by undirected cycles. Through simultaneous use of both graph theory and elasticity values of transitions in identifying loops, the proposed approach provides a systematic, unambiguous, and formal way to identify the different directed cycles an individual may follow in a life cycle. In addition, the relative influences of these pathways on the growth rate are determined.

The utility of loop analysis in demographic studies is ultimately determined by its appropriateness in answering the questions posed by any particular study. It is hoped that the proposed rules of thumb and the accompanying codes render the loop analysis a more amenable tool for life-history studies and that they will facilitate more practical implementation of the demographic loop analysis.

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APPENDIX A

Some graph-theoretic concepts relevant to the proposed methodology (*Ecological Archives* E088-127-A1).

APPENDIX B

An example of how unrealistic loops can arise from life-cycle graphs and a modification to Wardle's loop redefinition approach that eventually leads to an ecologically meaningful loop set (*Ecological Archives* E088-127-A2).

SUPPLEMENT

Matlab codes for the implementation of the methodology and short descriptions of the codes (*Ecological Archives* E088-127-S1).