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On Net Reproductive Rate and the Timing of Reproductive Output

T. de-Camino-Beck[1,*] **and M. A. Lewis**[1,2,†]

1. Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton, Alberta T6G 2G1, Canada;
2. Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2G1, Canada

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abstract: Understanding the relationship between life-history patterns and population growth is central to demographic studies. Here we derive a new method for calculating the timing of reproductive output, from which the generation time and its variance can also be calculated. The method is based on the explicit computation of the net reproductive rate (R_0) using a new graphical approach. Using nodding thistle, desert tortoise, creeping aven, and cat's ear as examples, we show how R_0 and the timing of reproduction is calculated and interpreted, even in cases with complex life cycles. We show that the explicit R_0 formula allows us to explore the effect of all reproductive pathways in the life cycle, something that cannot be done with traditional analysis of the population growth rate (λ). Additionally, we compare a recently published method for determining population persistence conditions with the condition $R_0 > 1$ and show how the latter is simpler and more easily interpreted biologically. Using our calculation of the timing of reproductive output, we illustrate how this demographic measure can be used to understand the effects of life-history traits on population growth and control.

Keywords: matrix model, net reproductive rate, biological control, generation time, reproductive output, persistence.

Persistence of biological populations is the result of the evolution of life-history patterns that have consequences for population growth. Early theoretical work by Cole (1954) showed how changes in reproductive schedules can have consequences in population growth rate. Cole's work established the foundations of demographic analysis—based on the estimation of parameters such as growth rate, net reproductive rate, and length of a generation—and provided the foundation for theoretical and empirical work on population demography (e.g., Cole 1960; Murdoch 1966; Charnov and Schaffer 1973; Goodman 1975). Since Cole's work, substantial theoretical advances have been achieved, in particular with the use of matrix models popularized and summarized in a book by Caswell (2001).

Matrix models provide an intuitive modeling strategy where the life cycle of the organisms can be described explicitly in terms of life ages or stages. Demographic parameters of population growth rate (λ), net reproductive rate (the lifetime reproductive output of an individual; R_0), and generation time (the time it takes for the population to increase by R_0) have also been derived for matrix models (Caswell 2001), providing a direct connection between life cycle structure and these demographic parameters.

In general, most of the analysis in matrix models has been based on the numerical calculation of λ and the sensitivity of λ to model parameters. In particular, elasticity or sensitivity analysis of λ to age/stage transitions in matrix models has become a standard method in demographic analysis in ecology, management, and evolution (Silvertown et al. 1993; Franco and Silvertown 1996; Pfister 1998; Oli and Dobson 2003, 2005; Gaillard et al. 2005; Shea 2004). In all but the simplest matrix models, calculation of the population growth rate and elasticity requires numerical estimates, thus restricting results to the particular population parameter estimates.

Although total reproductive output and timing of reproduction have an impact on population growth and persistence, parameters like R_0 and generation time have not been well studied using matrix models. The calculation of R_0 is thought to be too complicated to perform analytically (Hastings and Botsford 2006*b*), and its numerical calculation for stage-structured models (Cushing and Zhou 1994) has rarely been made, in favor of the calculation of λ and elasticity/sensitivity analysis of λ. The dif-

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[*] E-mail: tomasd@math.ualberta.ca.

[†] E-mail: mlewis@math.ualberta.ca.

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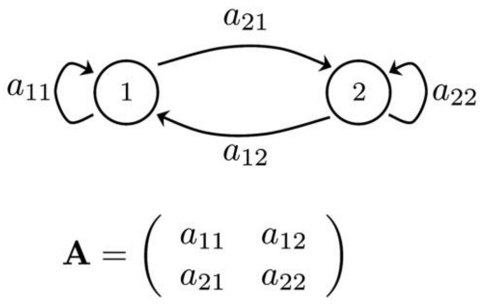
ficult calculation of generation time in stage-structured models (Cochran and Ellner 1992; Lebreton 2005) had dissuaded demographers from using R_0 as a measure of the impacts of reproduction and survival on population growth and persistence, primarily because the interpretation of R_0 without an estimate of generation time can be misleading (Birch 1948; Cole 1960; Caswell 2001). Here we show that both R_0 and mean generation time can be directly calculated for stage-structured models.

In a previous article (de-Camino-Beck and Lewis 2007), we developed a graphical method for calculating R_0 explicitly, and we showed how it can be applied in the context of biological control. In this article, we derive a formula for calculating the timing of reproductive output based on the R_0 equation. This formula allows for the calculation of the timing of reproductive output, the mean generation time, and the mean generation time variance for stage-structured models. We start by giving the theoretical background in matrix models and life cycle graphs. Then, we briefly describe the graph-theoretic method to calculate R_0 and the timing of reproductive output. Later, we show with four examples how R_0 and timing of reproductive output are calculated, and we discuss the implications for demographic analysis. Additionally, we compare the condition $R_0 > 1$ with a persistence condition for matrix models derived by DeAngelis et al. (1986) and recently rederived by Hastings and Botsford (2006*b*), and we discuss its implication in the management and control of organisms.

Net Reproductive Rate, Generation Time, and Persistence

In this section, we briefly introduce matrix models. First, we show how to calculate the net reproductive rate using a graphical approach. Next, we show that the concept of the net reproductive rate can be extended to determine not only the total number of offspring produced but also their distribution over the life span of the parent. Then, we describe the persistence condition proposed by DeAngelis et al. (1986) and Hastings and Botsford (2006*b*), which we will call the Hastings-Botsford persistence condition, and compare this with $R_0 > 1$.



$$\mathbf{A} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$$

Figure 1: Simple 2 × 2 matrix **A** and its associated graph. There is a directed edge in the graph for every a_{ij} entry in the matrix. In the graph, for a transition a_{ij}, the edge is directed from node j to node i.

Matrix Models

Stage-structured models are population dynamics models where life cycle stages are explicitly defined. Stages can be size classes or life forms (e.g., larvae, juvenile, seeds, seedling, adult plants). In matrix form, a stage-structured model is defined as

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t, \tag{1}$$

where $\mathbf{n}_t$ is a vector of stages at time t and $\mathbf{A}$ is an $n \times n$ projection matrix. Each entry, a_{ij}, in the matrix $\mathbf{A}$ represents the contribution from stage j in time t to stage i in time $t+1$. The projection matrix $\mathbf{A}$ can also be represented as a life cycle graph where each node in the graph corresponds to a stage and each arrow represents transitions, a_{ij} (fig. 1).

The matrix $\mathbf{A}$ is composed of survivorship and fecundity transitions. These can be decomposed into a transition matrix $\mathbf{T}$ and a fecundity matrix $\mathbf{F}$. Transition matrix entries, t_{ij}, describe survivorship, the probability of survival from stage j to i. The fecundity matrix entries, f_{ij}, describe fecundities, the maximum reproductive output from stage j to i. This decomposition is not mathematically unique but is uniquely determined by the biology of the organism.

Net Reproductive Rate R₀

Given an initial distribution of stages $\mathbf{n}_0$, the number of offspring produced by the individuals initially present is

$$\begin{aligned} \mathbf{F}\mathbf{n}_0 + \mathbf{F}\mathbf{T}\mathbf{n}_0 + \mathbf{F}\mathbf{T}^2\mathbf{n}_0 + \cdots &= \mathbf{F}(\mathbf{I} + \mathbf{T} + \mathbf{T}^2 + \cdots)\mathbf{n}_0 \\ &= \mathbf{F}(\mathbf{I} - \mathbf{T})^{-1}\mathbf{n}_0. \end{aligned} \tag{2}$$

The first term on the left-hand side of the first line of the equation represents first-year fecundity, the second term represents fecundity following a year of survival, and the third term represents fecundity following two years of survival and so forth. The matrix $\mathbf{F}(\mathbf{I} - \mathbf{T})^{-1}$ is referred to as the next-generation matrix (Cushing and Zhou 1994; Li and Schneider 2002).

The net reproductive rate, R_0, is the average number of offspring that a single reproducing individual can produce

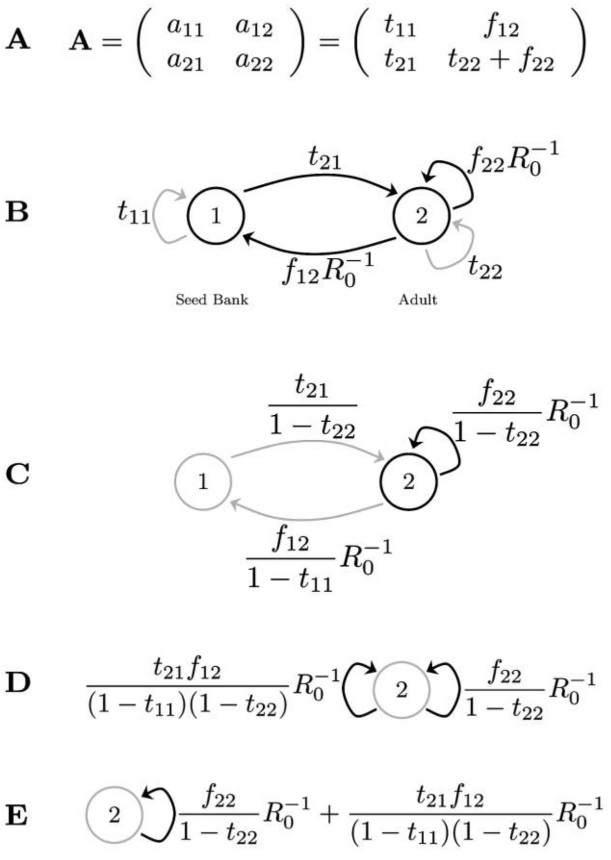


Figure 2: *A* shows the transition matrix and its decomposition in survivorship and fecundities. In *B*, fecundities are multiplied by R_0^{-1}. Then, using rule *A* in figure 3, self-loops (*gray*) are eliminated, yielding the graph in *C*. Node 1 is eliminated by multiplying the two edges in gray (rule in fig. 3*C* to produce the graph in *D*). The resulting loops are added together (rule in fig. 3*B* to obtain *E*). Applying step 5 in *E* to the single node graph yields R_0.

over its lifetime and is mathematically defined as the dominant eigenvalue of the next-generation matrix

$$R_0 = \rho[\mathbf{F}(\mathbf{I} - \mathbf{T})^{-1}], \tag{3}$$

where $\rho(\cdot)$ denotes the dominant eigenvalue. An $R_0 > 1$ implies $\lambda > 1$, and $R_0 < 1$ implies $\lambda < 1$ (Li and Schneider 2002). Thus, conditions on model parameters that satisfy $R_0 > 1$ also guarantee that $\lambda > 1$ and vice versa. However, the calculation of R_0 using formula (3) is not always algebraically straightforward. A recently discovered method provides a simple alternative (de-Camino-Beck and Lewis 2007). This uses graph reduction methods on the life cycle graph to calculate R_0. The calculation starts with the description of the projection matrix as a life cycle graph, similar to the one shown in figure 2*A*. Once the life cycle graph has been specified, the procedure is as follows. (1) Identify survivorship and fecundity transitions. (2) Multiply all fecundity transitions f_{ij} in the graph by R_0^{-1}. (3) Eliminate survivorship self-loops, using rule *A* in figure 3. (4) Reduce the graph using the graph reduction rules defined in figure 3 until only nodes with fecundity self-loops are left. When a node is eliminated, all pathways that go through that node have to be recalculated. (5) When only one node with a single self-loop is left, eliminate the final node by setting the self-loop equal to 1 and solve this equation for R_0.

Note that the resulting R_0 formula is the same regardless of the order by which nodes are eliminated. As an example, consider the hypothetical graph in figure 2*B*. After applying the graph reduction method as shown in figure 2*B*–2*E*, the resulting R_0 is

$$R_0 = \underbrace{\frac{f_{22}}{(1-t_{22})}}_{\text{reproduction from adult to adult}} + \underbrace{\frac{t_{21}f_{12}}{(1-t_{11})(1-t_{22})}}_{\text{reproduction going through seed bank}}. \tag{4}$$

The population persists if $R_0 > 1$. The R_0 formula shows two reproductive pathways. If either is >1, then the population persists. The first pathway accounts for the reproduction of plants that start as adults and produce reproducing adults immediately the next year. The second pathway represents seeds that go to the seed bank that take at least an extra year to become adults again. The terms $(1 - t_{ii})^{-1}$ are interpreted as the average time an individual stays in stage *i*.

Typically, the net reproductive rate formula can be writ-

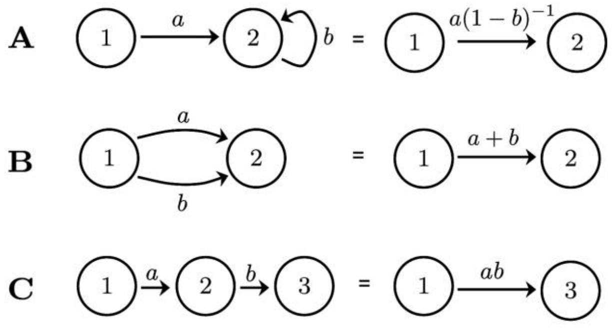


Figure 3: Graph reduction rules. *A*, Self-loop elimination with $b < 1$. *B*, Parallel path elimination. *C*, Node elimination. Rules *A* and *B* show elimination of paths, and rule *C* shows the elimination of node 2. Graph reduction is done by repeatedly applying these rules until only one node is left.

ten explicitly as the sum of fecundities for m pathways as follows:

$$R_0 = R_1 + R_2 + \cdots + R_m, \tag{5}$$

where R_i is the fecundity for a pathway that ends in reproduction. We will call each R_i a fecundity pathway. Because the pathways are summed, the population will persist if any $R_i > 1$. From the previous example, the first pathway is $R_1 = f_{22}/(1 - t_{22})$, and the second is $R_2 = t_{21}f_{12}/[(1 - t_{11})(1 - t_{22})]$. If R_1, R_2, or the sum $R_1 + R_2$ is >1, then the population will persist.

This graph reduction method for calculating R_0 (de-Camino-Beck and Lewis 2007) relates to a different established method for calculating the eigenvalues λ of the projection matrix $\mathbf{A}$. There, each entry a_{ij} of the life cycle graph is multiplied by λ^{-1}, and the graph reduction steps of figure 3 are used to yield a characteristic polynomial for the eigenvalues λ (Caswell 2001). The difference between the methods (multiplying f_{ij} by R_0^{-1} [step 2] rather than multiplying each $a_{ij} = t_{ij} + f_{ij}$ by λ^{-1} [above]) is sufficient to yield the reproductive rate R_0 rather than λ. In other words, R_0 is the dominant eigenvalue of the next-generation matrix $\mathbf{F}(\mathbf{I} - \mathbf{T})^{-1}$, while λ is the dominant eigenvalue of the projection matrix $\mathbf{T} + \mathbf{F}$ (Caswell 2001). The population growth rate, λ, can be calculated with the graph method as well. However, the procedure yields a higher-degree polynomial where the interpretation is not intuitive. For example, the characteristic polynomial for the eigenvalues associated with the life cycle graph in figure 2 is

$$\lambda^2 - (t_{11} + t_{22} + f_{22})\lambda + [t_{11}(t_{22} + f_{22}) - t_{21}f_{12}] = 0, \tag{6}$$

which has dominant eigenvalue

$$\lambda = \frac{1}{2}\left\{t_{11} + t_{22} + f_{22} + \sqrt{(t_{11} + t_{22} + f_{22})^2 - 4[t_{11}(t_{22} + f_{22}) - t_{21}f_{12}]}\right\}. \tag{7}$$

While this eigenvalue gives the population persistence condition as $\lambda > 1$, there is no intuitive interpretation of the condition, unlike the fecundity pathways used for R_0. When the number of stages in the life cycle is three or more, it is difficult or impossible to calculate the dominant eigenvalue explicitly, and numerical methods must instead be used.

Timing of Reproductive Output

Since the work by Cole (1954), timing of reproductive output and its implications for fitness have been the subject of widespread study (Beckerman et al. 2002; Ranta et al. 2002; Oli and Dobson 2003; Coulson et al. 2006). In this section, we show our calculation of how R_0 can be extended to yield the total number of offspring produced as well as their distribution over the life span of the parent. To explore timing of reproduction in a stage-structured model using R_0, the time that it takes to go through each pathway has to be included in the R_0 formula. Rather than grouping terms according to fecundity pathway terms, equation (5), in the net reproductive rate, formula can be grouped according to the number of time steps taken to complete a pathway. For example, equation (4) can be rewritten as

$$\begin{aligned}
R_0 &= f_{22}(1 + t_{22} + t_{22}^2 + \cdots) \\
&\quad + t_{21}f_{12}(1 + t_{11} + t_{11}^2 + \cdots)(1 + t_{22} + t_{22}^2 + \cdots) && (8) \\
&= \underbrace{f_{22}}_{\text{one time step to reproduction}} \\
&\quad + \underbrace{(f_{22}t_{22} + t_{21}f_{12})}_{\text{two time steps to reproduction}} && (9) \\
&\quad + \underbrace{(f_{22}t_{22}^2 + t_{21}f_{12}t_{11} + t_{21}f_{12}t_{22})}_{\text{three time steps to reproduction}} + \cdots \\
&= S_1 + S_2 + S_3 + \cdots. && (10)
\end{aligned}$$

If the population is growing ($\lambda > 1$), offspring produced after several time steps will contribute less to population growth than those produced immediately. This motivates us to connect R_0 to λ by using the current value of future reproduction. The current value of future reproductive output is assigned on the basis of the contribution that the future reproductive output will make to the overall population growth. Formally, we define $\tau = \lambda^{-1}$ and start by multiplying each pathway that takes n time steps to complete by the weight τ^n. From the example above, pathway $S_2 = (f_{22}t_{22} + t_{21}f_{12})$ takes two time steps to complete ($n = 2$); thus, the pathways with its associated weights are $S_2\tau^2 = (f_{22}t_{22} + t_{21}f_{12})\tau^2$. Thus, $\lambda > 1$ means $\tau < 1$, and the reproductive output two steps hence is diminished by the factor τ^2. Summing across all possible values of n yields the present value of all future reproduction

$$S(\tau) = \sum_{n=1}^{\infty} S_n\tau^n. \tag{11}$$

By analogy with generating functions in probability theory, we also refer to this as the R_0-generating function. Equation (11) can also be found by taking the z transform of the life cycle graph with $z = \tau^{-1}$. For details of applying a z transform, see Caswell (2001, chap. 7). For life cycle graphs, a more compact representation of equation (11) arises from simply multiplying each survivorship and fecundity term by τ. For example, applying this method to equation (4) yields

$$S(\tau) = \frac{f_{22}\tau}{(1-t_{22}\tau)} + \frac{t_{21}f_{12}\tau^2}{(1-t_{11}\tau)(1-t_{22}\tau)}. \tag{12}$$

Because equation (11) is a Taylor series representation for the function $S(\tau)$, the number of direct descendants in n time steps, S_n, can be recovered as the Taylor series coefficients from the nth derivative of $S(\tau)$:

$$S_n = \frac{1}{n!}\frac{d^nS}{d\tau^n}(0). \tag{13}$$

The net reproductive rate can be recovered from $S(\tau)$ by recognizing that it is the total number of new individuals produced that are direct descendants of the original individual, and hence $R_0 = S(1) = \sum_{n=1}^{\infty} S_n$.

Generation time can be interpreted as the length of time it takes the population to increase by a factor of R_0. In stage-structured models, the calculation of generation time is difficult since stage is not related to age and individuals can stay in a stage for a long period of time (Cochran and Ellner 1992; Lebreton 2005). There are several approximate methods for estimating generation time (Caswell 2001). The simplest is given by

$$\tilde{T} = \frac{\log R_0}{\log \lambda}. \tag{14}$$

The mean generation time can be understood exactly by considering a randomly selected direct descendant of the original reproducing individual. The year in which the descendant is produced is a random variable T with mean μ_T and variance σ_T^2:

$$\begin{aligned} \mu_T &= \frac{S'(1)}{R_0}, \\ \sigma_T^2 &= \frac{S''(1)}{R_0} + \frac{S'(1)}{R_0} - \frac{S'^2(1)}{R_0^2}. \end{aligned} \tag{15}$$

See the appendix in the online edition of the *American Naturalist* ("Generation Time Derivation") for a detailed derivation. The mean generation time μ_T, equation (15), is an alternative to the previous approximation $\tilde{T}$ (eq. [14]). The relationship with equation (14) can be found by writing the population N_t at time t in terms of individuals from previous time steps using the renewal equation,

$$N_t = \sum_{n=1}^{\infty} S_n N_{t-n}, \tag{16}$$

with N_0 given and $N_n = 0$ for $n < 0$. A population growing at rate λ takes the form $N_t = c\lambda^t$. Substitution of this form into equation (16) yields the Euler-Lotka equation for the population growth rate,

$$1 = \sum_{n=1}^{\infty} S_n \lambda^{-n} = S(\lambda^{-1}). \tag{17}$$

Hence, the population growth rate is given by $S(\lambda^{-1}) = 1$. Consider now an entire population reproducing at time $\tilde{T}$. Then,

$$S_n = \begin{cases} 0, & n \neq \tilde{T} \\ R_0, & n = \tilde{T} \end{cases}. \tag{18}$$

The Euler-Lotka equation gives $1 = R_0\lambda^{-\tilde{T}}$, and therefore equation (14) follows. In other words, $\tilde{T}$ is an approximation to the true generation time, μ_T, which is found under the assumption that there is a single, episodic reproductive event at time $\tilde{T}$ rather than continual reproduction. Equation (15) not only gives an exact generation time, μ_T, but also yields the variability in the generation time, σ_T^2.

Caswell (1989), in the first edition of his book, applies a similar approach, using the z transform of a graph with no disjoint loops to obtain R_0. However, Caswell uses equation (14) to calculate generation time. We go further by deriving the R_0-generating function from which the timing of reproductive output and formulas for the mean generation time and the generation time variance can be derived.

Hastings-Botsford Persistence Conditions and R$_0$

As shown in "Net Reproductive Rate R_0," the formula for R_0 provides a threshold condition for population growth ($R_0 > 1$), which is easier to calculate than the population growth rate threshold $\lambda > 1$. Also, it can be understood biologically as a parent's total contribution to the next generation arising from each of the possible fecundity pathways (see eq. [5]). It is natural to ask whether there are any other simple threshold conditions for population growth other than $R_0 > 1$ and $\lambda > 1$. Indeed, there is a condition, first derived by DeAngelis et al. (1979, 1986) and rederived and applied by Hastings and Botsford (2006*a*, 2006*b*). However, these Hastings-Botsford conditions have two limitations that do not arise in the analysis of R_0. First, for a given model, there may be many conditions to check as opposed to a single one ($R_0 > 1$). Second, the conditions cannot be interpreted biologically in a manner similar to the condition $R_0 > 1$.

The Hastings-Botsford conditions are strict mathematical conditions for population persistence. For an $n \times n$ matrix **A**, the Hastings and Botsford (2006*a*, 2006*b*) persistence condition states that a population will persist if and only if $a_{ii} > 1$ or if any principal minor,

$$(-1)^{m+1} \det(\mathbf{J}) > 0, \qquad (19)$$

where **J** is an m-dimensional principal submatrix of $\mathbf{Q} = \mathbf{A} - \mathbf{I}$ including **Q**. The principal minors of **Q** are the determinants of the submatrices obtained by deleting the same $n - m$ rows and columns in **Q**.

In other words, when the population persists ($R_0 > 1$), at least one of the self-loops a_{ii} exceeds 1 or one of the principal minors of $\mathbf{A} - \mathbf{I}$ is positive (eq. [19]). When the population does not persist ($R_0 < 1$), all self-loops are <1, and all the principal minors are negative. While the Hastings-Botsford persistence condition is mathematically analogous to $R_0 > 1$, their analytical formula comes at a cost. Unlike $R_0 > 1$, the condition has limited biological interpretation.

Consider the example from figure 2. On the basis of the Hastings-Botsford conditions, the population will persist if a_{11} or $a_{22} > 1$ or if

$$\begin{aligned}(-1)^3 \det(\mathbf{Q}) &= (-1)^3 \det(\mathbf{A} - \mathbf{I}) \\ &= (-1)^3[(a_{11} - 1)(a_{22} - 1) - a_{21}a_{12}] > 0,\end{aligned}$$

in other words, if

$$\frac{a_{21}a_{12}}{(1 - a_{11})(1 - a_{22})} > 1. \qquad (20)$$

To compare this condition with $R_0 > 1$, we rewrite the Hastings-Botsford condition in equation (20) using the survivorship and fecundity decomposition shown in figure 2*A*. The population will persist if $t_{22} + f_{22} > 1$, or, given $t_{22} + f_{22} < 1$, if

$$\frac{t_{21}f_{12}}{(1 - t_{11})[1 - (t_{22} + f_{22})]} > 1. \qquad (21)$$

Now, consider R_0 calculated for the same example in equation (4). The population will persist if

$$R_0 = \frac{f_{22}}{1 - t_{22}} + \frac{t_{21}f_{12}}{(1 - t_{11})(1 - t_{22})} > 1. \qquad (22)$$

These two conditions are equivalent (i.e., they hold or fail under identical conditions on the parameters), even though they are expressed differently. This can be shown by multiplying both sides of equation (21) by $[1 - (t_{22} + f_{22})]/(1 - t_{22})$. Equation (22) is the sum of fecundity pathways that yield the lifetime reproductive output. There is no similar interpretation for equation (21).

In this simple example, the condition on the sign of principal minors (eq. [19]) reduces to a single condition. However, as indicated by Hastings and Botsford (2006*b*), for large matrices, all the principal minors need to be calculated. In many cases, and in all examples given by Hastings and Botsford (2006*b*), it is sufficient to check condition (19) for the largest submatrix (i.e., $\mathbf{J} = \mathbf{Q}$) in equation (19). However, it is possible to come up with counterexamples where this condition is not sufficient and all principal minors must be checked (see "Creeping Aven").

Examples

To further illustrate the calculation of R_0, the timing of reproductive output, and the mean generation time μ_T, we reconsider Hastings and Botsford (2006*b*) examples of the persistence of nodding thistle ("Nodding Thistle") and the desert tortoise ("Desert Tortoise"). We also include examples that demonstrate more complicated life cycles and show how the calculation of R_0 is straightforward and simple. For creeping aven ("Creeping Aven"), the full set of Hastings-Botsford inequalities (26 in all) must be checked, whereas the condition $R_0 > 1$ is easy to calculate as a single inequality. An example of invading cat's ear is presented in the appendix ("Cat's Ear, Jury Test, and R_0"). For nodding thistle, desert tortoise, and creeping aven, we also calculate the timing of reproductive output and the mean and variance of the generation time, on the basis of parameter estimates from the literature.

Each of the examples considered in this section has also been previously analyzed by other authors using eigenvalue analysis (Doak et al. 1994; Shea and Kelly 1998; De Kroon et al. 2000; Weppler et al. 2006). In these analyses, the population growth rate λ was numerically calculated, and conclusions were drawn about the impact of model parameters on λ (elasticity analysis).

Nodding Thistle

Population Persistence. The nodding thistle (*Carduus nutans*) matrix model (Shea and Kelly 1998) provides a good example of the calculation and analysis of R_0, timing of reproduction, and the calculation of generation time. This thistle causes damage to grazing lands in New Zealand and Australia, and the life cycle graph is shown in figure 4*A*. Using graph reduction, we obtain

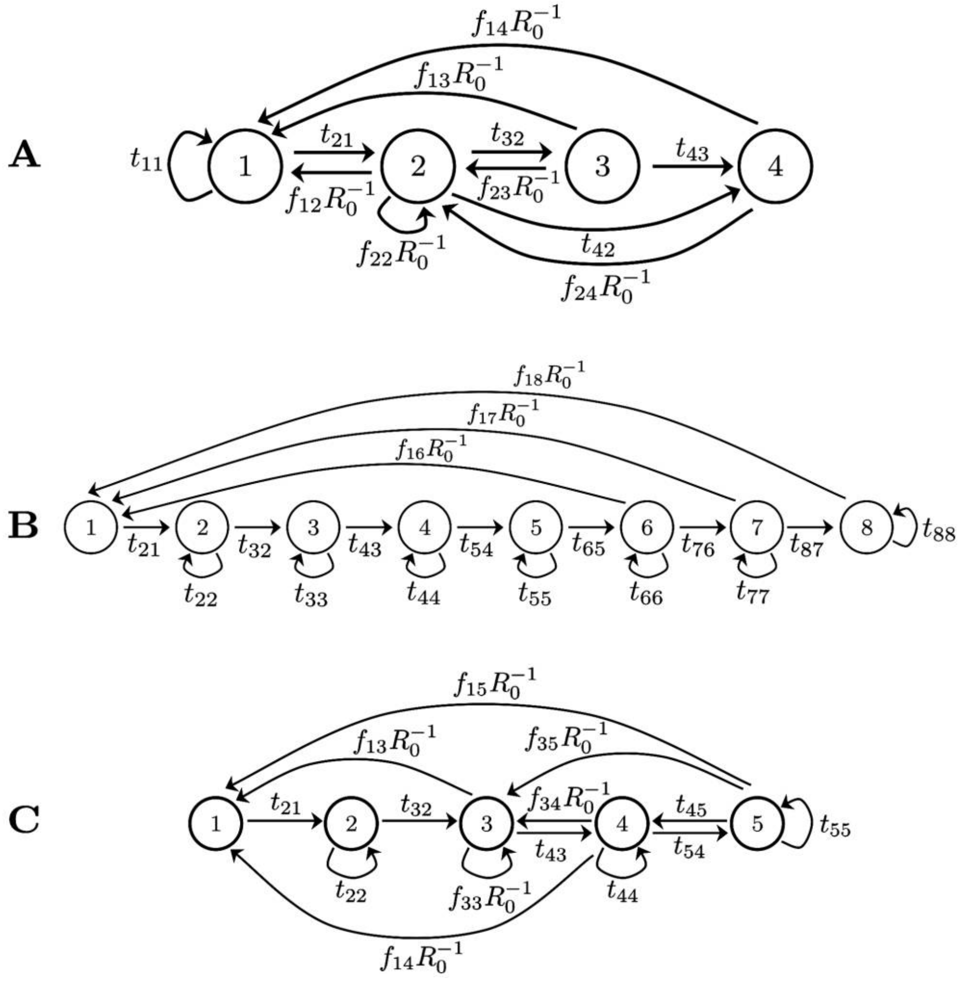


Figure 4: Life cycle graphs of nodding thistle (*A*), desert tortoise (*B*), and creeping aven (*C*). Fecundity transitions f_{ij} are multiplied by R_0^{-1} to proceed with the graph reduction. Survivorship transitions are labeled t_{ij}. The life cycle of *Geum reptans* (*C*) is as described by Weppler et al. (2006). Node 1 = seedling, node 2 = juvenile, node 3 = small adult, node 4 = medium adults, and node 5 = large adults. Clonal reproduction fecundities are f_{33}, f_{34}, and f_{35}. Sexual reproduction is f_{13}, f_{14}, and f_{15}.

$$R_0 = \underbrace{f_{22} + t_{32}f_{23} + \overbrace{t_{42}f_{24} + t_{32}t_{43}f_{24}}^{\text{large plant reproduction}}}_{\text{pathways without the seed bank}} + \underbrace{\frac{t_{21}f_{12} + t_{21}t_{32}f_{13} + \overbrace{t_{21}t_{42}f_{14} + t_{32}t_{43}t_{21}f_{14}}^{\text{large plant reproduction}}}{1 - t_{11}}}_{\text{pathways that visit the seed bank}}. \quad (23)$$

From equation (23), it is clear that the population will persist if any of the terms or the sum of any term in R_0 is >1. There are two stages, seed bank and small plants (nodes 1 and 2), that are common in all pathways and that could be used for control. Reduction in these transitions would maximize the number of pathways affected by control. The fecundities f_{i4} from node 4 (large plants) to other plants appear in four of the eight fecundity pathways, but f_{i3} occurs in only two of them. This would suggest that large plants should also be targets of control. In contrast to the results of Shea and Kelly (1998), these observations are qualitative and do not require numerical estimates. These results are consistent with previous work (Jongejans et al. 2006). Previous studies used elasticity analysis from parameter estimates for populations in Australia, New Zealand, and its native range in Eurasia to determine strategies for control. However, inspection of the R_0 formula reveals that thistle has many pathways that lead to reproduction. Higher elasticity of matrix transitions indicates higher impact on λ, but this does not ensure that a reduction in the transition will be sufficient to ensure $\lambda < 1$. On the other hand, if total eradication is desired, then each pathway or sum of pathways in equation (23) has to be <1. See the appendix ("Hastings-Botsford Persistence Conditions for Nodding Thistle") for comparison of the condition $R_0 > 1$ with the Hastings-Botsford condition for nodding thistle.

Timing of Reproduction. Using parameter estimates from Shea and Kelly (1998; their table 2), the number of new individuals over time (fig. 5*A*), starting with one reproducing individual, is calculated using equation (13). As seen in figure 5*A*, this thistle has short generation times with low variance, and most of the reproductive output occurs in the first 2 years of the life cycle. It can also be seen that for this particular set of parameter estimates, reproduction seems to become negligible after the fourth year of introduction of the original individual. For an effective control strategy, it would be reasonable to ensure the application of control measures for at least the duration of the timing of reproduction (approximately 4 years).

We also estimated generation time and variance using equation (15). For Midland, $R_0 = 4.1116$, $\mu_T = 1.9789$, and $\sigma_T^2 = 0.5375$, and for Argyll, $R_0 = 1.8113$, $\mu_T = 1.6909$, and $\sigma_T^2 = 0.3429$. There are large differences in R_0 but not in timing of reproductive output. This suggests that environmental differences change the overall output but do not change reproductive strategies. For comparison, the generation time $\tilde{T}$ calculated with equation (14) for both sites is 1.779 and 1.630, respectively.

Desert Tortoise

Population Persistence. Using graph reduction, we calculated R_0 for the desert tortoise (*Gopherus agassizii*) matrix model (Doak et al. 1994). The calculated R_0 formula is

$$R_0 = \overbrace{\frac{t_{21}t_{32}t_{43}t_{54}t_{65}f_{16}}{(1-t_{22})(1-t_{33})(1-t_{44})(1-t_{55})(1-t_{66})}}^{\text{pathway to reproduction at age 6 and higher}} + \overbrace{\frac{t_{21}t_{32}t_{43}t_{54}t_{65}t_{76}f_{17}}{(1-t_{22})(1-t_{33})(1-t_{44})(1-t_{55})(1-t_{66})(1-t_{77})}}^{\text{pathway to reproduction at age 7 and higher}} + \underbrace{\frac{t_{21}t_{32}t_{43}t_{54}t_{65}t_{76}t_{87}f_{18}}{(1-t_{22})(1-t_{33})(1-t_{44})(1-t_{55})(1-t_{66})(1-t_{77})(1-t_{88})}}_{\text{pathway to reproduction at age 8 and higher}} . \qquad (24)$$

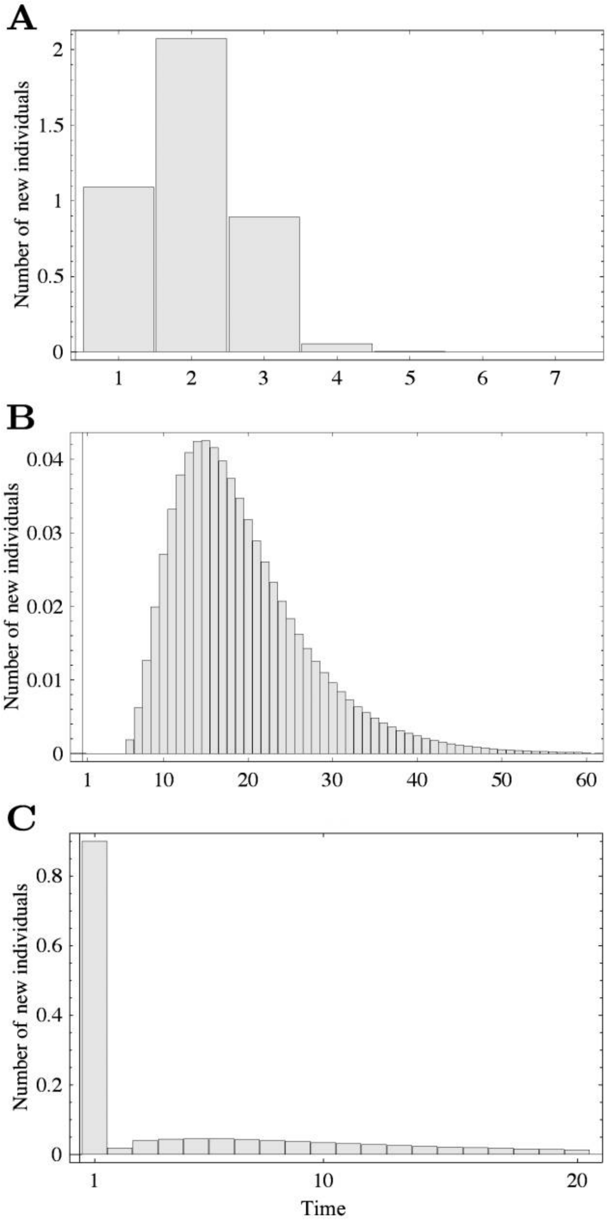


Figure 5: Number of new individuals obtained after *n* time iterations, starting with one reproductive individual. Iterations are calculated using equation (13). *A*, Nodding thistle data taken from Shea and Kelly (1998). *B*, Desert tortoise data taken from Doak et al. (1994). *C*, Creeping aven data taken from Weppler et al. (2006).

The matrix for the desert tortoise is an Usher matrix, a stage-structured matrix where all reproduction goes to a newborn stage. When individuals can stay in one stage *i*, such as in the desert tortoise, a term $(1 - t_{ii})^{-1}$ will appear in the fecundity pathway where stage *i* is involved. Relabeling equation (24) with the same notation as that used by Hastings and Botsford (2006*b*), the condition $R_0 > 1$ is written as

$$\begin{aligned} R_0 = {} & \frac{a_{10}a_{21}a_{32}a_{43}a_{54}f_5}{(1-a_{11})(1-a_{22})(1-a_{33})(1-a_{44})(1-a_{55})} \\ & + \frac{a_{10}a_{21}a_{32}a_{43}a_{54}a_{65}f_6}{(1-a_{11})(1-a_{22})(1-a_{33})(1-a_{44})(1-a_{55})(1-a_{66})} \\ & + \frac{a_{10}a_{21}a_{32}a_{43}a_{54}a_{65}a_{76}f_7}{(1-a_{11})(1-a_{22})(1-a_{33})(1-a_{44})(1-a_{55})(1-a_{66})(1-a_{77})} > 1. \end{aligned} \tag{25}$$

In this particular case, the condition $R_0 > 1$ and the first Hastings-Botsford persistence condition are identical (Hastings and Botsford 2006*b*). Each term in equation (24) corresponds to a pathway from birth to reproduction (as indicated by the parentheses in the equation). As indicated before, the population will persist if any of the terms or the sum of any term in R_0 is >1. If the population starts with one newborn individual, then the first reproduction would occur at stage 6, as indicated by the first pathway in the equation. Each pathway shares the survivorship until stage 6. Doak et al. (1994) found using numerical elasticity analysis that survival of adult females contributed the most to population growth rate. This can also be seen from simple observation of equation (24), where the terms $1 - t_{ii}$ lie in the denominator, allowing R_0 to grow quickly as t_{ii} approaches 1. With R_0, we also note that at the same time, the pathway to adult female ($t_{21}t_{32}t_{43}t_{54}t_{65}$) must be maintained if maximizing reproductive output is the goal.

Timing of Reproduction. Using the matrix from Doak et al. (1994; their table 5), we calculated the timing of reproductive output. Figure 5*B* shows the number of offspring over time, when the population starts with one reproducing individual. The maximum number of new individuals resulting from one new individual peaks at about 15 years, with $R_0 = 0.696$, mean generation time $\mu_T = 19.209$, and variance $\sigma_T^2 = 67.443$. Using equation (14), the mean generation time is $\tilde{T} = 19.872$. The high variance indicates that individuals can stay for long periods in one stage before moving to the next one.

The high variance and spread out reproductive output (fig. 5*B*) are a consequence of individuals being able to stay for long periods in one stage class. If adults are protected, in principle, this would improve reproductive output. However, improved adult tortoise survival does not guarantee survival of new generations. Thus, conservation strategies that substantially exceed the mean generation time (20 years) would be required if persistence of this species needs to be ensured.

Creeping Aven

Population Persistence. Creeping aven (*Geum reptans*) is a clonal perennial rosette that grows in alpine conditions. The life cycle for creeping aven is shown in figure 4*C* (Weppler et al. 2006).

Using graph reduction, the calculated R_0 is

$$\begin{aligned} R_0 = {} & \overbrace{f_{33} + \frac{t_{43}f_{34}}{1-t_{44}} + \frac{t_{43}t_{54}t_{45}f_{34}}{(1-t_{44})^2(1-\tau_{45})} + \frac{t_{43}t_{54}f_{35}}{(1-t_{44})(1-\tau_{45})}}^{\text{vegetative reproduction}} \\ & + \Bigg[\overbrace{\frac{t_{21}t_{32}f_{13}}{1-t_{22}} + \frac{t_{21}t_{32}t_{43}f_{14}}{(1-t_{22})(1-t_{44})}}^{\text{sexual reproduction}} \\ & \underbrace{+ \frac{t_{21}t_{32}t_{43}t_{54}t_{45}f_{14}}{(1-t_{22})(1-t_{44})^2(1-\tau_{45})} + \frac{t_{21}t_{32}t_{43}t_{54}f_{15}}{(1-t_{22})(1-t_{44})(1-\tau_{45})}\Bigg]}_{\text{sexual reproduction}}, \end{aligned} \tag{26}$$

where $\tau_{45} = (t_{45}t_{54})/[(1-t_{44})(1-t_{55})]$ and $(1-\tau_{45})^{-1}$ is the time an individual spends looping between stages 4 and 5. The population will persist if any of the terms or the sum of any terms in R_0 is >1. Transitions t_{ii} occur in almost all fecundity pathways. This means that the time an individual stays in one stage could have a large impact on R_0 and on population growth. Terms $(1-t_{44})^{-2}$ appear because in those pathways, stage 4 is visited twice. Weppler et al. (2006) used elasticity analysis of λ to determine which transitions contribute most to population growth. They found that t_{ii} had the greatest contribution, and our analysis of R_0 is consistent with their observation. However, we use only the analytical solution to R_0 and no numerical estimates. Weppler et al. (2006) determined that for creeping aven, both sexual and clonal reproduction seem to be equally predominant. Looking at the pathways in the R_0 equation reveals that there are many pathways that lead to both types of reproduction. However, vegetative reproduction pathways are shorter, which suggests faster reproduction through clonal reproduction. Additionally, the equation for R_0 (eq. [26]) shows that if transition $f_{33} > 1$, then population will persist, regardless of longer reproductive pathways. This leads us to conclude that vegetative reproduction may be predominant when f_{33} is large.

This analysis goes beyond a simple condition for determining persistence. The R_0 formula shows explicitly all the pathways for vegetative or sexual reproduction, whereas the Hastings-Botsford condition simply tests for persistence. The full Hastings-Botsford conditions (eq. [19]) comprise 26 inequalities that must be individually evaluated. These can be simplified to three inequalities, any one of which, if satisfied, guarantees persistence (see

"Hastings-Botsford Persistence Conditions for Creeping Aven" in the appendix). We have not been able to evaluate these inequalities directly to $R_0 > 1$, although this may be possible.

Timing of Reproduction. Using transition entries from Weppler et al. (2006; their table 1), we calculated the net reproductive rate and mean generation time. As an example, we consider parameter values for only one of the sites ("vandret da Porchabella") for 2000–2001. The number of new descendants over time is shown in figure 5*C*. This figure indicates that the largest reproductive output is predominant in the first year. This is consistent with our previous analysis of transitions f_{33} in the R_0 formula. From the second year, there is a mixture of sexual and clonal reproduction that spreads out for longer than 20 years, resulting in a large variance. This analysis suggests two phases of reproduction: short-term clonal reproduction and longer-term reproduction with a mixture of sexual and clonal. The first phase yields the potential for fast short-term growth under good environmental conditions, whereas the second phase would "time-average" possible variations in long-term environmental conditions. The dominance of these phases may be determined by environmental stochasticity and other environmental factors. With $R_0 = 1.581$, the mean generation time is $\mu_T = 6.446$ with variance $\sigma^2_{\tilde{T}} = 96.912$. Equation (14) results in a generation time of $\tilde{T} = 6.912$.

Cat's Ear

The example of cat's ear can be found in "Cat's Ear, Jury Test, and R_0" in the appendix. This case is unusual in that it leads to a quadratic equation for the net reproductive rate R_0. We do not provide a proof, but we believe that the quadratic equation results when there are disjoint reproductive pathways (reproductive pathways that are independent of each other). This is the only life cycle we know of that does this, and we include the example for completeness.

Discussion

Matrix models have established a formal foundation for the study of the effect of life-history changes in population dynamics, given a biological description of life cycle events. It has been widely shown that elasticity/sensitivity analyses of λ are powerful measures of the consequences of life-history events on population growth rate (Caswell 2001). The development by de-Camino-Beck and Lewis (2007) of a method for calculating the reproductive rate, R_0, explicitly allows for analysis to complement demographic studies. In this article, we take this a step further, deriving the calculation of the timing of reproductive output, which further allows for the calculation of mean and variance of the generation time. Once the life cycle has been described as a matrix model, R_0 can be easily calculated from the graph representation, even for complex life cycles. The analytical R_0 formula can be used to perform qualitative analysis of life cycle structure and persistence. When matrix transition estimates exist, the timing of reproductive output can be used to study early versus late reproduction strategies as well as the mean generation time to determine how spread reproduction occurs, and generation time variance can be used to study differences in reproductive strategies. From the next-generation matrix shown in "Net Reproductive Rate R_0," the per generation reproductive value can be calculated as the left eigenvector of this matrix, in a fashion similar to that described for the per year reproductive value (left eigenvector of the projection matrix) by Caswell (2001).

Although we do not fully address evolutionary questions about semelparity and iteroparity, like the ones posed by Cole (1954), in this article, we believe that the R_0-generating function and the timing of reproduction will assist in understanding these types of life histories. With R_0, it is possible to study how changes in life cycle structure affect fecundity pathways and the timing of reproduction. For instance, it can be seen from the R_0-generating function that when $\lambda \gg 1$, $\tau \ll 1$; hence, the value of late reproductive output is very low, and early reproduction has a stronger impact on population persistence (the weight τ^n becomes increasingly smaller as n becomes large). It can also be seen that when an individual can stay a long time in one stage, $(1 - a_{ii})^{-1}$ becomes large, which in turn results in a more spread out timing of reproduction.

When we compare our analysis using R_0 to the previous analysis using λ, several themes emerge. First, qualitative conclusions regarding the effect of key model parameters on population persistence are similar between the two analyses. However, depiction of R_0 as a sum of fecundity pathways allows us to explore the effects of secondary (less key) pathways on population persistence. The reproduction through these pathways can actually be sufficient to allow the population to persist. These results can be missed using typical sensitivity/elasticity analyses of λ. Second, the explicit formula R_0 allows a simple (nonnumerical) analysis of the role of model parameters on population persistence. This contrasts with the numerical methods needed to analyze the dependence of λ to model parameters. The R_0 fecundity pathways analysis is different from a method known as loop analysis (van Groenendael et al. 1994). Loop analysis shows life cycle loop contributions to population growth rate, but these loops do not necessarily correspond to directed fecundity pathways, and it depends on the calculation of elasticities. In contrast, the

R_0 analysis presented here focuses on directed reproduction pathways and does not require numerical estimates of vital rates. Last, while we know that $R_0 > 1$ and the Hastings-Botsford conditions are mathematically equivalent, the condition $R_0 > 1$ can be interpreted biologically and intuitively in terms of fecundity pathways, whereas the Hastings-Botsford conditions cannot. In all cases but one (creeping aven), we show how to algebraically connect the two conditions. From the R_0 formula, it is easy to see that if any term (pathway) is >1, or if the sum of combination of terms is >1, then the population will persist.

In terms of control of invading organisms, R_0 analysis, as shown in the examples, complements sensitivity/elasticity analyses of λ. The analytical solution of R_0 can be used to understand fecundity pathways and assist in the experimental design of demographic studies or assist in finding the best short- and long-term control strategies for pest species. As shown in the thistle example ("Nodding Thistle"), one strategy could be targeting transitions that affect the most fecundity pathways. A second factor to consider is how spread out the timing of reproduction is. Targeting transitions that affect early reproduction may result in reduction of population growth rate; however, if control efforts are not maintained for a long period and if the timing of reproductive output indicates that there is still late reproduction, a reinvasion may occur.

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