

A net reproductive number for periodic matrix models

J.M. Cushing^{a*} and A.S. Ackleh^b

^aDepartment of Mathematics, Interdisciplinary Program in Applied Mathematics, University of Arizona, Tucson, AZ 85721-0089, USA; ^bDepartment of Mathematics, University of Louisiana at Lafayette, Lafayette, LA 70504-1010, USA

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We give a definition of a net reproductive number R_0 for periodic matrix models of the type used to describe the dynamics of a structured population with periodic parameters. The definition is based on the familiar method of studying a periodic map by means of its (period-length) composite. This composite has an additive decomposition that permits a generalization of the Cushing–Zhou definition of R_0 in the autonomous case. The value of R_0 determines whether the population goes extinct ($R_0 < 1$) or persists ($R_0 > 1$). We discuss the biological interpretation of this definition and derive formulas for R_0 for two cases: scalar periodic maps of arbitrary period and periodic Leslie models of period 2. We illustrate the use of the definition by means of several examples and by applications to case studies found in the literature. We also make some comparisons of this definition of R_0 with another definition given recently by Bacaër.

1. Introduction

Matrix models of the form $x(t + 1) = Px(t)$ have been widely used to describe the (discrete) time dynamics of structured populations since the seminal papers of Lewis [19], Leslie [17, 18] and Lefkovich [16]. To this day, they continue to be used to address both theoretical and applied questions concerning biological populations structured by means of an ever increasing spectrum of classification schemes (chronological age, body size or weight, life cycle stage, disease stages, gender, genetic characteristics, epidemiological categories, spatial locals, etc.) [6,10,11]. Matrix models usually have a plethora of class-specific parameters that appear in the entries of the projection matrix P (survivorships, fertility, growth rates, etc.). There are, however, two fundamental composite parameters that determine the long-term fate of a population: the population growth rate r and the net reproductive number R_0 . (In the case of nonlinear matrix models with $P = P(x)$, key parameters are the *inherent* population growth rate and net reproductive numbers, which are calculated from $P(0)$ [10,11].) The growth rate r is the dominant eigenvalue of the $n \times n$ matrix P . Under the common assumption that P is primitive, r is strictly dominant. The net reproductive number R_0 has a mathematically more complicated definition. The projection matrix P is additively decomposed into fertility and transition matrices

$$P = F + T \tag{1}$$

*Corresponding author. Email: cushing@math.arizona.edu

and, under suitable assumptions on F and T , the net reproductive number is the dominant eigenvalue of $F(I - T)^{-1}$ [12] (also see [6,10,11,20]). These two quantities have different biological interpretations and each has its importance in relation to the study of population dynamics: r measures the growth or decay rate of (each classification category of) the population, and R_0 is a measure of individual expected lifetime reproduction. Although not obvious at first glance, it turns out that r and R_0 are on the same side of 1 (or are both equal to 1) and, as a result, either quantity can be used to determine the asymptotic fate of $x(t)$. This fact was proved in [12] and, under slightly weaker assumptions, in [20].

An interesting fact is that R_0 is frequently more analytically tractable than r and often an explicit formula for R_0 in terms of the model parameters appearing in P exists, even for large matrix models, when there is no such formula for r . See [10,12] for examples. This is due basically to the fact that in most population models F has low rank, which is in turn due to the fact that newborns generally lie in only a few categories (indeed, often only one category) in the classification scheme on which the matrix model is based. Thus, by using R_0 one can often analytically relate the asymptotic dynamics of the matrix model to the model parameters in P in an explicit way. Such formulas permit, e.g., an assessment of population viability on specific class of parameters and a sensitivity analysis of population viability as measured by R_0 .

The definition of R_0 given above is for autonomous matrix equations, i.e., when F and T are constant matrices. This assumes that all population vital rates and parameters are unchanged in time. In this paper, we give a definition of R_0 for the case when $F = F(t)$ and/or $T = T(t)$ (and hence $P = P(t)$) are periodic matrices of a common period p , a case that arises when population parameters oscillate periodically. Such periodic forcing can arise, e.g., when a population inhabits a periodically fluctuating (e.g., seasonal) environment. Our approach is mathematically straightforward in that it uses the standard approach for studying the asymptotic dynamics of periodic difference equations, which is to study the period composite map. This map is defined by an autonomous projection matrix the eigenvalues of which determine the population's asymptotic dynamics. This approach is the discrete time analog of Floquet theory for continuous flows. We are motivated by the ecological studies reported in [1,7,8,14,15] which use periodic matrix models to account for seasonal periodicities and in which the authors utilize the definition of R_0 we give here.

Following Caswell [7] for the period $p = 2$ case, we show in Section 2 that the coefficient matrix of the composite map can be additively decomposed in a fashion analogous to Equation (1) in which reproductive and class transition processes during one period are separated. That is to say, the composite projection matrix for maps of period p has the form $F^{(p-1)} + T^{(p-1)}$ in which the terms $F^{(p-1)}$ and $T^{(p-1)}$ account, respectively, for accumulated offspring and all possible class transitions that occur during a full periodic cycle. Again following Caswell [7], we define R_0 as in [12], namely, as the dominant eigenvalue of $F^{(p-1)}(I - T^{(p-1)})^{-1}$. We give some illustrative examples and applications in Sections 4 and 5.

2. A definition of R_0 for periodic matrix equations

Let R^n denote n -dimensional Euclidean space and $x = \text{col}(x_i) \in R^n$ be a column vector. Let \bar{R}_+^n denote the closure of the positive cone and let $Z_+ = \{0, 1, 2, \dots\}$. We consider the periodically forced matrix equation

$$x(t+1) = P(t)x(t), \quad t \in Z_+, \quad (2)$$

where the $n \times n$ projection matrix $P(t)$ satisfies the following conditions:

$$\begin{aligned} P(t) &= F(t) + T(t), \quad F(t) = (\varphi_{ij}(t)), \quad T(t) = (\tau_{ij}(t)), \\ \varphi_{ij} : Z^+ &\rightarrow \bar{R}_+^1, \quad \tau_{ij} : Z^+ \rightarrow [0, 1] \\ \varphi_{ij}(t+p) &= \varphi_{ij}(t), \quad \tau_{ij}(t+p) = \tau_{ij}(t), \quad t \in Z^+. \end{aligned} \quad (3)$$

Since the transition matrix $T(t)$ accounts only for survivorship and movement among classes, the column sums of its entries satisfy [10,12,20]

$$\sum_{i=1}^n \tau_{ij}(t) \leq 1 \quad \text{for } t \in Z^+. \quad (4)$$

The entries in these matrices have the following interpretations:

$\varphi_{ij}(t)$ = number of newborns in the i -class at time $t + 1$ produced by a j -class individual alive at time t

$\tau_{ij}(t)$ = probability a j -class individual alive at time t is alive and in the i -class at time $t + 1$.

In this paper, we use the product notation for the multiplication of a sequence of matrices M_t , $t = 0, \dots, m$, defined as follows (note the order of subscripts):

$$\prod_{t=0}^m M_t = M_m M_{m-1} \cdots M_1 M_0.$$

Using the matrices satisfying the conditions in (3), we define

$$\begin{aligned} F^{(m)} &\stackrel{\circ}{=} \prod_{t=0}^m [F(t) + T(t)] - \prod_{t=0}^m T(t), \\ T^{(m)} &\stackrel{\circ}{=} \prod_{t=0}^{m-1} T(t). \end{aligned}$$

In what follows, among the individuals present at time $t \geq 1$, we distinguish between *original individuals* who were present at time $t = 0$ and those individuals who were not (and hence were born at some later time). The latter individuals we call *offspring*. At $t = 1$, the offspring of an original individual consist solely of newborns. At $t > 1$ the offspring of an original individual include all of its descendants. Note that $F^{(0)} = F(0)$ and $T^{(0)} = T(0)$ and hence the entries of

$$\begin{aligned} F^{(0)} &= (\varphi_{ij}^{(0)}) = (\varphi_{ij}(0)), \\ T^{(0)} &= (\tau_{ij}^{(0)}) = (\tau_{ij}(0)) \end{aligned}$$

have the interpretations

$\varphi_{ij}^{(0)}$ = number of offspring in the i -class at time $t = 1$ produced by a j -class original individual,
 $\tau_{ij}^{(0)}$ = probability a j -class original individual is alive and in the i -class at time $t = 1$.

LEMMA 1 Assume $P(t)$ satisfies Equation (3). The entries in $F^{(m)} = (\varphi_{ij}^{(m)})$ and $T^{(m)} = (\tau_{ij}^{(m)})$ have the following interpretations for $m \geq 0$:

$$\varphi_{ij}^{(m)} = \text{number of offspring in the } i\text{-class at time } m + 1 \text{ descended from a } j\text{-class original individual ,} \tag{5}$$

$$\tau_{ij}^{(m)} = \text{probability a } j\text{-class original individual is alive and in the } i\text{-class at time } m + 1. \tag{6}$$

Proof As noted above the interpretations (5)–(6) are correct for $m = 0$. For purposes of induction we assume these interpretations are correct for $m = q \geq 1$ and prove they are correct for $m = q + 1$. Under this induction hypothesis we can write

$$\prod_{t=0}^q [F(t) + T(t)] = F^{(q)} + T^{(q)},$$

where the entries of $F^{(q)}$ and $T^{(q)}$ have interpretations (5)–(6). Then for $m = q + 1$ we have

$$\begin{aligned} \prod_{t=0}^{q+1} [F(t) + T(t)] &= [F(q + 1) + T(q + 1)][F^{(q)} + T^{(q)}] \\ &= F(q + 1)F^{(q)} + F(q + 1)T^{(q)} + T(q + 1)F^{(q)} + T(q + 1)T^{(q)} \end{aligned}$$

and hence

$$F^{(q+1)} = F(q + 1)F^{(q)} + F(q + 1)T^{(q)} + T(q + 1)F^{(q)}, \tag{7}$$

$$T^{(q+1)} = T(q + 1)T^{(q)}. \tag{8}$$

We account for the offspring (of original individuals) who are alive at time $q + 2$ in three ways:

- (i) newborns produced by offspring alive at time $q + 1$,
- (ii) newborns produced by original individuals alive at time $q + 1$,
- (iii) offspring alive at $q + 1$ who survive to time $q + 2$.

This bookkeeping procedure produces the three additive terms in the formula (7) for the matrix $F^{(q+1)} = (\varphi_{ij}^{(q+1)})$ the entries of which are

$$\varphi_{ij}^{(q+1)} = \sum_{k=1}^n \varphi_{ik}(q + 1)\varphi_{kj}^{(q)} + \sum_{k=1}^n \varphi_{ik}(q + 1)\tau_{kj}^{(q)} + \sum_{k=1}^n \tau_{ik}(q + 1)\varphi_{kj}^{(q)}. \tag{9}$$

To see this we look at each sum in detail.

- (i) If we sum the quantities

$$\begin{aligned} \varphi_{ik}(q + 1)\varphi_{kj}^{(q)} &= \text{number of newborns in the } i\text{-class at time } q + 2 \text{ produced by a } k\text{-class} \\ &\quad \text{individual alive at time } q + 1 \text{ multiplied by the number of offspring in} \\ &\quad \text{the } k\text{-class at time } q + 1 \text{ descended from a } j\text{-class original individual} \\ &= \text{number of newborns in the } i\text{-class at time } q + 2 \text{ produced by those} \\ &\quad \text{descendants of a } j\text{-class original individual in the } k\text{-class at time } q + 1 \end{aligned}$$

over all classes k , we obtain

$$\sum_{k=1}^n \varphi_{ik}(q+1)\varphi_{kj}^{(q)} = \text{number of newborns in the } i\text{-class at time } q+2 \text{ produced by} \\ \text{descendents of a } j\text{-class original individual and alive at time } q+1. \quad (10)$$

(ii) If we sum the quantities

$$\varphi_{ik}(q+1)\tau_{kj}^{(q)} = \text{number of newborns in the } i\text{-class at time } q+2 \text{ produced by a } k\text{-class} \\ \text{individual alive at time } q+1 \text{ multiplied by the probability that a} \\ j\text{-class original individual is alive and in the } k\text{-class at time } q+1 \\ = \text{number of newborns in the } i\text{-class at time } q+2 \text{ produced by a} \\ j\text{-class original individual who is in the } k\text{-class at time } q+1$$

over all classes k , we obtain

$$\sum_{k=1}^n \varphi_{ik}(q+1)\tau_{kj}^{(q)} = \text{number of newborns in the } i\text{-class at time } q+2 \text{ produced by a} \\ j\text{-class original individual who is alive at time } q+1. \quad (11)$$

(iii) Finally, if we sum the quantities

$$\tau_{ik}(q+1)\varphi_{kj}^{(q)} = \text{probability a } k\text{-class individual alive at time } q+1 \text{ is alive and in the} \\ i\text{-class at time } q+2 \text{ multiplied by the number of offspring in the} \\ k\text{-class at time } q+1 \text{ descended from a } j\text{-class original individual} \\ = \text{number of descendents of a } j\text{-class original individual who are in the} \\ k\text{-class at time } q+1 \text{ and who are in the } i\text{-class at time } q+2$$

over all classes k , we obtain

$$\sum_{k=1}^n \tau_{ik}(q+1)\varphi_{kj}^{(q)} = \text{number of descendents of a } j\text{-class original individual who are} \\ \text{in the } i\text{-class at time } q+2. \quad (12)$$

The sum of the three quantities (10)–(12) gives the total number of i -class offspring alive at time $q+2$ descended from a j -class original individual. Thus, we find from formula (9) that the interpretation (5) holds at $m = q+1$. This completes the induction step for interpretation (5).

To validate the induction step for interpretation (6), see from formula (8) that the entries in the matrix $T^{(q+1)} = (\tau_{ij}^{(q+1)})$ are

$$\tau_{ij}^{(q+1)} = \left(\sum_{k=1}^n \tau_{ik}(q+1)\tau_{kj}^{(q)} \right).$$

If we sum the quantities

$$\begin{aligned} \tau_{ik}(q+1)\tau_{kj}^{(q)} &= \text{probability a } k\text{-class individual alive at time } q+1 \text{ is alive and in the } i\text{-class} \\ &\quad \text{at time } q+2 \text{ multiplied by the probability that a } j\text{-class original individual} \\ &\quad \text{is alive and in the } k\text{-class at time } t=q+1 \\ &= \text{probability a } j\text{-class original individual, who is in the } k\text{-class at time } q+1, \\ &\quad \text{is alive and in the } i\text{-class at time } q+2 \end{aligned}$$

over all classes k , we obtain

$$\begin{aligned} \sum_{k=1}^n \tau_{ik}(q+1)\tau_{kj}^{(q)} &= \text{probability a } j\text{-class original individual is alive and in the} \\ &\quad i\text{-class at time } q+2, \end{aligned}$$

that is to say, interpretation (6) holds for $m = q + 1$. This completes the induction step. ■

The analysis summarized in Lemma 1 was carried out from time $t = 0$ to $m + 1$. If we apply this result with $m = p - 1$ to the periodic matrix model (2)–(3), the entries in $F^{(p-1)}$ and $T^{(p-1)}$ have the interpretations

$$\begin{aligned} \varphi_{ij}^{(p-1)} &= \text{number of offspring in the } i\text{-class at time } p \text{ descended from a} \\ &\quad j\text{-class original individual,} \end{aligned}$$

$$\tau_{ij}^{(p-1)} = \text{probability a } j\text{-class original individual is alive and in the } i\text{-class at time } p.$$

Since the entries in the projection matrix of Equation (2) are p -periodic, we can carry out an equivalent analysis with similar results and interpretations from time $t = p$ to $t = 2p$ or indeed over any interval of time with length p .

COROLLARY 1 *For the periodic matrix model (2)–(3), the entries of the matrices $F^{(p-1)} = (\varphi_{ij}^{(p-1)})$ and $T^{(p)} = (\tau_{ij}^{(p-1)})$ have the following interpretations:*

$$\begin{aligned} \varphi_{ij}^{(p-1)} &= \text{for a } j\text{-class individual, this is the number of its descendants who are in the} \\ &\quad i\text{-class after one period of time has elapsed} \end{aligned}$$

$$\tau_{ij}^{(p-1)} = \text{probability an individual in the } j\text{-class is alive and in the } i\text{-class after one period} \\ \text{of time has elapsed.}$$

Another way in which the quantity $\varphi_{ij}^{(p-1)}$ could be described in more succinct language is

$$\varphi_{ij}^{(p-1)} = \text{number of } i\text{-class descendants produced by a } j\text{-class individual per period.}$$

As is well known, the asymptotic dynamics of periodic matrix equations (2) can be determined from the asymptotic dynamics of the autonomous equation obtained from the $(p - 1)$ -composite

of the equation. This autonomous equation has a coefficient matrix $\prod_{t=0}^{p-1} P(t)$, which by Corollary 1, has the additive decomposition

$$\prod_{t=0}^{p-1} P(t) = F^{(p-1)} + T^{(p-1)} \tag{13}$$

into a fertility matrix $F^{(p-1)}$ and a transition matrix $T^{(p-1)}$ (just as does the projection matrix $P(t)$ at each point in time t). We will use this decomposition to define R_0 for the periodic matrix equation (2).

For an $n \times n$ matrix M , let the spectral radius $\rho[M]$ denote the maximum of the absolute values of its eigenvalues. We make the following assumptions:

$$\prod_{t=0}^{p-1} P(t) = \prod_{t=0}^{p-1} (F(t) + T(t)) \text{ is irreducible,} \tag{14a}$$

$$\rho \left[\prod_{t=0}^{p-1} T(t) \right] < 1. \tag{14b}$$

The inequalities (4) on $T(t)$ imply that the entries in $\prod_{t=0}^{p-1} T(t)$ also satisfies those same inequalities. Those inequalities in turn imply $\rho \left[\prod_{t=0}^{p-1} T(t) \right] \leq 1$ but they are not sufficient for the strict inequality (14b). The assumption (14b) is needed for Theorem 1 below. Biologically it means that an individual has a finite expected life span.

As a generalization of the definitions of r and R_0 for the autonomous case $p = 1$, we make the following definitions for the general periodic case.

DEFINITION 1 *Assume that the matrix $P(t) = F(t) + T(t)$ satisfies the properties in (3) and (14a,b). We define the net reproductive number R_0 and the population growth rate r as*

$$R_0 \doteq \rho[F^{(p-1)}(I - T^{(p-1)})^{-1}], \quad r \doteq \rho \left[\prod_{t=0}^{p-1} P(t) \right],$$

where

$$F^{(p-1)} = \prod_{t=0}^{p-1} P(t) - \prod_{t=0}^{p-1} T(t), \quad T^{(p-1)} = \prod_{t=0}^{p-1} T(t).$$

Alternatively, we can write

$$R_0 = \rho \left[\left(\prod_{t=0}^{p-1} (F(t) + T(t)) - \prod_{t=0}^{p-1} T(t) \right) \left(I - \prod_{t=0}^{p-1} T(t) \right)^{-1} \right]. \tag{15}$$

The asymptotic dynamics of the periodic matrix model (2) and (3) are determined by r . The extinction equilibrium $x = 0$ is (globally asymptotically) stable if $r < 1$ and is unstable if $r > 1$ (in fact, the equation is uniformly persistent with respect to $x = 0$). Alternatively, the dynamics can also be determined by R_0 under appropriate assumptions. Specifically, under the assumptions (14) we have all the conditions necessary for an application of Cushing–Zhou Theorem to the matrix $\prod_{t=0}^{p-1} P(t) = F^{(p-1)} + T^{(p-1)}$ [10,12] (see in particular Theorem 3.3 in [20]).

THEOREM 1 Assume the periodic projection matrix $P(t)$ satisfies Equations (3) and (14). Let r and R_0 be given as in Definition 1. Then

$$r < 1 \iff R_0 < 1, \quad r > 1 \iff R_0 > 1, \quad r = 1 \iff R_0 = 1.$$

Remark 1 The assumptions on the composite matrix $\prod_{t=0}^{p-1} P(t)$ in (14a,b) are satisfied if those assumptions are satisfied at each time t , i.e., if

$$P(t) \text{ is irreducible and } \rho[T(t)] < 1 \text{ for each } t = 0, 1, \dots, p - 1.$$

3. Biological interpretation of R_0

From Corollary 1, it follows that the entries in the matrix $(I - T^{(p-1)})^{-1} = (e_{ij}^{(p-1)})$ are

$e_{ij}^{(p-1)}$ = life time expected number of periods a j -class original individual will begin a period in the i -class

and the entries in the matrix defining R_0

$$F^{(p-1)}(I - T^{(p-1)})^{-1} = (R_{ij}^{(p-1)})$$

are

$$R_{ij}^{(p-1)} = \sum_{k=1}^n \varphi_{ik}^{(p-1)} e_{kj}^{(p-1)}.$$

If we sum the quantities

$\varphi_{ik}^{(p-1)} e_{kj}^{(p-1)}$ = number of i -class offspring produced per k -class individual per period multiplied by the life time expected number of periods a j -class original individual will begin a period in the k -class
 = life time expected number of i -class offspring, per period, of a j -class original individual, calculated over those periods when the j -class individual is in the k -class at the start of the period

over all k classes, we obtain

$R_{ij}^{(p-1)}$ = life time expected number of i -class offspring, per period, of a j -class original individual.

In what follows, we use the vector norm

$$\|x\| = \sum_{i=1}^m |x_i|.$$

For the autonomous (period $p = 1$) case, R_0 in Definition 1 is the dominant eigenvalue of $F(I - T)^{-1}$ where $F = F(0)$, $T = T(0)$. A newborn class is represented in F by those rows

that do not consist entirely of zeroes. If there are $\ell \leq n$ newborn classes and if we index these classes first (i.e., the newborn classes are classes $i = 1, 2, \dots, \ell$), then

$$F(I - T)^{-1} = \begin{pmatrix} R^{(0)} & S \\ 0 & 0 \end{pmatrix},$$

where $R^{(0)} = (R_{ij}^{(0)})$ is an $\ell \times \ell$ non-negative matrix and S is an $\ell \times (n - \ell)$ non-negative matrix. (The zero matrices appearing in this block matrix have appropriate dimensions.) The dominant eigenvalue R_0 of $F(I - T)^{-1}$ is the dominant eigenvalue of $R^{(0)}$. If $v^{(0)} \in R_+^\ell$ is a distribution of newborns, then $\|R^{(0)}v^{(0)}\|$ is the total expected number of newborns from all classes, and $\|R^{(0)}v^{(0)}\|/\|v^{(0)}\|$ is the per capita expected number of newborns, produced by the distribution $v^{(0)}$. If we choose $v^{(0)}$ to be an eigenvector of $R^{(0)}$, then $\|R^{(0)}v^{(0)}\|/\|v^{(0)}\| = R_0$. Note that $v = \text{col}(v^{(0)}, 0)$, $0 \in R^{n-\ell}$, is an eigenvector of $F(I - T)^{-1}$ associated with R_0 which consists solely of individuals from the newborn classes. It follows, when $p = 1$, that R_0 is the per capita expected number of newborns produced by a distribution of newborns equal to an eigenvector of $F(I - T)^{-1}$.

Analogous reasoning with F and T replaced by $F^{(p-1)}$ and $T^{(p-1)}$ shows that for arbitrary period R_0 is the per capita expected number of offspring produced (per period) by a distribution of offspring equal to an eigenvector of $F^{(p-1)}(I - T^{(p-1)})^{-1}$.

Remark 2 Another interpretation of R_0 is obtained from the formula

$$\rho[M] = \max_{x \in R_+^n, \|x\|=1} \min_{x_i > 0} \frac{(Mx)_i}{x_i}$$

for the spectral radius $\rho[M]$ of a nonnegative, irreducible matrix M [5]. Applying this to $M = F^{(p-1)}(I - T^{(p-1)})^{-1}$, we have

$$R_0 = \max_{x \in R_+^n, \|x\|=1} \min_{x_i > 0} \frac{\sum_{j=1}^n R_{ij}^{(p-1)} x_j}{x_i}$$

and we obtain the following:

$$R_0 = \max_{x \in R_+^n, \|x\|=1} \min_{x_i > 0} (\text{expected number of } i\text{-class offspring, per period,}$$

from the distribution $x = \text{col}(x_i)$ relative to the number of

i -class individuals in the distribution). (16)

If, after one period of time, no distribution x of individuals can produce offspring in class k , then the k th row in $F^{(p-1)}$, and hence in $F^{(p-1)}(I - T^{(p-1)})^{-1}$, will consist entirely of zeros. If a distribution x is chosen with $x_k > 0$ in formula (16), then since $\sum_{j=1}^n R_{kj}^{(p-1)} x_j = 0$ the minimum will be zero for such a distribution. This means in the formula (16) for R_0 one need consider only distributions x which consist of classes that can produce offspring alive at the end of the period.

Remark 3 If those classes that can contain offspring after one period are indexed by $i = 1, 2, \dots, \ell$ then

$$F^{(p-1)}(I - T^{(p-1)})^{-1} = \begin{pmatrix} R^{(p-1)} & S \\ 0 & 0 \end{pmatrix},$$

where $R^{(p-1)} = (R_{ij}^{(p-1)})$ is an $\ell \times \ell$ non-negative matrix and S is an $\ell \times (n - \ell)$ non-negative matrix. R_0 is the dominant eigenvalue of $R^{(p-1)}$. If ℓ is significantly smaller than n , then the

calculation of R_0 becomes more tractable because of the smaller dimension of $R^{(p-1)}$. This is the source of the well-known tractability of R_0 in the autonomous case ($p = 1$) when the number of newborn classes is small. A classic example is the autonomous Leslie age-structured model for which $\ell = 1$ and R_0 is simply the upper left corner entry in $F(I - T)^{-1}$. In a periodic matrix model, if the number of classes in which offspring produced after one period can belong is less than the total number n of classes, then there is some simplification in calculating R_0 due to the reduced dimension of $R^{(p-1)}$. This might not be the case, however, even for periodic models in which newborns always lie in one class. See Section 4.2 for examples involving periodic Leslie models. If the period is long compared with n then the likelihood of a drop in dimension in $R^{(p-1)}$, and an accompanying gain in analytic simplification in the calculation of R_0 , is reduced.

4. Examples

We give two examples to illustrate the calculation of R_0 for periodic models using the formula (15). In both cases, the general $n = 1$ dimensional case and the general Leslie age-structured model, we provide an analytic formula for R_0 in terms of the demographic parameters in the projection matrix $P(t)$.

4.1. Periodic scalar equations

For the scalar ($n = 1$) periodic equation

$$x(t + 1) = (\varphi(t) + \tau(t))x(t), \quad (17)$$

Definition 1 gives

$$R_0 = \left(\prod_{t=0}^{p-1} (\varphi_t + \tau_t) - \prod_{t=0}^{p-1} \tau_t \right) \left(1 - \prod_{t=0}^{p-1} \tau_t \right)^{-1}. \quad (18)$$

Here, for notational convenience, we have defined

$$\varphi_t \doteq \varphi(t), \quad \tau_t \doteq \tau(t).$$

The first factor in this formula for R_0 counts the number of offspring acquired during a period (see formula (7)). The second factor is the expected number of periods in the life of an individual (i.e., newborns, since there is only one newborn class in this case). The interpretation of R_0 is

$$R_0 = \text{life time expected number of offspring per period per individual.} \quad (19)$$

To illustrate a use of the formula for R_0 , we give a toy application.

Example 1 We can use the period $p = 2$ case for equation (17) to investigate the dynamics of a population exposed periodically to good and bad seasons. We term the second season as “bad” in the sense that fertility φ_1 during that season is equal to or near 0 (relative to the good season fertility $\varphi_0 > 0$). We suppose the population has a capability, by re-allocating available resources, to increase fertility φ_1 during the bad season, but only at the expense of decreasing survivorship τ_1 during the bad season. The question we ask is: what strategy should the population take so as to increase R_0 ? Should it increase or decrease fertility during the bad season?

We model the bad season fertility/survivorship trade-off by setting $\tau_1 = \tau_1(\varphi_1)$ where $\tau_1(\cdot)$ is a continuously differentiable, positive valued, and decreasing function defined on an open interval

containing 0 with $\tau_1(0) < 1$. Holding all other parameter values fixed, we treat $R_0 = R_0(\varphi_1)$ as a function of bad season fertility φ_1 . We are interested in the sign of the derivative $R'_0(\varphi_1)$ (i.e., the sensitivity of R_0 with respect to φ_1) for small values of $\varphi_1 \gtrsim 0$. If this sensitivity is positive, then the population should increase its fertility φ_1 during the bad season (at the expense of a lower survivorship). If the sensitivity is negative, then it should not.

Since $p = 2$, from the formula (18) we have

$$R_0(\varphi_1) = \frac{\varphi_1\varphi_0 + \varphi_1\tau_0 + \tau_1(\varphi_1)\varphi_0}{1 - \tau_1(\varphi_1)\tau_0}, \quad R_0(0) = \frac{\varphi_0\tau_1(0)}{1 - \tau_0\tau_1(0)},$$

$$R'_0(0) = \frac{(1 - \tau_1(0)\tau_0)(\tau_0 + \varphi_0) + \varphi_0\tau'_1(0)}{(1 - \tau_1(0)\tau_0)^2}.$$

Thus, the sensitivity of R_0 to φ_1 at $\varphi_1 = 0$ is dependent on τ_1 . Specifically,

$$R'_0(0) > 0 \quad \text{if } \tau'_1(0) > -\tau^*,$$

$$R'_0(0) < 0 \quad \text{if } \tau'_1(0) < -\tau^*,$$

where the threshold $-\tau^*$ is defined by

$$\tau^* \doteq \frac{1 - \tau_1(0)\tau_0}{\varphi_0}(\tau_0 + \varphi_0) > 0.$$

The conclusion is that, in order to increase R_0 , the population should increase (low values of) bad season fertility φ_1 , at the expense of decreased bad season survivorship τ_1 , provided the sensitivity of τ_1 to φ_1 is not too large (i.e., $|\tau'_1(0)| < \tau^*$). Otherwise, it should decrease fertility in favour of survivorship during the bad season.

As a final observation from formula (18) we note for the scalar equation (17) the net reproductive number R_0 and the population growth rate r bear a linear relationship:

$$R_0 = \left(r - \prod_{t=0}^{p-1} \tau_t \right) \left(1 - \prod_{t=0}^{p-1} \tau_t \right)^{-1}.$$

4.2. Periodic Leslie models

The standard Leslie matrix model for the dynamics of an age structured population has a projection matrix $P = F + T$ of the form

$$F = \begin{pmatrix} \varphi_{11} & \varphi_{12} & \cdots & \varphi_{1,n-1} & \varphi_{1n} \\ 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 \end{pmatrix}, \quad T = \begin{pmatrix} 0 & 0 & \cdots & 0 & 0 \\ \tau_{21} & 0 & \cdots & 0 & 0 \\ 0 & \tau_{32} & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & \tau_{n,n-1} & 0 \end{pmatrix}.$$

We consider a $p = 2$ periodic Leslie matrix for a population that experiences two “seasons” of length 1 during a “year” of length 2. The age-specific fertilities and survivorships in the Leslie projection matrix are allowed to vary from season to season. For notation convenience, we denote

the two seasonal fertility and transition matrices by

$$F(0) = \begin{pmatrix} f_1 & f_2 & \cdots & f_{n-1} & f_n \\ 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 \end{pmatrix}, \quad F(1) = \begin{pmatrix} \phi_1 & \phi_2 & \cdots & \phi_{n-1} & \phi_n \\ 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & 0 & 0 \end{pmatrix},$$

$$T(0) = \begin{pmatrix} 0 & 0 & \cdots & 0 & 0 \\ s_1 & 0 & \cdots & 0 & 0 \\ 0 & s_2 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & s_{n-1} & 0 \end{pmatrix}, \quad T(1) = \begin{pmatrix} 0 & 0 & \cdots & 0 & 0 \\ \sigma_1 & 0 & \cdots & 0 & 0 \\ 0 & \sigma_2 & \cdots & 0 & 0 \\ \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & \cdots & \sigma_{n-1} & 0 \end{pmatrix}$$

in which the seasons are distinguished by Latin and Greek letters, respectively. For this $p = 2$ periodic case, R_0 is the dominant eigenvalue of the upper left 2×2 sub-matrix Q of the $n \times n$ matrix

$$((F(1) + T(1))(F(0) + T(0)) - T(1)T(0))(I - T(1)T(0))^{-1}.$$

For example, in the $n = 3$ dimensional case this matrix is

$$\begin{aligned}
 & ((F(1) + T(1))(F(0) + T(0)) - T(1)T(0))(I - T(1)T(0))^{-1} \\
 &= \begin{pmatrix} \phi_2 s_1 + \phi_1(f_1 + s_1 \sigma_2 f_3) & s_2 \phi_3 + \phi_1 f_2 & \phi_1 f_3 \\ \sigma_1(f_1 + s_1 \sigma_2 f_3) & \sigma_1 f_2 & \sigma_1 f_3 \\ 0 & 0 & 0 \end{pmatrix}
 \end{aligned}$$

and R_0 is the dominant eigenvalue of the sub-matrix

$$Q = \begin{pmatrix} \phi_2 s_1 + \phi_1(f_1 + s_1 \sigma_2 f_3) & s_2 \phi_3 + \phi_1 f_2 \\ \sigma_1(f_1 + s_1 \sigma_2 f_3) & \sigma_1 f_2 \end{pmatrix}. \tag{20}$$

By an induction argument, one can show that in general the entries in the matrix $Q = (q_{ij})$ are, for even n ,

$$\begin{aligned}
 q_{11} &= \sum_{i=1}^{n/2} \left(\prod_{j=1}^i s_{2j-1} \prod_{k=1}^i \sigma_{2k-2} \right) \phi_{2i} + \phi_1 \left(f_1 + \sum_{i=2}^{n/2} \left(\prod_{j=1}^{i-1} s_{2j-1} \prod_{k=1}^i \sigma_{2k-2} \right) f_{2i-1} \right), \\
 q_{12} &= \sigma_1^{-1} \left(\sum_{i=2}^{n/2} \left(\prod_{j=1}^{i-1} s_{2j} \prod_{k=1}^{i-2} \sigma_{2k-1} \right) \phi_{2i-1} + \phi_1 \sum_{i=1}^{n/2} \left(\prod_{j=1}^i s_{2j-2} \prod_{k=1}^i \sigma_{2k-1} \right) f_{2i} \right), \\
 q_{21} &= \sigma_1 \left(f_1 + \sum_{i=2}^{n/2} \left(\prod_{j=1}^{i-1} s_{2j-1} \prod_{k=1}^i \sigma_{2k-2} \right) f_{2i-1} \right), \\
 q_{22} &= \sum_{i=1}^{n/2} \left(\prod_{j=1}^i s_{2j-2} \prod_{k=1}^i \sigma_{2k-1} \right) f_{2i}
 \end{aligned}$$

and for odd n are

$$\begin{aligned}
 q_{11} &= \sum_{i=1}^{n-1} \left(\prod_{j=1}^i s_{2j-1} \prod_{k=1}^i \sigma_{2k-2} \right) \phi_{2i} + \phi_1 \left(f_1 + \sum_{i=2}^{(n+1)/2} \left(\prod_{j=1}^{i-2} s_{2j-1} \prod_{k=1}^i \sigma_{2k-2} \right) f_{2i-1} \right), \\
 q_{12} &= \sigma_1^{-1} \left(\sum_{i=2}^{(n+1)/2} \left(\prod_{j=1}^{i-1} s_{2j} \prod_{k=1}^{i-2} \sigma_{2k-1} \right) \phi_{2i-1} + \phi_1 \sum_{i=1}^{(n-1)/2} \left(\prod_{j=1}^i s_{2j-2} \prod_{k=1}^i \sigma_{2k-1} \right) f_{2i} \right), \\
 q_{21} &= \sigma_1 \left(f_1 + \sum_{i=2}^{(n+1)/2} \left(\prod_{j=1}^{i-2} s_{2j-1} \prod_{k=1}^i \sigma_{2k-2} \right) f_{2i-1} \right), \\
 q_{22} &= \sum_{i=1}^{(n-1)/2} \left(\prod_{j=1}^i s_{2j-2} \prod_{k=1}^i \sigma_{2k-1} \right) f_{2i},
 \end{aligned}$$

where for convenience $\sigma_0 = \tau_0 = 1$. While complicated, these formulas defining Q provide a formula

$$R_0 = \frac{1}{2}(q_{11} + q_{22} + \sqrt{(q_{11} - q_{22})^2 + 4q_{21}q_{12}}) \tag{21}$$

that explicitly relates R_0 to the age-specific fertilities and survivorships during each season. It thus provides a way to study the effect that changes in any specific demographic parameter in the projection matrices for either season have on R_0 . For example, one can calculate derivatives (sensitivities) of R_0 with respect to any of the entries in the fertility and/or transition matrices at either season. We give an example that utilizes such a use of these formulas for a size $n = 3$ Leslie matrix. This example investigates the same question as that in Example 1, but for a population with a juvenile and adult structure.

Example 2 We use the matrix Q given by formula (20) to calculate R_0 for a 3×3 Leslie matrix of period $p = 2$ in the following environmental and biological context. We view the periodicity in the model as accounting for two seasons (lasting one unit of time each), a “good” season and a “bad” season. The population has a juvenile stage the length of which is one season (thus $f_1 = \phi_1 = 0$) and an adult stage that lasts two seasons (a “year”), so that $f_2 = f_3 = f > 0$ and $\phi_2 = \phi_3 = \phi > 0$. We assume that normally in the bad season survivorships and adult fertility are reduced by a factor w_0 , $0 < w_0 < 1$, so $\phi = w_0 f$ and $\sigma_i = w_0 s_i$ where $0 < w_0 < 1$.

The question we consider is the following. Suppose adults have an option to re-allocate the resources that are available during the bad season to increase fertility at the cost of decreased survivorship (or vice versa). What strategy should the adults adopt in order to increase R_0 ? We model this trade-off by setting

$$\begin{aligned}
 \phi_2 &= wf, & \phi_3 &= wf, \\
 \sigma_1 &= w_0 s_1, & \sigma_2 &= \frac{w_0}{1 - w_0} (1 - w) s_2,
 \end{aligned}$$

where the strategy w to be adopted satisfies $0 < w < 1$. The periodic matrix model setup is then

$$F(0) = \begin{pmatrix} 0 & f & f \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}, \quad F(1) = \begin{pmatrix} 0 & wf & wf \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix},$$

$$T(0) = \begin{pmatrix} 0 & 0 & 0 \\ s_1 & 0 & 0 \\ 0 & s_2 & 0 \end{pmatrix}, \quad T(1) = \begin{pmatrix} 0 & 0 & 0 \\ w_0 s_1 & 0 & 0 \\ 0 & \frac{w_0}{1-w_0} (1-w)s_2 & 0 \end{pmatrix}.$$

If $w = w_0$, then we have the baseline situation described above. If, on the other hand, $w > w_0$ then in bad seasons adult fertility increases while survivorship decreases. The opposite holds if $w < w_0$. We consider strategies near $w = w_0$ and use the formula derivable from the matrix (20) for $R_0 = R_0(w)$ to calculate $R'_0(w)$ at $w = w_0$.

The derivative of the dominant eigenvalue

$$R_0(w) = \frac{1}{2} s_1 f \left(w + w_0 + \sqrt{(w - w_0)^2 + \frac{4w_0^2}{1-w_0} s_2^2 w(1-w)} \right)$$

of

$$Q = \begin{pmatrix} w s_1 f & w s_2 f \\ \frac{w_0^2}{1-w_0} (1-w) s_1^2 s_2 f & w_0 s_1 f \end{pmatrix}$$

with respect to w equals, when evaluated at $w = w_0$, is

$$R'_0(w_0) = \frac{f s_1}{1-w_0} (s_2 \sqrt{w_0} (1-2w_0) + 1-w_0).$$

The sign of this derivative is that of the second factor. An investigation of the second factor shows

$$R'_0(w_0) < 0 \text{ if } w_0 > \frac{1}{2} \quad \text{and} \quad s_2 > s_2^* \doteq \frac{1-w_0}{(2w_0-1)\sqrt{w_0}}$$

$$R'_0(w_0) > 0 \text{ if } w_0 < \frac{1}{2} \quad \text{or} \quad s_2 < s_2^*.$$

In other words, if the decreases in baseline adult fertility and survivorship in bad seasons are not high ($w_0 > \frac{1}{2}$) and adult survivorship in good seasons is sufficiently high ($s_2 > s_2^*$), then the adult population should adopt a strategy that decreases fertility and increases survivorship during bad seasons (i.e. decrease w). On the other hand, in the opposite case – when decreases in baseline vital adult rates in bad seasons are high ($w_0 < \frac{1}{2}$) or adult survivorship in good seasons is low ($s_2 < s_2^*$) – then the adult population should adopt the opposite strategy in bad seasons, namely, adults should increase fertility at the expense of decreased survivorship. Note that these conclusions are not dependent on the good season fertility rate f nor juvenile survivorship rate s_1 .

As a final observation concerning periodic Leslie matrices, we point out that for periods $p \geq n + 1$ it follows that $R_0 = r$. This is because $\prod_{t=0}^{p-1} T(t) = 0$ for $T(t)$ in a Leslie matrix and hence

$$\left(\prod_{t=0}^{p-1} (F(t) + T(t)) - \prod_{t=0}^{p-1} T(t) \right) \left(I - \prod_{t=0}^{p-1} T(t) \right)^{-1} = \prod_{t=0}^{p-1} (F(t) + T(t)).$$

By Definition 1, R_0 is the dominant eigenvalue of the matrix on the left-hand side and r is the dominant eigenvalue of the matrix on the right-hand side of this equation. In fact, this observation holds for any matrix model in which $T(t)$ has zeros on and above (or below) the diagonal.

5. Applications

We illustrate the calculation of R_0 for two case study applications that involved periodic projection matrices.

5.1. Green treefrog dynamics

In [2], a discrete time model was developed to describe the seasonal population dynamics of the urban green treefrog *Hyla cinerea*. In this model, the population is divided into three life-cycle stages: tadpoles, nonbreeders (sexually immature frogs) and adult breeders (sexually mature frogs). The time unit is equal to one week, which is appropriate for comparison with the field data given in [2,22]. Accordingly, the tadpole stage is further split into five age classes each of which is one week long (it takes approximately five weeks for a tadpole to metamorphose). The nonbreeder stage is divided into 52 age classes n_i (it takes approximately one year for a frog to become sexually mature). The demographic state vector $x(t)$ for the matrix model lies in \bar{R}_+^{58} . The 58×58 projection matrix $P(t) = F(t) + T$ has period $p = 52$ (one year). In this model, the transition matrix is constant and its only nonzero entries are $\tau_{i+1,i}$ and $\tau_{58,58}$. The only nonzero entry in the fertility matrix $F(t) = (\varphi_{ij}(t))$ is the adult birth rate $\varphi_{1,58}(t)$ which was estimated from field calling data (see blue line in Figure 4 in [2]).

By Definition 1 the net reproductive number for this model (an extended Leslie matrix model) is

$$R_0 = \rho \left[\left(\prod_{t=0}^{51} (F(t) + T) - T^{52} \right) (I - T^{52})^{-1} \right].$$

Because of the large size of the matrices and the long period, an analytic formula for R_0 is not readily available. For parameter estimates given in [2], namely for survival rates

$$\begin{aligned} \tau_{i+1,i} &= 0.6111 \text{ for } i = 1 \text{ to } 5 \text{ (tadpoles),} \\ \tau_{i+1,i} &= 0.9999 \text{ for } i = 6 \text{ to } 57 \text{ (nonbreeders),} \\ \tau_{58,58} &= 0.9203 \text{ (adults),} \end{aligned}$$

we numerically calculate $R_0 \approx 3.8279$.

The matrix model derived and studied in [2] is nonlinear. This is because survival rates in that model are assumed to be density-dependent. The value of R_0 we calculated here is the *inherent* net reproductive number, i.e., is calculated under the assumption of low (technically 0) population densities. This relates to the nonlinear model in the following way. A fundamental theorem for autonomous nonlinear matrix models states that the extinction equilibrium loses stability as R_0 increases through 1 and that the population is uniformly persistent for $R_0 > 1$ [10,11]. (Moreover, non-extinction equilibria bifurcate from the extinction equilibrium at $R_0 = 1$.) This fundamental theorem is also valid for nonlinear, periodically forced matrix models [9,13]. Therefore, $R_0 > 1$ in the nonlinear model of [2] implies that the green treefrog population in that field study [2] is persistent.

5.2. A size-structured model for a soft coral

McFadden [21] used a periodic matrix model to study the dynamics of an intertidal soft coral (*Alcyonium* sp.). There are four colony size classes and a larval class in this 5×5 periodic matrix model which has period $p = 2$ to account for seasonal variations. McFadden estimated parameter values from field data and studied several variants of the model in order to investigate differing scenarios relating to the presence or absence of either sexual or clonal reproduction. In this same

spirit, we will illustrate the calculation of R_0 for this periodic model in the case when clonal reproduction is absent. Using the data from Table 2 and Figure 6 (Tatoosh Island, site T2) in [21] we obtain the following matrices

$$F(0) = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix}, \quad F(1) = \begin{pmatrix} 0 & 0.06 & 0.16 & 0.17 & 2.99 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix},$$

$$T(0) = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ 0.0070 & 0.39 & 0.30 & 0.01 & 0 \\ 0 & 0.15 & 0.30 & 0.17 & 0.03 \\ 0 & 0.01 & 0.16 & 0.36 & 0.26 \\ 0 & 0 & 0.12 & 0.19 & 0.14 \end{pmatrix}, \quad T(1) = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ 0 & 0.68 & 0.02 & 0 & 0 \\ 0 & 0.23 & 0.67 & 0.04 & 0 \\ 0 & 0.02 & 0.31 & 0.39 & 0.09 \\ 0 & 0.04 & 0 & 0.25 & 0.43 \end{pmatrix}.$$

From formula (15) with $p = 2$ we calculate that $R_0 = 4.9414 \times 10^{-3} < 1$. This indicates the lack of persistence of the coral population in the absence of clonal reproduction (all other factors remaining unchanged).

6. Some concluding remarks

In Sections 2 and 3 we considered a definition of R_0 for a periodically forced matrix equation (2) based on its composite map (Floquet theory for periodic maps). This definition was utilized in several applications of matrix models to structured populations in a seasonally fluctuating environment [1,7,8,14,15] and our main goal in this paper was to develop the general theory and investigate the properties of this particular definition of R_0 .

We show that the projection matrix of the composite map has an additive decomposition (13) into a fertility matrix plus a transition matrix. The composite of a periodic map defines an autonomous map, which leads to a definition of R_0 based on this decomposition as given in [12] for autonomous matrix equations. It follows from results in [12] (also see [10,11,20]) that this R_0 determines the asymptotic properties of solutions of the periodic matrix equation, i.e., R_0 and r are on the same side of 1 (where r is the dominant eigenvalue of the composite projection matrix). This fact implies that R_0 is also useful in the study of nonlinear periodic matrix equations with $P = P(t, x)$. The linearization principle applied at the extinction equilibrium $x = 0$ yields a periodic matrix equation with projection matrix $P(t, 0)$ the stability properties of which are determined by R_0 . Moreover, R_0 as defined in Definition 1 arises as a natural parameter to use in a bifurcation analysis of non-extinction (positive) periodic solutions that occurs at $R_0 = 1$ where the extinction state loses stability [9,13].

As a measure of reproductive output we saw that the number R_0 defined by Definition 1 can be interpreted as the per capita expected number of offspring (per period) of individuals from a certain (eigenvector) distribution of newborns. Other measures of reproductive output for populations modelled by periodic matrix equations are possible. Bacaër [3] defines R_0 for a periodic matrix model (2) to be the dominant eigenvalue $\rho[B]$ of the $np \times np$ matrix $B = \Phi N^{-1}$ where

$$\Phi = \begin{pmatrix} F(0) & 0 & \dots & 0 \\ 0 & F(1) & \dots & 0 \\ \vdots & \vdots & & \vdots \\ 0 & 0 & \dots & F(p-1) \end{pmatrix}, \quad N = \begin{pmatrix} -T(0) & I & 0 & \dots & 0 \\ 0 & -T(1) & I & \dots & 0 \\ \vdots & \vdots & \vdots & & \vdots \\ 0 & 0 & 0 & \dots & I \\ I & 0 & 0 & \dots & -T(p-1) \end{pmatrix}. \tag{22}$$

Several properties and interpretations of this R_0 are given in [3,4]: it is the spectral radius of a next generation matrix, a measure of the control effort, and the asymptotic per generation growth rate. Furthermore, it is shown in [3] that R_0 lies on the same side of 1 as r and therefore determines the stability of the matrix equation (2). This definition of R_0 and that given in Definition 1 are sometimes, but not always, equal. This can be seen from examples in Section 4. For the scalar case $n = 1$ with period $p = 2$, Definition 1 gives

$$R_0 = (\varphi_1\varphi_0 + \varphi_1\tau_0 + \tau_1\varphi_0) \frac{1}{1 - \tau_1\tau_0}$$

and the dominant eigenvalue of B is

$$R_0 = \frac{1}{2} [\tau_0\varphi_1 + \tau_1\varphi_0 + ((\tau_0\varphi_1 + \tau_1\varphi_0)^2 + 4\varphi_1\varphi_0(1 - \tau_1\tau_0))^{1/2}] \frac{1}{1 - \tau_1\tau_0}.$$

It is not difficult to see that these are identical if and only if $\varphi_1\varphi_0 = 0$, i.e., if and only if at one point in time during a period the population is infertile (otherwise the latter is closer to 1 than is the former). For the period $p = 3$ case Definition 1 gives

$$R_0 = \frac{1}{1 - \tau_2\tau_1\tau_0} (\varphi_2\varphi_1\varphi_0 + \varphi_2\tau_1\tau_0 + \tau_2\varphi_1\tau_0 + \tau_2\tau_1\varphi_0 + \varphi_2\varphi_1\tau_0 + \varphi_2\tau_1\varphi_0 + \tau_2\varphi_1\varphi_0).$$

A formula for the dominant eigenvalue R_0 of

$$B = \frac{1}{1 - \tau_2\tau_1\tau_0} \begin{pmatrix} \tau_2\tau_1\varphi_0 & \tau_2\varphi_0 & \varphi_0 \\ \varphi_1 & \tau_2\varphi_1\tau_0 & \varphi_1\tau_0 \\ \varphi_2\tau_1 & \varphi_2 & \varphi_2\tau_1\tau_0 \end{pmatrix}$$

is not as conveniently tractable, although we can see, by examining some special cases, that under some conditions the two definitions of R_0 are identical and that under other conditions they are not. For example, if the population is infertile during the last two steps of the period, i.e., if $\varphi_1 = \varphi_2 = 0$, then both equal

$$R_0 = \frac{\tau_2\tau_1\varphi_0}{1 - \tau_2\tau_1\tau_0}.$$

If, on the other hand, the population is infertile during only the last step of the period, i.e., if $\varphi_2 = 0$ and $\varphi_0\varphi_1 > 0$, then the two definitions (Definition 1 and Bacaër's) give, respectively

$$R_0 = \frac{1}{1 - \tau_2\tau_1\tau_0} (\tau_2\varphi_1\tau_0 + \tau_2\tau_1\varphi_0 + \tau_2\varphi_1\varphi_0),$$

$$R_0 = \frac{1}{1 - \tau_2\tau_1\tau_0} \frac{1}{2} [\tau_2\varphi_1\tau_0 + \tau_2\tau_1\varphi_0 + ((\tau_2\varphi_1\tau_0 + \tau_2\tau_1\varphi_0)^2 + 4\tau_2\varphi_1\varphi_0(1 - \tau_2\tau_1\tau_0))^{1/2}].$$

Straightforward algebraic manipulations show that these quantities are not identical (and the latter is closer to 1 than is the former).

Similar comparative conclusions hold for structured models of dimension $n > 1$ as well. For example, for the period $p = 2$ Leslie age-structured models considered in Section 4.2 we used a computer algebra program to calculate the characteristic polynomial of B for $n = 2$ to 7 and found it has the form $\lambda^{2n-2} p(\lambda)$ where $p(\lambda)$ is a quadratic polynomial. We then calculated the

Table 1. For a Leslie matrix of period $p = 2$, the difference between the characteristic quadratic $q(\lambda)$ of Q and $p(\lambda)$, quadratic factor of the characteristic polynomial $\lambda^{2n-2}p(\lambda)$ of B , is a multiple k of $\lambda - 1$. Note that the second factor in k is a sum of non-negative terms and can vanish if and only if each of these terms equals 0.

Dimension n	k
2	$\phi_1 f_1$
3	$\phi_1 (f_1 + s_1 \sigma_2 f_3)$
4	$\phi_1 (f_1 + s_1 \sigma_2 f_3)$
5	$\phi_1 (f_1 + s_1 \sigma_2 f_3 + s_1 s_3 \sigma_2 \sigma_4 f_5)$
6	$\phi_1 (f_1 + s_1 \sigma_2 f_3 + s_1 s_3 \sigma_2 \sigma_4 f_5)$
7	$\phi_1 (f_1 + s_1 \sigma_2 f_3 + s_1 s_3 \sigma_2 \sigma_4 f_5 + s_1 s_3 s_5 \sigma_2 \sigma_4 \sigma_6 f_7)$

difference $q(\lambda) - p(\lambda)$ where $q(\lambda)$ is the characteristic quadratic of Q . The results show that the difference between these two polynomials is a multiple of $\lambda - 1$, i.e., $q(\lambda) - p(\lambda) = -k(\lambda - 1)$ for a constant $k > 0$ given in Table 1.

If $k \neq 0$, then $q(\lambda)$ and $p(\lambda)$ have no root in common (other than 1) and hence the two definitions of R_0 differ. (Moreover, a little analytic geometry shows that $R_0 = \rho[B]$ is closer to 1 than is R_0 defined by Definition 1.) On the other hand, if $k = 0$ then $q(\lambda)$ and $p(\lambda)$ are identical and the two definitions give the same value for R_0 . One can see what the biological consequences of $k = 0$ are by referring to Table 1. We will not interpret here the various biological possibilities that give rise to $k = 0$ except to point out that for the dimensions $n = 2$ to 7 (and we conjecture that for all dimensions) $\phi_1 = 0$ implies the definitions are identical.

The following theorem gives a case when the two definitions of R_0 are identical, namely when reproduction occurs at only one point in time during a period. The proof appears in the appendix.

THEOREM 2 *Suppose $F(t)$ is the p -periodic extension of*

$$F(t) = \begin{cases} 0 & \text{for } t \in \{0, 1, \dots, p - 1\} \setminus \{k\}, \\ F & \text{for } t = k. \end{cases}$$

Then $\rho[F^{(p-1)}(I - T^{(p-1)})^{-1}] = \rho[B]$.

Even when the two definitions of R_0 are not identical they both determine the asymptotic stability properties of the periodic matrix equation. They will not, however, necessarily give the same results when put to other uses, such as a sensitivity analysis. For example, if one carries out the analysis in Example 1 using the definition $R_0 = \rho[B]$, one finds a similar threshold phenomenon but with a different threshold value for $\tau'_1(0)$, namely, $\tau^{**} = (1 - \tau_1(0)\tau_0)/\varphi_0\tau_1(0)$. A numerical comparison of the sensitivities with respect to φ_1 in this example appears in Figure 1.

Finally, we point out that in the applications in Section 5 the two definitions of R_0 are equal. In the soft coral application this follows from Theorem 2. For the greentree frog application, this is corroborated by a numerical calculation (the matrix B is of size 3016×3016), at least to five significant digits. However, changes in the fertility of the frogs can cause the inequality. For example, if $f_{1,20}(t)$ is changed from 0 to $b(t)$ (allowing frogs of age 15 weeks to reproduce at the same rate as frogs of age 52 weeks), then calculations show that Definition 1 gives $R_0 \approx 3.9328$ and $R_0 = \rho[B] \approx 3.8547$.

As a final remark we point out that R_0 given in Definition 1 is for a specific periodic schedule of vital rates which gives the composite map $\prod_{t=0}^{p-1} P(t) = F^{(p-1)} + T^{(p-1)}$ where $F^{(p-1)} = \prod_{t=0}^{p-1} P(t) - \prod_{t=0}^{p-1} T(t)$ and $T^{(p-1)} = \prod_{t=0}^{p-1} T(t)$. In general, the p periodic schedules give rise

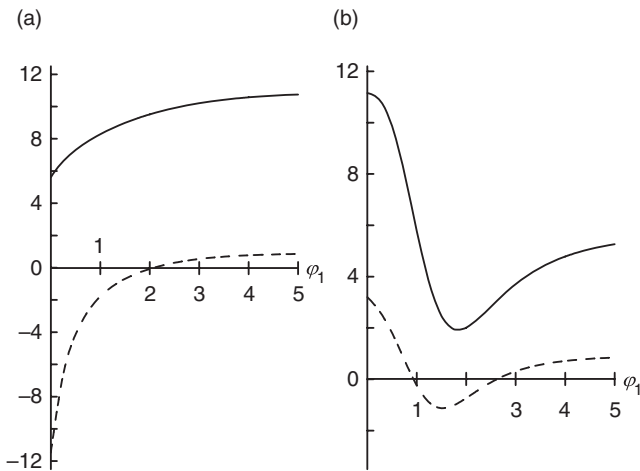


Figure 1. Plots of the sensitivities of R_0 defined by Definition 1 (solid line) or $\rho[B]$ (dashed line) as functions of φ_1 in Example 1 are shown for two illustrative cases. (a) For the exponential trade-off function $\tau_1 = 0.45e^{-\varphi_1}$ and parameter values $\varphi_0 = 10$ and $\tau_0 = 0.9$, we see that the sensitivities have opposite signs for small values of bad season fertility φ_1 . This is because $\tau'_1(0) = -0.45$ lies between the two thresholds $-\tau^* = -0.64855$ and $-\tau^{**} = -0.13222$. Note that the sensitivities do have the same sign for larger values of φ_1 . (b) For the trade-off function $\tau_1 = 0.6(1 + 0.1\varphi_1^3)^{-1}$ and parameter values $\varphi_0 = 5$ and $\tau_0 = 0.8$, we see that the sensitivities have the same signs for small values of bad season fertility φ_1 . This is because $\tau'_1(0) = 0$ is greater than both thresholds $-\tau^* = -0.5336$ and $-\tau^{**} = -0.1733$. Note, however, that the sensitivities do not always have the same signs for all values of φ_1 .

to composite maps of the form $\prod_{t=j}^{p+j-1} P(t)$, $j = 0, \dots, p - 1$, each of which can be additively decomposed as

$$(F^{(p-1)})_j + (T^{(p-1)})_j,$$

where

$$(F^{(p-1)})_j = \prod_{t=j}^{p+j-1} P(t) - \prod_{t=j}^{p+j-1} T(t), \quad (T^{(p-1)})_j = \prod_{t=j}^{p+j-1} T(t).$$

These composite maps can be used to define schedule-dependent net reproductive numbers, namely

$$R_{0,j} = \rho[(F^{(p-1)})_j(I - (T^{(p-1)})_j)^{-1}], \quad j = 0, \dots, p - 1. \tag{23}$$

Note that the schedule $j = 0$ results in Equation (15), i.e., $R_{0,0}$ in Equation (23) is the R_0 given in Definition 1. In general, these net reproduction numbers may not have the same value. Individuals in a population beginning at a favourable time (or “season”) and those in an identical population beginning at an unfavourable time, for example, will not in general have the same long-term reproductive output as measured by R_0 . (This fact about R_0 , as defined by Definition 1, has also been pointed out to us by H. Caswell, who views it as a useful feature in applications (personal communication).)

Here is an example to illustrate this fact. For a size $n = 2$ Leslie matrix of period $p = 2$ define the projection matrix $P(t) = F(t) + T(t)$ by

$$F(0) = \begin{pmatrix} 1 & 5 \\ 0 & 0 \end{pmatrix}, \quad T(0) = \begin{pmatrix} 0 & 0 \\ 0.7 & 0.9 \end{pmatrix},$$

$$F(1) = \begin{pmatrix} 5 & 3 \\ 0 & 0 \end{pmatrix}, \quad T(1) = \begin{pmatrix} 0 & 0 \\ 0.4 & 0.8 \end{pmatrix}.$$

A calculation using formula (23) yields $R_{0,0} \approx 69.5$ and $R_{0,1} \approx 24.9$.

Under special circumstances it can turn out that all the periodic schedules give the same net reproductive number. See Corollary 2 for an example. Regardless of the schedule, however, Theorem 1 holds, and for any $j = 0, \dots, p - 1$, $R_{0,j}$ and r always lie on the same side of 1.

The following Corollary shows, for the case considered in Theorem 2 where reproduction occurs at only one point in time during the period, that the definition of R_0 is independent of the schedule. The proof appears in the Appendix.

COROLLARY 2 *Under the assumptions of Theorem 2, the definition of R_0 is independent of the schedule, i.e. the numbers $R_{0,j}$, $j = 0, \dots, p - 1$, given in formula (23) are equal.*

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Appendix

For notational purposes, we let $T_t = T(t)$, $F_t = F(t)$ and

$$\prod_{t=m}^n T_t = \begin{cases} T_n T_{n-1} \cdots T_m & \text{for } n \geq m, \\ I & \text{for } n < m. \end{cases}$$

The following lemma can be verified by a direct calculation of NN^{-1} for N in formula (22).

LEMMA A1 Define the $n \times n$ matrices G_{ij} for $1 \leq i, j \leq p$ by

$$G_{ij} = \begin{cases} \prod_{t=j}^{p+i-2} T_t \left(I - \prod_{t=j}^{p+j-1} T_t \right)^{-1} & \text{for } i \leq j, \\ \prod_{t=j}^{j-2} T_t \left(I - \prod_{t=j}^{p+j-1} T_t \right)^{-1} & \text{for } i > j. \end{cases}$$

Then $N^{-1} = (G_{ij})$.

As examples, for periods $p = 2$ and $p = 3$ we have, respectively,

$$N^{-1} = \begin{pmatrix} T_1(I - T_0T_1)^{-1} & (I - T_1T_0)^{-1} \\ (I - T_0T_1)^{-1} & T_0(I - T_1T_0)^{-1} \end{pmatrix},$$

$$N^{-1} = \begin{pmatrix} T_2T_1(I - T_0T_2T_1)^{-1} & T_2(I - T_1T_0T_2)^{-1} & (I - T_2T_1T_0)^{-1} \\ (I - T_0T_2T_1)^{-1} & T_0T_2(I - T_1T_0T_2)^{-1} & T_0(I - T_2T_1T_0)^{-1} \\ T_1(I - T_0T_2T_1)^{-1} & (I - T_1T_0T_2)^{-1} & T_1T_0(I - T_2T_1T_0)^{-1} \end{pmatrix}.$$

LEMMA A2 The following identity holds:

$$\left(\prod_{t=k+1}^{p-1} T_t \right) \left(I - \prod_{t=k+1}^{p+k} T_t \right)^{-1} = \left(I - \prod_{t=0}^{p-1} T_t \right)^{-1} \left(\prod_{t=k+1}^{p-1} T_t \right).$$

Proof We first note that

$$\begin{aligned} \left(\prod_{t=k+1}^{p-1} T_t \right) \left(I - \prod_{t=k+1}^{p+k} T_t \right)^{-1} &= \left(\prod_{t=k+1}^{p-1} T_t \right) \left(I + \sum_{i=1}^{\infty} \left(\prod_{t=k+1}^{p+k} T_t \right)^i \right) \\ &= \left(\prod_{t=k+1}^{p-1} T_t \right) \left(I + \sum_{i=1}^{\infty} \left(\prod_{t=k+1}^{p+k} T_t \right)^{i-1} \left(\prod_{t=k+1}^{p+k} T_t \right) \right) \\ &= \left(\prod_{t=k+1}^{p-1} T_t \right) \left(I + \sum_{i=1}^{\infty} \left(\prod_{t=k+1}^{p+k} T_t \right)^{i-1} \left(\prod_{t=p}^{p+k} T_t \right) \left(\prod_{t=k+1}^{p-1} T_t \right) \right) \\ &= \left(\prod_{t=k+1}^{p-1} T_t \right) + \left(\prod_{t=k+1}^{p-1} T_t \right) \sum_{i=1}^{\infty} \left(\prod_{t=k+1}^{p+k} T_t \right)^{i-1} \left(\prod_{t=p}^{p+k} T_t \right) \left(\prod_{t=k+1}^{p-1} T_t \right) \\ &= \left(I + \sum_{i=1}^{\infty} \left(\prod_{t=k+1}^{p-1} T_t \right) \left(\prod_{t=k+1}^{p+k} T_t \right)^{i-1} \left(\prod_{t=p}^{p+k} T_t \right) \right) \left(\prod_{t=k+1}^{p-1} T_t \right). \end{aligned}$$

Because of the periodicity we can write $\prod_{t=p}^{p+k} T_t = \prod_{t=0}^k T_t$. This allows us to re-associate factors in the product

$$\begin{aligned} \left(\prod_{t=k+1}^{p-1} T_t\right) \left(\prod_{t=k+1}^{p+k} T_t\right)^{i-1} \left(\prod_{t=p}^{p+k} T_t\right) &= \left(\prod_{t=k+1}^{p-1} T_t\right) \left(\prod_{t=p}^{p+k} T_t \prod_{t=k+1}^{p-1} T_t\right)^{i-1} \left(\prod_{t=p}^{p+k} T_t\right) \\ &= \left(\prod_{t=k+1}^{p-1} T_t\right) \left(\prod_{t=0}^k T_t \prod_{t=k+1}^{p-1} T_t\right)^{i-1} \left(\prod_{t=0}^k T_t\right) \\ &= \left(\prod_{t=0}^{p-1} T_t\right) \left(\prod_{t=0}^{p-1} T_t\right)^{i-1} \\ &= \left(\prod_{t=0}^{p-1} T_t\right)^i \end{aligned}$$

and thus

$$\left(\prod_{t=k+1}^{p-1} T_t\right) \left(I - \prod_{t=k+1}^{p+k} T_t\right)^{-1} = \left(I + \sum_{i=1}^{\infty} \left(\prod_{t=0}^{p-1} T_t\right)^i\right) \left(\prod_{t=k+1}^{p-1} T_t\right).$$

Proof of Theorem 2 Since

$$\begin{aligned} \prod_{t=0}^{p-1} (F_t + T_t) - \prod_{t=0}^{p-1} T_t &= \left(\prod_{t=k+1}^{p-1} T_t\right) (F + T_k) \prod_{t=0}^{k-1} T_t - \prod_{t=0}^{p-1} T_t \\ &= \left(\prod_{t=k+1}^{p-1} T_t\right) F \prod_{t=0}^{k-1} T_t + \left(\prod_{t=k+1}^{p-1} T_t\right) T_k \prod_{t=0}^{k-1} T_t - \prod_{t=0}^{p-1} T_t \\ &= \left(\prod_{t=k+1}^{p-1} T_t\right) F \prod_{t=0}^{k-1} T_t \end{aligned}$$

it follows for R_0 defined by Definition 1 that

$$R_0 = \rho \left[\left(\prod_{t=k+1}^{p-1} T_t\right) \left(F \prod_{t=0}^{k-1} T_t\right) \left(I - \prod_{t=0}^{p-1} T_t\right)^{-1} \right]. \tag{A1}$$

We now turn our attention to R_0 defined as $\rho[B]$. From formula (22) we find that all (block) rows of B consist of p zero ($n \times n$) block matrices, except for the k^{th} block row, i.e.,

$$B = \Phi N^{-1} = \begin{pmatrix} 0 & \cdots & 0 & \cdots & 0 \\ \vdots & & \vdots & & \vdots \\ FG_{k+1,1} & \cdots & FG_{k+1,k+1} & \cdots & FG_{k+1,p} \\ \vdots & & \vdots & & \vdots \\ 0 & \cdots & 0 & \cdots & 0 \end{pmatrix}.$$

Consequently, by Lemma A1

$$\begin{aligned} \rho[B] &= \rho[FG_{k+1,k+1}] = \rho \left[F \prod_{t=k+1}^{p+k-1} T_t \left(I - \prod_{t=k+1}^{p+k} T_t\right)^{-1} \right] \\ &= \rho \left[\left(F \prod_{t=p}^{p+k-1} T_t\right) \left(\prod_{t=k+1}^{p-1} T_t\right) \left(I - \prod_{t=k+1}^{p+k} T_t\right)^{-1} \right] \\ &= \rho \left[\left(F \prod_{t=0}^{k-1} T_t\right) \left(\prod_{t=k+1}^{p-1} T_t\right) \left(I - \prod_{t=k+1}^{p+k} T_t\right)^{-1} \right]. \end{aligned}$$

Using Lemma A2 we can write

$$\rho[B] = \rho \left[\left(F \prod_{t=0}^{k-1} T_t \right) \left(I - \prod_{t=0}^{p-1} T_t \right)^{-1} \left(\prod_{t=k+1}^{p-1} T_t \right) \right].$$

Since the spectrum of a product AB is the same as the spectrum of BA we have

$$\rho[B] = \rho \left[\left(\prod_{t=k+1}^{p-1} T_t \right) \left(F \prod_{t=0}^{k-1} T_t \right) \left(I - \prod_{t=0}^{p-1} T_t \right)^{-1} \right],$$

which is the same as formula (A1). ■

Proof of Corollary 2 Recall that in Theorem 2, R_0 corresponds to the specific periodic schedule $j = 0$ which is based on the composite map $\prod_{t=0}^{p-1} P(t) = P(p-1) \cdots P(k) \cdots P(0)$ (where $P(t) = F(t) + T(t)$ and $F(t) = F$ at the point $t = k$ and zero everywhere else). Consider any other periodic schedule j and assume $0 < j < k$ (similar argument holds for $k \leq j \leq p-1$). Then the net reproductive number corresponding to the composite map $\prod_{t=j}^{p+j-1} P(t) = P(j-1) \cdots P(0)P(p-1) \cdots P(k) \cdots P(j)$ is defined as

$$\begin{aligned} R_{0,j} &= \rho \left[\left(\prod_{t=k+1}^{p+j-1} T_t \right) \left(F \prod_{t=j}^{k-1} T_t \right) \left(I - \prod_{t=j}^{p+j-1} T_t \right)^{-1} \right] \\ &= \rho \left[\left(\prod_{t=0}^{j-1} T_t \prod_{t=k+1}^{p-1} T_t \right) \left(F \prod_{t=j}^{k-1} T_t \right) \left(I - \prod_{t=0}^{j-1} T_t \prod_{t=j}^{p-1} T_t \right)^{-1} \right]. \end{aligned} \tag{A2}$$

We want to show that $R_{0,j}$ in formula (A2) is equal to R_0 in Theorem 2. To this end, first note that for matrices A and B we have: 1) $\rho[AB] = \rho[BA]$ and 2) $(I - BA)^{-1}B = B(I - AB)^{-1}$ (which can be easily shown using the expansion $(I - M)^{-1} = I + M + M^2 + \dots$). Hence,

$$\begin{aligned} R_{0,j} &= \rho \left[\left(\prod_{t=0}^{j-1} T_t \right) \left(\prod_{t=k+1}^{p-1} T_t \right) \left(F \prod_{t=j}^{k-1} T_t \right) \left(I - \prod_{t=0}^{j-1} T_t \prod_{t=j}^{p-1} T_t \right)^{-1} \right] \\ &= \rho \left[\left(\prod_{t=k+1}^{p-1} T_t \right) \left(F \prod_{t=j}^{k-1} T_t \right) \left(I - \prod_{t=0}^{j-1} T_t \prod_{t=j}^{p-1} T_t \right)^{-1} \left(\prod_{t=0}^{j-1} T_t \right) \right] \\ &= \rho \left[\left(\prod_{t=k+1}^{p-1} T_t \right) \left(F \prod_{t=j}^{k-1} T_t \prod_{t=0}^{j-1} T_t \right) \left(I - \prod_{t=j}^{p-1} T_t \prod_{t=0}^{j-1} T_t \right)^{-1} \right] \\ &= \rho \left[\left(\prod_{t=k+1}^{p-1} T_t \right) \left(F \prod_{t=0}^{k-1} T_t \right) \left(I - \prod_{t=0}^{p-1} T_t \right)^{-1} \right] = R_0. \end{aligned}$$

■